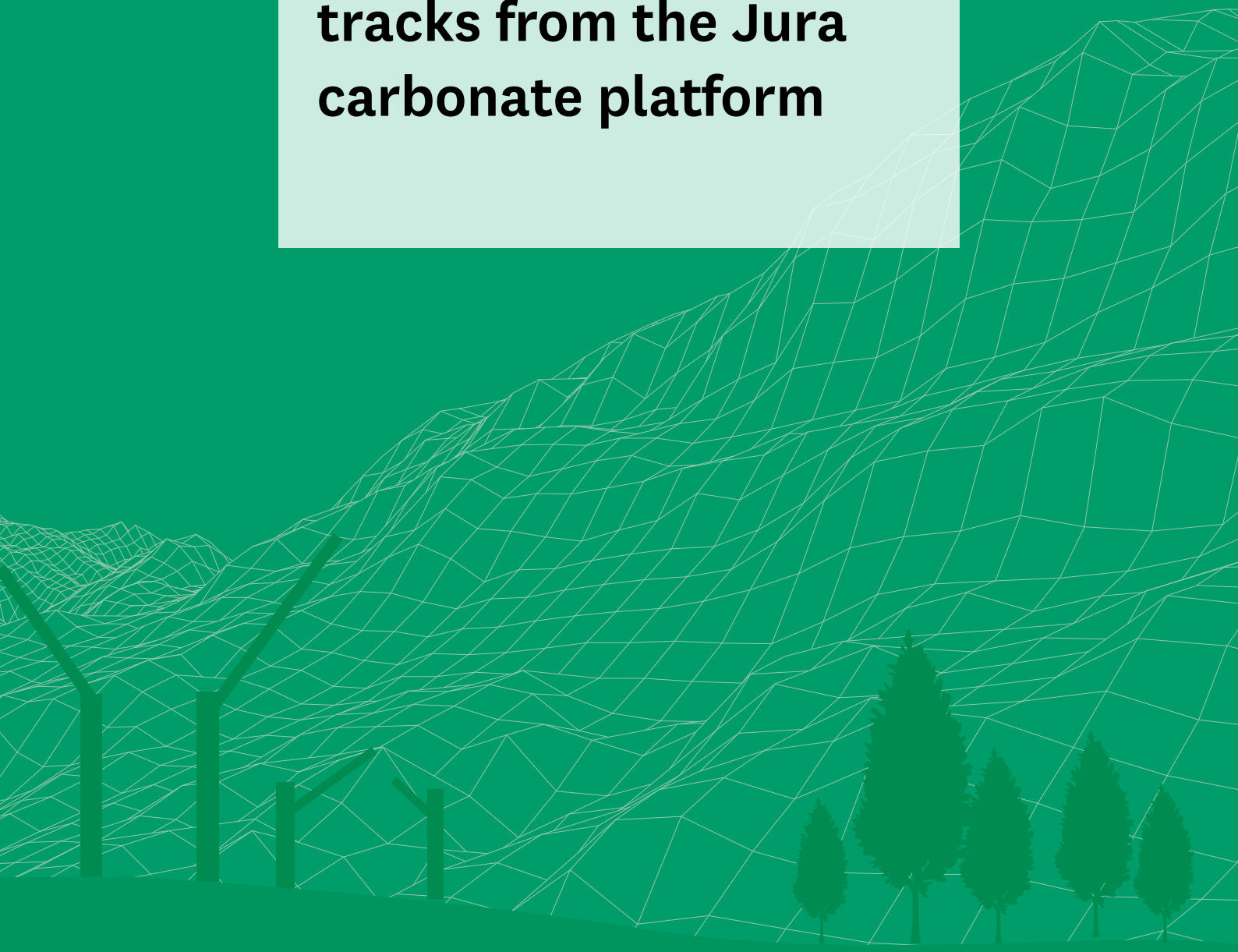
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Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform



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GeoFocus volume 21

Daniel MARTY

Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez—Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology



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"Tracking is an ancient art, once practised by the whole human race and still a part of daily life for hunting and gathering peoples. It has almost completely gone out of fashion in the modern world. (...) An experienced (aboriginal) tracker can read the ground like a storybook. If the tracks are those of a mammal, he can probably tell you, from the size and 'weight' or depth of the tracks, its gender and approximate age. If the animal is a female, he will know by the spacing of the hind legs whether or not it is 'parapu' (carrying young). He will usually be able to tell you the species of a lizard and not only which way a snake is travelling, and its size, but how fast it is moving and whether it is harmless or venomous."

Pat Lowe (2002)

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Cover photo: Chevenez—Combe Ronde tracksite, excavation area 3, main track level: Two trackways (S12, S13) of tiny sauropods heading to the top are crossed by a trackway (S11) of a small sauropod heading from the upper left to the lower right. Also visible are desiccation cracks and a normal fault in the middle part of the picture. Photo by B. Migy.
Photographs: If not otherwise stated, all photographs in this work were taken by Daniel Marty. All photographs of the Chevenez—Combe Ronde and Courtedoux—Sur Combe Ronde tracksites (tracks, samples, etc.) are courtesy of the PAL A16, ©OCC–SAP (*République et Canton du Jura, Office de la culture, Section d'archéologie et paléontologie, Paléontologie A16, Hôtel des Halles, C.P. 64, 2900 Porrentruy 2, Switzerland*), and the originals are archived in the photo database of the PAL A16. All other photographs are courtesy of Daniel Marty.
Figures: Some of the figures with tracks and trackways in this work (Figs. 4.16, 4.17A, 4.18, 5.12, 5.14, 5.17, 5.26, 5.27A, 5.29, 5.30, 5.34B, 5.40A, Annex 5.1) are based on track digitalisations made by the PAL A16, and the original digitalisations are archived by the PAL A16. A 1:50 map of excavation area 3 (similar to Figs. 5.29 & 5.30) is not included in this work due to its large size, but is archived by the PAL A16.
Studied material: All studied fossil material (casts of tracks and trackways, track slabs, recovered tracks, sedimentological samples, thin-sections) is courtesy of the PAL A16. This material is currently housed in the collections of the PAL A16 but will later be transferred to the collection of the *Musée jurassien des sciences naturelles de Porrentruy* (institutional abbreviation: MJSN). Lists of the studied material are archived by the PAL A16.
Original documentations: All original documentations (maps, track descriptions and drawings, track and trackway parameters, sedimentological logs) are archived by the PAL A16.
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* * *

Abstract

Dinosaur tracks are biogenic, sedimentary structures and not body fossils or biological objects in the common sense. They result from the complex interaction of the kinematics of the trackmaker, its foot anatomy, and the substrate properties, and from taphonomic processes acting prior to the incorporation of the tracks into the sedimentary record. The objective of this work is an interdisciplinary study of a large sample of dinosaur tracks and trackways linking sedimentology with vertebrate ichnology, palaeontology, and palaeoecology.

Excellent conditions are provided by the Late Jurassic (Kimmeridgian) Chevenez—Combe Ronde tracksite, which is one of several tracksites located on the future course of the Transjurane highway near Porrentruy (Canton Jura, NW Switzerland). Here, eight superimposed dinosaur track-bearing surfaces were systematically excavated level-by-level within a 0,65 m thick laminite interval, unearthing almost 1400 dinosaur tracks. The main track level, located at the base of the interval, is the most diverse ichnoassemblage composed of 14 trackways of tiny (Pes Length < 25 cm) and small (25 cm < PL < 50 cm) sauropods and 43 trackways of minute (PL < 10 cm), small (10 cm < PL < 20 cm), and medium-sized (20 cm < PL < 30 cm) bipedal, tridactyl dinosaurs.

The main issues are: (1) identification of true tracks, undertracks, and overtracks, and their relationships with substrate properties, their link with the exposure index, and their utility in the reconstruction of the palaeoenvironment; (2) implications of the main track level ichnoassemblage for dinosaur behaviour, the terrestrial palaeoecosystem, and vertebrate ichnofacies; (3) relationships between variability in trackway patterns and configurations with locomotion speed, behaviour, and substrate properties as well as implications for locomotion capabilities; (4) Quantification and relevance of sauropod trackway gauge; and (5) interpretation of manus-dominated and pes-only sauropod trackways.

The approach is first actualistic by studying human footprints and processes acting during their formation and preservation on modern tidal-flats. In these highly structured environments, microbial mats are ubiquitous, strongly facies-specific, and occupy a key position during and after footprint formation. Undertracks readily form in biolaminated sediment, whilst underprints and deep tracks are common in unlaminated, water-saturated sediment. Most consolidated vertebrate tracks are affected by taphonomic processes, including renewed and/or repeated growth of microbial mats leading to the formation of modified true tracks, internal overtracks (track fills), and overtracks.

The sauropod tracks and the encasing laminite interval of the Combe Ronde site are then subject of detailed sedimentological and taphonomical analyses. This discloses the sediment properties at the time of track formation and reveals the processes modifying the tracks during subaerial exposure and integrating them into the sedimentary record. Track morphology, associated track features, and sedimentary features can be linked with the exposure index, identifying the palaeoenvironment as a supratidal flat not located in close proximity to a coastline. These flats were susceptible for track recording only during short periods after wetting due to a rainy period or due to occasional storms. Longer periods of subaerial exposure prior to burial are indicated by the presence of internal overtracks and/or overtracks, and rapid covering up is indicated by the lack of overtracks on top of tracks with large displacement rims. Cross-sections of sauropod tracks provide insight into the consolidation history of the substrate prior to track formation and into the walking dynamics of dinosaurs, confirming that sauropods put their hindfeet in a pronounced plantigrade way on the ground.

The level-by-level superimposition of the studied surfaces enables to identify true tracks, undertracks, and overtracks. The best-defined true tracks (anatomical morphotypes) of the main track level are then used for ichnotaxonomy and trackmaker identification, and the detailed analyses of trackway parameters, including trackway gauge, provide insight into the locomotion capabilities of dinosaurs.

The best-defined minute and small tridactyl tracks can be assigned to the ichnogenus *Carmelopodus*, extending it from the Middle Jurassic into the Late Jurassic. These tracks were likely left by a small theropod dinosaur similar in size to *Compsognathus* or *Juravenator*. The medium-sized tridactyl tracks of morphotype II exhibit some of the typical features of the ichnogenus *Therangospodus* (attributed to large and robust theropods) but also some of ornithopod ichnotaxa.

The sauropod trackways show a wide range of patterns and configurations but are all medium- to wide-gauge. Therefore, they are assigned tentatively to the ichnogenus *Brontopodus* attributed to derived "brachiosaurid" or "titanosaurid" dinosaurs. The variability of the trackways reflects the general locomotion capabilities of the trackmakers and is an expression of individual walking style and behaviour, which may be related to substrate properties. Trackway patterns (the degree of manus overprinting by the pes) and different trackway configurations including trackway gauge are not only related to locomotion speed, and they provide no evidence of a relationship with ontogeny.

The gauge of sauropod trackways can be quantified with the pes trackway ratio and the here defined [WAP/PL]-ratio (Width of the pes Angulation Pattern / Pes Length). Gauge is possibly related to the substrate and the behaviour of the trackmaker adapting to it, but this does not change the overall medium-gauge to wide-gauge appearance of the trackways. The manus-dominated and pes-only sauropod trackways of the Combe Ronde site are explained by trackmakers exerting more pressure on the manus than the pes, and by overprinting of the manus by the pes, respectively.

The alignment of trackways on the main track level shows no evidence of a nearby shoreline and of interactions between the different groups of dinosaurs. It indicates gregarious behaviour amongst tiny and small sauropods, and suggests that minute and small bipedal dinosaurs were frequent visitors on the supratidal flats.

The ichnoassemblage of the main track level is the first one found in the Jura Mountains displaying abundant minute and small tridactyl tracks. This is also typical for the other Ajoie ichnoassemblages, which further exhibit tracks of tiny to large (up to 1,1 m PL) sauropods, and tracks of medium-sized to large (up to 0,8 m PL) bipedal dinosaurs. Sauropod trackways include narrow-gauge and wide-gauge trackways indicating the presence of "basal" and derived sauropods. This suggests that dwarfed insular animals can be excluded as trackmakers of the tiny and small sauropod trackways of the Ajoie ichnoassemblages and the Combe Ronde tracksite and that the Jura carbonate platform was connected with the landmasses of the London-Brabant Massif and the Massif Central during periods of emersion. Dinosaurs used the Jura carbonate platform for the establishment of *in situ,* predominantly saurischian dinosaur populations, but also as a migration corridor between the massifs.

Because the Ajoie ichnoassemblages are dominated by small tridactyl tracks, they differ from other Jurassic tetrapod ichnofacies in carbonate settings, notably from the *Brontopodus* ichnofacies. In the case of those ichnoassemblages commonly attributed to the *Brontopodus* ichnofacies, the lack or rareness of small tridactyl tracks may indicate the absence of small trackmakers in those palaeoenvironments or unsuitable conditions for the formation and preservation of small tracks.

This study highlights the benefits of systematic and interdisciplinary analyses of dinosaur tracks, which disclose variations related to behaviour and to differences in substrate. This allows recognizing anatomical morphotypes and trackway configurations representative of typical trackmaker behaviour. The latter can then also be used in ichnotaxonomical classification. Similar approaches should be in the focus of future work and performed on the other tracksites and ichnoassemblages of the Ajoie. Together with the evidence from other tracksites of the Jura Mountains, this will contribute towards a better understanding of the terrestrial palaeoenvironments and palaeogeography, and of dinosaur palaeoecology and palaeobiogeography on the Jura carbonate platform.

* * *

Résumé

Les traces de dinosaures sont des structures biogéniques et sédimentaires, mais pas des organismes fossiles à proprement parler. Elles résultent de l'interaction complexe entre le mode de déplacement d'un animal, l'anatomie de ses pieds et de ses mains, et les propriétés du substrat, mais aussi des processus taphonomiques. En ce sens, ce travail est une étude interdisciplinaire d'un échantillon riche en traces et en pistes de dinosaures, associant des données sédimentologiques, ichnologiques, paléontologiques et paléoécologiques.

Le site à traces de Chevenez—Combe Ronde, daté du Kimméridgien (Jurassique supérieur), offre d'excellentes conditions d'étude de traces de dinosaures inédites. Il s'agit d'un des sites à traces de dinosaures situés sur le futur tracé de l'autoroute Transjurane dans les environs de Porrentruy (canton du Jura, nord-ouest de la Suisse). Huit niveaux à traces successifs, contenus dans un intervalle de 0,65 m de calcaire laminé, ont été fouillés de manière systématique, livrant près de 1400 traces de dinosaures. Le niveau principal, situé à la base de l'intervalle, présente l'assemblage ichnologique le plus diversifié, avec 14 pistes de petits (25 cm < Longueur du Pied < 50 cm) voire très petits (LP < 25 cm) sauropodes et 43 pistes de dinosaures bipèdes et tridactyles de taille très petite (LP < 10 cm) et petite (10 cm < LP < 20 cm) à moyenne (20 cm< LP < 30 cm).

Les objectifs principaux de cette étude sont : (1) identifier les vraies empreintes (*true tracks*), les sous-empreintes (*undertracks*) et les sur-empreintes (*overtracks*), définir leur lien avec les propriétés du substrat et l'indice d'exposition (*exposure index*) ainsi que leur utilité pour la reconstitution d'un paléoenvironnement ; (2) définir les implications de l'assemblage ichnologique du niveau principal pour reconstituer le comportement des dinosaures, le paléoécosystème terrestre et l'ichnofaciès ; (3) déterminer les relations entre la variabilité du *pattern* et de la configuration des pistes et les capacités locomotrices, la vitesse de déplacement, le comportement et les propriétés du substrat ; (4) discuter de la signification de la largeur de voie des pistes de sauropodes ; (5) interpréter les pistes particulières de sauropodes, dominées par les empreintes de mains ou constituées uniquement d'empreintes de pieds.

L'approche est tout d'abord actualiste, avec l'étude d'empreintes humaines et des processus agissant durant leur formation et leur préservation dans des vasières actuelles. Dans ces environnements, les tapis microbiens sont ubiquistes, fortement spécifiques au type de faciès, et jouent un rôle clé dans la formation et la préservation des empreintes. Les sous-empreintes se forment dans un sédiment biolaminé, alors que les *underprints* et les empreintes profondes (*deep tracks*) sont fréquentes dans un sédiment non laminé, saturé en eau. La plupart des traces de vertébrés sont affectées par des processus taphonomiques, incluant le renouvellement et/ou la croissance des tapis microbiens, ce qui modifie les vraies empreintes, mais forme également des sur-empreintes internes (*internal overtracks*, remplissages des vraies empreintes) et des sur-empreintes.

Les traces de sauropodes de l'intervalle de calcaire laminé du site de Combe Ronde ont également été soumises à des analyses détaillées de sédimentologie et de taphonomie. Ces analyses mettent en évidence les propriétés du sédiment lors de la formation des

traces, mais aussi les processus ayant modifié les traces durant leur exposition sub aérienne et leur enregistrement dans le sédiment. La morphologie des traces, les structures associées aux traces et les structures sédimentaires peuvent être reliées à l'indice d'exposition, indiquant un paléoenvironnement de type vasière supratidale éloignée de la ligne de côte. Ces vasières sont favorables à la préservation d'empreintes uniquement durant de courtes périodes où le substrat est humide, suite à une période de pluie ou à l'occasion d'une tempête. De longues périodes d'exposition sub aérienne avant l'enfouissement sont indiquées par la présence de sur-empreintes internes et/ou de sur-empreintes, alors qu'un recouvrement rapide est indiqué par l'absence de sur-empreintes sur des traces ayant d'importants bourrelets d'expulsion (de boue carbonatée). Des coupes longitudinales d'empreintes de sauropodes fournissent des informations sur le mode de consolidation du substrat avant la formation des traces et sur la locomotion des dinosaures, confirmant que les sauropodes posaient leurs pieds de manière plantigrade.

La superposition niveau par niveau des surfaces étudiées permet de discerner les vraies empreintes, les sous-empreintes et les sur-empreintes. Les vraies empreintes les mieux définies (morphotypes anatomiques) du niveau principal sont alors utilisées pour l'ichnotaxonomie et l'identification de l'auteur des traces. Les analyses détaillées des paramètres de pistes, incluant la largeur de voie des pistes, fournissent des informations sur le mode de déplacement des dinosaures.

Les pistes tridactyles de taille très petite à petite sont attribuées à l'ichnogenre *Carmelopodus*, ce qui étend la répartition stratigraphique de cet ichnotaxon du Jurassique moyen au Jurassique supérieur. Ces empreintes ont été formées par un petit dinosaure théropode de taille similaire à *Compsognathus*. Un second morphotype partage certains caractères avec l'ichnogenre *Therangospodus*, attribué à de grands et robustes théropodes, mais aussi avec des ichnotaxons typiques d'ornithopodes.

Les pistes de sauropodes montrent un spectre varié de *patterns* et de configurations mais ont toutes une largeur de voie moyenne à large. Elles sont attribuées avec précaution à l'ichnogenre *Brontopodus*, ichnotaxon associé à des brachiosauridés ou des titanosaures. La variabilité des pistes reflète les capacités locomotrices. Elle est l'expression de différents types de locomotion et de comportement individuel liés aux propriétés du substrat. Le *pattern* (le degré de recouvrement de la main par le pied) et les différentes configurations (incluant la largeur de voie) des pistes ne sont pas seulement liées à la vitesse de déplacement et n'indiquent pas de changement au cours de l'ontogénie.

La largeur de voie des pistes de sauropodes peut être quantifiée avec le *pes trackway ratio* et le *[WAP/PL]-ratio*, le rapport entre la largeur de voie (*Width of the pes Angulation Pattern*) et la longueur des pieds (*Pes Length*). La largeur de voie est probablement liée au substrat et au comportement du sauropode, mais sans que cela change l'aspect général des pistes dont la largeur de voie est moyenne à large. Les pistes du site de Combe Ronde dominées par les empreintes de mains ou uniquement composées d'empreintes de pieds, sont interprétées comme laissées par des sauropodes exerçant respectivement plus de pression sur les mains que sur les pieds ou par un recouvrement des empreintes de mains par celles des pieds.

L'alignement des pistes du niveau principal ne suggère pas de proximité d'une ligne de côte et d'interactions entre différents groupes de dinosaures. Il indique un comportement grégaire parmi les sauropodes de taille très petite à petite et suggère que les dinosaures bipèdes de taille très petite à petite étaient des visiteurs fréquents de ces vasières supratidales.

L'assemblage ichnologique du niveau à traces principal est le premier découvert dans la chaîne du Jura avec une abondance d'empreintes tridactyles de tailles très petite à petite. Les assemblages ichnologiques d'Ajoie sont généralement caractérisés par une prédominance d'empreintes tridactyles de taille très petite à petite, puis d'empreintes de sauropodes de taille très petite à grande (LP jusqu'à 1,1 m), puis de traces de dinosaures bipèdes de taille moyenne à grande (LP jusqu'à 0,8 m) incluant de grands théropodes. La voie des pistes de sauropodes est étroite à large, ce qui indique la présence de formes à la fois « basales » et évoluées de sauropodes. Ceci suggère que la plateforme carbonatée du Jura était, durant les périodes d'émersion, régulièrement connectée avec les masses continentales du Massif de London-Brabant et du Massif Central, permettant le maintien *in situ* de populations de dinosaures saurischiens et écartant la possibilité de formes insulaires « naines » de sauropodes pour les pistes aux empreintes de taille très petite à petite du site de Combe Ronde.

Parce que les assemblages ichnologiques d'Ajoie sont dominés par les petites empreintes tridactyles, elle diffèrent des autres ichnofaciès à tétrapodes connus dans des environnements carbonatés du Jurassique, en particulier de l'ichnofaciès *Brontopodus*. La rareté des petites empreintes tridactyles dans l'ichnofaciès *Brontopodus* signifie soit l'absence de ces petits animaux dans les paléoenvironnements représentés, soit des conditions défavorable pour la formation ou la préservation des petites empreintes.

Cette étude souligne l'avantage d'analyses systématiques d'échantillons riches en traces et en pistes, afin de discerner la variation due au comportement et aux propriétés du substrat. Ceci permet de définir des morphotypes anatomiques et des configurations de pistes caractéristiques du comportement des animaux. Ces éléments peuvent également être utilisés pour l'ichnotaxonomie. Des approches similaires devraient être appliquées dans le cadre des études menées sur la très importante base de données des assemblages ichnologiques d'Ajoie en comparaison avec les données des autres sites à traces de l'arc jurassien. Ceci permettra de mieux comprendre les paléoenvironnements terrestres, mais aussi la paléobiogéographie et la paléoécologie des dinosaures de la plateforme carbonatée du Jura.

Translation by Jean-Paul Billon-Bruyat and Damien Becker (PAL A16)

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Zusammenfassung

Dinosaurierspuren sind biogene, sedimentäre Strukturen und keine Körperfossilien oder biologische Objekte im herkömmlichen Sinn. Sie entstehen durch das komplexe Wechselspiel zwischen der Bewegung und der Anatomie des Fusses des Verursachers einerseits und Sediment mit unterschiedlichen Eigenschaften andererseits; zusätzlich können die Spuren vor ihrer Fossilisation durch taphonomische Prozesse verändert werden. Das Ziel der vorliegenden Arbeit ist ein interdisziplinäres Studium von Dinosaurierspuren mittels Methoden der Sedimentologie, Wirbeltier-Ichnologie, -Paläontologie und -Paläoökologie.

Hervorragende Voraussetzungen für solch eine Studie fanden sich an der spätjurassischen Fundstelle Chevenez—Combe Ronde, einer von mehreren Fundstellen auf der zukünftigen Autobahn A16 (Transjurane) nahe Pruntrut (Kanton Jura, NW Schweiz). Ein 0,65 m mächtiges Intervall, bestehend aus laminiertem, mergeligem Kalkstein, wurde hier systematisch ausgegraben. So wurden acht übereinanderliegende Horizonte mit nahezu 1400 Dinosaurierspuren zu Tage gefördert. Der Hauptfährtenhorizont an der Basis dieses Intervalls ist die Spurenassoziation mit der grössten Diversität. Diese besteht aus 14 Sauropoden-Fährten von sehr kleinen (d.h. Fusslänge < 25 cm) und kleinen (25 cm < FL < 50 cm) Individuen und 43 Fährten mit dreizehigen Fussabdrücken von winzigen (FL < 10 cm), kleinen (10 cm < FL < 20 cm) und mittelgrossen (20 cm < FL < 30 cm) bipeden Dinosauriern.

Die Hauptfragestellungen dieser Arbeit sind:

(1) die Identifizierung von *true tracks* (echte Spuren, auf der ursprünglichen Bodenoberfläche abgedrückt), *undertracks* (Pausspuren), und *overtracks* (Oberspuren) sowie die Zusammenhänge zwischen den verschiedenen Arten von Spuren einerseits und den Sedimenteigenschaften und dem *exposure index* (Mass für die Anzahl Tage pro Jahr, an denen die Bodenoberfläche nicht mit Wasser bedeckt ist) andererseits; (2) die Spurenassoziation (*ichnoassemblage*) des Hauptfährtenhorizontes und mögliche Rückschlüsse auf das Verhalten der Dinosaurier, ihr Paläoökosystem und ihre Ichnofazies; (3) die Beziehungen zwischen der Variabilität der Muster (*pattern*) und Konfigurationen der Fährten einerseits und andererseits den Sedimenteigenschaften, sowie der Fortbewegungsgeschwindigkeit, dem Verhalten, und den Fortbewegungsfähigkeiten der Dinosaurier; (4) die Bedeutung der Gangbreite

von Sauropodenfährten; (5) die Interpretation von Sauropodenfährten, welche nur oder mehrheitlich Adrücke der Hinterfüsse respektive der Vorderfüsse zeigen.

Die Vorgehensweise ist zunächst aktualistisch: Menschliche Fussspuren und die Prozesse, die heute während ihrer Bildung und Erhaltung in intertidalen bis supratidalen Ablagerungsräumen stattfinden, werden analysiert. In diesen verschiedenartigen Ablagerungsräumen spielen die allgegenwärtigen und fazies-spezifischen Mikrobenmatten während und nach der Bildung von Fussspuren eine Schlüsselrolle. In biolaminiertem Sediment bilden sich *undertracks*; in unlaminiertem, wassergesättigtem Sediment dagegen sind *underprints* und *deep tracks* (das sind beide spezielle Formen echter Spuren) typisch, welche die ursprüngliche Bodenoberfläche durchbrechen. Es zeigt sich, dass die meisten verhärtet vorgefundenen Spuren durch taphonomische Prozesse beeinträchtigt wurden. So führt erneutes und/oder wiederholtes Wachstum von Mikrobenmatten zur Bildung von *modified true tracks* (modifizierten echten Spuren), *internal overtracks* (internen Oberspuren), und *overtracks*.

Darauf folgend werden die Sauropodenspuren und das sie umgebende Gestein der Fundstelle Combe Ronde detaillierten sedimentologischen und taphonomischen Analysen unterzogen. Das ergibt Hinweise auf die Sedimenteigenschaften zur Zeit der Spurenbildung und auf die Prozesse, welche die Spuren modifizierten und konservierten. Die verschiedenen Spurenmorphologien, ihre assoziierten Strukturen, und andere sedimentäre Merkmale werden mit dem *exposure index* in Beziehung gebracht und kennzeichnen den ehemaligen Lebensraum als supratidal und nicht in der Nähe einer Küstenlinie liegend. Spuren konnten in diesem supratidalen Ablagerungsraum nur während kurzer Zeit nach Regenperioden oder Stürmen hinterlassen werden. Dass die Bodenoberfläche während längerer Zeit nahezu unverändert bestehen blieb, wird durch *internal overtracks* und/oder *overtracks* angezeigt, ein schnelles Zudecken der Oberfläche dagegen durch das Fehlen von *overtracks*. Querschnitte durch Sauropodenspuren ermöglichen Einblicke in die Konsolidierungsgeschichte des Sediments vor der Bildung der Spuren und in die Fusskinematik ihrer Verursacher. Das bestätigt, dass Sauropoden ihre Hinterfüsse plantigrad auf das Sediment aufsetzten.

Durch die Überlagerung der Spurenpläne von übereinander liegenden Flächen können *true tracks*, *undertracks* und *overtracks* unterschieden werden. Die am besten erhaltenen Spuren des Hauptfährtenhorizonts werden in der Folge für ichnotaxonomische Beschreibungen und Bestimmungen sowie für die Identifizierung der Verursacher verwendet. Die detaillierte Analyse aller Fährtenparameter, unter besonderer Berücksichtigung der Gangbreite, ergibt einen Einblick in die Fortbewegungsfähigkeiten der Dinosaurier.

Bei den dreizehigen Spuren können zwei Morphotypen unterschieden werden. Die am besten definierten, kleinen Spuren können dem Ichnogenus *Carmelopodus* zugeordnet werden, was sein zeitliches Auftreten von der Mittleren bis in die Späte Jurazeit ausdehnt. Diese Spuren wurden von einem kleinen Theropoden in der Grössenordnung von *Compsognathus* oder *Juravenator* hinterlassen. Ein zweiter, mittelgrosser Morphotyp zeigt Merkmale, die auf Theropoden (Ichnogenus *Therangospodus*), aber auch auf Ornithopoden hinweisen.

Die Sauropodenfährten zeigen eine grosse Bandbreite an Mustern und Konfigurationen. Sie sind aber alle durch eine hohe Gangbreite ausgezeichnet, und werden deshalb provisorisch dem Ichnogenus *Brontopodus* zugerechnet. Dieses wird mit „brachiosauriden“ oder „titanosauriformen“ Sauropoden in Verbindung gebracht.

Die Variabilität der Sauropodenfährten reflektiert die allgemeinen Bewegungsfähigkeiten ihrer Verursacher und ist ein Ausdruck von individueller Gangart und Verhalten, was auch mit den Sedimentbedingungen in Zusammenhang stehen mag. Die verschiedenen Muster und Konfigurationen (einschliesslich der Gangbreite) hängen nicht von der Grösse der Tiere und nur bedingt von der Fortbewegungsgeschwindigkeit ab.

Die Gangbreite kann mit dem *pes trackway ratio* und dem in dieser Arbeit neu eingeführten Quotienten *[WAP/PL]-ratio*, das ist das Verhältnis zwischen der Gangbreite (Width of the pes Angulation Pattern = WAP) und der Fusslänge (PL = Pes Length), quantifiziert werden. Die Gangbreite kann von den Sedimenteigenschaften und einem dadurch hervorgerufenen Verhalten abhängen, was aber nichts an einem eher schmalen oder weiten Erscheinungsbild einer Fährte ändert. Fährten mit nur oder mit mehrheit-

lich den Abdrücken der Vorderfüsse entstehen wenn die Sauropoden mehr Druck auf die Vorderfüsse als die Hinterfüsse ausüben. Fährten ohne Abdrücke der Vorderfüsse sind durch das Übertreten der Abdrücke der Vorderfüsse durch die Hinterfüsse bedingt.

Die Anordnung der Fährten auf dem Hauptfährtenhorizont deutet weder auf eine nahe Küstenlinie noch auf Interaktionen zwischen den verschiedenen Gruppen von Dinosauriern hin. Die unregelmässige Anordnung ihrer Spuren lässt vermuten, dass die kleinen bipeden Dinosaurier den supratidalen Ablagerungsraum regelmässig aufsuchten. Klar ersichtlich ist hingegen ein Herdenverhalten unter den kleinen Sauropoden.

Die Spurenassoziation des Hauptfährtenhorizontes ist die erste aus dem Juragebirge wo kleine dreizehige Spuren nachgewiesen werden. Dies ist auch typisch für die anderen Spurenassoziationen der Ajoie (*Ajoie ichnoassemblages*), die zudem Spuren von sehr kleinen bis gigantischen (Fusslänge bis 1,1 m) Sauropoden, und von von mittelgrossen bis grossen (Fusslänge bis 0,8 m) bipeden Dinosauriern (zumeist Theropoden) beinhaltet. Die Sauropodenfährten beinhalten schmale und weite Fährten, was auf das Vorhandensein von primitiven („*basal*“) und höher entwickelten (*derived*) Sauropoden schliessen lässt. Zwergwüchsige Sauropoden können als Verursacher der sehr kleinen Spuren ausgeschlossen werden, da sehr kleine und sehr grosse Spuren zusammen vorkommen. Das bedeutet auch, dass die Jura Karbonat-Plattform während Zeiten niedrigen Meeresspiegels mit den grösseren Landmassen des London-Brabant Massifs und des Massif Central verbunden war, und dass Dinosaurier diese Landbrücke als Lebensraum einerseits und als Migrationsroute zwischen den Massiven andererseits benutzten.

Da die Spurenassoziationen der Ajoie von kleinen dreizehigen Spuren dominiert werden, unterscheiden sie sich von anderen Jurassischen Tetrapoden-Ichnofazien aus karbonatischen Ablagerungsräumen, insbesondere von der *Brontopodus* Ichnofazies. Das Fehlen kleiner dreizehiger Spuren in der *Brontopodus* Ichnofazies bedeutet entweder, dass diese kleinen Tiere in den entsprechenden Ablagerungsräumen nicht vorkamen oder, dass dort die Bedingungen für die Bildung und Erhaltung solch kleiner Spuren nicht gegeben waren.

Die vorliegende Studie unterstreicht die Bedeutung der systematischen und interdisziplinären Auswertung ichnologischer Daten. So können durch das Verhalten der Verursacher oder Unterschiede in den Sedimenteigenschaften hervorgerufene Variationen in der Spurenmorphologie unterschieden und anatomische Morphotypen und typische Fährtenkonfigurationen erkannt werden. Letztere können dann auch für ichnotaxonomische Klassifikationen herangezogen werden. Eine ähnliche Vorgehensweise sollte bei der zukünftigen wissenschaftlichen Bearbeitung der Spurenassoziationen der Ajoie im Vordergrund stehen. Zusammen mit den Befunden anderer Dinosaurierspuren Fundstellen im Jura-gebirge wird das zu einem besseren Verständnis der terrestrischen Ablagerungsräume und der Paläogeographie, sowie der Paläobiogeographie und Paläoökologie der Dinosaurier auf der Jura Karbonat-Plattform beitragen.

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* * *

1 - Introduction

Although the most vivid (scientific) impression of a dinosaur as a living animal is provided by the interpretation of a well-preserved trackway, which is the epitome of its dynamic behaviour (Farlow & Chapman, 1997; Lockley, 1997b), it was only during the last thirty years that the study of dinosaur tracks came into the focus of scientific research (e.g., Lockley, 1986, 1987, 1989, 1991a, 1998a, 1999).

Lockley & Meyer (2000) stated that "the classic Jura region is full of tracks that were previously not known to exist". Indeed, since the initial discovery of dinosaur tracks in the Lommiswil quarry (Meyer, 1990), many more tracksites were discovered in the Jura Mountains (Meyer & Thüring, 2003a), culminating in the discoveries in the Ajoie (Canton Jura, NW Switzerland) along the Transjurane highway and in the Chevenez – Courtedoux area. Consequently, dinosaur tracks became useful not only regarding palaeontological research, but also regarding the high level of media and public interest and their great educational value. Today, the tracksites of the Jura Mountains are generally considered as geotopes, or as important parts of the natural heritage (e.g., Marty et al., 2004). Accordingly, the larger sites are now in the focus of a more popular and touristic interest.

In the year 2000, a new palaeontological survey project, the Palaeontology A16 (abbreviation: PAL A16), was established in the Canton Jura (NW Switzerland). This palaeontological project is part of the *Section d'archéologie et paléontologie* (abbreviation: SAP), which is under the responsibility of the Office of Culture of the Canton Jura (*Office de la culture de la République et Canton du Jura*). It is in charge of the excavation and documentation of the palaeontological heritage of the future course of the Transjurane highway (federal highway A16) prior to its construction, and of making this heritage accessible for scientific research (e.g., Marty, 2003a; Marty & Becker, 2003; Marty & Hug, 2003; Hug et al., 2004; Marty et al., 2004, 2007a; Ayer et al., 2005, 2006). These excavations resulted in the discovery of several large dinosaur tracksites unearthing dozens of ichnoassemblages with thousands of dinosaur tracks (Marty et al., 2007a) in this work referred to as Ajoie ichnoassemblages.

The present PhD thesis project was established in 2004 thanks to a joint venture between the Palaeontology A16 (Office of Culture of the Canton Jura) and the University of Fribourg. The aim of the thesis is a detailed sedimentological and ichnological analysis of one of the Ajoie dinosaur tracksites, namely the Chevenez—Combe Ronde tracksite (abbreviation: Combe Ronde site; CHE-CRO), which is located on a feeder road to the Transjurane highway near Porrentruy (Canton Jura, NW Switzerland). This tracksite was discovered in 2003 by the Palaeontology A16, excavated from 2003 to 2007, and it is meanwhile protected by the extension of a highway bridge.

1.1 Objectives

Dinosaur tracks are trace fossils and not body fossils in the common sense (e.g., Bertling, 2007). They are deformed sediment resulting from the complex interaction of the foot anatomy and the kinematics of the trackmaker with the substrate (e.g., Padian & Olsen, 1984; Unwin, 1989). Wilson (2005) stated that "trackways should be interpreted in the context of behavioural variation (is the trackway representative of "typical" trackmaker behaviour?), taphonomic variation (is trackway morphology altered by preservation?), and taxonomic variation (is the trackmaker "typical" of the larger taxon it represents?)". This highlights that the study of vertebrate ichnology is inherently interdisciplinary connecting sedimentology with vertebrate ichnology, palaeontology, locomotion, and behaviour.

The main objective of this work is to perform such an interdisciplinary approach based on a large sample of tracks and trackways. This is provided by the Chevenez—Combe Ronde tracksite where a 0,65 m thick interval of laminated to biolaminated, marly limestone was subjected to a systematic level-by-level excavation. This revealed seven dinosaur track-bearing surfaces superimposed on the main track level, the latter with the most diversified ichnoassemblage composed of tracks of both sauropod and bipedal dinosaurs including tracks of very small animals of both groups.

The sedimentology of this laminite interval and the sedimentological and stratigraphical framework of previous studies suggest that the dinosaur tracks of the Combe Ronde tracksite were left approximately at the boundary from the Early to the Late Kimmeridgian (about 152 million years ago) on tidal-flats of the Jura carbonate platform.

However, several commonly addressed issues concerning the dinosaur tracks of the Jura carbonate platform are not clear at the moment. Were they chance visitors migrating to reach new territories? Or were these tidal-flat and carbonate platform environments one of their favourite haunts and *in situ* dinosaur populations were during periods of emersion? What do the tracks tell us about the behaviour of the dinosaurs in those environments and what about the terrestrial palaeoecosystem? What about the locomotion capabilities of the trackmakers and were they able to swim?

To find answers to some of these questions and in order to get a better insight into the palaeoenvironments of the Late Jurassic Jura carbonate platform, the following major issues will be analysed in this work:

1. Identification of true tracks (preservational and anatomical morphotypes), undertracks, and overtracks
2. Relationships between substrate properties and track morphology
3. Consolidation and burial of palaeosurfaces and tracks: role of microbial mats and other sedimentary processes
4. Reconstruction of sauropod foot kinematics from cross-sections of tracks
5. Link between sauropod tracks and exposure index
6. Importance of sauropod tracks for the reconstruction of the (tidal-flat) palaeoenvironment and its evolution
7. Quantification and relevance of trackway gauge for sauropod ichnotaxonomy and identification of possible trackmakers
8. Ichnotaxonomy of tridactyl tracks and distinction between theropod and ornithischian trackmakers
9. Relationships between variability in trackway patterns and configurations with locomotion speed, behaviour, and substrate properties: implications for locomotion capabilities of the trackmakers and ichnotaxonomy
10. Interpretation of manus-dominated and pes-only sauropod trackways
11. Ichnodiversity and trackway alignment of the ichnoassemblage of the main track level: implications for the behaviour of the trackmakers, the dinosaur community and population structure, and vertebrate ichnofacies.

1.2 Approach

The approach of this work is first actualistic: human footprints and processes acting during their formation and taphonomy are studied on modern tidal flats. These processes are thought to be similar to those acting during the Late Jurassic, even though global climatic conditions and amplitudes of sea-level changes were quite different from today.

Afterwards, the sauropod tracks and the encasing laminite interval of the Combe Ronde site are subjected to detailed sedimentological and taphonomical analyses. It will be tried to recognize similar processes as those inferred from the Holocene and to use them for the interpretation of the palaeoenvironment.

The better understanding of these processes will then allow identifying well-preserved and unmodified true tracks, which can be used for ichnotaxonomical analyses and trackmaker identification. Finally, trackway data will be subjected to detailed analyses because trackways are direct evidence of how dinosaurs moved. This will provide insight into the general locomotion capabilities of the trackmakers, and relationships between trackway configurations and patterns with the behaviour of the trackmakers and/or substrate properties may be recognized.

* * *

2 - General setting of the Chevenez—Combe Ronde tracksite, ichnological terminology and methodology

This chapter gives an overview of the dinosaur tracks in the Jura Mountains, and those discovered by the Palaeontology A16 since 2002 in the Ajoie and on the future course of the Transjurane highway. The latter include the Chevenez—Combe Ronde tracksite, which will be in the focus of detailed descriptions and analyses in Chapter 4 and Chapter 5. Here, the history of the excavations carried out at the Chevenez—Combe Ronde tracksite is detailed and the studied data are specified. The general geographical, geological, and stratigraphical frame is given and the applied ichnological terminology and methodology is explained.

2.1 Dinosaur tracks in the Jura Mountains

Dinosaur bones of *Cetiosauriscus greppini* Huene 1927 were discovered already in the 19th century in the Early Kimmeridgian of the Basse Montagne quarry, which is located near Moutier, Canton Berne (Greppin, 1870; von Huene, 1922, 1926; Schwarz et al., 2007a). However, the first dinosaur tracks were discovered only in 1989 in the Lommiswil quarry near Solothurn (Meyer, 1990). This attested for the first time unequivocally the presence of larger and connected landmasses on the Jura carbonate platform during the Late Jurassic (Meyer, 1993). Since this initial track discovery, more than 20 tracksites have been discovered in the Late Jurassic of the Swiss Jura Mountains, and are reviewed in Meyer & Thüring (2003a) (Table 2.1). Apart from the large Lommiswil and Moutier sites, the Swiss tracksites are rather small in size, do often not show distinct trackways, and because most of the tracks were also exposed in natural outcrops to weathering over long time periods, they are often not well preserved. All Swiss tracksites are either located in the Kimmeridgian Reuchenette Formation or in the Tithonian Twannbach Formation (review in Meyer & Thüring, 2003a).

Dinosaur tracks are also reported from the French part of the Jura Mountains. In 2004, at least nine sauropod trackways were discovered in the Tithonian near Coisia (*Département du Jura*) and attributed to the ichnotaxon *Parabrontopodus* (Le Loeuff et al., 2005, 2006). Sauropod tracks and trackways were furthermore discovered in the Late Oxfordian, in a large quarry near Loulle (Mazin & Hantzpergue, 2006). Loulle is the oldest tracksite of the Jura Mountains and hence marks the first unequivocal formation of larger terrestrial areas on the Jura carbonate platform in connexion either with the Massif Central to the SW, the Rhenish Massif and the London-Brabant Massif to the N-NW, or the Bohemian Massif to the NE, which allowed a subsequent immigration of dinosaurs during the Late Oxfordian. The formation of larger landmasses by the Middle to Late Oxfordian is confirmed by the fossil record of dinosaurs, notably the sauropod remains found near Damparis, France (Lapparent, 1943; Buffetaut, 1988) and an isolated theropod tooth from Röschenz, NW Switzerland (Meyer & Thüring, 2003a), but also by numerous remains of charophytes and plants known from Middle to Late Oxfordian deposits (e.g., Ziegler, 1956; Oertli & Ziegler, 1958; Barale & Contini, 1976; Enay, 1980; Philippe, 1995; Van Konijnenburg-van Cittert & Meyer, 1996; Mojon, 2002; Gee et al., 2003). Sauropod tracks were also discovered in the Berriasian (Early Cretaceous) of the Department Ain, France (Charollais et al., 2008). This suggests the recurrent presence of dinosaurs at least from the Late Jurassic to the Berriasian, and fits well with recurrent periods of emersion on the Jura carbonate platform during the Late Jurassic and Early Cretaceous as indicated by the sedimentary record (e.g., Remane, 1991; Hillgärtner, 1999; Colombié, 2002; Hug, 2003; Rameil, 2005; Tresch, 2007).

Name of tracksite (Community)	Location Country	Lithostratigraphy Age	Tracks and trackways	References
Bürenberg (Romont)	Canton Bern Switzerland	Reuchenette Formation Late Kimmeridgian	Sauropod tracks, pes-only sauropod trackway	Meyer & Hauser, 1994; Meyer & Lockley, 1996
Chevenez—Combe Ronde (Chevenez)	Highway A16, Canton Jura Switzerland	Reuchenette Formation Early / Late Kimmeridgian	1400 tracks including 26 sauropod trackways and 49 bipedal trackways	Marty et al., 2006a; Marty et al., 2007a, this work
Chevenez—Crat (Chevenez)	Highway A16, Canton Jura Switzerland	Reuchenette Formation Early / Late Kimmeridgian	Tracks and trackways of sauropods and tridactyl dinosaurs	Marty et al., 2007a
Chevenez—La Combe (quarry) (Chevenez)	Ajoie, Canton Jura Switzerland	Reuchenette Formation Early / Late to Late Kimmeridgian	Tracks and trackways of sauropods and tridactyl dinosaurs	Marty et al., 2007a
Coisia (Coisia)	Département du Jura France	Couches du Chailley Formation Tithonian	>170 sauropod pes & manus tracks 9 sauropod trackways	Bernier, 1984; Le Loeuff et al., 2005, 2006
Corcelles (Corcelles)	Canton Bern Switzerland	Reuchenette Formation Late Kimmeridgian	Sauropod tracks	Meyer, 2000; Meyer & Thüring, 2003a
Courtedoux—Béchat Bovais (Courtedoux)	Highway A16, Canton Jura Switzerland	Reuchenette Formation Early / Late Kimmeridgian	Tracks and trackways of sauropods and tridactyl dinosaurs	Marty et al., 2007a
Courtedoux—Bois de Sylleux (Courtedoux)	Highway A16, Canton Jura Switzerland	Reuchenette Formation early Late Kimmeridgian	Tracks and trackways of sauropods and tridactyl dinosaurs	Marty et al., 2007a
Courtedoux—Dessus Latchire (Courtedoux)	Ajoie, Canton Jura Switzerland	Reuchenette Formation early Late Kimmeridgian	Tracks and trackways of sauropods	Unpublished data of the PAL A16
Courtedoux—Oratoire (Courtedoux)	Ajoie, Canton Jura Switzerland	Reuchenette Formation early Late Kimmeridgian	Tracks and trackways of sauropods	Billon-Bruyat et al., 2007
Courtedoux—Pommerat (Courtedoux)	Ajoie, Canton Jura Switzerland	Reuchenette Formation early Late Kimmeridgian	Tracks and trackways of sauropods and tridactyl dinosaurs	Unpublished data of the PAL A16
Courtedoux—Sur Combe Ronde (Courtedoux)	Highway A16, Canton Jura Switzerland	Reuchenette Formation early Late Kimmeridgian	Tracks and trackways of sauropods and tridactyl dinosaurs	Marty et al., 2003, 2004; Marty & Cavin, 2003
Courtedoux—Tchâfouè (Courtedoux)	Highway A16, Canton Jura Switzerland	Reuchenette Formation early Late Kimmeridgian	Tracks and trackways of sauropods and tridactyl dinosaurs	Marty et al., 2006a, 2007a, c
Frinvilier (Frinvilier)	Canton Bern Switzerland	Reuchenette Formation Early Kimmeridgian	1 sauropod trackway	Ayer & Claude, 2001
Gänsbrunnen (Gänsbrunnen)	Canton Solothurn Switzerland	Reuchenette Formation Late Kimmeridgian	Sauropod tracks	Meyer, 2000; Meyer & Thüring, 2003a
Gex/Echenevex (Quarry d'En Rati)	Département de l'Ain France	Pierre Châtel Formation Middle Berriasian	Sauropod tracks and trackways	Charollais et al., 2008
Glovelier—Contournement (aka Glovelier I) (Glovelier)	Canton Jura Switzerland	Reuchenette Formation Early / Late Kimmeridgian	Parallel trackways of sauropods	Hostettler, 1999; Tschudin, 2001; Jank et al., 2006b
Glovelier—Côte du Crêt (aka Glovelier II) (Glovelier)	Canton Jura Switzerland	Reuchenette Formation Early / Late Kimmeridgian	1 trackway of a large theropod	Beuchat, 1999
Grenchenberg I & II (Grenchen)	Canton Solothurn Switzerland	Reuchenette Formation Late Kimmeridgian	Sauropod tracks	Meyer, 2000; Meyer & Thüring, 2003a
La Heutte I, III, & IV (La Heutte—Fôret de l'Envers)	Canton Bern Switzerland	Reuchenette Formation Late Kimmerdigian	Tracks of sauropods	Meyer & Hauser, 1994; Meyer & Lockley, 1996
La Heutte II (La Heutte—Fôret de l'Envers)	Canton Bern Switzerland	Reuchenette Formation Late Kimmerdigian	Tracks of sauropods and of a large theropod	Meyer & Hauser, 1994; Meyer & Lockley, 1996
La Plagne (La Plagne—Vâcherie Hirschi)	Canton Bern Switzerland	Reuchenette Formation Late Kimmerdigian	Isolated sauropod tracks	Meyer & Hauser, 1994; Meyer, 2000
Rochefort—Les Grattes (Rochefort)	Canton Neuchâtel Switzerland	Twannbach Formation Tithonian	Single sauropod trackway	Unpublished data of Marty et al.
Lommiswil (aka Lommiswil quarry) (Lommiswil)	Canton Solothurn Switzerland	Reuchenette Formation Late Kimmeridgian	>340 sauropod tracks, 9 sauropod trackways	Meyer, 1990, 1993
Loulle (Loulle)	Département du Jura France	Pierre bleue de Loulle Late Oxfordian	Sauropod tracks and trackways	Mazin & Hantzpergue, 2006
Montbautier (Montbautier)	Canton Bern Switzerland	Reuchenette Formation Late Kimmeridgian	Sauropod trackway	Mouchet, 1993; Meyer, 1994b
Moutier Gorges (aka Moutier I-IV) (Moutier)	Canton Bern Switzerland	Reuchenette Formation Early Kimmeridgian	>2000 isolated sauropod pes and manus tracks	Meyer & Lockley, 1996; Meyer, 1997; Lockley & Meyer, 2000
Pierre Pertuis I-IV (Tavannes)	Canton Bern Switzerland	Twannbach Formation Early Tithonian	Isolated sauropod tracks	Meyer & Lockley, 1996; Meyer, 2000
Reconvilier (Reconvilier)	Canton Bern Switzerland	Reuchenette Formation Early Kimmeridgian	Sauropod tracks	Meyer, 1996; Meyer, 2000
Tavannes (Tavannes)	Canton Bern Switzerland	Reuchenette Formation Early Kimmeridgian	Sauropod tracks	Meyer & Thüring, 2003a
Twannberg (aka Burgflue) (Twann)	Canton Bern Switzerland	Twannbach Formation Early Tithonian	Isolated sauropod tracks	Meyer & Lockley, 1996; Meyer, 2000

Table 2.1: Overview of the published dinosaur tracksites of the Jura Mountains including the Kimmeridgian tracksites of the Transjurane highway (Canton Jura, NW Switzerland).

2.2 Dinosaur track excavations of the Palaeontology A16

Prior to the excavations of the Palaeontology A16 (PAL A16), dinosaur tracks have already been found near Glovelier on a construction site, which was, even though not located on the main course of the highway, closely related to the construction of the Transjurane highway (e.g., Hostettler, 1999; Tschudin, 2001). These tracks were briefly mentioned in Lockley & Meyer (2000; p. 173), but have not yet been studied in greater detail.

The Courtedoux—Sur Combe Ronde tracksite, discovered in the year 2002, was the first larger dinosaur tracksite on the main course of the Transjurane highway discovered and excavated by the PAL A16. Preliminary reports on that site were subsequently published by Marty et al. (2003, 2004), who mentioned from the main track level of that site 17 sauropod trackways assigned to the ichnogenus *Parabrontopodus*, and two tridactyl, bipedal trackways, which they attributed to large theropods.

After the discovery of the Courtedoux—Sur Combe Ronde tracksite the Chevenez—Combe Ronde site, which is in the focus of this work, was the second tracksite discovered on the future course of a feeder road to the Transjurane highway. Note the very similar name of both tracksites, which are in close proximity to each other (Fig. 2.2A) but not located in the same track-bearing levels (Fig. 2.5).

On the Transjurane highway, dinosaur tracks were found and (partially) excavated on six extensive tracksites, in a nearby quarry in Chevenez (associated with the construction of the highway), and also due to cantonal prospecting in the Ajoie beside the Transjurane highway (Fig. 2.1). The excavations on the Transjurane highway so far resulted in several large-scale outcrops including continuous sections and contiguous bedding planes of several 100 to 1000 m^2 (review of the tracksites in Marty et al., 2007a).

All tracksites are named in a binomial way: first the community is indicated, followed by the name of the site, e.g., Chevenez—Combe Ronde is the Combe Ronde tracksite on the parish area of Chevenez, and Courtedoux—Sur Combe Ronde is the Sur Combe Ronde tracksite on the parish area of Courtedoux. For each site an acronym is defined, which is composed of two times three capital letters, separated by a hyphen, e.g., CHE-CRO for the Chevenez—Combe Ronde site. This acronym is also used for the labelling of samples, e.g., CHE-CRO004-1 is sample number 1 of the year 2004 of the Chevenez—Combe Ronde site.

The particularity of these sites is that they reveal tracks within three stratigraphic intervals, and each of these intervals yields tracks on several superimposed levels. Currently, tracks have been found on over thirty distinct levels. This resulted (by the end of 2006) in the systematic excavation and documentation of over 4200 dinosaur tracks including 129 trackways of sauropods and 151 trackways of bipedal dinosaurs (Marty et al., 2007a). Because many tracks were located on superimposed levels and had to be destroyed by the ongoing excavations, dozens of casts were fabricated and large track-bearing surfaces were displaced and recovered, resulting in a large track collection actually stored in the repositories of the PAL A16 in Porrentruy. Additionally, many of these surfaces were also documented by laser scanning and photogrammetry. All this resulted in a huge ichnological data base and track collection, which are currently in a phase of organization and assessment.

The study of all currently available track data from the Transjurane tracksites is clearly outside of the scope of this work. In the focus here is the study of the Chevenez—Combe Ronde tracksite, and Chapters 4 and 5 provide a detailed case study on that tracksite. Nonetheless, some comparisons with the Courtedoux—Sur Combe Ronde tracksite described by Marty et al. (2003) and the Ajoie ichnoassemblages are made at the end of Chapter 5. Thus, if it is referred to discoveries or evidence of other tracksites this is always clearly stated in the text.

2.2.1 The Chevenez—Combe Ronde tracksite

The Chevenez—Combe Ronde tracksite is located about 6 km southwest of the city of Porrentruy, the capital of the Ajoie district, on a feeder road to the Transjurane highway (Fig. 2.2). It is situated in close proximity to the Courtedoux—Tchâfouè and the Courtedoux—Sur Combe Ronde sites, which both exhibit the intermediate and upper levels, but not the lower levels as does the Chevenez—Combe Ronde site (Fig. 2.5).

2.2.1.1 History of excavation

The Combe Ronde site was discovered in August 2003 during palaeontological and archaeological prospecting by the PAL A16. The importance of the site was quickly recognized, because it is older than the Courtedoux—Sur Combe Ronde site, because the tracks are well-defined, and because of the presence of tracks of both sauropods and bipedal, tridactyl dinosaurs including small tracks. Systematic excavations were planed and carried out by the PAL A16 from autumn 2003 until November 2005. These were followed by emergency excavations in June 2006 and February 2007.

Systematic excavations (Plates 2.1 & 2.2)

Systematic excavations started in autumn 2003 and lasted until November 2005 in the excavation areas 1, 2, and 3 (Fig. 2.2 C; Marty, 2004a, 2005; Marty & Strasser, 2005; Marty et al., 2005; Billon-Bruyat et al., 2006, 2007).

Excavation area 3 is the largest surface, excavation areas 1 and 2 are clearly smaller (Fig. 2.2 C). Excavation areas 2 and 3 are only slightly affected by normal faults and epikarstification, whereas excavation area 1 is highly affected by karstification and disintegrated, especially in its exterior parts. The faults within the excavation

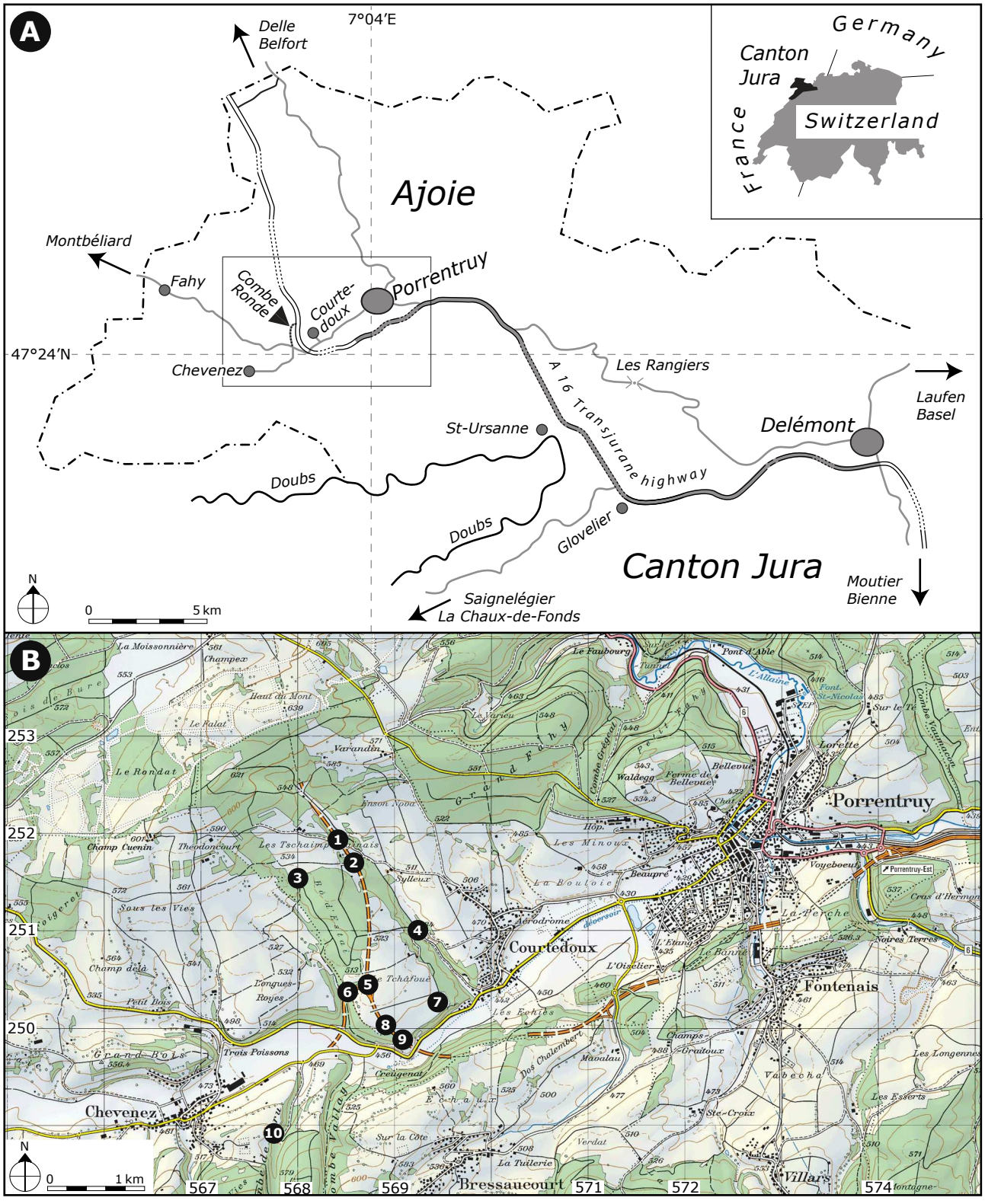


Fig. 2.1: A: Geographical setting of the Ajoie district (NW Switzerland) and the tracksites along the Transjurane highway; inset shows location within Switzerland. The box encompasses the map shown in B; the approximate position of the Chevenez—Combe Ronde tracksite is indicated. After Marty et al. (2007a). **B:** Extract of the Swiss National Map 1:25'000 sheet 1085—St-Ursanne (reproduction authorised by Swisstopo - BA081389), with the tracksites of the Transjurane highway and the trackways outside the highway indicated. From north to south: (1) Courtedoux—Béchat Bovais, (2) Courtedoux—Bois de Sylleux, (3) Courtedoux—Pommerat, (4) Courtedoux—Oratoire, (5) Courtedoux—Tchâfouè, (6) Chevenez—Combe Ronde, (7) Courtedoux—Dessus Latchire, (8) Courtedoux—Sur Combe Ronde, (9) Chevenez—Crat, and (10) Chevenez—La Combe (quarry).

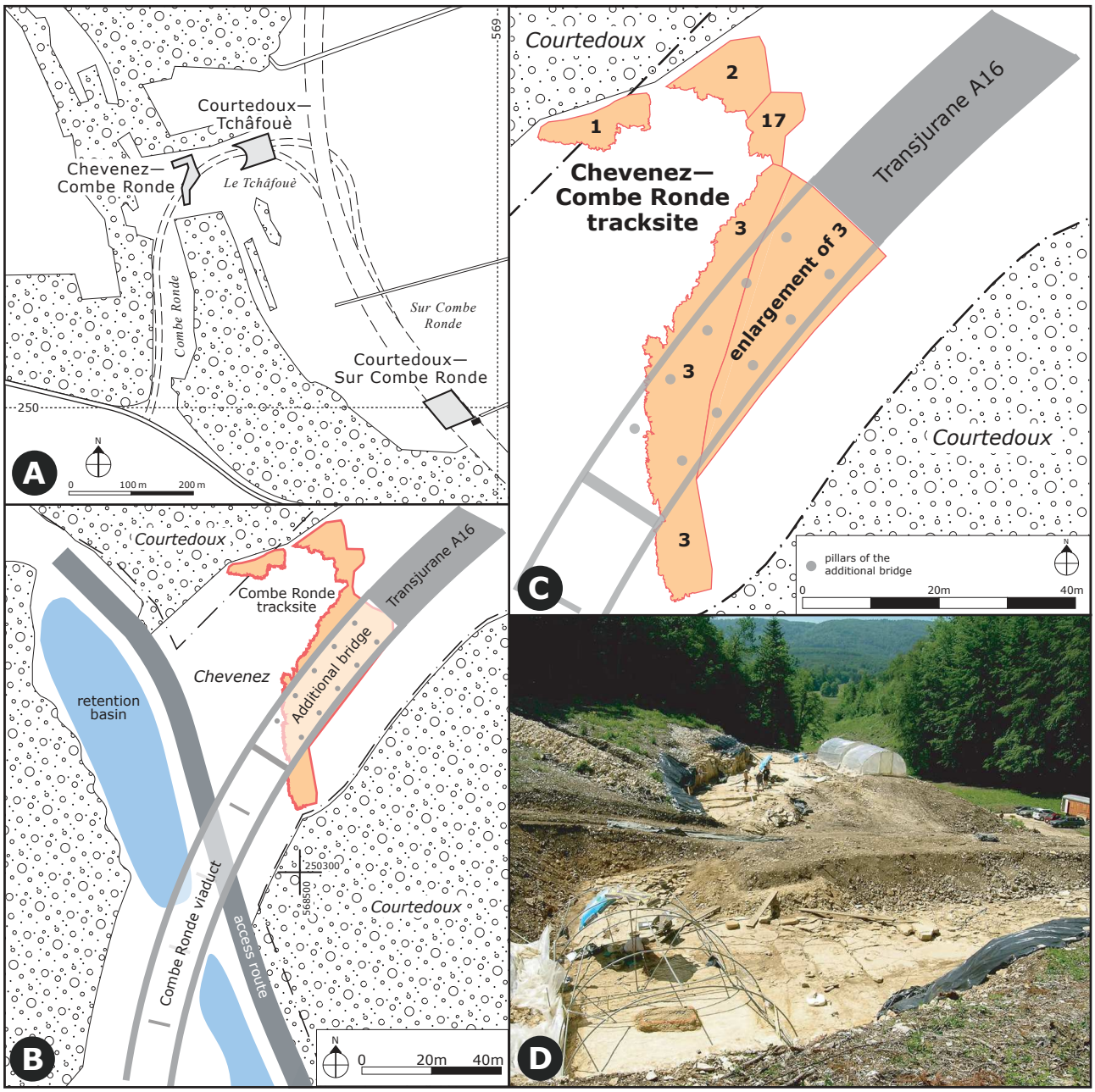


Fig 2.2: Geographical setting of the Chevenez—Combe Ronde tracksite and excavation areas. **A:** Future course of the Transjurane highway and the feeder road showing the location of the Chevenez—Combe Ronde, Courtedoux—Tchâfouè, and Courtedoux—Sur Combe Ronde tracksites. Redrawn after Billon-Bruyat et al. (2007). **B:** Close-up of A: The initial Combe Ronde viaduct of the feeder road to the Transjurane highway has been extended by the construction of an additional bridge, which now crosses and protects the main track level. **C:** Close-up of B: Excavation areas (1, 2, 3, enlargement of 3, and 17) of the Chevenez—Combe Ronde tracksite. Note that the data of excavation area 17 and of the enlargement of 3 are not included in this work. **D:** Overview of the Chevenez—Combe Ronde tracksite in June 2004 during the systematic excavation. View towards the southwest.

areas are generally small with vertical displacements between 0 cm and 30 cm (see also Braillard, 2006b). Only one fault between the excavation areas 1 and 2 is more important and displaces area 1 about 2 m downwards in comparison to areas 2 and 3, which lie on the same height. As the initial excavation area 3 (as-is state of end 2005) was first supposed to be destroyed by the construction of the Combe Ronde viaduct (Fig. 2.2B), the main track level in this area was also documented by laserscanning and photogrammetry, and silicon casts were fabricated of all trackways.

The 0,65 m thick laminite interval was excavated and documented level-by-level on a total surface of nearly 600 m^2 (Ayer & Iberg, 2004; Marty, 2004a, b, c; Marty et al., 2005; Billon-Bruyat et al., 2006). Within the laminite interval, dinosaur tracks and trackways were found on eight superimposed levels, named levels 500, 505, 510, 515, 520, 530, 540, and 542. The main track level, located at the base of the laminite sequence, was the largest surface, revealed the best preserved tracks and the most diverse ichnoassemblage with different size classes of tracks of both sauropod and bipedal, tridactyl dinosaurs. All superimposed surfaces revealed tracks of sauropods only.

Horizontal bedding makes the site well accessible and facilitated excavations. All levels were carefully excavated by hand. However, as the laminites were in places heavily altered and/or displaced and fractured by normal faults, not all levels could be excavated over the total available excavation surface. Generally speaking, lower lying levels were uncovered on larger surfaces than higher levels, and at the end of the excavation the main track level, which marks the base of the laminite sequence, was uncovered over 600 m^2.

During field work, all excavated surfaces were first analysed for tracks, sometimes also during night using artificial light. The reported tracks and trackways were then highlighted with chalk and labelled. Afterwards a 1:20 graphical documentation including all dinosaur tracks and enigmatic traces, desiccation cracks and faults was accomplished and later digitized. 1:1 drawings on transparent films, and silicon casts were made of selected tracks and trackways. All tracks and trackways were photographed (sometimes using artificial light), described, and their parameters were measured according to Chapter 2.7. Additionally photogrammetry and laser scanning (Cyrax 2500, 3D SmartScan technology; Leica Geosystems, 2003) were achieved of the main track level.

Excavated tracks were exhaustively sampled including their track fills. Several selected tracks were extracted in blocs and cut into serial-sections. A thorough documentation and description of other macrosedimentary features (desiccation cracks, wave ripples, invertebrate burrows) and their association and interactions with the tracks was also accomplished.

Emergency excavations (Plate 2.3)

At the end of 2005 it was decided to protect the main track level of the Combe Ronde site by the extension of the Combe Ronde viaduct. The construction of this additional bridge implied a considerable enlargement of excavation area 3 (approximately 300 m^2) towards the northeast (Fig. 2.2C).

In June 2006, just before the construction of this additional bridge, the main track level of the concerned area (an additional surface of approximately 350 m^2) was uncovered with heavy shovel excavators and documented during an emergency excavation. The overlying track-bearing levels were not excavated, because of lack of time and because they were mostly amalgamated (Billon-Bruyat et al., 2007). After excavation, this surface was covered up with about 1 m of sand and gravel in order to protect it and to enable the construction of the bridge. The subsequent construction of the bridge in 2006 only slightly affected the main track level, in as far that several pillars had to be put down into the main track level, and a wall had to be constructed at the eastern end of the bridge for stability reasons.

In February 2007 another small surface (excavation area 17), the connection between excavation areas 2 and 3, was excavated due to the construction of the highway canalisation. On this surface, the main track level revealed one sauropod (S15) and one bipedal trackway (T49). A part of this surface was destroyed, but a connection between the main track level of excavation areas 2 and 3 still does exist.

Meanwhile, the Combe Ronde tracksite is crossed and protected by the additional highway bridge. Thus, it is the first large palaeontological site in Switzerland, which has been protected and not destroyed by the construction of a federal highway. However, the site remains covered up until the Canton Jura makes the site accessible for public viewing. During this final phase of site development, additional surfaces are likely to be excavated.

2.2.1.2 Studied data and used material

By the end of 2007, all excavations together had revealed nearly 1400 dinosaur tracks including 26 trackways of sauropods and 49 trackways of bipedal dinosaurs. However, the present study is based only on the data of the systematic excavations achieved by the end of 2005. The tracks from the emergency excavations are not yet included in this study, because the site was recovered quickly and time was too short to properly correlate the trackways with those of excavation area 3, and to study them in detail. Thus, the data of the emergency excavation are in need of revision.

By the end of 2005, 1167 dinosaur tracks including 25 sauropod (thereof 14 on the main track level), and 43 bipedal trackways (all on the main track level) were documented on eight levels during the systematic excavations. The main track level exhibited a rich and diverse ichnoassemblage composed of 14 trackways of sauropods and 43 trackways of bipedal, tridactyl dinosaurs on a total surface of roughly 600 m^2. Additionally, many well-defined enigmatic traces were unearthed. The ichnological study of the ichnoassemblage of the main track level is in the focus of Chapter 5.

Above the main track level seven superimposed surfaces were excavated exhibiting exclusively tracks and trackways of sauropods. In comparison with the main track level, most of these tracks were rather poorly defined, and because of the high dinoturbation index of several levels (notably levels 510, 515, 520), trackways were often difficult to identify (see Annex 5.1). Nonetheless, quadrupedal, pes-only, and manus-dominated trackways with reasonably to well-defined tracks were found on levels 530 and 540 and will be described in greater detail in Chapter 5. The other sauropod tracks are in the focus of the sedimentological and taphonomical analyses carried out in Chapter 4.

All studied material (casts, slabs, samples, thin-sections) is currently housed in the collections of the PAL A16 but will be integrated into the *Musée jurassien des sciences naturelles de Porrentruy* (institutional abbreviation: MJSN). All original documentations (maps, descriptions, trackway parameters, logs) are courtesy of the PAL A16 and archived in Porrentruy.

2.3 Geographical and geomorphological setting

The Chevenez—Combe Ronde tracksite and all other dinosaur track excavation sites of the PAL A16 are located in the Ajoie district of the Canton Jura (NW Switzerland), situated on a plateau between Courtedoux and Chevenez about 6 km to the southwest

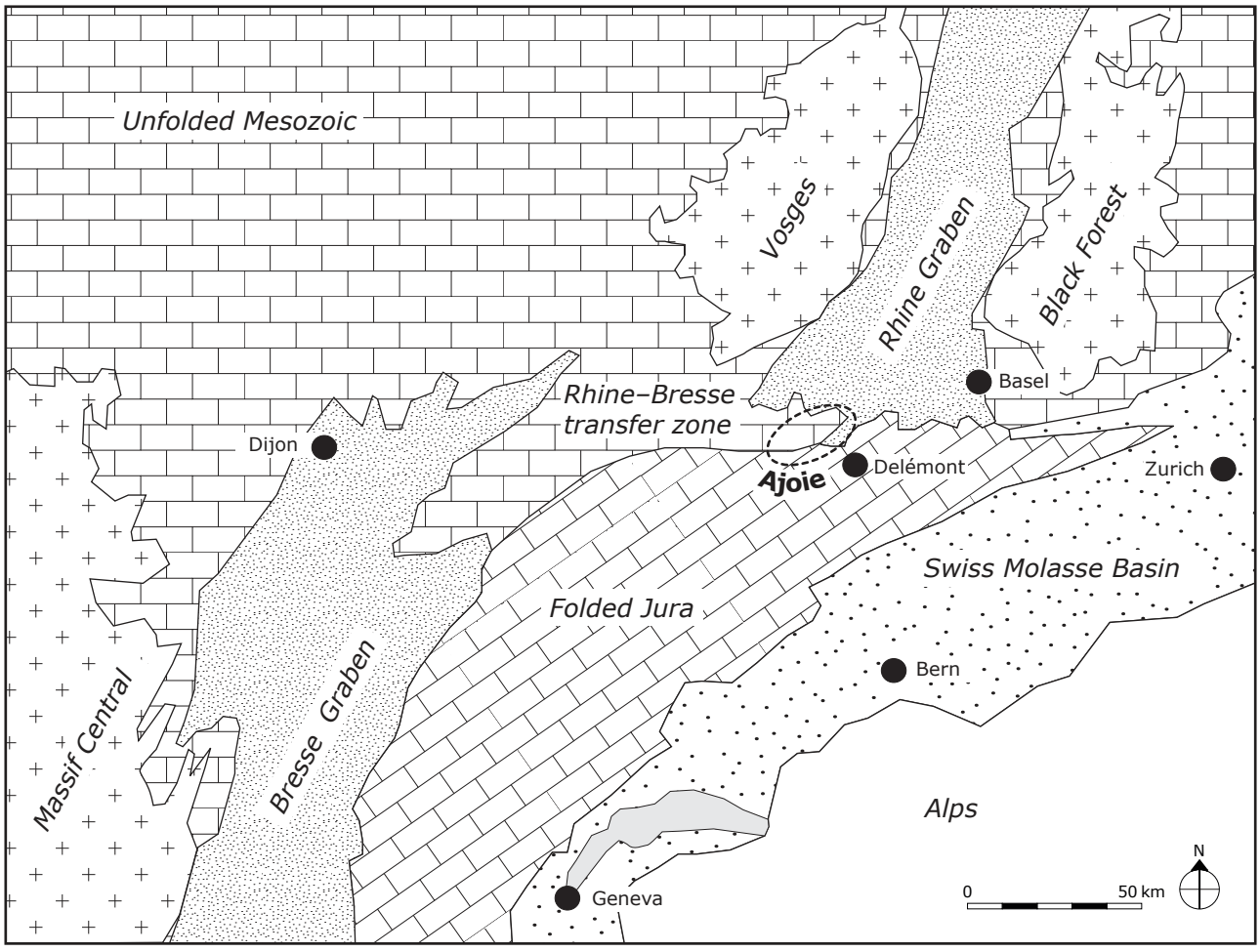


Fig. 2.3: Geological setting of the Jura arc and the Ajoie. Redrawn after Braillard (2006a, b) and modified from Marty et al. (2007a).

of Porrentruy (Fig. 2.1). The Ajoie district borders in the south the Delémont and Franches-Montagnes districts, and most parts are relatively flat with a mean elevation around 500 m. The dominant morphological features are dry valleys, which have been generated by karstic dissolution (main process) and fluviatile erosion (accessory process) along faults (Braillard 2006a, b). This karstification also caused an important subterranean fluviatile network, and only three small superficial streams occur in the Ajoie.

2.4 Geological setting

The Ajoie is located at the eastern end of the Rhine-Bresse transfer zone between the Folded Jura Mountains to the south and east and the Upper Rhine Graben and Vosges Mountains to the north (Fig. 2.3). It belongs almost entirely to the Tabular Jura, which consists of slabs of subhorizontally layered Mesozoic strata, separated by narrow dislocation belts (Trümpy, 1980). Near the front of the Folded Jura (Mont Terri anticline), detached folds of the Folded Jura are overthrusted onto the Tabular Jura (Tschopp, 1960). From the Eocene to the Pleistocene, five tectonic phases created a complex set of fractures in the bedrock, as well as small, low amplitude anticlines (Giamboni et al., 2004; Ustaszewski et al., 2005; Braillard 2006b).

2.4.1 Palaeogeographical setting

During the Late Jurassic, the domain of today's Jura Mountains was located at the northern margin of the oceanic Ligurian Tethys (e.g., Gygi, 1990; Thierry et al., 2000; Stampfli & Borel, 2002) as a large, structurally complex carbonate platform (Fig. 2.4). This platform was at a palaeolatitude of around 30° N, at the threshold between the Paris Basin to the northwest and the Tethys Ocean to the south and thus, influenced by both the Tethyan and Boreal realms

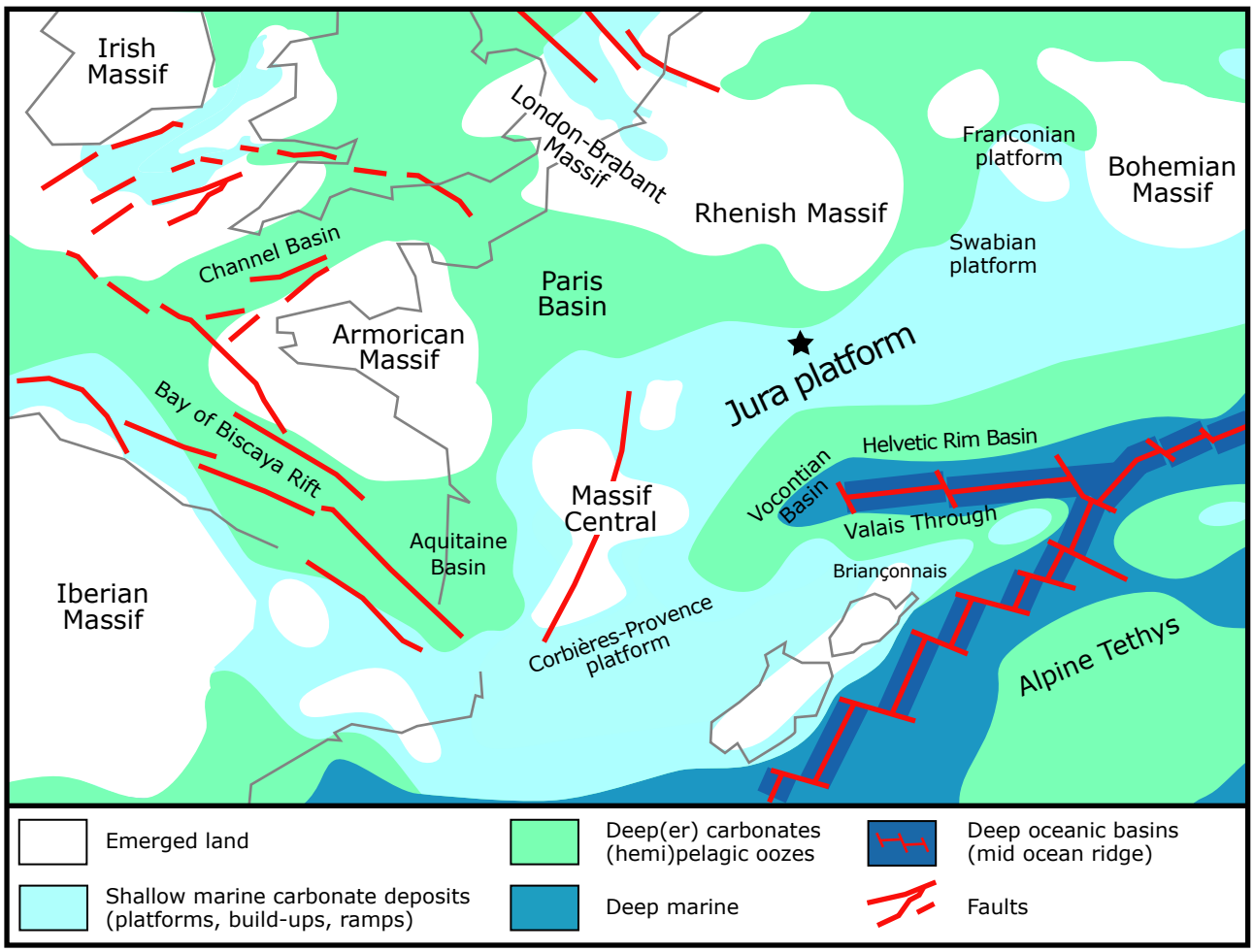


Fig. 2.4: Palaeogeographical setting of the Jura carbonate platform during the Kimmeridgian (Late Jurassic, approximately 152 Ma). After Thierry et al. (2000) and Thierry & Barrier et al. (2000). The palaeogeographical position of Corsica and Sardinia is interpreted differently in other reconstructions (e.g., Stampfli et al., 2002). Asterisk marks the approximate position of the study area.

(Ziegler, 1988; Meyer & Schmidt-Kaler, 1989; Dercourt et al., 1994; Smith et al., 1994; Dercourt et al., 2000; Thierry, 2000a, b).

During the Late Jurassic, the western Tethys was already subjected to sinistral translative movements between Africa and Laurasia induced by northward propagation of the Atlantic spreading axis. As a consequence of these movements, compressional stresses developed in the eastern parts of the Tethys, whereas in the western parts sea-floor spreading diminished. Supported by accelerated rifting in the North Atlantic, this led to a general thermal doming and associated sea-level fall, which caused widespread emergence (Late Kimmerian unconformity) of the Armorican, London-Brabant, Rhenish, and Bohemian Massifs and the Massif Central (Meyer & Schmidt-Kaler, 1989; Dercourt et al., 2000; Thierry, 2000a, b).

2.4.2 Palaeoenvironmental setting

During the Late Jurassic, the Jura carbonate platform was subdivided into land surfaces, tidal flats, internal lagoons, lagoons, and (reef) barriers (e.g., Pümpin, 1965; Thalmann, 1966; Bläsi, 1980; Meyer, 1994a; Mouchet, 1995; Colombié, 2002; Hug, 2003; Colombié & Strasser, 2005; Jank et al., 2005, 2006a; Rameil, 2005; Védrine, 2007; Védrine et al., 2007). Consequently, the Late Jurassic of the Ajoie is essentially made up of shallow marine carbonates and marls, in function of terrestrial input related to eustatic sea-level changes and climatic conditions.

Sedimentological analyses of the tracksites suggest the presence of several juxtaposed depositional environments ranging from shallow lagoon to beach and to supratidal flats and marshes (Marty & Strasser, 2005). Similar zonations in laminated sediments have been described from Shark Bay (Australia), the Persian Gulf, and the Bahamas (e.g., Logan et al., 1970; Purser, 1973; Hardie, 1977a, respectively). In such environments, the preservation of dinosaur

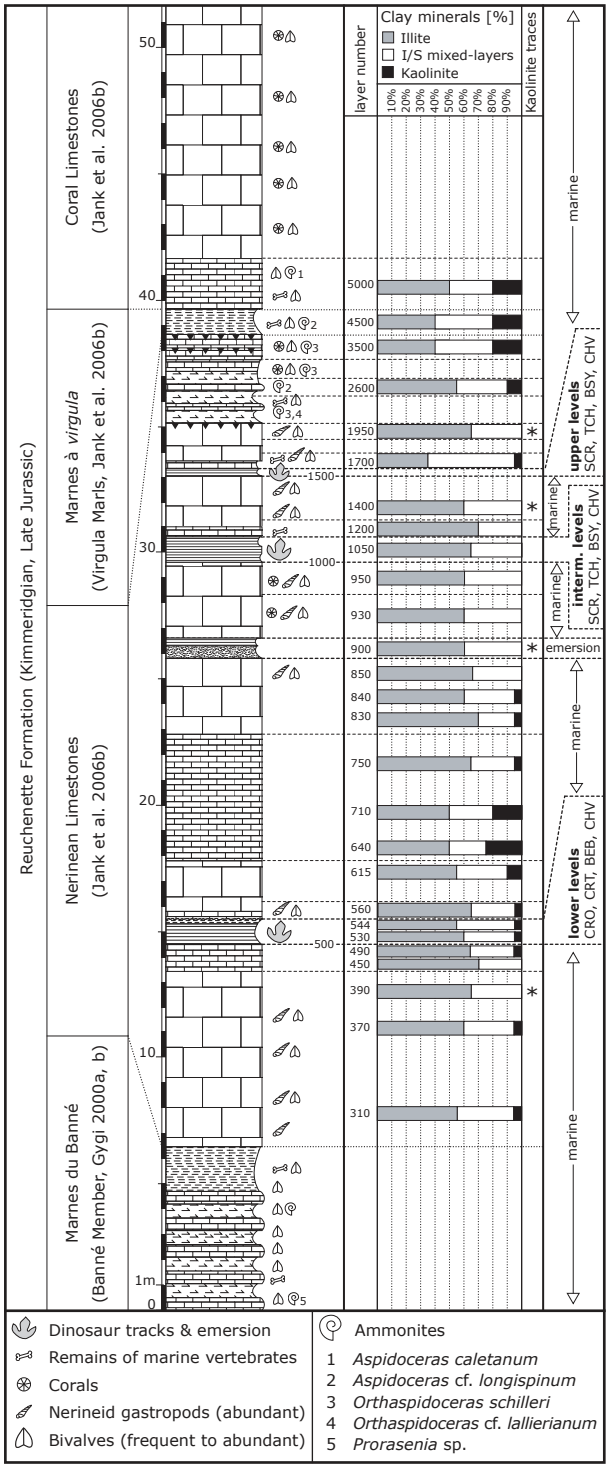


Fig. 2.5: Schematic figure of the lithological succession of the Reuchenette Formation between the Marnes du Banné and the Marnes à *virgula*, as logged between the Chevenez — Combe Ronde site and the Courtedoux—Tchâfouè site. So far, three track-bearing intervals, named the lower levels, intermediate levels, and the upper levels have been identified in the Tabular Jura of the Ajoie and are indicated in the right column. The abbreviations indicate which levels crop out at which tracksites, from bottom to top: CRO = Chevenez—Combe Ronde; CRT = Chevenez—Crat; BEB = Courtedoux—Béchat Bovais; CHV = Chevenez—La Combe (quarry); SCR = Courtedoux—Sur Combe Ronde; TCH = Courtedoux—Tchâfouè; BSY = Courtedoux—Bois de Sylleux. Also indicated is the position of ammonites, and for selected layers the clay mineralogy, which was analysed by J.-F. Deconinck (University of Dijon). Note that the laminite sequence of the Combe Ronde tracksite corresponds to the lower levels and is located about 10 m above the Marnes du Banné. After Marty et al. (2007a).

tracks basically depends on the nature of superficial microbial mats and the underlying sediment, which results in a wide range of track morphologies (see also chap. 3). The implications of track morphology for the interpretation of the palaeoenvironment are discussed in detail in Chapter 4.

Small-scale sea-level drops repeatedly created vast emergent areas as is proven by the numerous tracksites of the Jura arc. Hence, dinosaurs habitually entered this coastal marine tidal-flat environment of the Jura carbonate platform from the south-eastern border of the London-Brabant Massif (located in the NE), or from the Massif Central (located in the SW) (Meyer & Lockley, 1996; Meyer et al., 2006) (Fig. 2.4).

2.4.3 Palaeoclimatological setting

During the Kimmeridgian, the climate of the Jura carbonate platform was subtropical, and is generally considered semi-arid to arid (e.g., Hallam, 1984, 1985; Frakes et al., 1992; Moore et al., 1992; Ross et al., 1992; Moore & Ross, 1994; Weissert & Mohr, 1996; Bertling & Insalaco, 1998; Billon-Bruyat et al., 2005). This is also supported by the generally low content of kaolinite in the clay mineral fraction of the interval between the Marnes du Banné and the Marnes à *virgula* (Fig. 2.5). A more detailed discussion on the palaeoclimatology and the clay mineralogy of the Combe Ronde site is provided in Chapter 4.4.5.

2.5 Stratigraphical setting

The Ajoie district is almost entirely composed of sedimentary rocks, which can be attributed to the St. Ursanne, Vellerat, Courgenay, and Reuchenette formations, which are Middle Oxfordian to Late Kimmeridgian in age (e.g., Gygi, 1995, 2000a, b; Gygi et al., 1998).

All dinosaur track excavations of the PAL A16 are located in the Reuchenette Formation within three emersive intervals, named here lower levels, intermediate levels, and upper levels. These intervals are situated in the "Nerinean Limestones" of Jank et al. (2005, 2006a, b), enclosed by the Marnes du Banné at the base (Banné Member *sensu* Gygi, 2000a, b) and the Marnes à *virgula* (Virgula Member *sensu lato* of Gygi, 2000a, b; northern Virgula Marls in Jank et al., 2006a; Virgula Marls in Jank et al., 2006b; lower Virgula Member in Colombié & Rameil, 2007) at the top.

The track-bearing lower levels of the Chevenez—Combe Ronde tracksite correspond to the lower levels, which are situated approximately 10 m above the Marnes du Banné and approximately 25 m below the Marnes à *virgula*. The track-bearing intermediate levels of the Courtedoux—Sur Combe Ronde tracksite are situated approximately 9 m below the Marnes à *virgula* (Fig. 2.5). Note that at Glovelier sauropod track-bearing laminite levels occur below and above the Marnes du Banné (Tschudin, 2001; Jank et al., 2006b), and that the levels above the Marnes du Banné may be coeval with some of the levels of the Ajoie. However, in the Ajoie no dinosaur tracks were found as yet below the Marnes du Banné, even though in the quarry "Ecorchevez" near Vendlincourt a laminite interval with desiccation cracks can be observed within the "Lower Grey & White Limestones" of Jank et al. (2005, 2006a, b), about 3 m below the Marnes du Banné (Jank et al., 2005, Fig. 7-2).

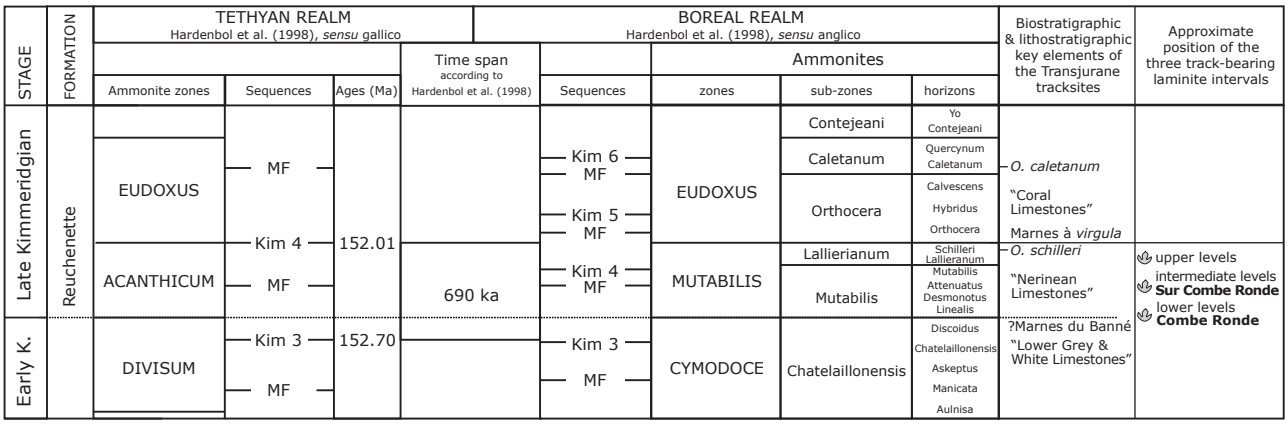


Fig. 2.6: Chrono-, bio- and lithostratigraphical context of the Kimmeridgian Reuchenette Formation and the three track-bearing levels of the dinosaur tracksites of the Ajoie, Canton Jura: Tethyan (*sensu gallico*) and boreal (*sensu anglico*) ammonite zonations, sequence boundaries Kim3 to Kim4, and maximum-flooding surface (MF) according to Hantzpergue et al. (1997) and Hardenbol et al. (1998).

The Reuchenette Formation was originally defined by Thalmann (1966). In the Ajoie region it has a maximum thickness of more than 140 m (Jank et al., 2006a). Until recently, the bio- and lithostratigraphy of the Reuchenette Formation within the Ajoie region was poorly understood, due to a lack of biostratigraphical markers (mainly ammonites) related to scant outcrop conditions (Gygi, 2000a, b). However, since the construction of the Transjurane highway, associated quarrying at several localities and the excavations of the PAL A16 started, many ammonites have been discovered. These ammonites established a well-defined biostratigraphical frame for the Reuchenette Formation of northwestern Switzerland (Jank et al. 2005, 2006a, b). This also proofed that the Reuchenette Formation contains no Tithonian ("Portlandian") sediments, contrary to what is indicated on the geological map of St. Ursanne (Laubscher, 1948; Diebold, 1960). This is further corroborated by mineralo-stratigraphic, sequence-stratigraphic, and cyclostratigraphic studies carried out during the last few years by Mouchet (1995, 1998), Colombié (2002), Colombié & Strasser (2003, 2005), Jank et al. (2005, 2006a, b), and Keller et al. (2006) in the Kimmeridgian, and by Rameil (2005) in the Late Kimmeridgian and Tithonian. Finally, all this new evidence enabled to put forward a Tethyan-to-Boreal correlation for the Kimmeridgian (Jank et al., 2005, 2006a; Colombié & Rameil, 2007).

The recently discovered ammonites place the interval encompassed by the Marnes du Banné and the Marnes à *virgula* between the late Early Kimmeridgian and the early Late Kimmeridgian. The lower levels of the Chevenez—Combe Ronde site are positioned approximately at the boundary from the Early and the Late Kimmeridgian, that is somewhere in between the Tethyan sequence boundaries Kim3 and Kim4 (Hardenbohl et al., 1998; Fig. 2.6). The sequence boundary Kim4 probably corresponds to the laminites of the upper levels (situated approximately 5 m below the Marnes à *virgula*), even though it was placed by Colombié & Rameil (2007, Fig. 10) in the intermediate levels (situated approximately 9 m below the Marnes à *virgula*). Assuming that Kim4 corresponds to the upper levels, the intermediate levels could be correlated with the laminated beds of the small-scale sequence 22 of Colombié (2002, Fig. 5.1) and of the small-scale sequence 52 of Strasser (2007, Fig. 10) (W.A. Hug, pers. comm.). The Marnes à *virgula* can be interpreted as transgressive and/or maximum flooding deposits of small-scale sequence 24 of Colombié (2002) and small-scale sequence 54 of Strasser (2007). Accordingly, a small-scale depositional sequence, corresponding to the 100 kyr Mylankovitch cycle (Strasser et al., 1999, 2006), can be postulated for the deposits between the upper levels and the Marnes à *virgula* (W.A. Hug, pers. comm.).

2.6 Ichnological terminology

In vertebrate ichnology there is not always consensus about the used terminology. However, it is important to use a clear nomenclature. In order to be as consistent as possible in terminology, the most commonly used ichnological terms in this work are explained and defined:

Associated track features
This encompasses all features forming at the time of track formation on the tracked surface and below a track (e.g., displacement rims, pressure release structures, displaced discs, expulsed sediment, ejecta, cracks, undertracks) or after track formation (internal overtracks, overtracks, modified true tracks, weathered tracks).

Brontopodus *ichnofacies*
The *Brontopodus* ichnofacies was introduced for repeated ichnocoenoses of sauropod-dominated track assemblages with a large number of tracks of large, robust theropods in carbonate and evaporitic facies associated with carbonate platform environments or alkaline-saline-carbonate lake deposits situated at low palaeolatitudes (Lockley et al., 1994a). Later, this label was generalized and used to accommodate any recurrent association of sauropod tracks (including *Parabrontopodus* and related types) with large theropod tracks (e.g., Meyer & Pittman, 1994; Lockley & Meyer, 2000; Marty et al., 2003). However, Hunt & Lucas (2006, 2007) argued that the *Brontopodus* ichnofacies *sensu* Lockley et al. (1994a) should be considered as an ichnocoenosis. They defined the *Brontopodus* ichnofacies as consisting of several ichnocoenoses embracing the *Ceratopsipes*, *Carichnium*, and *Brontopodus* ichnocoenoses, which are all typically found in coastal-plain and clastic or carbonate marine-shoreline environments. In this work ichnofacies is used *sensu* Lockley et al. (1994a).

Deep track
True tracks made by a trackmaker sinking deeply into soft mud have been named deep tracks (Gatesy, 2003). In this case the foot penetrates through the sediment and the true track (the surface having been in direct contact with the foot) is located within the sediment and may reveal information about how the foot was

placed (Gatesy, 2003). After withdrawal, the foot may be covered with sediment.

Dinoturbation and dinoturbation index
Dinoturbation is the trampling of substrate by dinosaurs (Dodson et al., 1980). According to Lockley & Conrad (1989) the dinoturbation index reflects the degree of vertebrate trampling and its intensity (light: 0-33%, moderate: 34-66%, and heavy: 67-100% of the total surface trampled) is used in this work to characterize the dinoturbation of a given surface.

Displacement rim (raised-rim, expulsion rim, bourrelet)
Depending on the substrate consistency, a marginal rim of displaced material may form on the surface around the track. This may be associated with marginal thrusts in the rim and radial fractures in the sediment around the track (e.g., Allen, 1997), and with pressure release structures (Brown, 1999). Displacement rims are always higher than the tracked surface (positive epirelief).

Elite track
Has the connotation of a well-preserved, visually-clear true track with anatomical details of the foot and that is not distorted by overprinting or taphonomic processes (e.g., Lockley, 1993; Lockley & Hunt, 1995; Lockley & Meyer, 2000).

Footprint (print, track)
An impression (negative epirelief) of the autopodium (or a part of the autopodium) of a tetrapod on a surface (Leonardi, 1987). The term footprint is used in a general way, without specifying the precise nature of

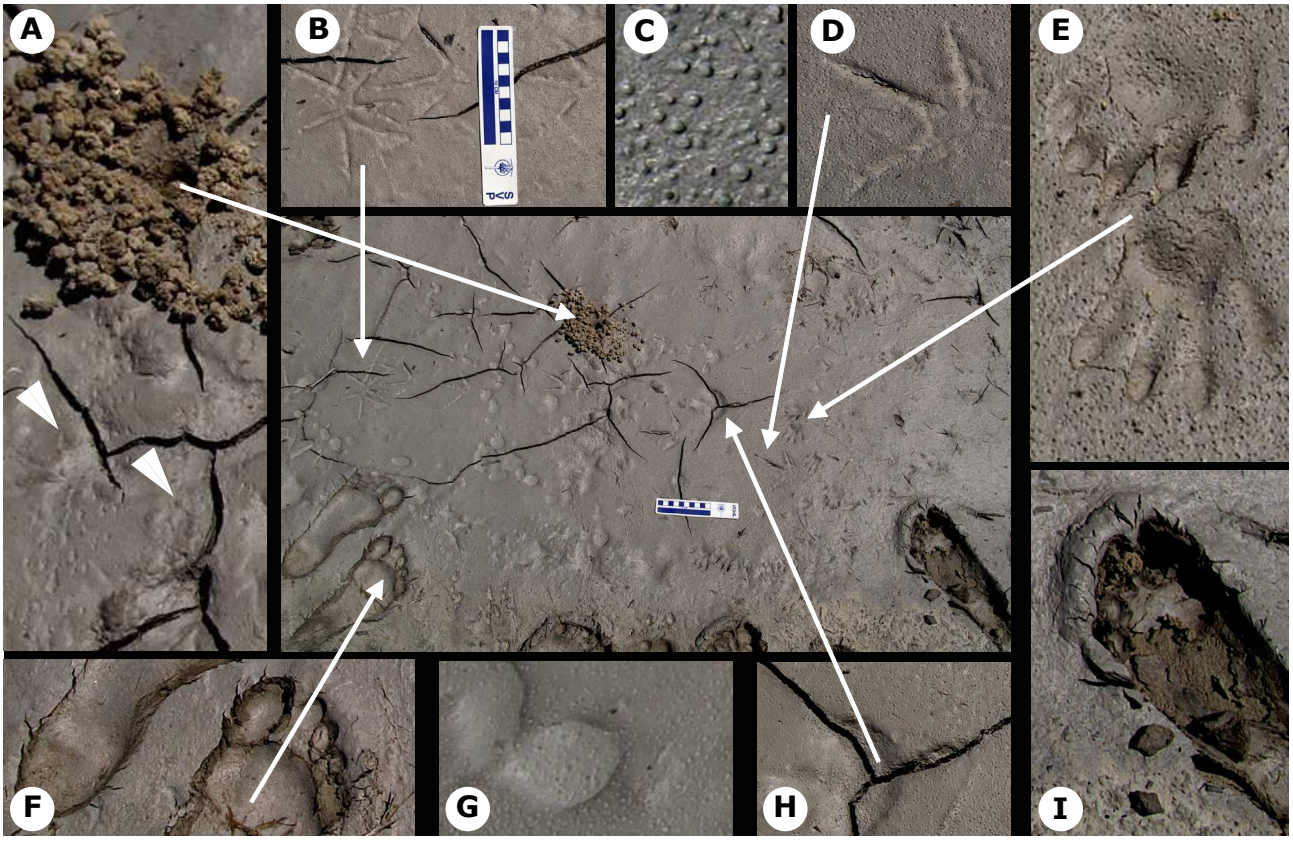


Fig. 2.7: The concept of vertebrate ichnoassemblage demonstrated by an example from a supratidal, microbial mat-covered flat south of San Pedro Town (Ambergris Caye, Belize). The pictures were taken after a heavy rainfall, when the flat was susceptible for track recording. Two days later, the same surface was completely desiccated and the traces consolidated. Accordingly, time-averaging is minor and the assemblage is likely to record at least a part of the biocoenosis of the surrounding area and also the behaviour of the trackmakers in that environment. **A:** Burrow with pellets of a decapod crustacean, note the trails heading away from and to the burrow (arrows). **B:** Faint shorebird tracks left in an area with rather firm sediment. **C:** Gas-bubble escape structures related to the decay of organic matter within the sediment. **D:** Reasonably-defined bird track of a shorebird. **E:** Well-defined tracks of *Iguana* with digit impressions, organized in a trackway. **F**: Well-defined footprints with toe impressions left by the author. **G**: Marks of large raindrops. **H:** Initial desiccation cracks. **I:** Reasonably-defined footprint surrounded by displacement rims left by the author. This track can be considered as an underprint because the surficial layer was squeezed outwards and/or lifted away. Scale bars in B and in the picture in the middle are 10 cm.

the footprint (e.g., true track, undertrack, overtrack). Footprint refers to a single print, not to a sequence of tracks or a trackway. In this work it is especially used in the context of human footprints.

Footprint consolidation and lithification
The term consolidation is used to describe recent footprints, which are cohesive or hard and difficult to disintegrate. In the case of modern tracks, this is often related to the presence of a dry, coherent microbial mat. Lithification means that the sediment has been (at least partially) stabilized by early cementation (e.g., precipitation of carbonates).

Ichnoassemblage
In invertebrate ichnology an assemblage of ichnofossils in a single rock unit (layer), is conceptually equivalent to an assemblage of body fossils (Bromley, 1990, 1996), and may not reflect an actual community because processes such as taphonomic filtering, ecological tiering, and biological succession time-average a given assemblage (e.g., Bromley, 1996). However, if the term ichnoassemblage is used in vertebrate ichnology for an association of true tracks left on a single horizon (palaeosurface), time-averaging is much less relevant (Cohen et al., 1993) (Fig. 2.8). In this case an ichnoassemblage is hardly affected by above cited processes and it is good evidence for a single biocoenosis. In order to avoid the ambiguities encompassing the term ichnocoenosis, the term ichnoassemblage is used in this work to refer to an association of true tracks of vertebrates found on a single palaeosurface (Fig. 2.7).

Ichnocoenosis (ichnocoenose, palaeoichnocoenosis)
In vertebrate ichnology an ichnocoenosis is an association of trace fossils produced by a single association of living organisms (biological community, biocoenosis), and it is properly used for the trace fossil association from a single level only (Leonardi, 1987; Lockley et al., 1994a). However, this term is also used for a trace fossil assemblage produced by a biological community that can be characterized by morphological criteria, independent of depositional environment or biological affinities (e.g., Bromley, 1996, McIlroy, 2004). In this work, ichnocoenosis is referred to recurrent ichnoassemblages (*sensu* Hunt & Lucas, 2006, 2007), implying that the term ichnocoenosis is not confined to an assemblage of tracks of a single level.

(Invertebrate) Ichnofacies
Term introduced by Seilacher (1964, 1967) for "general trace associations, or types of ichnocoenoses, representing certain facies with a long geologic range". This definition is generally referred to as Seilacherian or archetypal (e.g., Frey & Pemberton, 1987; Bromley, 1996; MacEachern et al., 2007), and there is consensus that ichnofacies should refer to recurrent (multiple) ichnocoenoses that represent a significant portion of Phanerozoic time (e.g., Hunt & Lucas, 2007). In invertebrate ichnology the ichnofacies concept is today critically viewed and has been expanded with the concept of ichnofabric (e.g., Ekdale et al., 1984; Droser & Bottjer, 1986, 1989; Pemberton et al., 1992; Goldring, 1993).

Vertebrate (nonmarine tetrapod) Ichnofacies
The ichnofacies concept was introduced in vertebrate ichnology by Lockley et al. (1994a) referring to "multiple ichnocoenoses that are similar in ichnotaxonomic composition and show recurrent association in particular definite environments". However, more recently Hunt & Lucas (2006, 2007) argued that all tetrapod ichnofacies defined prior to 2005 (notably also the *Brontopodus* ichnofacies of Lockley et al., 1994a) should be considered as ichnocoenoses, as they represent the traces of specific communities that lack the stratigraphic and geographic range that would warrant their consideration as archetypal ichnofacies. These authors defined vertebrate ichnofacies as "recurrent

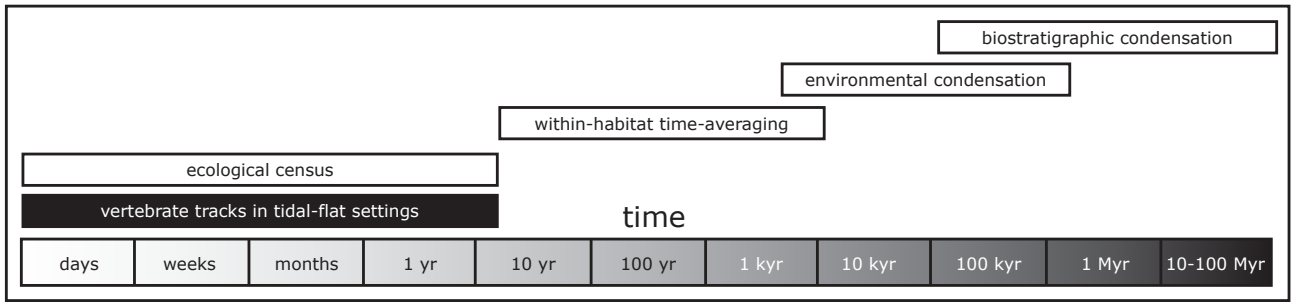


Fig. 2.8: Time-averaging of vertebrate track ichnoassemblages in tidal-flat settings can be considered as "ecological census assemblages". After Kidwell & Bosence (1991).

ichnocoenoses that represent a significant portion of Phanerozoic time" and they defined five archetypal tetrapod ichnofacies for nonmarine environments: *Chelichnus, Grallator, Brontopodus, Batrachichnus* and *Characichichnos*.

Ichnofauna (palichnofauna, palaeoichnofauna)
A fauna whose existence and composition are revealed (wholly or largely) by the evidence of trace fossils. This term has an ampler meaning than ichnocoenosis and can also be used for trace fossil associations of either one level or from a complete series (Leonardi, 1987; Thulborn, 1990).

Ichnology (palichnology, palaeoichnology)
The study of trace fossils or the traces of the activity of organisms (plants and animals).

Ichnotaxonomy
Trace fossils including vertebrate footprints are named in a binomial (Linnean) way consisting of ichnogenus and ichnospecies (ICZN, 1999), even though they are not biological objects in a strict sense but biogenic, sedimentary structures. Reviews of problems frequently encountered in ichnotaxonomy can be found for instance in Pemberton & Frey (1982), Billon-Bruyat & Mazin (2003), Bertling et al. (2006), Bertling (2007), and Lockley (2007).

Internal overtrack
Forms by draping of the track bottom (the true track *sensu stricto* inside the overall track) without covering the entire tracked surface. They are commonly induced by repeated growth of microbial mats in the wetter track interior, by the trapping of sediment, or by an alternation of both processes.

Megatracksite ("dinosaur freeway")
A megatracksite is "a regionally extensive single surface, or a very thin package of beds, that is track-bearing over a large area on the order of hundreds to thousands of square kilometres" (Lockley, 1991b, 1997a, b).

Modified (true) track
This term is introduced in order to describe true tracks which have been modified by physico-chemical (e.g., weathering) and/or biological influences after they were made. Biological processes include modification through the growth of microbial mats, which do not cover the whole tracked surface or the whole track bottom. The terms slightly-, moderately-, and strongly-modified are used to characterize the degree of modification. They differ from true tracks in that they will not reveal fine details of the anatomy of the foot anymore, and from overtracks in that the tracked surface is not covered but disintegrated.

Natural cast
A homogeneous sediment fill a true overall track forms a natural cast (Lockley, 1991b).

Overtrack (ghost track)
An overtrack appears in a horizon above the tracked surface. It forms by draping of the entire true track (overall track and the tracking surface) with sediment and/or by repeated growth of microbial mats and associated binding of sediment particles. A rapid and important sedimentation event may bury the overall track and the tracked surface without leaving behind an overtrack. In such a way, a homogeneous track fill (sediment fill) or natural cast of the overall track is formed.

Palaeosurface
A palaeosurface is the surface of an ancient depositional landform that is preserved in the rock record with its original topography and surface sculpture intact (Smith, 1993; Widdowson, 1997). A palaeosurface is an omission surface *sensu* Heim (1924, 1934), which is synonymous with discontinuity surface (Clari et al., 1995). They mark temporary halts in deposition, but involve little or no erosion (Bromley, 1975). Hillgärtner (1998) characterized discontinuity surfaces by geometry, lateral extent, surface morphology, biological activity, mineralization, facies contrast, early diagenetic contrast and biostratigraphy, and differentiated four types of discontinuity surfaces: related to subaerial exposure, to stratigraphic condensation, to subaqueous erosion, or to changes of facies and/or texture.

Trace fossil (ichnite, ichnofossil, Lebensspur)
Reflection of the biological activity of ancient organisms. Dinosaur trace fossils encompass tracks, trackways, nests, eggs, coprolites (feces), tooth marks, gastroliths (stomach stones), burrows, and dens.

Track (footprint, print)
Track is used synonymously with footprint, and not in the sense of trackway. The term track is used in this work in the context of dinosaur tracks.

Track outline (internal and external)
The external track outline is either marked by displacement rims or, if such are absent, by the upper limit of the track walls. The internal track outline marks

the limit of the true track, i.e., the sediment which was in contact with the foot. Especially in shallow tracks with poorly-defined track walls the external and internal track outlines are difficult to identify and named poorly defined. Well-defined internal track outlines, which accurately reflect the dimensions of the trackmaker's feet, are only found in well-defined, unmodified true tracks.

Track preservation
For the preservational classification the terminology of Seilacher (1964) is used, i.e., positive and negative epirelief or hyporelief. The latter two terms corresponding to epichnia and hypichnia, respectively, of Martinsson (1970). To facilitate the descriptions of the footprints, the terms poorly-, reasonably-, and well-defined or -preserved are used. The first refers to tracks, which show only the typical gross outline of the foot but which lack any further anatomical details. The latter refers to tracks with a well-defined outline and which may exhibit the impressions of digits, claws, and foot pads in the case of sauropod tracks and of the phalangeal pads and claws in the case of tridactyl tracks.

Track wall
Inclined to vertical walls surrounding the track bottom (the true track *sensu stricto*). If the track walls are not vertical, the track intersection with the tracked surface is larger than the dimensions of the trackmaker's foot and is termed the overall track (Brown, 1999).

Tracked surface (tracking surface)
The tracked surface is the surface on which the animal (trackmaker) walks (Fornós et al., 2002) or the surface, which is exposed at the time of track formation. In a more proper sense, the tracked surface is the sediment that has been in direct contact with the foot. In underprints and deep tracks, the track bottom does not correspond to the initially exposed sediment surface.

Trackway
A series of tracks (commonly a minimum of three consecutive hindfoot prints in the case of a bipedal animal), left by a single animal (Leonardi, 1987; Thulborn, 1990). However, sequences of two consecutive tracks, which obviously belong to the same animal, are occasionally also described as trackways.

True track
Lockley (1991b) called the track emplaced on the actual tracked surface true track, and the term true track is used in this work in this sense. Only the bottom of the track contains the direct impression of the trackmaker's foot. This is the true track *sensu stricto* or track bottom, which may under appropriate substrate conditions and if the foot is placed in an ideal way reveal information about the anatomy of the trackmaker's foot. Such tracks were also named elite tracks, which have the connotation of well-preserved, visually-clear true tracks that are not distorted (e.g., Lockley & Hunt, 1995; Lockley & Meyer, 2000). A true overall track is the true track *sensu stricto* with the track walls and all associated track features (e.g., displacement rims, pressure release structures) visible on the tracked surface.

Track penetration depth
In a track cross-section, this is the maximum depth (measured from the tracked surface) where undertracks or deformation of the sediment are still discernable.

Underprint (subtrace)
Unlike undertracks, underprints are true tracks which are produced when the foot penetrates or breaks through the uppermost or through several layers of sediment, and leaves the true track on sediment below the initially exposed sediment surface. If in this case the sediment is split open at successively deeper layers, the overall track will be found to be less and less complete (Thulborn, 1990), whilst the true track *sensu stricto* may still reveal the anatomy of the foot. If the track bottom of an underprint is disintegrated, a modified true track will form.

Undertrack (transmitted print, ghost print)
A track that is formed in (bio-) laminated and plastic substrate when the foot does not penetrate the sediment but compresses it in a way that it creates a miniature stratigraphic sequence or stack of transmitted prints (stack of casts and moulds) (Thulborn, 1990; Lockley, 1991b). Undertracks most likely form in biolaminated sediment. After consolidation, the (laminated) sediment package may split at successively deeper bedding planes and reveal correspondingly shallower and less detailed versions of the track at different horizons.

Unmodified true track
A true track, which remained unmodified until its final incorporation into the sedimentary record.

Weathered (altered, eroded) track
This term refers to modified true tracks, which have been modified by erosional processes, disintegrating the true track and the tracked surface.

2.7 Ichnological methodology

2.7.1 Labelling and numbering of tracks and trackways

Tracks and trackways are numbered sequentially per level. Thereby the acronym S is used as an abbreviation for a sauropod trackway, and T for a bipedal trackway with tridactyl tracks.

Tracks in sauropod trackways are labelled with R (right) and L (left) P (pes) and M (manus), i.e., LP1 stands for left pes 1 or RM3 for right manus 3. Tracks in trackways of bipedal dinosaurs are labelled with L and R only, i.e., L3 for left pes 3 (Fig. 2.9).

Isolated tracks, which can not unambiguously be assigned to a distinct trackway, and other enigmatic traces are labelled with E (for French: *empreinte*) and numbered sequentially. At the very beginning of the excavations at the Combe Ronde site, isolated tracks were labelled with the acronym T (for French: *trace*), but this was then changed to E because of ambiguity with the labelling of the tridactyl trackways. However, this acronym still occurs in some of the cross-sectioned isolated sauropod tracks, which are described in greater detail in Chapter 4.

A trackway usually includes a minimum of three sequential pes-manus track sets in quadrupedal sauropods or three sequential tracks in bipedal dinosaurs. However, in the case of a pes-only sauropod trackway, it may also be defined by three sequential pes tracks. Exceptionally, two sequential tridactyl tracks were labelled as a bipedal trackway if it was obvious that they were left by the same animal.

2.7.2 Illustrating of tracks

Information about a track's surface morphology forms the foundation of ichnological analysis and needs to be documented as objectively as possible, especially when specimens remain in the field or if they are threatened by erosion or destruction (e.g., Sarjeant, 1989; Gatesy et al., 2005a; Lockley & Matthews, 2007). However, it is generally difficult to produce objective illustrations of tracks, because many have rounded margins rather than exact, sharp

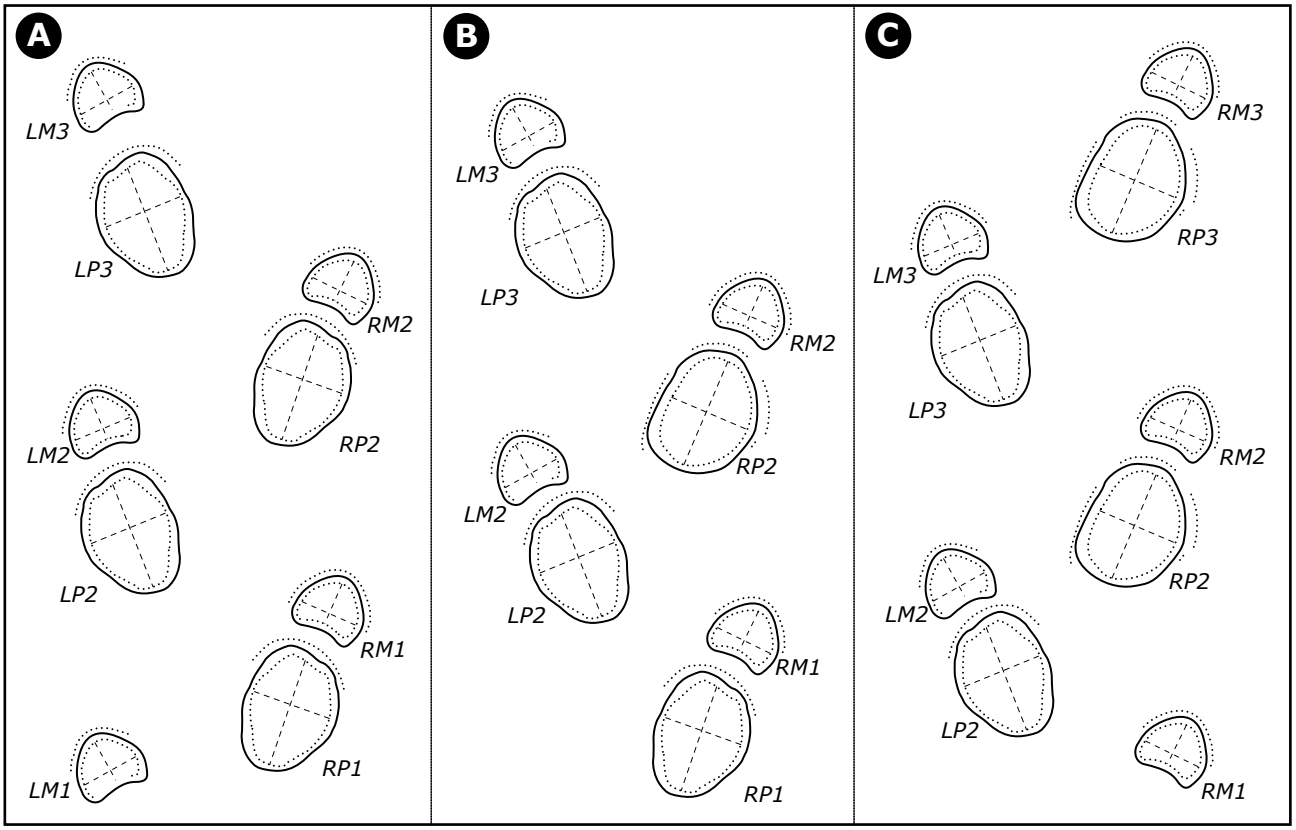


Fig. 2.9: Schematic sauropod trackways explaining the numbering of pes and manus tracks. Numbering theoretically starts with LP1. If LP1 is missing, numbering starts with LM1 (**A**), and if LM1 is missing as well, with RP1 and RM1 (**B**). If a trackway starts with a right manus, then it is named RM1, and the subsequent left pes and manus are labelled LP2 and LM2 (**C**).

boundaries (Thulborn, 1990). Outline drawings are often over-simplified and represent one's person interpretation of a complex three-dimensional object, and photographs depend on the angle of illumination (e.g., Thulborn, 1990; Gatesy et al., 2005a).

Hence, more sophisticated methods have been applied to document more objectively the three-dimensional morphology of tracks or the track outline. For single tracks these methods include for instance *Moiré Topography* (Ishigaki & Fujisaki, 1989), 3-D photographs (Goto et al., 1996), 3-D digitizer / high resolution laserscanning (e.g., Farlow & Lockley, 1993; Azuma et al., 2002; Gatesy et al., 2005b), landmark analysis (Rodrigues & Santos, 2004), or stereo-photographic techniques and anaglyph stereo imaging (e.g., Gatesy et al., 2005a). However, most of these methods have never been applied systematically because they are generally too time-consuming and expensive for the documentation of complete tracksites.

Since tracksites are considered as geosites or geotopes and an important part of the natural heritage (e.g., Lockley & Meyer, 1997; Marty et al., 2004), many efforts were undertaken to document complete tracksites by means of new technological methods, which are in particular laserscanning (e.g., Hurum et al., 2006; Meyer & Thüring, 2006; Thüring et al., 2007), photogrammetry (e.g., Breithaupt & Matthews, 2001; Matthews & Breithaupt, 2001; Matthews et al., 2006), low-altitude aerial photogrammetry (Matthews et al., 2002), terrestrial light detection and range (Lidar) imaging (Bates et al., 2008), or by a combination of several of these methods (e.g., Breithaupt et al., 2004).

Since 2002 high-resolution (in the order of 1-2 mm) laserscanning (with a *Cyrax* 3D scanner) and extreme close-range photogrammetry (2-10 m from camera to object) are systematically used on the track excavations of the PAL A16 (e.g., Leica Geosystems, 2003; Marty et al., 2003, 2007a). These technologies were also applied at the Combe Ronde tracksite, in order to document the main track level. Combined laserscan and photogrammetry allow the subsequent generation of a 3D model of the main track level with a resolution in the order of a few millimetres. This is quite a high resolution for the sauropod tracks but may still be insufficient for more detailed studies of very small tridactyl tracks. Therefore, silicon casts of the most important tracks and trackways have also been fabricated.

2.7.2.1 Illustrating with outline drawings

The benefit of outline drawings is that they represent the distinct and essential characters of a track or a trackway; they highlight aspects of interest. Nonetheless, they have to be viewed with some reservation, because they represent an interpretation or abstraction of a complex three-dimensional object.

In this work, in all outline drawings of tracks, the continuous line marks the exterior track outline, which is defined by the intersection of the track wall with the tracked surface. The continuous line marks the crest of a displacement rim, if it is exteriorly surrounded by a dotted line. If the continuous line is not surrounded exteriorly by a dotted line, then a displacement rim is absent. The dotted line within the continuous line marks the internal track outline (the actual imprint of the foot) and defines the track dimensions (Fig. 2.10). Dashed lines are used for the external outline of very shallow and faint tracks which are almost indiscernible, and for enigmatic structures, which can not (unambiguously) be identified as vertebrate tracks.

2.7.2.2 Illustrating with photographs

Besides outline drawings, photographs provide much information about tracks. However, the angle of illumination may considerably change the appearance of the track in the photograph (e.g., Sarjeant, 1989; Gatesy et al., 2005a), and especially small tracks may only become visible if they are specifically illuminated. Additionally, monocular photographs are subjected to distortion.

If not otherwise stated, all photographs were taking at daylight. Such photographs may have suffered from suboptimal lightening, because the sun does not always shine when pictures have to be taken during a systematic excavation, and seldom provides the ideal angle of illumination. Several photographs of tridactyl tracks of the main track level and of extracted samples of the Combe Ronde site were taken using artificial lightning, if possible always from the upper left corner. The direction of illumination is indicated in all figured tracks.

2.7.3 Track and trackway parameters

Even though the most important track and trackway parameters such as pace or stride are commonly measured in a similar way, many different terminologies exist for the measuring of track and trackway parameters of tetrapods and for the used reference points (e.g., Peabody, 1948, 1959; Baird, 1952; Lessertisseur, 1955; Heyler & Lessertisseur, 1963; Haubold, 1971, 1974, 1984; Leonardi, 1987; Thulborn, 1990; Lockley, 1991b). Leonardi (1987) provided an exhaustive overview of ichnological terms and methods.

In this work, parameters were measured in a consistent fashion from one track or trackway to the next, by always using the same reference points. Thereby it was important to use a terminology, which is easily applicable in the field, especially concerning the tridactyl tracks. The parameters of all tracks and trackways of the Combe Ronde tracksite were entered by C. Lovis (PAL A16) into standardized *Excel* worksheets. These data, notably the mean track and trackway parameters, are subject of more detailed analyses in Chapter 5.

In addition to the parameters measured directly on the tracks and trackways, several parameters were calculated either based on measured values (e.g., index of track size, locomotion speed) or on measurements on magnified outline drawings (e.g., trackway ratio, [WAP/PL]-ratio).

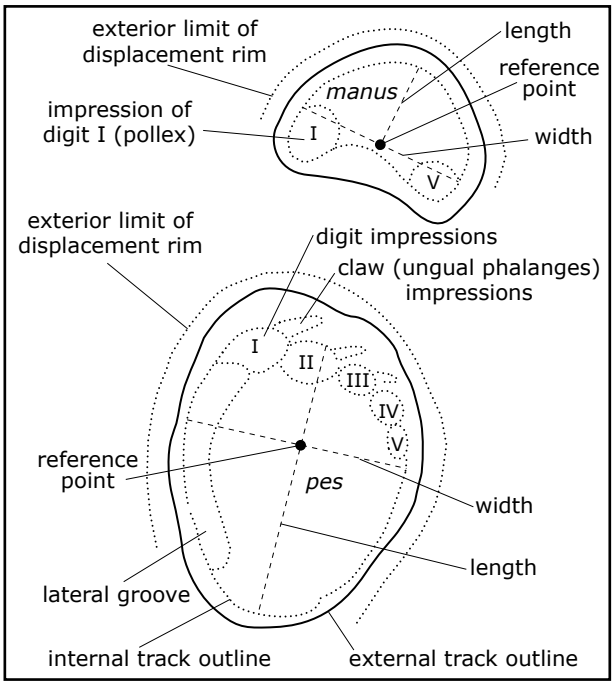


Fig. 2.10: Schematic outline drawing of a sauropod pes and manus track explaining the methodology of the outline drawings and characteristic features of sauropod pes and manus tracks. Note that ungual phalanges are denoted as claws in this work.

2.7.3.1 Tracks of quadrupedal dinosaurs

Track length and track width

Length and width are measured inside the displacement rim, as discussed by Lockley et al. (2002a; Fig. 8). They are defined by the internal track outline and correspond approximately to the dimensions of the true track *sensu stricto* or the imprint of the foot.

In pes tracks, the length was measured from the middle of the anterior internal track outline (claws not considered) to the middle of the posterior interior track outline, the axis dividing the track in two approximately equal halves. Pes width was measured roughly perpendicular to the long axis, at the point of greatest track width. In manus tracks the length was measured from the middle of the anterior internal track outline to the middle of the posterior internal track outline. Manus width was measured as the greatest width perpendicular to the length axis (Fig. 2.10).

In sauropod pes tracks the length is always larger than the width, and in manus tracks the length is generally smaller than the width (Fig. 2.10). In manus tracks the width better characterizes the size of the tracks because it is less variable than the length, which is strongly affected by the kinematics of the trackmaker.

Index of track (footprint) size

This parameter is calculated following Thulborn (1990, p. 234), from the track length and width for both pes and manus tracks and is expressed in the same units of measurements of length and width:

Index of track size (IS) = $(\text{length} \times \text{width})^{0,5}$
Index of pes track size (IPS) = $(\text{PL} \times \text{PW})^{0,5}$
Index of manus track size (IMS) = $(\text{ML} \times \text{MW})^{0,5}$

(Maximum) track depth

Distance between the deepest point of the track and the highest point of the displacement rim or the surrounding tracked surface, if no displacement rim is discernable.

Heteropody

Lockley et al. (1994) defined heteropody as the difference in area (total track area) between the pes

and manus tracks in a given trackway of a quadrupedal animal. In this work heteropody is estimated by counting squares on grids and indicated as an approximate (pes/manus)-ratio. Furthermore, the ratio between the indices of pes and manus track sizes is used to characterize heteropody.

2.7.3.2 Trackways of quadrupedal dinosaurs

The measured trackway parameters include pace, stride, rotation, and width of the angulation pattern for both pes and manus tracks (Fig. 2.11). Furthermore, the gleno-acetabular distance, the total trackway length, and the trackway orientation were measured.

Because the sauropod tracks did not consistently exhibit clearly defined reference points such as the imprint of the first digit, in both pes and manus tracks the intersection of length and width was used as the reference point for the measurement of the trackway parameters (cf. Leonardi, 1987; Thulborn, 1990; Lockley, 1991b) (Fig. 2.10). This is suggested to be the best-defined reference point, even though it is also not always easy to define, notably in partially overprinted manus tracks.

Stride length

This is the distance between the reference points of two consecutive tracks made by the same foot (pes or manus), that is left-to-left or right-to-right (Thulborn, 1990; Lockley, 1991b) (Fig. 2.11).

Pes and manus rotation

When a track is directed outward with respect to the line connecting it with the consecutive track (the stride), it shows a positive (outward) rotation (indicated by positive angle values). If the track is directed inward, it shows a negative (inward) rotation (indicated by negative angle values). This definition was suggested by Demathieu (1970), Leonardi (1987), and Lockley (1991b). However, other ichnologists have used these terms in the opposite sense, i.e., the defined outward rotation as negative values (e.g., Haubold, 1971; Thulborn, 1990; Marty et al., 2003). This parameter was also called "divarication of foot from midline" (Leonardi, 1987). In the present work the rotation is not measured with respect to the trackway midline but with respect to the stride line towards the subsequent pes or manus track, or exceptionally towards the precedent pes or manus track if the subsequent pes or manus track is lacking (Fig. 2.11).

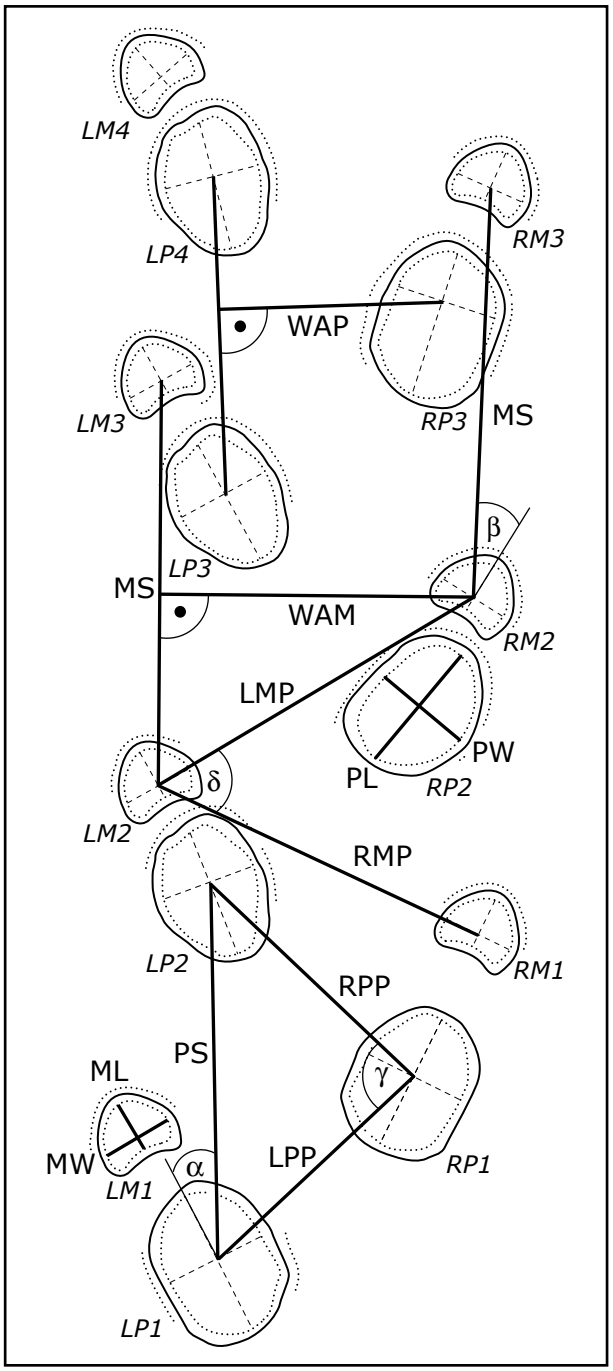


Fig. 2.11: Schematic sauropod trackway showing the essential pes and manus track and trackway parameters measured:
Pes length (PL), pes width (PW), pes rotation (α) (here the left rotation is shown), left pes pace length (LPP) and right pes pace length (RPP), pes stride length (PS), pes pace angulation (γ), width of the pes angulation pattern (WAP) or pes trackway width;
Manus length (ML), manus width (MW), manus rotation (β) (here the right rotation is shown), left manus pace length (LMP) and right manus pace length (RMP), manus stride length (MS), manus pace angulation (δ), width of the manus angulation pattern (WAM) or manus trackway width.

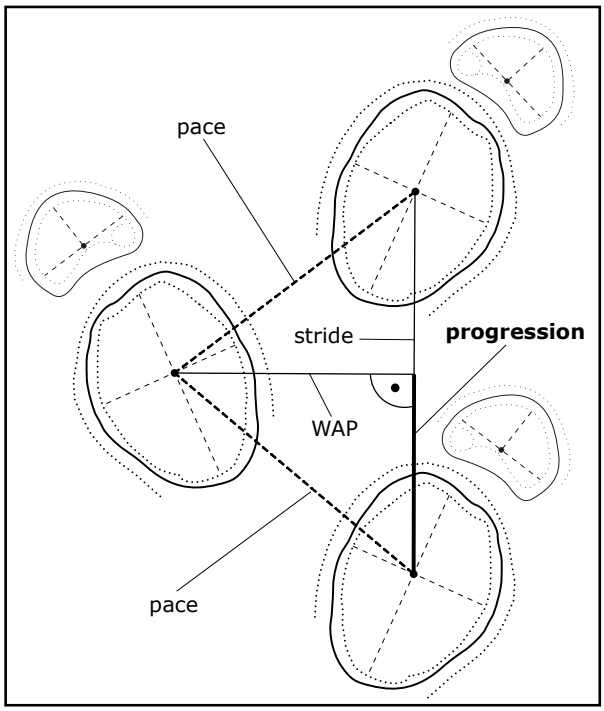


Fig. 2.12: Schematic sauropod trackway, illustrating the concept of the progression, in this case the right pes progression.

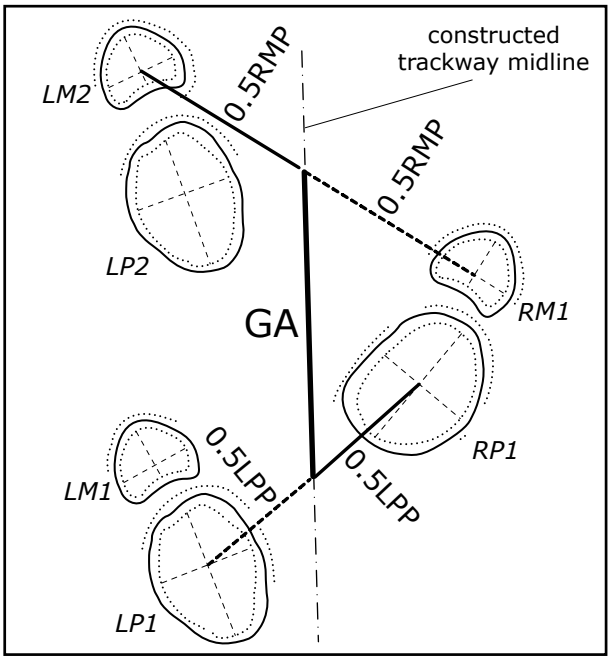


Fig. 2.13: Schematic sauropod trackway, illustrating how the gleno-acetabular distance is measured. Note that the trackway midline is constructed, contrary to the hypothetical trackway midline shown in Figure 2.9. The constructed trackway midline intersects the midpoint of the pace of two subsequent and opposite pes tracks and the midpoint of the pace of the subsequent manus tracks. The distance between the two midpoints is the gleno-acetabular distance and it lies on the constructed trackway midline. For abbreviations see Fig. 2.11.

Pace (step) length

Distance between the reference point in two successive (consecutive) tracks (pes or manus), that is left-to-right (LPP or LMP) or right-to-left (RPP or RMP) (Thulborn, 1990; Lockley, 1991b) (Fig. 2.11). Left and right pace are separately indicated in the tables.

Progression

This parameter is calculated with the Pythagoras' theorem from the measurements of the pace and the trackway width:

$$\text{Progression} = [(\text{pace})^2 - (\text{WAP})^2]^{0,5}$$

The progression represents the forward movement of the trackmaker in the direction of the trackway during one footfall (pace), and is calculated for the left and right pes and manus tracks (Fig. 2.12).

Pace angulation

Pace angulation was measured according to Figure 2.10 for both pes and manus tracks, and not calculated from pace and stride measurements by the law of cosines (e.g., Farlow et al., 1989).

Gleno-acetabular distance

The gleno-acetabular distance is an indication of body size, and it corresponds from an anatomical point of view to the distance between the centre of the shoulder joint (glenoid cavity) and the centre of the hip joint (acetabular cavity). For quadrupedal animals it may be estimated from their trackways by measuring the distance between the midpoint of a line connecting two consecutive pes tracks (left and right or vice versa) and the midpoint of a line connecting the next two manus tracks (cf. Demathieu, 1970; Leonardi, 1987; Thulborn, 1990) (Fig. 2.13).

Width of the angulation pattern (WAP, trackway width)

The width of the angulation pattern (Thulborn, 1990) was measured in order to characterize trackway width. Other parameters such as internal and external trackway width (e.g., Leonardi 1987, Thulborn, 1990; Marty et al., 2003), side width and overall width (Romano et al., 2007), or width of pace, commonly used to characterize trackway width, have not been measured because they are less-clearly defined.

The width of the angulation pattern corresponds to the distance between the reference point of a given pes or manus and the stride between the opposite, antecedent and subsequent pes or manus tracks. This distance comprises a right angle with the stride (Fig. 2.11). Note that this parameter does

not significantly vary when using another reference point. In a regular trackway it can be approximately calculated with the Pythagoras' theorem from pace and stride length, if it is assumed that the width of the angulation pattern intersects the stride under a right angle and approximately at the midpoint of the stride. For a more precise calculation refer to Farlow (1989).

(Width of the angulation pattern / track size)-ratios

Two ratios are calculated and each for pes and manus tracks:

1. Width of the pes angulation pattern / pes length [WAP/PL]-ratio
2. Width of the pes angulation pattern / index of pes track size [WAP/IPS]-ratio
3. Width of the manus angulation pattern / manus width [WAM/MW]-ratio
4. Width of the manus angulation pattern / index of manus track size [WAM/IMS]-ratio

These ratios can be used to characterize trackway gauge for pes and manus tracks. The ratio between both of them, i.e., the ([WAP/PL]/[WAM/MW])-ratio, can be used to characterize whether manus tracks are closer or further away from the trackway midline than pes tracks. In this work, only the [WAP/PL]-ratio is in the focus of further discussion and comparison (see also chap. 5.7.1.1).

Pes trackway ratio (PTR)

This parameter was recently introduced by Romano et al. (2007) in order to characterize the gauge of quadrupedal trackways (Fig. 5.39):

PTR = [side width (SW) / overall width (OW)] x 100%

Note that in this work side width and overall width have been estimated from magnified outline drawings and have not been measured directly on the trackways in the field. The same ratio can also be measured for the manus tracks, which was, however, not done in this work.

Trackway gauge

Farlow (1992) first classified sauropod trackways using trackway gauge. He defined narrow-gauge trackways by "tracks close (to) or even intersecting the trackway midline", and wide-gauge trackways by "tracks well away from the trackway midline". This definition readily identifies narrow-gauge and very wide-gauge trackways, but it is difficult to characterize medium-gauge and not very wide-gauge trackways.

However, without a clear quantification, trackway gauge is often difficult to identify, particularly regarding trackways with small tracks, because these often appear narrower than they actually are. In order to quantify trackway gauge, Romano et al. (2007) introduced the trackway ratio (see above). Based on measurements of selected, published sauropod trackway outline drawings they suggested trackway ratios of 35% for the wide-medium, and 50% for the medium-narrow transition as provisional boundaries (Romano et al., 2007). The significance of these boundaries and their correlation with the [WAP/PL]-ratio is discussed in Chapter 5.7.1.1.

2.7.3.3 Tracks and trackways of bipedal, tridactyl dinosaurs

In this work the terms "tracks/trackways of bipedal dinosaurs", "bipedal trackways", or "bipedal, tridactyl trackways" are used to refer to tridactyl tracks and trackways.

The trackway parameters were measured as described above for the sauropod trackways according to Figure 2.13. The distal extremity (tip without the impression of the claw) of digit III was used as reference point.

Owing to the particular morphology of tridactyl tracks, the measured parameters differ from those of the sauropod tracks and have to be clearly defined:

Digital axis

An axis going through the most anterior point (tip without claw) of a digit imprint, and separating the digit imprint in two approximately symmetrical halves (Fig. 2.15B). Note that using this definition the digital axes of all three digits generally do not intersect at a single point at the posterior end of the track.

Track length and width

Track length is measured from the most anterior point (tip without claw) of digit III, along or approximately parallel to the digital axis of the principal digit III, to the posterior end of the track (Fig. 2.15A). The total length may include the impression of the heel or the metapodium.

Track width is measured as the distance between the most anterior point (tip without claw) of digit II and digit IV (Fig. 2.15A). Consequently, the measured

track width is not necessarily at a right angle to track length and does not necessarily correspond to the maximum track width.

Digit length and digit width

Length and width were measured for all three digits. However, because digits are often curved, irregular in shape, or poorly marked, it was difficult to maintain a consistent technique for measuring them. Digit length was generally measured from the most anterior point (tip without claw), along the digital axis to the most posterior point (Fig. 2.15C). Digit length was difficult to measure when the digits merged into an imprint made by the distal end of the metapodium. The digit width was generally measured as maximum width at a right angle to the digital axis (Fig. 2.15C).

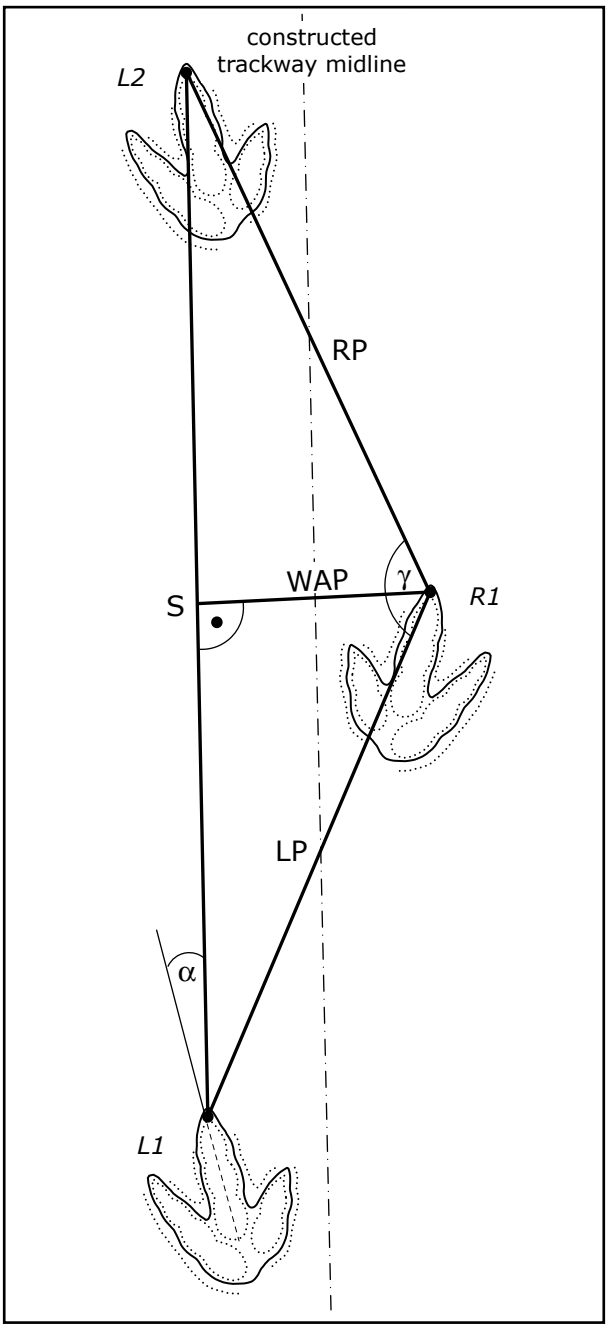


Fig. 2.14: Schematic theropod trackway illustrating the measured trackway parameters: track rotation (α) here figured an outward (positive) rotation, left pace length (LP) and right pace length (RP), stride length (S), pace angulation (γ), and width of the pes angulation pattern (WAP) or trackway width.

Interdigital divarication angles II-III and III-IV

The interdigital divarication angles were measured between the digital axes (Thulborn, 1990; Fig. 4.5a). The total divarication (II-IV) angle is defined as the angle between the digital axes of digit II and digit IV, and it corresponds to the sum of the two interdigital angles II-III and III-IV (Fig. 2.15B).

2.7.4 Trackway patterns and configuration

Leonardi (1987) defined trackway pattern as "the complex of characteristics of the trackway with the exception of those characteristics belonging specifically to the pes or manus tracks", and in ichnotaxonomical diagnoses trackway characteristics are commonly integrated. However, in ichnological literature the term pattern in association with trackway either refers to the general trackway characteristics *sensu* Leonardi (1987) (e.g., Farlow & Pianka, 2000; Farlow et al., 2000; Lockley & Meyer, 2000), to the walking (gait) pattern of the trackway (e.g., Herreid & Full, 1986; Lee & Huh, 2002; Padian, 2003; Lee & Lee, 2006; Li et al., 2006; Marty et al., 2006b), or to the pattern of the distribution of trackway orientation on a given tracksite (trackway orientation pattern). For the description of the trackway characteristics, the terms trackway configuration (e.g., Foster et al., 1999; Meyer & Thüring, 2003b) or simply trackway parameters (e.g., Romano et al., 2007) have also been applied, but trackway pattern is more frequently used.

2.7.4.1 Trackway patterns

In this work, trackway pattern refers to the general pattern of a trackway of a quadrupedal animal (Marty et al., 2006b). Depending on the presence or absence of pes and manus tracks, the sauropod trackways are described with five different trackway patterns as illustrated in Figure 2.16:

1. *Quadrupedal trackways*: manus and pes tracks always present
2. *Pes-only trackways*: without any evidence of manus tracks (primary overstep of Peabody, 1959)

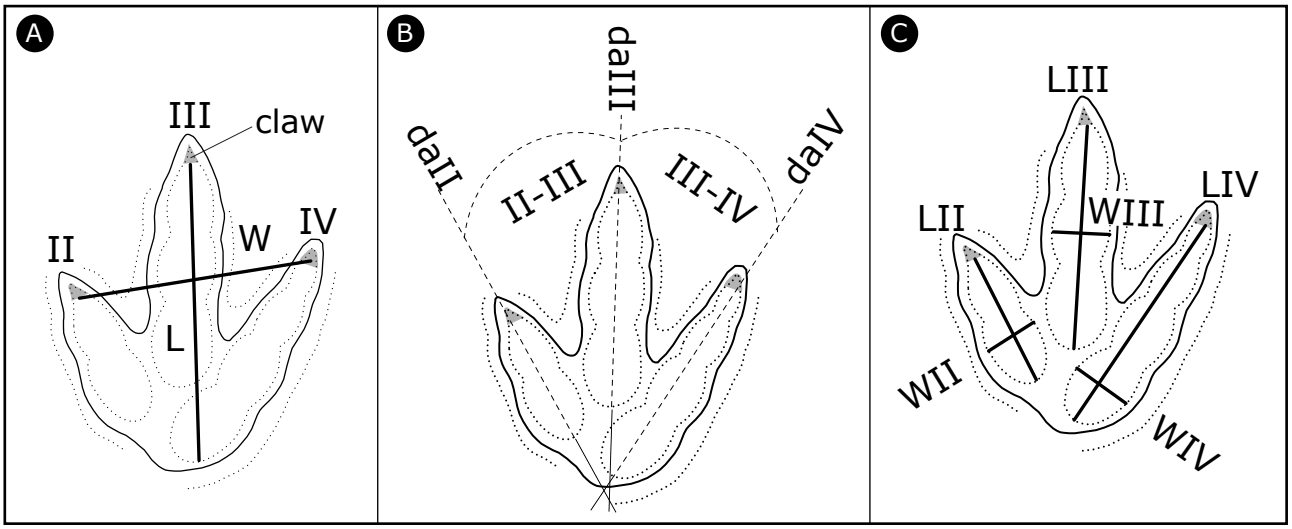


Fig. 2.15: Schematic tridactyl tracks showing the track parameters measured. **A:** Track length (L) and width (W). **B:** Digital axis (da) and (interdigital) divarication angles II-III and III-IV. Note that the digital axes do only occasionally intersect at a single point. **C:** Digit length (L) and width (W), measured along the digital axes.

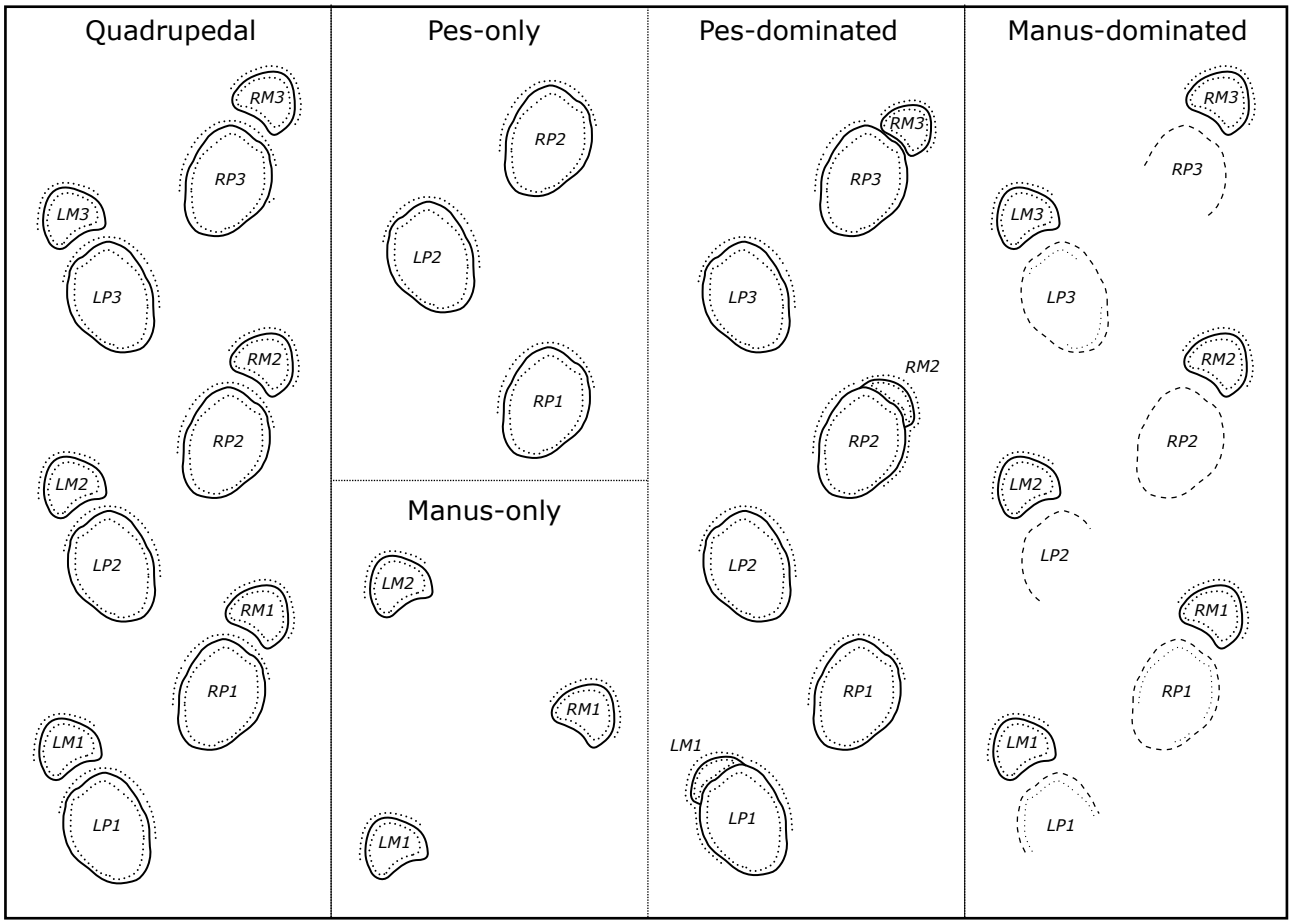


Fig. 2.16: Schematic sauropod trackways illustrating the different possible trackway patterns that can be observed on the trackways of quadrupedal animals.

3. *Manus-only trackways*: without any evidence of pes tracks
4. *Pes-dominated trackways*: some manus tracks absent (completely overprinted) and/or (partially) deformed
5. *Manus-dominated trackways*: (deep) manus tracks and some shallow and barely visible pes tracks

Lack of manus tracks is due to overprinting by the pes, whereas the (partial) lack of pes tracks generally is a preservational artefact. Manus-only trackways led to the debate about the swimming capacities of sauropods, which is discussed in greater detail in Chapter 5.7.1.7.

2.7.4.2 Trackway configuration

In quadrupedal animals, trackway configuration refers to the general trackway characteristics, such as the arrangement of pes and manus tracks (e.g., whether the pes or manus tracks are closer to the trackway midline), their orientation, and the trackway width (gauge). These features may be used for ichnotaxonomical diagnosis because they are – at least to a certain degree – an expression of the general stance (posture) and gait, and locomotor capabilities of the trackmaker. With the exception of the regular quadrupedal trackway pattern, the trackway patterns can be considered as subcategories of the trackway configuration, indicating a special behaviour of the trackmaker or special substrate properties. Consequently, they should not be included in ichnotaxonomical diagnosis.

	size class	pes track length (PL)
sauropod dinosaurs	tiny	PL < 25 cm
	small	25 cm < PL < 50 cm
	medium sized	50 cm < PL < 75 cm
	large	PL > 75 cm
bipedal dinosaurs	minute	PL < 10 cm
	small	10 cm < PL < 20 cm
	medium sized	20 cm < PL < 30 cm
	large	PL > 30 cm

Table 2.2: Terminology of track size classes used for the classification of tracks of sauropods and bipedal, tridactyl dinosaurs.

For bipedal dinosaurs, the trackway configuration is mainly characterized by the pes rotation (e.g., outward or inward rotation) and the trackway width (gauge), even though both parameters may considerably vary as a function of the behaviour (e.g., locomotion speed) of the trackmaker.

2.7.5 Track size classes

Often, dinosaur tracks are referred to small, medium-sized or large animals without a clear definition of these size classes (e.g., Lockley, 1994). Thulborn (1990) for instance defined a foot length of 25 cm as the boundary between small and large theropods or bipedal dinosaurs in general, and Dalla Vecchia (1998b) used track lengths of 15 and 25 cm between small, medium-sized, and large theropod tracks, respectively. Moreno & Benton (2005) considered sauropod tracks measuring less than 20 cm as small, and tracks measuring more than 22,5 cm as medium-sized.

Because there is no concordance between commonly used size classes, for the sake of simplicity, the size classes of Marty et al. (2007c) are used here and defined based on the length of the pes tracks (PL) as shown in Table 2.2. Note that this classification is tentative and not based on any statistical analysis. Thus, the boundaries do not have any precise palaeoecological meaning (i.e., age classes).

2.7.6 Calculation of locomotion speed

How fast certain dinosaurs could move and what kind of locomotion such as walking or running they used is an intriguing question. Trackways offer the only direct insight into dinosaur locomotor capacity. This information is coupled with skeleton-based biomechanical approaches such as estimations of the strength of leg bones (e.g., Farlow et al., 1995) or muscle mass (e.g., Hutchinson & Garcia, 2002; Hutchinson et al., 2005), indispensable for the reconstruction of the precise motions of dinosaurs.

Calculation of locomotion speed from trackways derives from the relationship obtained by Alexander (1976) between speed, body size (expressed by the height at the hip), and the stride length. Subsequently, the calculation of speed has been frequently estimated from dinosaur trackways (e.g., Russell & Béland, 1976; Tucker & Burchette, 1977; Kool, 1981; Thulborn, 1981; Farlow, 1982; Currie, 1983; Haubold, 1984; Lockley et al., 1986; Irby, 1996a, b; Mazzetta & Blanco, 2001; Mossman et al., 2003).

However, already Coombs (1978) pointed out the shortcomings of this empiric relationship because estimates of the hip height based on tracks size may be liable to serious error and because the trackmaker can rarely be precisely identified. He also concluded that this method has limited value in estimating the maximum running speed of dinosaurs for the simple reason that running animals generally use their top speed only rarely, and that trackways made at maximum speed are unlikely to be found. Meanwhile, it has been recognized that this method can not claim to be accurate, because it is unknown whether the relationship between relative stride length (S/h) and the Froude number (i.e., $[speed]^2$/ [leg length x g]) is the same for dinosaurs as for recent mammals (Alexander, 2006), and because the estimation of hip height from track length is subjected to a great source of errors (e.g., Henderson, 2003; Rainforth & Manzella, 2007). Thus, speed calculations are considered rough approximations (e.g., Hutchinson et al., 2005; Alexander, 2006; Rainforth & Manzella, 2007). This was also suggested by skeleton-based approaches for the calculation of speed (e.g., Thulborn, 1982; Demathieu, 1984, 1986). Even if this method could claim accuracy, maximum speed would still be hard to estimate, because running animals use their maximum speed only rarely (Alexander, 2006).

Nonetheless, Alexander's (1976) method is at least informative providing an approximation for the magnitude of the locomotion speed of a dinosaur and, more importantly, for the relative speed of a given sample of trackways. The latter is interesting when interpreting the behaviour of trackmakers from trackways (e.g., gregarious behaviour from parallel trackways). Speed is calculated in this work to better understand the observed differences in trackway patterns and configurations of the Combe Ronde trackways. Based on this, assumptions about the general locomotion capabilities and possible behaviour of the trackmakers can then be made.

2.7.6.1 Equations used in this study

From the study of locomotion of living terrestrial vertebrates, Alexander (1976) found a relationship to calculate locomotion speed from trackways:

(eq. 1) $(S/h) \approx 2{,}3(v^2/gh)^{0{,}3}$ (Alexander, 1976)

Where S=stride length [m], h=hip height [m], v=speed of locomotion [m/s], g=gravitational constant (9,81 m/s^2), (s/h) is also called relative stride length and is dimensionless.

Alexander (1976) pointed out that this empiric formula can be applied to dinosaur trackways, since the stride length can be measured directly and the hip height (size) of the dinosaur can be estimated from the size of its tracks. In order to calculate locomotion speed, equation 1 can be transformed to give:

(eq. 2) $v \approx 0{,}25g^{0{,}5} S^{1{,}67}h^{-1{,}17}$ for $(S/h)<2{,}0$ (Alexander, 1976)

Mammals generally shift from a walking to a trotting or running gait when relative stride length reaches a value of about 2,0. Alexander (1976) and Alexander et al. (1977) suggested that equation 1 applies best for trackways with an estimated S/h of less than 2,0 because equation 1 gives low estimates when compared to data gathered from African ungulates moving with a faster gait. They found the following equation 3 to be valid for a wide range of animals at a wide range of speeds:

(eq. 3) $S/h \approx 2{,}3[v(gh)^{-0{,}5}]^{0{,}6}$ (Alexander et al., 1977)

Alexander et al. (1977) also indicated that the change from trotting to galloping occurs when:

(eq. 4) $v(gh)^{-0{,}5} \approx 1{,}5$ (Alexander et al., 1977)

From equations 3 and 4 Thulborn (1982) estimated that the transition from trotting to galloping occurs when the relative stride length is larger than approximately 2,9. Thulborn & Wade (1984) revised equation 3 of Alexander et al. (1977) and proposed the following equation to calculate the speed of running dinosaurs:

(eq. 5) $v \approx [gh(S/1{,}8h)^{2{,}56}]^{0{,}5}$ for $(S/h)>2{,}9$ (Thulborn & Wade, 1984)

Thulborn & Wade (1984) also suggested the mean of equations 2 and 5 to be used for trotting gaits, or when the relative stride is between 2,0 and 2,9:

(eq. 6) $v \approx [(eq.2)+(eq.5)]/2$ for $2{,}0<(S/h)<2{,}9$ (Thulborn & Wade, 1984)

In this work, equation 2 is used for the calculation of locomotion speed for $(S/h)<2{,}0$ (walking gaits), equation 5 for $(S/h)>2{,}9$ (running gaits), and equation 6 for $2{,}0<(S/h)<2{,}9$ (trotting gaits). Thereby, the mean value of the stride lengths of a given trackway was used.

2.7.6.2 Estimation of hip height

One of the major problems in calculating locomotion speed from a trackway is to estimate the hip height of the *a priori* unknown trackmaker, based on its footprints (e.g., Rainforth & Manzella, 2007). Nonetheless, hip height (h) is considered to be the most convenient measure of body size in dinosaurs (Thulborn, 1990), and Alexander (1976) defined it as the height of the hip from ground, and suggested that hip height equals approximately 4 times the foot length (PL). This factor is generally considered as a thumb rule.

Thulborn & Wade (1984) defined the skeletal hip height as the height above the ground of the hip joint in a dinosaur skeleton. "Height of the hindlimb from the summit of the femur to the sole of the foot" has been defined as combined lengths of femur, tibia and longest metatarsal, plus an increment of 9% to account for the ankle bones and soft tissues (Thulborn, 1982). Based on his preceding work (Thulborn, 1982, 1984; Thulborn & Wade, 1984; Thulborn, 1989), Thulborn (1990) assumed that these various estimations for hip height were roughly equivalent, and that the skeletal foot length (the sum of the phalanges) was roughly equivalent to the length of the third metatarsal. In order to calculate the hip height from footprint length, Thulborn (1989, 1990) proposed, based on cursory analysis of osteometric data, several morphometric ratios for different groups and size classes of dinosaurs. He stated that these factors are convenient for the preliminary analysis of trackway data, especially for small, tridactyl dinosaurs, where the length of the metatarsus may be roughly equivalent to the footprint length. In the case of larger dinosaurs such as sauropods, however, footprint length is exaggerated by a substantial cushion of soft tissues in the "heel" region and, consequently, it is difficult to predict any skeletal dimension on the basis of footprint length (Thulborn, 1990).

In this work, the following morphometric parameters were used to calculate the hip height from pes track length (PL):

Sauropods in general

(1) h = 4,0PL (Alexander, 1976)
(2) h = 5,9PL (Thulborn, 1989, 1990)

Bipedal dinosaurs (PL<25 cm)

h = 4,5PL (Thulborn, 1989, 1990)

Bipedal dinosaurs (PL>25 cm)

h = 4,9PL (Thulborn, 1989, 1990)

Thereby, the mean value of the measured track lengths of a given trackway was used. In bipedal, tridactyl trackways the mean value of the length of digit III (e.g., Thulborn, 1990, Day et al., 2002b; Mossman et al., 2003) was not used because it could not always be reliably measured due to the often rather poor preservation of the tracks.

* * *

3 - Formation and taphonomy of human footprints in microbial mats of present day tidal-flat environments: implications for the study of fossil footprints

3.0 Preliminary note

This chapter was submitted by Daniel Marty, Andreas Strasser & Christian A. Meyer to a special volume on hominid footprints in Ichnos (Marty et al., 2008a), edited by M.G. Lockley (see also Lockley et al., 2007a), reviewed and accepted for publication, and the manuscript that has been accepted for publication is hereafter reproduced. For reasons of continuity the manuscript was formatted according to this work, and in order to avoid duplications, the terminology part of the accepted manuscript was included in Chapter 2.6. Note also that the size of the figures was slightly adapted to fit into the GeoFocus layout, and that an additional figure (Fig. 3.10) is provided here, which was not included in the accepted manuscript.

3.1 Abstract

This chapter concerns the formation, taphonomy, and preservation of human footprints in microbial mats of present-day tidal-flat environments. Due to differences in water content and nature of the microbial mats and the underlying sediment, a wide range of footprint morphologies was produced by the same trackmaker. Most true tracks are subjected to modification due to taphonomic processes, leading to modified true tracks. In addition to formation of biolaminites, microbial mats play a major role in the preservation of footprints on tidal flats. A footprint may be consolidated by desiccation or lithification of the mat, or by ongoing growth of the mat. The latter process may lead to the formation of overtracks. Amongst consolidated or (partially) lithified footprints found on present-day tidal flats, poorly-defined true tracks, modified true tracks, and overtracks were most frequently encountered while unmodified and well-defined true tracks are rather rare. We suggest that modified true tracks and overtracks make up an important percentage of fossil footprints and that they may be as common as undertracks. However, making unambiguous distinctions between poorly-defined true tracks, modified true tracks, undertracks, and overtracks in the fossil record will remain a difficult task, which necessitates systematic excavation of footprints combined with careful analysis of the encasing sediment.

3.2 Introduction

The preservation of fossil vertebrate tracks in laminated sediments, in particular in tidal-flat environments, is frequently explained by the presence of microbial mats, which are thought to have covered and stabilised the tracks (e.g., Thulborn, 1990; Avanzini, 1998; Kvale et al., 2001; Freytet, 2003; Conti et al., 2005; Marty, 2005). It has also been suggested that undertracks commonly form in well-laminated microbially-bound sediment (Lockley, 1991b). Also, the relative abundances of true tracks and undertracks in the sedimentary record (e.g., Thulborn, 1990; Lockley, 1991b; Nadon, 2001; Milàn & Bromley, 2006), and the importance of correct interpretation of undertracks (Milàn & Bromley, 2006) have been discussed. Lockley (1991b) spoke about tracks as traps (low energy pockets) and Paik et al. (2001) provided a model for overtrack formation by sediment accumulation (trapping) within the true track. However, overtracks and modified true tracks have not as yet been included in the "true track vs. undertrack" discussion.

Generally, only fine anatomical details such as digit impressions, claw marks, or skin impressions clearly identify true tracks. Unfortunately, such details are often not recorded because the trackmaker's feet aren't suitable to leave such traces, or because the animal is too heavy or too light to leave recognizable prints. Moreover, ill-defined prints are created during running or jumping, because the soles are covered with mud, because the substrate is too dry or too soft, or simply because weathering or erosion destroys the footprints (e.g., Cohen et al., 1991; Demathieu, 1991; Nadon, 2001; Henderson, 2006a; Milàn, 2006; Scott et al., 2007). Consequently, one of the major challenges of vertebrate ichnology is the unambiguous identification of (modified) true tracks and their distinction from under- and overtracks and from other extramorphological features that distort true foot morphology. This is the prerequisite for meaningful ichnotaxonomical procedure, and the interpretation of behavioural patterns and the reconstruction of the palaeoenvironment.

Experimentation and modelling has contributed considerably to the understanding of the formation and characteristics of true tracks and undertracks (e.g., Peabody, 1959; Brand, 1996; Allen, 1997; Manning, 2004; Diedrich, 2005; Henderson, 2006a; Milàn, 2006; Milàn & Bromley, 2006; Uchman & Pervesler, 2006; Davis et al., 2007). Nonetheless, the role of microbial mats in the formation and preservation of footprints has so far not been analysed in greater detail.

Microbial mats are ubiquitous on modern and ancient carbonate and siliciclastic tidal flats and have been described in many classical works on peritidal environments (review in Gerdes & Krumbein, 1994; Gerdes et al., 2000; Schieber et al., 2007a). Their important role in the formation and preservation of sedimentary structures is more and more recognized (e.g., Gerdes et al., 1993; Schieber et al., 2007a), and they commonly bear vertebrate footprints in the Recent as well as in the geologic record. Microbial mats consist of benthic microbial communities, which are usually dominated by photosynthetic prokaryotes, particularly cyanobacteria and photosynthetic bacteria, and occasionally by eukaryotic microalgae such as diatoms (e.g., Bauld, 1984; Cohen et al., 1984; Krumbein et al., 2003; Levit & Krumbein, 2003). They grow best where they can obtain the maximum amount of sunlight and yet remain moist and in water contact (Kendall & Skipwith, 1968). Microbial mats can either agglutinate sediment particles onto their sticky mucilaginous sheaths or act as bafflers that trap sediment washed into the tangle of filaments (Demicco & Hardie, 1994). Trapping and binding is regulated by microbial activity which, in turn, may be stimulated when the mat is covered by a thin sediment layer (Burne & Moore, 1987). Microbial mats commonly display a complex vertical distribution of microbial communities that create and are adapted to specific geochemical conditions. In many cases, the sediment below a dense mat becomes anoxic (Dupraz et al., 2004).

Additionally, microbial mats may quickly lithify by the precipitation of calcium carbonate (e.g., Krumbein & Cohen, 1977; Chafetz & Buczynski, 1992; Dupraz et al., 2004; Dupraz & Visscher, 2005), and consequently enhance the preservation potential of footprints and other traces. Microbial mats are particularly abundant in low latitudes where protected microtidal lagoons occur more frequently and provide varied ecospaces such as persisting thin water sheets, permanently water-filled ponds, flats subjected to daily tidal flooding, or surfaces that are water-covered only during spring-tides or storms (Gaillard et al., 1994; Gerdes & Krumbein, 1994). The products of benthic microbial communities are called "biolaminites" or "biolaminations" for the flat laminated type of stromatolites (Gerdes et al., 1991), or "biolaminoids" for less significantly laminated sediment that accumulated through the activity of microbial communities (Gerdes & Krumbein, 1987; Brehm et al., 2002).

This chapter addresses a number of issues concerning the formation, taphonomy, and preservation of vertebrate footprints in microbial mats of present-day tidal-flat environments:

1. Relationships between the physical properties of the microbial mat (e.g., water content, mat thickness, elasticity/plasticity) and footprint morphology
2. Modification of footprint morphology by continued growth of the microbial mat
3. Consolidation of footprints by desiccation and/or lithification of the microbial mat.

These observations in modern environments are relevant for a better understanding of the taphonomy of vertebrate footprints in fossil biolaminites and for the evaluation of the relative abundances of (modified) true tracks, undertracks, and overtracks. Consequently, they help in understanding ichnotaxonomy, palaeoecology, and palaeoenvironment. Finally, the results contribute

to the study of fossil hominid footprint preservation especially in environments comparable to those studied here (review of fossil hominid footprint sites in Lockley et al., 2007a).

3.3 Geographical, environmental, and climatic settings

The data presented herein were gathered during fieldtrips to Ambergris Caye (Belize), Eleuthera Island (Bahamas), southern Tunisia, and southern Sinai (Egypt). Vertebrate tracks in microbial mats were observed in different tidal-flat environments including intertidal flats, supratidal flats and marshes, and sabkhas. These environments differ from each other mainly in respect to the thickness and nature of the microbial mats, the properties of the underlying sediment, and the water content related to tidal range and climate.

3.3.1 Ambergris Caye (Belize)

In February 2007, footprints were studied in Belize on Ambergris Caye SW of San Pedro Town (87°59'00''W, 17°54'11''N), in mangrove swamps near South Beach, and on supratidal flats and marshes SW of the airport (Fig. 3.1A). Belize lies in the tropical zone, and the climate on Ambergris Caye is one of seasonally varying rainfall and evaporation rates with a drier season in winter and a rainy season in summer (Gregg et al., 1992).

The supratidal flats and marshes are topographically featureless with a maximum relief of 1-2 m above mean sea level, locally heavily vegetated by mangroves and almost completely covered with microbial mats (Figs. 3.2A and 3.2B). Generally, these mats are smooth and flat; blistering seldom occurs. To the SW of San Pedro Town, vast surfaces have recently been subjected to deforestation (Fig. 3.2A), probably for new construction sites, offering perfect conditions to study footprints in dead and lithified (dolomitized) microbial mats. As these flats were visited during the dry season, it is not known whether the microbial communities were killed by the deforestation or due to the drought. However, it is probable that new communities will install themselves on top during the wet season.

3.3.2 Eleuthera Island (Bahamas)

In May 2004, footprints were studied on Eleuthera Island on a supratidal flat around No Name Pond, located in the northern part of the island (76°34'31''W, 25°24'28''N), about 3 km NW of Gregory Town (Fig. 3.1B). Eleuthera forms part of the northeastern and windward margin of the Great Bahama Bank. It is located in the subtropical zone and, due to the seasonal shifting of climatic belts, experiences warm-temperate conditions in winter and a tropical regime with occasional hurricanes in summer (Bosart & Schwartz, 1979).

No Name Pond is a hypersaline lake. Both the lake and the surrounding flats display prolific microbial mats whose morphology and consistency are clearly related to the water content (Fig. 3.3). The microbial mats are mainly built up by the cyanobacterium *Microcoleus* sp. and the coccoid cyanobacteria *Gloeocapsa* sp. and *Entophysalis* sp. (Dupraz et al., 2004). From the shallower parts of the lake, Dupraz et al. (2004) described more or less continuous carbonate crusts, which form by early high-Mg calcite precipitation in the uppermost layer of the mats.

3.3.3 Southern Tunisia

In May 2005, we studied two areas: Sabkha Bou Jemel (11°06'39''E, 33°16'56''N), located about 10 km S of Zarzis, and the Hassi Jerbi tidal flat (10°59'60''E, 33°38'38''N) with its barrier-island system, connecting Jerba Island to the Tunisian coastline NW of the village of Hassi Jerbi (Fig. 3.1C). The climate in the wide coastal plain of southern Tunisia is subtropical semi-arid. Precipitation is very irregular with episodic catastrophic floodings followed by long periods of drought, which may extend over several years (Medhioub & Perthuisot, 1981). Tides are in the microtidal range.

The barrier-island NW of Hassi Jerbi is mainly composed of bioclastic sands and surrounded by intertidal sand flats, supratidal flats, and marshes (Davaud & Septfontaine, 1995). Footprints were studied in the intertidal and supratidal zones (Fig. 3.2C). On the lower intertidal sand flats, the microbial mats were just a thin film (biofilm) due to the grazing activity of cerithid gastropods (Fig. 3.5I), and footprints could easily be made. On higher intertidal flats to supratidal flats and marshes, on the other hand, the thick coherent mats were smooth to pustular, often multilaminated, consolidated in a way that they could only be disintegrated by cutting with a knife, and superimposed on well-laminated sediment, rich in organic material (inset in Fig. 3.2C). Here, no fresh imprints could be made, but earlier footprints left during wet conditions could be studied. For more detailed descriptions of the

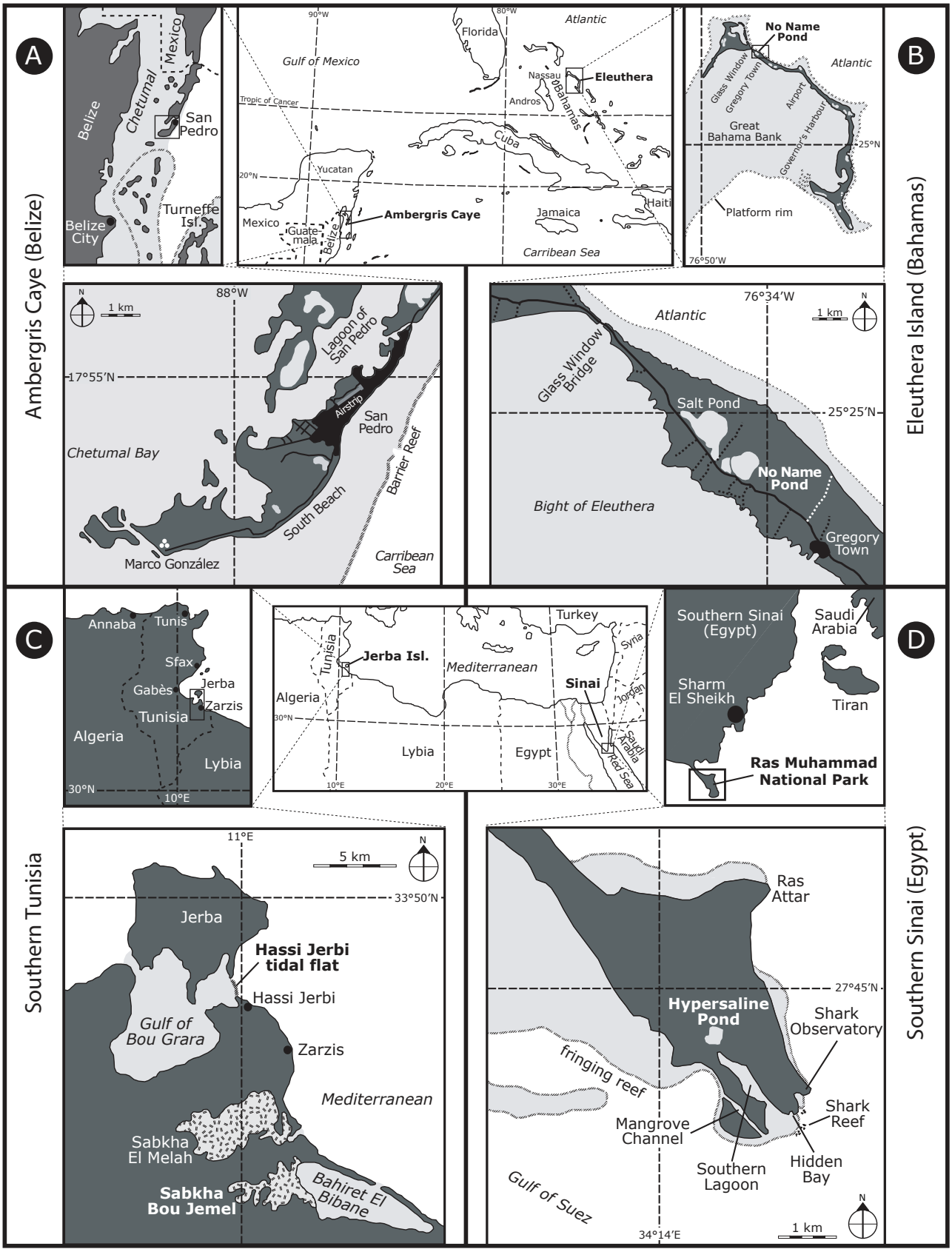


Fig. 3.1: Locations of the studied areas. **A:** Ambergris Caye SW of San Pedro Town (Belize). **B:** No Name Pond on Eleuthera Island (Bahamas). **C:** Hassi Jerbi tidal flat and Sabkha Bou Jemel (southern Tunisia). **D:** Hypersaline Pond in the Ras Muhammad National Park (southern Sinai, Egypt).

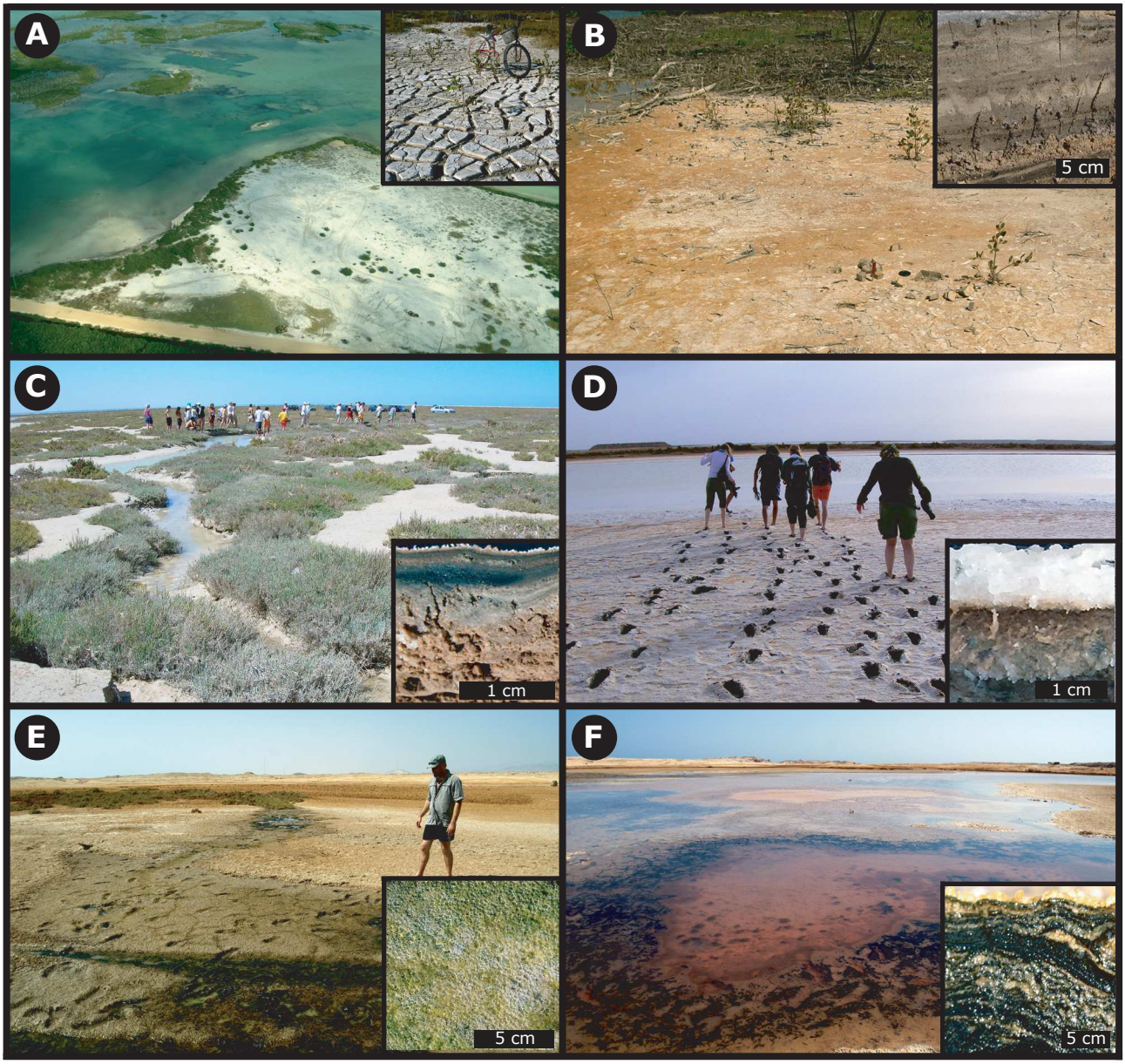


Fig. 3.2: Peritidal environments in Belize (A-B), Tunisia (C-D), and Egypt (E-F). **A:** Aerial view of a supratidal flat about 2 km SW of San Pedro airport. The white colour is due to the lithification (dolomitization) of microbial mats. Inset shows prism-cracked and completely dolomitized microbial mats. **B:** Supratidal mangrove swamp at South Beach, about 2 km SW of San Pedro. Inset shows a cross-section of the thick microbial mat on top of a well-laminated peat. **C:** Supratidal flats and marshes NW of Hassi Jerbi cut by small meandering tidal channels. Note the halophytic vegetation (*Salicornia*). Inset shows thick microbial mat on top of well-laminated, organic-rich sediment. **D:** Sabkha Bou Jemel. Inset shows thick microbial mat, covered by a cm-thick crust of halite. Whilst walking over the sabkha, one's feet sank deep into the underlying soft sediment forming deep tracks when the crust and mat were broken; otherwise, no tracks were left. Note the irregular and wide-gauge trackway of the person walking on the left, which is related to an unsure behaviour. **E:** Supratidal flats around Hypersaline Pond. Note the deep footprints in the water-saturated area at the bottom of the picture and the geologist who is unsure whether to pass or not. Inset shows gas bubbles on top of the microbial mat; **F:** Hypersaline Pond. Note the trampled ground (human footprints) of the pond at the bottom of the picture. Inset shows a cross-section of thick, gelatinous, and well-laminated microbial mat with halite crystals on the surface.

microbial mats and microbially induced sedimentary structures, the reader is referred to Gerdes et al. (2000) and Noffke et al. (2001a).

In addition, footprints were made in Sabkha Bou Jemel, which borders the restricted lagoon of Bahiret El Bibane (Fig. 3.1C). The lowest parts of the sabkha were filled with brine (Fig. 3.2D). On top of the water-saturated, peat-like and cerithid-bearing sediment, a thick, water-unsaturated microbial mat with a high yield strength was covered by a cm-thick crust of halite (inset in Fig. 3.2D).

3.3.4 Southern Sinai (Egypt)

In October 2006, footprints were studied in Egypt, in and on the flats surrounding the shallow Hypersaline Pond (34°14'29''E, 27°44'32''N), about 2 km NW of Shark Observatory in Ras Muhammad National Park, on the southernmost tip of the Sinai peninsula (Fig. 3.1D). This area is located in the subtropical zone. Receiving very little precipitation in any form, the climate is fully arid. The measured salinity of the pond was higher than 250 ‰ at the time of visit.

The area around the pond is desertic and xerophytic (Fig. 3.2E). The microbial mats of this pond are thick and gelatinous (inset in Fig. 3.2F). They appear to be similar to those of the well-studied Solar Lake, a small sea-margin pond located on the Gulf of Aqaba, 18 km south of Taba/Eilat, where the dominant cyanobacterium is *Microcoleus chthonoplastes* (e.g., Cohen, 1984; Krumbein et al., 1977).

3.4 Methodology

Human footprints in microbial mats were studied and documented in a wide range of present-day tidal-flat environments, which mainly differ from each other regarding the nature of the microbial mats (composition, thickness, water content, consistency) and the underlying sediment (composition, texture, water content). Only barefoot human footprints were analysed because they are easily left at any place and time, even though other vertebrate footprints of birds, dogs, and lizards were also frequently encountered. Selected footprints or parts of them (e.g., displacement rims) were sampled. The microbial mats were characterized from a morphological point of view, applying commonly used terminology

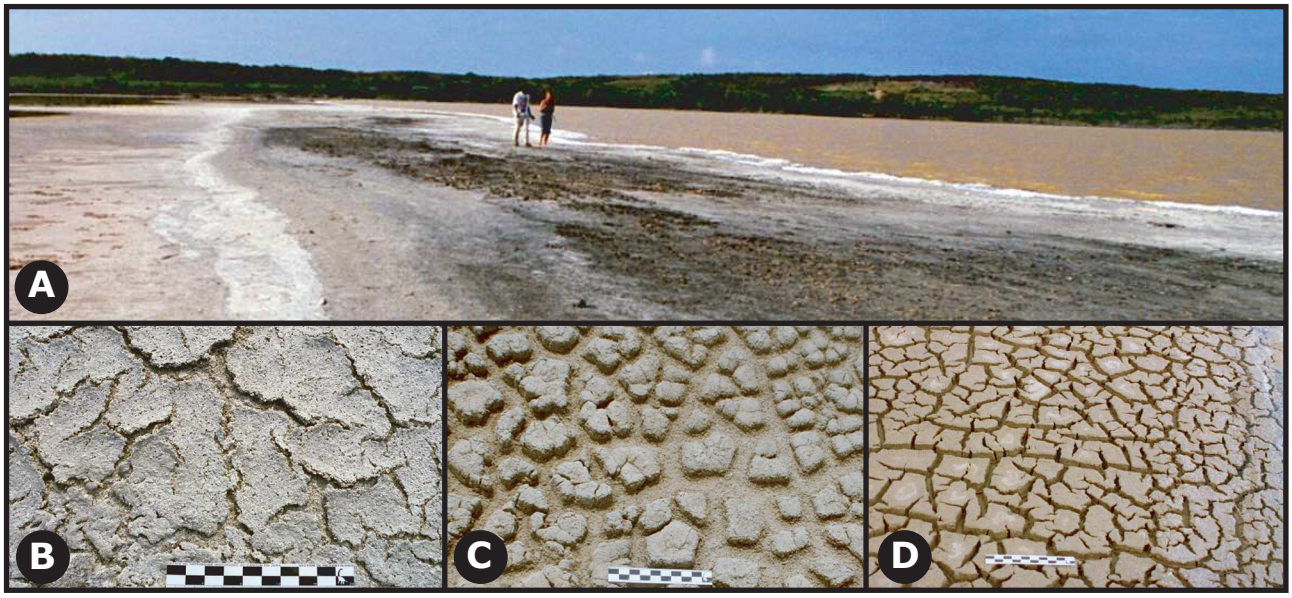


Fig. 3.3: A: Typical zonation of microbial mats on the supratidal flats of No Name Pond (Eleuthera Island). View towards the N, geologists for scale. **B:** Thin, brittle, and dry (crinkled and cracked surface with upcurled margins) mat on top of a consolidated cerithid packstone. When walking on this hard surface, the mat was slightly brecciated but no clear footprints were made. **C**: Thick and moist mat with healed shrinkage cracks, exhibiting a cauliflower pattern and rounded edges, caused by the renewed growth of a mat within the cracks. Situated on top of a water-unsaturated cerithid packstone. This mat had such a high elasticity that even when deformed under the pressure of the foot, no footprints were registered. **D:** Very thick and water-saturated smooth mat with a very low yield strength on top of a water-unsaturated poorly-laminated cerithid packstone. The formation of cracks, which extend about 10 cm into the sediment, may be explained by different surface tensions between the thick mat and the underlying sediment (cerithid packstone). Here it was difficult to walk, as one's feet sank deep into the sediment and got stuck, forming deep tracks. Scale bars in B, C, and D are 20 cm.

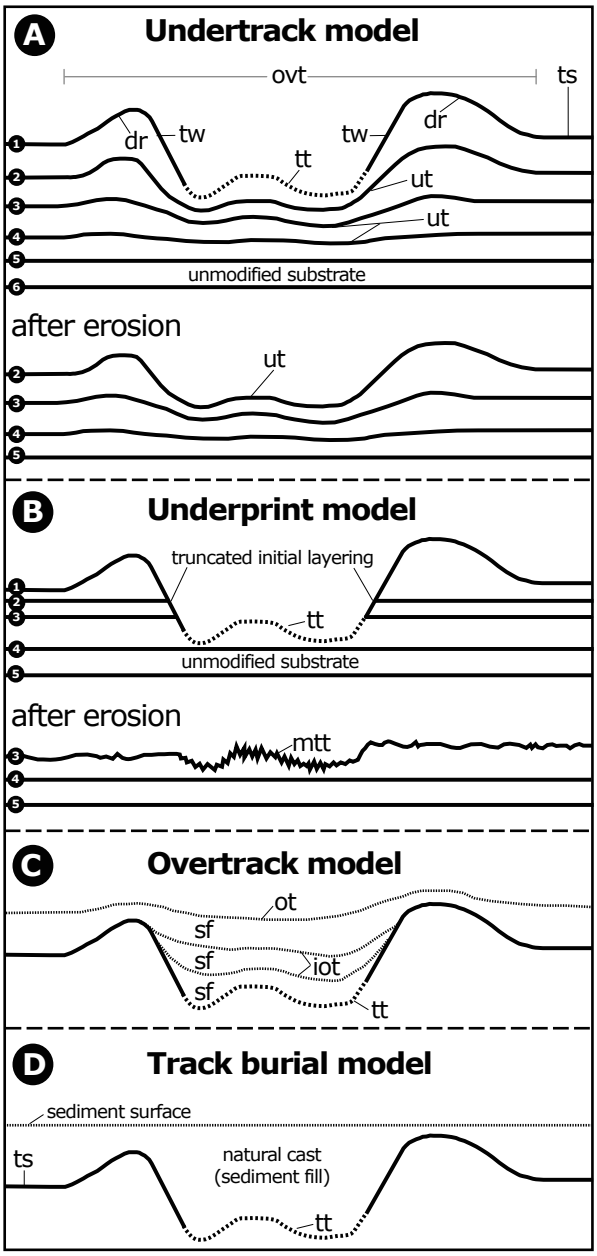


Fig. 3.4: Schematic longitudinal sections through a human footprint (following Allen, 1989, 1997), explaining the terminology used in this work: displacement rim (dr), overall track (ovt), sediment fill (sf), tracked surface (ts), track wall (tw), true track (tt), undertrack (ut). **A:** Undertrack model showing the formation of undertracks through the compression of well-laminated sediment by pressure of the foot. **B:** Underprint model: foot is breaking through the initial layering and the print is not left on the originally exposed sediment surface. When the sediment is split at a deeper layer the overall track is less complete. With ongoing erosion the overall track is less complete and the true track modified, leading to the formation of a modified true track (mtt). **C:** Overtrack model showing a stack of internal overtracks (iot) and an overtrack (ot). **D:** In the track burial model the track is filled up and buried by a rapid and important sedimentation event, forming a natural cast without overtrack on top of the overall track.

(e.g., Monty, 1972; Kendall & Skipwith, 1968; Davies, 1970; Logan et al., 1974; Hardie, 1977a). In order to characterize the properties of the underlying sediment and to understand the evolution of the different environments during the Holocene, up to 1 m-long sediment cores were taken by pushing or hammering a plastic tube into the unconsolidated sediment. Samples were solidified with epoxy, and thin-sections were made to characterize the sediment texture and facies.

3.4.1 Terminology

In order to avoid duplications, the terminology part of the accepted manuscript is integrated in Chapter 2.6.

3.5 Description of footprints

The formation and morphology of footprints in microbial mats depends not only on the nature (composition, thickness, water content, degree of consolidation, etc.) of the mat itself, but also on the characteristics (water content, grain size, lamination, degree of consolidation, presence of a lithified horizon) of the underlying sediment. Consequently, many different combinations are possible, which complicate a thorough description of the footprints. Nevertheless, it was found that the thickness of the microbial mat and the water content of the mat and of the underlying sediment are the most crucial factors for footprint morphology. The footprints in Figures 3.5, 3.6, and 3.7 were left by the first author (23 cm foot length, 70 kg weight). Figure 3.5 shows a series of footprints on thin and thick microbial mats with variable mat and underlying sediment water content. Note that the limit between thin and thick mats was arbitrarily fixed at 3 mm, that the water content is estimated, and that other substrate properties such as grain size or texture are not taken into account. Such a general approach is necessary because it is practically impossible to measure every variable in every footprint. Further footprints are illustrated in Figures 3.6 and 3.7.

3.5.1 Dry mats

Poorly-defined footprints were produced in thin and dry mats superimposed on dry but still soft (unconsolidated) sediment. In this case, the mat frequently cracked in such a way that the gross outline of the print was visible and extension of the crack pattern inside the print easily identified the shallow prints (Fig. 3.5A). Such prints may initiate further disintegration of the mat (e.g., overturning and

water content of the microbial mat & underlying sediment
dry
moist/damp
water unsaturated
water saturated
digit I
thin microbial mat
(< 3 mm)
thick microbial mat
(> 3 mm)
A
B
C
D
E
F
G
H
I
J
I
SVP
10 CM

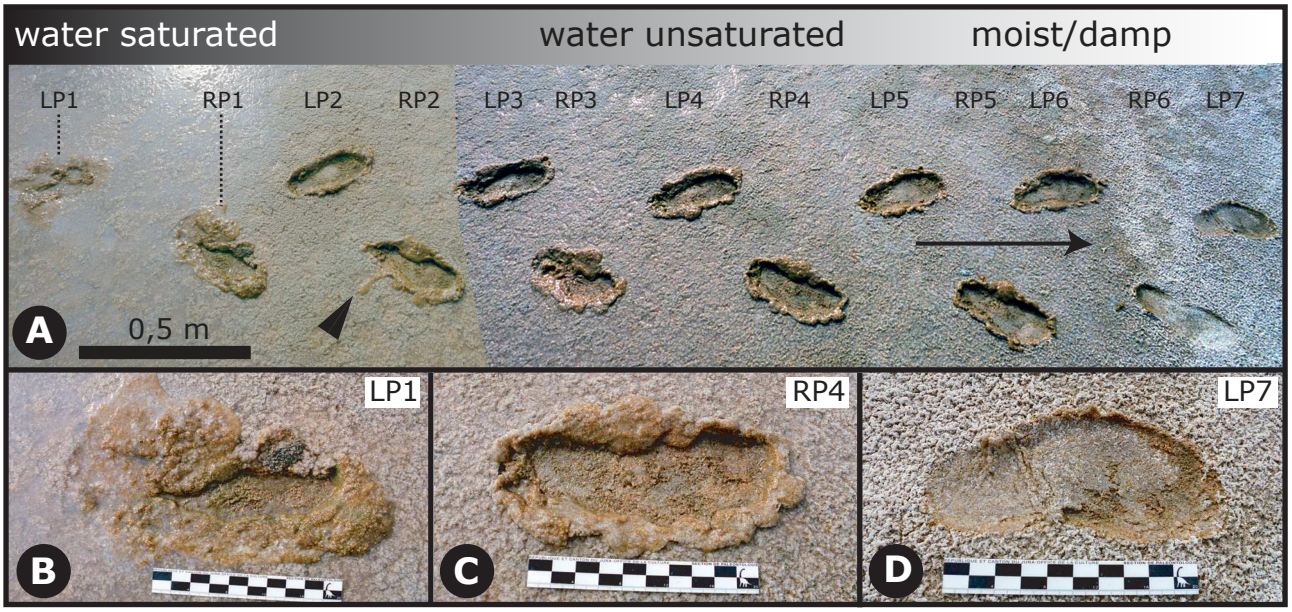


Fig. 3.6: A: Changing footprint morphology along a trackway left at the border of No Name Pond (Eleuthera Island, Bahamas). Here a lithified layer was covered with a 3-5 cm thick microbial mat with variable water content. LP stands for left pes, RP for right pes. Arrow on RP2 points to expelled sediment. The colour differences are due to a splicing of two photographs. **B:** Partially collapsed footprint (true track with extramorphological features) showing only the gross outline. **C:** Footprint with well-defined displacement rim and sediment collapse feature into the area of the foot's longitudinal arch. **D:** Shallow footprint without displacement rim. Scale bars in B, C, and D are 20 cm.



Fig 3.7 (right): Thick and almost dry (initial formation of desiccation cracks), smooth mat on top of a thick layer of water-saturated carbonate mud. In the left footprint, the microbial mat broke in the central part of the print and was pushed to the sides of the print. Consequently, the foot sank over 40 cm deep into the sediment, and formed a deep track. In the right other print the microbial mat broke at the border of the foot, and was pushed underneath the foot vertically into the sediment. Hammer for scale, No Name Pond (Eleuthera Island, Bahamas).

Fig. 3.5 (opposite page): Footprint morphology as a function of microbial mat thickness and water content of the mat and the underlying sediment. Arrows indicate the position of the big toe (digit I). All scale bars are 10 cm. See text for description and interpretation. **A, H:** Sabkha Bou Jemel (southern Tunisia). **B-G:** Mangrove swamps near South Beach and supratidal flats and marshes SW of San Pedro airport (Ambergris Caye, Belize). Arrow in D points to the heel. **I:** Intertidal sand flat NW of Hassi Jerbi (southern Tunisia), arrow points to grazing traces of cerithid gastropods, footprint is filled with water. **J:** Hypersaline Pond (southern Sinai, Egypt). This footprint was covered by 10 cm of water.

reworking pieces by tidal flooding, wind, or surges) and the formation of mud chips or even flat-pebble conglomerates. Consequently, these footprints are fragile and have a very low preservation potential unless they are immediately buried after formation.

In thick and dry microbial mats, no footprints were formed if the mat had a very high elasticity (Fig. 3.3C), if the underlying sediment had high yield strength, or if it was dry or (partly) lithified. However, as thick microbial mats may form a continuous, strongly cohesive zone of low permeability, separating the underlying sediment from the atmosphere and protecting it against water loss, the sediment below a dry mat is not necessarily dry ("confined aquifer") (Porada et al., 2007). Thus, if the underlying sediment was still moist and soft, the dry mat sometimes broke at the border of the foot, and was pushed underneath the foot vertically into the underlying sediment. Such prints have a typical cracked surface, exhibit the gross outline of the foot, and are clearly deeper (Fig. 3.5B). In the case of a dry microbial mat superimposed on water-saturated sediment (mud), deep tracks formed if the mat broke in the centre of the foot and was pushed to the sides of the print (Fig. 3.7). However, if in the same scenario the mat broke at the border of the foot and was pushed underneath the foot vertically into the underlying sediment, it acted as a sort of "snowshoe" (Fig. 3.7). Such footprints are a special case of true tracks since they exhibit the characteristics of a print left on a dry mat, but the initially exposed surface may be pushed relatively deep into the underlying sediment. Such prints may be easily preserved by simple filling up.

3.5.2 Moist mats

In thin and thick moist mats, the mat was compressed by the foot, and shallow but well-defined prints with anatomical details of the toes were formed, if the underlying sediment was of moderate yield strength and was not water unsaturated or water saturated (Fig. 3.5C). In thick, moist mats the footprints were shallow and clearly less well defined (Fig. 3.5D, RP6 in Fig. 3.6A, and Fig. 3.6D). When a moist mat was overlying water-saturated sediment, deep tracks formed if the mat broke in the centre of the print and was pushed to the sides of the print, forming vertical track walls.

3.5.3 Water-unsaturated mats

Here, a great variability in footprint morphology was produced, including well- and poorly-defined footprints. On thin and thick mats, well-defined footprints with anatomical details of the toes and well-defined displacement rims (with radial fractures in Fig. 3.5E) were formed if the underlying sediment still had relative high yield strength. Thus, the mat was not penetrated but compressed and plastically deformed (Figs. 3.5E & F and LP5 to LP6 in Fig. 3.6A). Badly-defined underprints exhibiting only the gross outline formed if the underlying sediment had a low yield strength or if it was water saturated (Figs. 3.5G & H). In Figure 3.5G the foot penetrated through the mat into the underlying sediment. Figure 3.5G further demonstrates how track morphology also depends on trackmaker weight, as on the same surface shorebirds left well-preserved tracks because their feet did not penetrate through the mat. In Figure 3.5H the foot formed a deep underprint, because it broke through a cm-thick layer of halite (inset in Fig. 3.2D) and the underlying water-unsaturated microbial mat and pushed them to the sides of the print, forming vertical track walls.

3.5.4 Water-saturated mats

In water-saturated mats, only poorly-defined footprints were made. In both thin and thick mats, footprint morphology mainly depended on the nature of the underlying sediment, as the foot easily penetrated through the gelatinous mats. If the underlying sediment was water-saturated but not very thick (Fig. 3.5I), or if it was consolidated (Fig. 3.6B), the prints display the gross outline of the foot. Figure 3.5J shows a footprint that was formed in a water-saturated, gelatinous mat on top of a water-saturated and thick layer of peat. In this case, the foot penetrated deep into the sediment and a deep track formed. The print LP1 in Figure 3.6B was left in a thixotropic microbial mat on top of a lithified sediment layer. It does barely exhibit the gross outline of the foot, as it collapsed after foot withdrawal. This track is best described as an underprint with extramorphological collapse features.

3.5.5 Consolidated footprints

Consolidated and/or (partially) lithified microbial mats preserved footprints, which were left while the mats were still moist and plastic. It is unknown when and under what circumstances (e.g., water content of the mat) the solidified footprints in Figures 3.8 and 3.9 were made.

Figure 3.8 shows several footprints, which were found in close proximity to each other on the supratidal

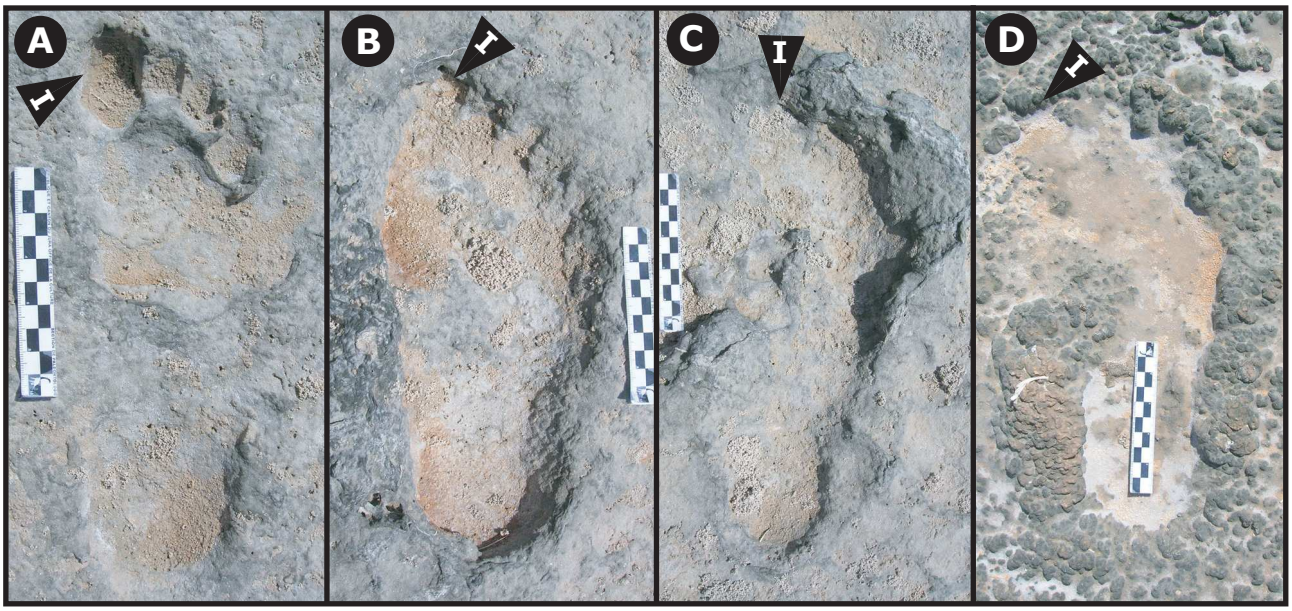


Fig. 3.8: Modification of footprint morphology by consolidation and/or continued growth of the microbial mat. All footprints are right pes prints of unknown individuals and the arrows indicate the position of the big toe (digit I). The microbial mats were dry, inactive, and consolidated in such a way that no further footprints could be made at the time the pictures were taken. All pictures are from the supratidal flats NW of Hassi Jerbi (southern Tunisia), scale bars are 10 cm. **A:** Well-defined footprint exhibiting anatomical details of the toes and heel. **B:** Footprint with a stack of internal overtracks. General outline is still well defined and the position of the digits can be recognized. **C:** Outline starts to disintegrate but the position of digits I and II can still be identified. Note increased growth of microbial mat on topographic highs (displacement rims on the upper right of the print). **D:** Blurring of the footprint by growth of a pustular microbial mat. The gross outline can still be recognized but the approximate position of digit I can only be estimated. This is a good example of the formation of an overtrack by the growth of a microbial mat.

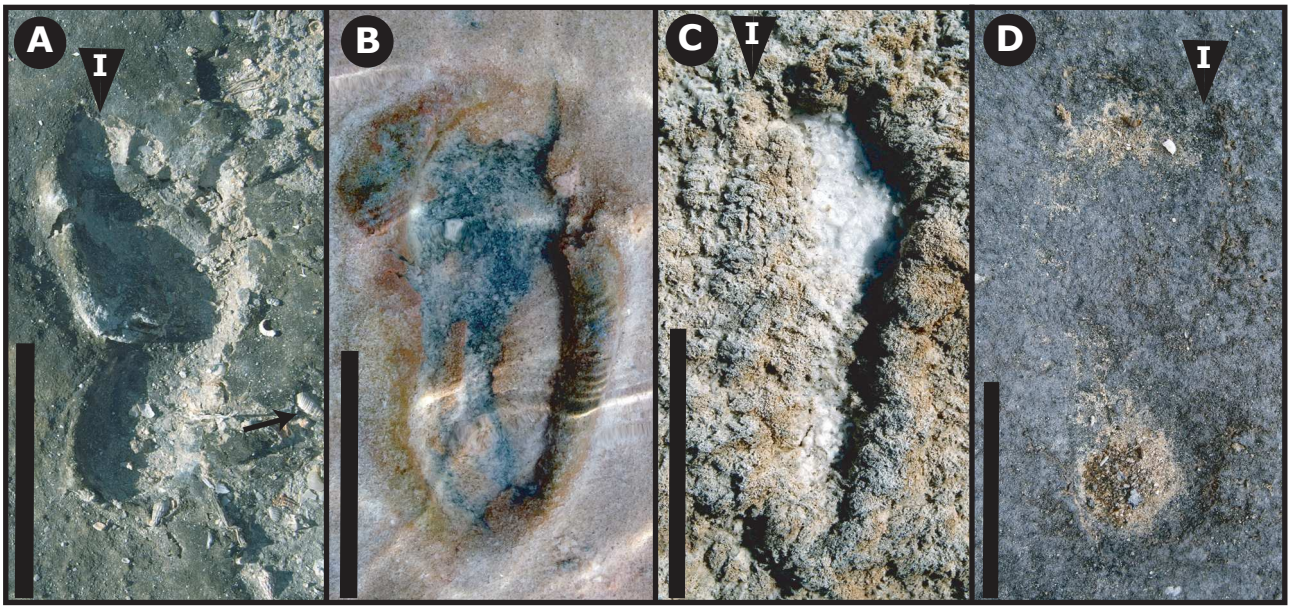


Fig. 3.9: Modification of footprint morphology by continued growth and/or consolidation of the microbial mat. Where possible, the position of digit I is indicated. Scale bars are 10 cm. **A:** Supratidal flat SW of San Pedro airport (Ambergris Caye, Belize). Modified true track. Note the presence of (dead) cerithid gastropods (arrow), the well-defined displacement rim at the inner (left) margin of the (right) print and the torn away mat in the upper right. **B:** Hypersaline Pond (southern Sinai, Egypt). Overtrack or modified true track with well-defined displacement rim on the right side of the print. **C:** Supratidal flat around Hypersaline Pond (southern Sinai, Egypt). Continued growth of the microbial mat and precipitation of halite led to a poorly-defined overtrack. **D:** Supratidal flat SW of San Pedro airport (Ambergris Caye, Belize). Very shallow and barely visible overtrack.

flats and marshes NW of Hassi Jerbi (Tunisia). Even if they are not part of a trackway, it is suggested that they were left more or less at the same time, whilst the microbial mat was still moist and active, after a rainy period or after an exceptionally high (storm) tide. Once the footprints were made, the mats kept growing as long as they remained moist. This growth modified the original morphology to different degrees and let to the formation of internal overtracks (Fig. 3.8B) and overtracks (Fig. 3.8D). Later, the mats dried up and consolidated or lithified.

Other consolidated footprints are shown in Figure 3.9. All such footprints could be incorporated into the sedimentary record. Some exhibit nothing more than the gross outline of the pes and would be difficult to identify as footprints of hominids. Figure 3.9A shows a footprint of a child with impressions of the toes. As this print has clearly started to suffer some alteration, it can be described as a consolidated modified true track. This print was left in a cm-thick microbial mat and was originally probably similar to the ones shown in Figures 3.5E and 3.5F. Figures 3.9B and 3.9C show footprints, which were left in a thick microbial mat, and which may initially have been as well defined as the footprints in Figures 3.5E and 3.5F. The print in Figure 3.9B was consolidated and then covered by about 10 cm of water. The one in Figure 3.9C was highly modified by the ongoing growth of the microbial mat and by precipitation of halite, which led to the formation of a poorly-defined overtrack. Finally, the footprint in Figure 3.9D was probably left in a moist microbial mat similar to the ones in Figures 3.5C and 3.5D. Prior to consolidation, this print suffered from the growth of the microbial mat, which blurred its original morphology and led to the formation of an overtrack.

3.6 Discussion

This study of hominid footprints in microbial mats of present-day tidal-flat environments reveals a great variability in footprint morphology. Even on an ideal substrate (moist to water-unsaturated, plastic microbial mat) it was difficult to deliberately register a perfect footprint with anatomical details such as the toe impressions, which could unequivocally be identified as an unmodified true track. A perfect footprint is even more unlikely to occur if the trackmaker produces different footprint morphologies due to changing behaviour (walking, running, jumping) (e.g., Thulborn & Wade, 1989; Milàn, 2006). In addition, footprint morphology is related to the properties (namely consistency) of the substrate being traversed (e.g., Farlow, 1992; Marty et al., 2006b; Uchman & Pervesler, 2006), and poor footprint registration can just be due to unsuitable substrate properties (e.g., Brand, 1996; Diedrich, 2002b). Identification of true tracks is further complicated in the fossil record where footprints undergo different stages of taphonomy and are at different stages within the diagenetic sequence of development. This corroborates Allen (1997) who stated that only a very small proportion of the tracks in a given area are capable of yielding diagnostic taxonomic information about the animals that made them, and McKeever & Haubold (1996) who showed that many Permian ichnotaxa are nothing more than substrate or behavioural variants of the same trackmaker.

3.6.1 Factors controlling footprint morphology

Footprint morphology is controlled and affected by substrate properties such as consistency, sediment composition, grain size, texture, yield strength, water content, rate of consolidation, and last but not least the presence and nature of microbial mats. Allen (1997) and Manning (2004) suggested that the water content and the yield strength of the sediment at the time of track formation are crucial and most strongly control track morphology. Scrivner & Bottjer (1986) and Allen (1997) classified footprint morphologies as a function of water (moisture) content and yield strength of the sediment (mud). Their classification can be summarized as pertaining to:

1. Dry and hard, stiff to firm mud
2. Moist or slightly damp stiff mud
3. Water-unsaturated soft mud
4. Water-saturated semi-liquid mud

In the present work, this classification proved very helpful for the gross characterization of microbial mats and the underlying sediment, even if the boundaries between these four categories are inherently gradational (see Fig. 3.6). Other factors were found to be of importance as well. First, the yield strength of a mat depends on its thickness and elastic limit. Furthermore, the consistency of the underlying sediment, presence or absence of a lithified layer below the microbial mat, and the position of the water table are also important for the formation and the morphology of a footprint. Consequently, different combinations of the properties of the microbial mat and the underlying sediment result in a broad range of morphologies for footprints

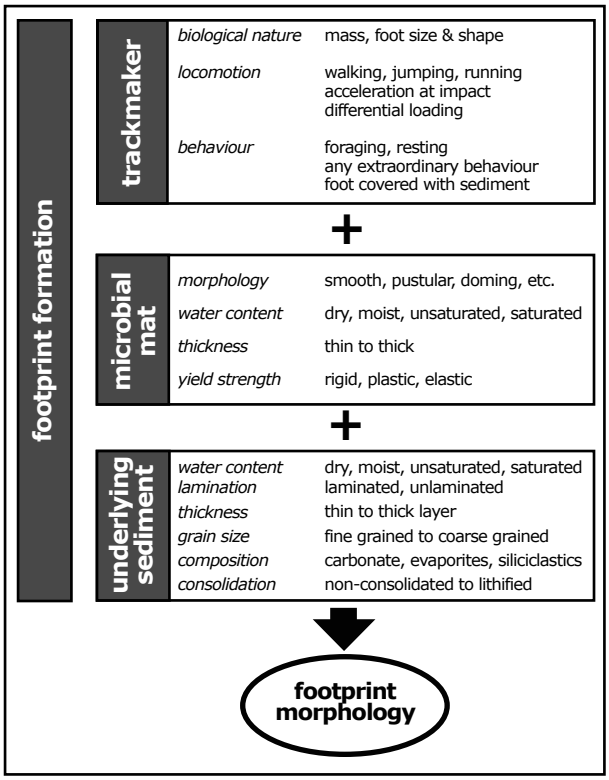


Fig. 3.10: Processes acting during footprint formation, determining the footprint morphology right after foot withdrawal, that is the morphology of the unmodified true track, underprint or deep track. Note that this figure is in addition to the submitted manuscript.

(true tracks, underprints, deep tracks) left by a single trackmaker (Fig. 3.10). The formation of undertracks is only possible in well-laminated and plastic, moist to water-saturated sediment.

On dry and consolidated mats overlying dry unconsolidated sediment, a footprint only forms if the trackmaker exerts enough pressure to crack the mat, which is basically only possible if the mat is very thin or the trackmaker very heavy. Dry and consolidated mats with a thickness of 3 mm or more were found to be either very elastic or, if already consolidated, very rigid and thus difficult to deform permanently. In the presence of a high water table it has been observed that dry and firm microbial mats were often superimposed on unlaminated and water-unsaturated to water-saturated sediment. In this scenario, the mat frequently broke around the foot and was pushed underneath the foot vertically into the sediment. This led to the formation of particular true tracks, because the footprint was left on the originally exposed microbial mat, which was pushed relatively deep into the underlying sediment. When the mat broke in the central part of the foot and was pushed to the sides of the print, a deep track or an underprint was formed. If in the latter case the mat is still slightly plastic, this could explain the formation of lateral, vertical scratch marks as sometimes observed on deep dinosaur footprints (e.g., Diffley & Ekdale, 2002; Milàn et al., 2005; Platt & Hasiotis, 2006).

The morphologically best-defined prints are produced in moist to water-unsaturated, very plastic and thick microbial mats on top of sediment with high yield strength. In water-saturated microbial mats, generally only poorly-defined footprints are left, even if sometimes reasonably well-defined prints form if a water-saturated mat is superimposed on a lithified layer. The formation of well-defined displacement rims (as frequently observed around the prints of large dinosaurs) occurs in thick, plastic, moist to water-unsaturated microbial mats on top of moist to water-unsaturated sediment. Our observations show that shallow prints left in moist to water-unsaturated microbial mats have the best-defined morphology and can be used for ichnotaxonomical purposes. Those left in dry or water-saturated mats are generally poorly defined, but they can be used for the reconstruction of the palaeoenvironment.

3.6.2 Footprint taphonomy

Preservation of animal footprints in the fossil record is strongly dependent on taphonomic processes, which occur after registration of the footprint (track survivorship curves of Cohen et al., 1991). Generally, exposed tracks degrade rapidly after formation and have a low preservation potential. The amount of time between footprint formation and burial affects their preservation potential (Laporte & Behrensmeyer, 1980), as well as the degree of time-averaging of the ichnoassemblage (Cohen et al., 1993).

Many taphonomical factors affect a footprint after its formation. Destructive processes include vertebrate trampling, insect and other invertebrate bioturbation, root growth, weathering processes (heavy rainfall, wind deflation, desiccation with associated cracking and fracturing), deformation through displacive growth of evaporites, flooding and subsequent wave and seiche reworking or fluctuations of the groundwater table (e.g., Tucker & Burchette, 1977; Laporte & Behrensmeyer, 1980; Cohen et al., 1991; Demathieu, 1991; Nadon, 2001; Scott et al., 2007). These processes hinder footprint preservation or at least modify or obliterate the original true track, leaving behind a modified true track. Taphonomic

processes that potentially preserve footprints are early cementation (of the sediment or within the microbial mat), rapid covering by sediment, and overgrowth by microbial mats (Fig. 3.11).

This study shows that microbial mats may enhance footprint preservation by binding and stabilizing the sediment in which the trace was made, by overgrowth, by consolidation through drying, and also by lithification (carbonate precipitation within the microbial mat and early-diagenetic cementation). Nonetheless, to preserve a perfectly-defined true track, the microbial mat must die and consolidate shortly after footprint formation, and the tracked surface must be covered by sediment prior to the development of a new microbial community. Ongoing growth of the mat after footprint formation consolidates the print but will also cover and obliterate its original morphology, producing an overtrack. It has been observed that growing microbial mats may thicken on top of positive reliefs such as the displacement rims. However, if humidity remains only within a deep footprint, the microbial mat continues to grow within the footprint but not around it, thus slowly filling it up and forming a stack of internal overtracks. Finally, mat growth also depends on other extrinsic factors such as sedimentation rate, light, salinity, and temperature (e.g., Dupraz et al., 2006).

Based on computational models, Henderson (2006a) suggested that a weathered (tridactyl) true track cannot be confused with a freshly exposed (simulated) undertrack. Nonetheless, depending on the degree of modification, our study implies that true tracks are difficult to identify unambiguously because they may also look very similar to overtracks. Furthermore, accretion and erosion may occur on many time-scales and a track can repeatedly be partly filled by sediment, or partly or wholly emptied (Allen, 1997). In the case of an underprint, its upper part may be modified by erosion before final burial.

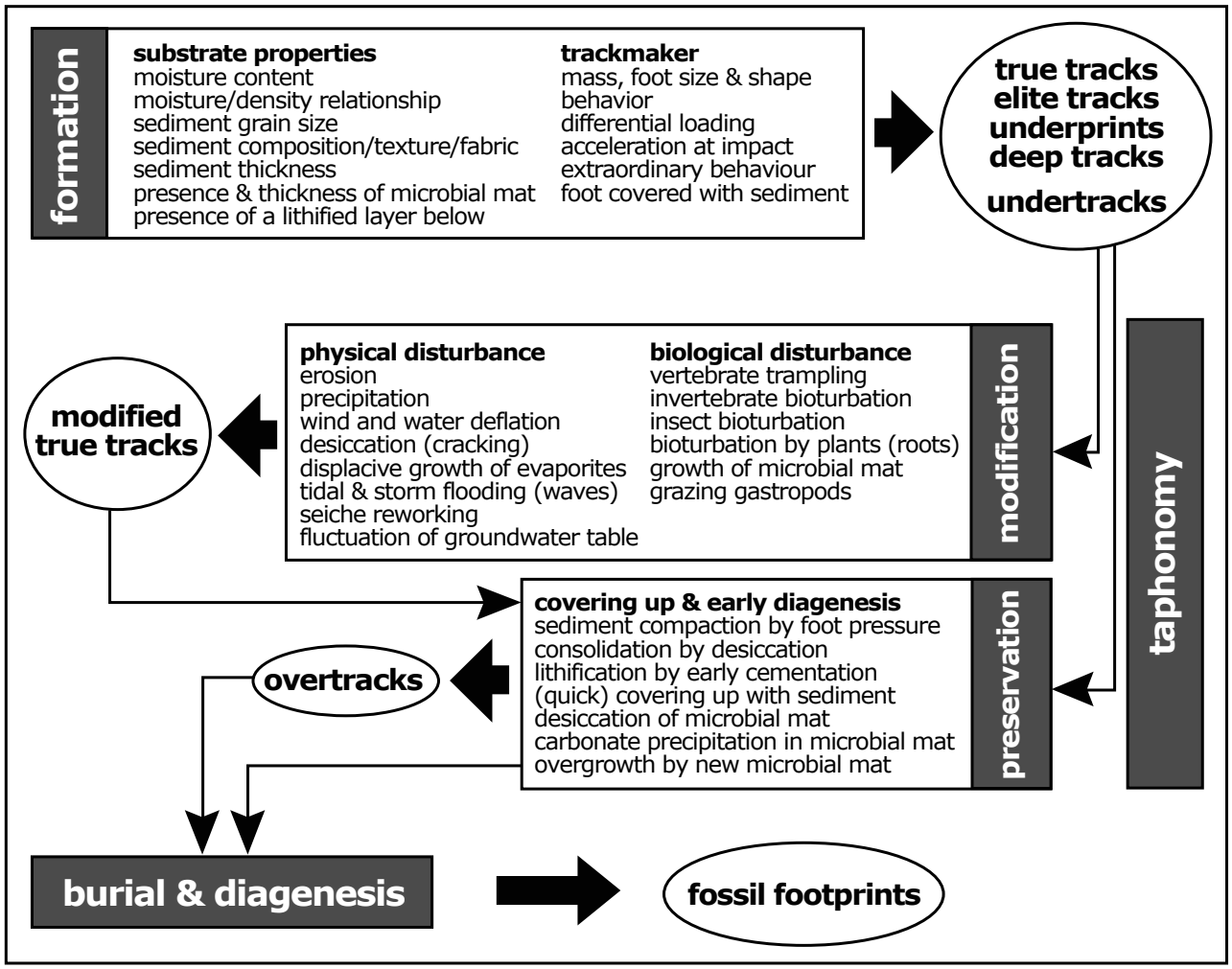


Fig. 3.11: Processes acting during footprint formation and taphonomy. Note that erosion is possible during different time frames, and even the fossil footprint itself may be subjected to erosion prior to discovery.

3.6.3 Footprint consolidation

The rapid consolidation of a footprint is crucial to prevent obliteration and deformation prior to and/or during subsequent burial (Phillips et al., 2007). Our observations show that consolidated or partly lithified footprints are commonly found in the higher intertidal zone and especially on supratidal flats and marshes. These footprints show a broad range of preservation states due to differences in substrate consistency at the time of formation, different degrees of overgrowth by microbial mats, and the different nature and morphology of microbial mats.

On the supratidal flats SW of San Pedro airport (Ambergris Caye, Belize) we found that completely lithified (dolomitized), mud-cracked biolaminites make up the upper 20 to 30 cm of the sediment (inset in Fig. 3.2A). Widespread dolomitization of peritidal flats on Ambergris Caye was already described by Mazzullo et al. (1987) and Gregg et al. (1992). Mazzullo et al. (1987) stated that these "massive beds of dolomite are characterized by a marked subtidal appearance, as they lack typical supratidal features". This is in contrast to our own observations because we found pronounced desiccation (prism) cracks (inset in Fig. 3.2A) and tetrapod footprints in the dolomitized microbial mats.

We also observed consolidation and (partial) lithification of microbial mats in the other study areas and we suggest that this is one of the major processes of footprint preservation in tidal-flat environments.

3.6.4 Footprints and environment

In microbial mats, footprints are generally only produced during wet conditions. During periods of drought, the mats consolidate rapidly, getting hard and rigid and making it almost impossible even for a heavy trackmaker to leave a footprint. Moreover, such consolidated microbial mats are difficult to disintegrate and even resist heavy rainfall. New footprints can only be made once a new microbial community is in place after renewed wetting. This narrows the time-frame during which footprints are registered and diminishes the time-averaging of an ichnoassemblage.

Ginsburg et al. (1977) introduced an exposure index for tidal-flat environments, which links characteristic sedimentary and organic features to the hydroperiod, i.e., to the time duration during which the ground surface at a given site is covered with water. In environments located far away from the coastline, the exposure index is higher and the hydroperiod shorter, as wetting only occurs sporadically during very high tides (spring tides, equinoxial tides, storm tides). On a surface with an exposure index higher than 90%, footprints can only be formed during the wet season or after a major storm. Consequently, if a large set of footprints is available, the general preservation state of footprints of trackmakers frequently traversing a tidal flat may yield additional important information about the exposure index of the different tidal-flat environments.

3.6.5 Incorporation of footprints into the sedimentary record

It is the sedimentation regime that finally determines if preservation will take place and if a footprint will be incorporated into the sedimentary record. The probability of footprint preservation is minimal during long-lasting periods of exposure without any sedimentation, and preservation is favoured by rapid and significant preservation events. Consequently, footprints are most commonly preserved in environments that experience periodic or cyclic accumulation of sediment (Thulborn, 1990), as typically observed on tidal flats.

While most of the upper intertidal zone is flooded at every high tide, flooding of supratidal flats and marshes only occurs during exceptionally high tides and with storms, resulting in a sudden influx of sediment-laden water even far inland from the coastal zone (e.g., Roehl, 1967; Monty, 1972; Hardie, 1977a; Boss & Neumann, 1993; Rankey et al., 2004; Bourrouilh-Le Jan, 2007). Important sediment influx covers up footprint-bearing surfaces. On top of these sediment layers, new microbial mats may grow and protect them from disintegration (Ginsburg & Hardie, 1975; Hardie & Ginsburg, 1977). Simultaneously, new footprints may form in these mats as long as they remain moist. Thus, repeated tide and/or storm sedimentation explains the preservation of superimposed footprint-bearing surfaces in biolaminites. On a larger time-scale, the preservation potential of tidal-flat sediments is best during transgression, when new accommodation space is created (e.g., Lockley et al., 1992). During relative sea-level or lake-level falls on the other hand, the enhanced erosional potential will most likely destroy the track-bearing surfaces.

3.6.6 Implications for the study of fossil footprints

The problem of the distinction between true tracks and undertracks has long been recognized

in vertebrate ichnology (Hitchcock, 1858). This distinction is important because only true tracks can give useful information relevant to ichnotaxonomic and palaeoecological studies. This problem is further complicated by the presence of true tracks with extramorphological features, modified true tracks and overtracks. Nadon (2001) and Milàn & Bromley (2006) suggested that undertracks are always less detailed than true tracks. However, in the case of a strongly modified true track, the undertrack may exceptionally reveal more information about the trackmaker (Milàn et al., 2004), or its behaviour (Avanzini, 1998; Gatesy et al., 1999).

Our study shows that consolidated overtracks and stacks of internal overtracks are frequently encountered in modern tidal-flat environments. It is often difficult to distinguish such tracks from true tracks, because consolidated, unmodified true tracks with anatomical details are only seldom found. We suggest that modified true tracks and overtracks are commonly incorporated into the sedimentary record and probably make up an important part of the fossil footprint record, and that unmodified true tracks, which can easily be identified as true tracks because of the presence of anatomical details, are the exception in the fossil record. The simple fact that even the least modified true track in the fossil record is lithified means some modification has occurred through the processes of lithification and diagenesis. Moreover, in fossil biolaminites, the rock does not necessarily split at the original tracked surface and thus, in the outcrop, we often observe undertracks or overtracks.

Undertracks are relatively easily incorporated into the sedimentary record because they are already within the sediment at the time of formation, while the original true track may be eroded prior to burial (Lockley, 1991b). However, they only form under very particular conditions and may thus not be as common.

3.7 Conclusions and perspectives

In recent microbial-mat-covered tidal-flat environments in differing tropical and subtropical climatic settings, a wide range of morphologies of human footprints was formed. This variability depends on the water content, thickness and nature of the microbial mat and the underlying sediment. Nature, thickness and water content of the mat are crucial for its yield strength, plasticity, and its elastic limit. If the mat is broken or penetrated by the pressure of the foot, the nature and water content of the underlying sediment becomes the determining factor for footprint morphology, and either an underprint or a deep track is produced.

Microbial mats are a significant factor for footprint preservation in modern tidal-flat environments. Once a footprint is left, it may be consolidated by simple desiccation of the microbial mat or by lithification due to carbonate precipitation within the mat. It may also be preserved by ongoing growth of the mat. However, continued microbial growth may seriously affect the initial footprint morphology and lead to the formation of a stack of internal overtracks or of an overtrack.

Amongst consolidated or lithified footprints, unmodified true tracks with anatomical details have only occasionally been found. Poorly-defined true tracks, modified true tracks, internal overtracks, and overtracks were most frequently observed. In the fossil record such footprints make ichnotaxonomy difficult but may be a valuable tool for palaeoenvironmental and palaeoecological reconstructions, when combined with sedimentological evidence.

We assume that the incorporation of an unmodified true track with anatomical details into the sedimentary record necessitates very particular conditions. Modified true tracks and overtracks are relatively easy incorporated into the sedimentary record and they may make up an important part of the fossil footprint record. They may even be more common than undertracks, because the latter only form under particular sediment conditions.

In fossil biolaminites the sediment often does not split at the original tracked surface and thus under- or overtracks are commonly exhibited in outcrop.

In the fossil record, the unambiguous distinction between poorly-defined true tracks, modified true tracks, undertracks, internal overtracks, and overtracks will remain a difficult task. True tracks may only be identified as such if they exhibit sufficient anatomical details, or if further evidence is gathered by detailed sedimentological studies of the footprint-bearing surface and the under- and overlaying layers. This underlines the importance of a systematic, three-dimensional study of footprints together with sedimentological analyses.

So far, these conclusions are based on empirical observations from several tidal-flat environments. Further research should focus on long-term surveys of footprints in living and dead microbial mats of known biological composition in suitable tidal-flat environments.

* * *

4 - Formation, taphonomy, and preservation of sauropod tracks: implications for the reconstruction of a Late Jurassic tidal-flat palaeoenvironment and its evolution

4.1 Introduction

Dinosaur tracks and namely tracks of saurischians (sauropod and theropod dinosaurs) are abundant in tidal-flat deposits of Mesozoic carbonate platforms (e.g., Lockley & Hunt, 1995; Meyer & Lockley, 1996; Lockley & Meyer, 2000; Meyer & Thüring, 2003a). On the other hand, skeletal remains of terrestrial vertebrates are rare because tidal-flat environments are often subjected to prolonged periods of subaerial exposure (e.g., Schäfer, 1972; Behrensmeyer, 1978; Weigelt, 1989), and because sedimentation only occurs episodically and is often linked to spring tides or storms, which are likely to disintegrate and disperse vertebrate carcasses. In tidal-flat deposits, most discoveries of skeletal remains are thus isolated bones or teeth (e.g., Von Huene, 1926; Meyer & Hunt, 1998), even though bone accumulations are sometimes found in pond (e.g., Greppin, 1870; Von Huene, 1922; Lapparent, 1943) or in palaeokarst deposits (e.g., Dalla Vecchia, 1998b; Boscarolli & Dalla Vecchia, 1999).

Consequently, dinosaur tracks complete the skeletal record, and they are important for the reconstruction of the terrestrial vertebrate ecosystem (Lockley, 1998a), and of palaeo(bio)geography (e.g., Meyer, 1993; Bosellini, 2002; Dalla Vecchia et al., 2001; Dalla Vecchia, 2003, 2005; Meyer & Thüring, 2003b; Conti et al., 2005; Nicosia et al., 2007). Tracks of sauropods and of large theropods from tidal-flat settings are commonly assigned to the *Brontopodus* ichnofacies (e.g., Farlow et al., 1989; Dalla Vecchia, 1994; Lockley et al., 1994a, b; Meyer & Pittmann, 1994; Pittman & Lockley, 1994; Avanzini et al., 1997; Dalla Vecchia, 2005; Mezga et al., 2006, 2007).

After the "renaissance" of vertebrate ichnology (e.g., Lockley, 1987, 1991a, 1998a; Gillette & Lockley, 1989), considerable progress has been made in experimental ichnology and neoichnology (e.g., Farlow, 1989; Brand, 1991, Cohen, 1991, 1993; Brand, 1996; Allen, 1997; Jackson, 2002, 2005; Manning, 2004; Diedrich, 2005; Milàn, 2006; Milàn & Bromley, 2006; Uchman & Pervesler, 2006; Davis et al., 2007; Scott et al., 2007). More attention has also been paid to sedimentological analyses of tracks and to track preservation (e.g., Benton, 1986; Lockley & Rice, 1990; McKeever, 1991; Fischer, 1998; Gatesy et al., 1999; Diffley & Ekdale, 2002; Gatesy, 2003; Milàn et al., 2004; Boutakiout et al., 2006; Loope, 2006; Milàn & Loope, 2007), and to the analysis of track cross-sections (e.g., Avanzini, 1998; Milàn et al., 2006). Vertebrate tracks have also been included in sedimentological studies of tidal-flat deposits (e.g., Pittman, 1989; Platt & Meyer, 1991; Meyer & Pittman, 1994; Gaillard et al., 1994; Avanzini et al., 1997). Because tidal flats of modern carbonate platforms are highly-diversified environments and sensitive ecosystems (e.g., Hardie, 1977a), vertebrate tracks may provide important additional information for the reconstruction of the palaeoenvironment and of the trackmaker behaviour and habitat.

Baird (1980) noted that "a footprint is not the natural mold of a morphological structure but the record of that structure in dynamic contact with a plastic substrate". This led Padian & Olsen (1984) to classify track morphology as a function of foot anatomy, kinematics of the limb, and substrate properties, expressed in the form of a ternary diagram (see also Fig. 5.18). Seilacher (1986) and Nadon (2001), on the other hand, suggested that footprints are a valuable sedimentological tool, as they can be seen as a palaeo-engineering tests of the substrate.

Large and heavy terrestrial animals are insensitive to microhabitat differences, and their tracks have a high survivorship potential (Cohen et al., 1991, 1993). They also have a strong impact on the substrate and even the environment, as is today for instance disclosed by "hippo trampling" in wetland environments (Ashley, 2002; Deocampo, 2002).

A similar impact on the sediment has been suggested for sauropod dinosaurs by Jones & Gustason (2006) and named dinovulsion, since sauropods were the largest terrestrial vertebrates in evolutionary history and reached masses of presumably more than 26 metric tons (e.g., McIntosh, 1990; Upchurch, 1995; Peczkis, 1994; Henderson, 2004; Upchurch et al., 2004). Their generally large tracks and associated track features (displacement rims, undertracks, internal overtracks, overtracks) are well-defined structures, and they may reveal important information about the sediment properties and consistency at the time of track formation, and the sedimentary processes after track formation. Consequently, they have a great potential in reconstructions of palaeoenvironments and of palaeoclimate, and may even be useful in sequence stratigraphic interpretations.

This chapter presents data from the excavation of the Chevenez—Combe Ronde tracksite, which provided a good opportunity to study sauropod tracks and associated track features on closely-spaced, superimposed surfaces, in cross-section, and thin-section. The sedimentological analysis of the track-bearing laminites of the lower levels (Fig. 2.5), of cross-sectioned sauropod tracks, and of the excavated levels and sauropod tracks are the main purpose of this chapter. A number of issues concerning the formation, taphonomy, and preservation of sauropod tracks in conjunction with tidal-flat environments of the Jura carbonate platform are addressed:

1. Identification of (modified) true tracks, undertracks, and (internal) overtracks
2. Relationships between substrate properties (namely water content) and track morphology
3. Identification of palaeosurfaces and bedding planes
4. Consolidation of palaeosurfaces and tracks
5. Sedimentary processes responsible for the burial of palaeosurfaces and tracks
6. Link between the preservational state of vertebrate tracks and exposure index
7. Importance of sauropod tracks for the reconstruction of the (tidal-flat) palaeoenvironment and its evolution.

4.2 Methodology

During the systematic level-by-level excavation, special attention was paid not only to the dinosaur tracks, but also to other macrosedimentary features (desiccation cracks, ripple marks, wrinkle marks, invertebrate burrows). Several detailed sedimentological sections of the laminites were logged to correlate the excavated bedding planes and to detect lateral variations. Thereby, a single number was attributed to each bed (=layer) and its upper bedding plane (=level).

All layers were exhaustively sampled, including the sauropod tracks (except tracks of the main track level) and their fills. Several large blocs and slabs containing sauropod tracks on one or multiple surfaces were recovered and solidified with epoxy. Some of these blocs were cut vertically into serial-sections with an industrial stone saw, either approximately along the longitudinal axis (axial vertical section *sensu* Allen, 1997) or perpendicular to the longitudinal axis along the short axis. Selected cross-sections were polished and used for detailed macroscopic descriptions. The counterpart of one of these sections has been used to make thin-sections.

The whole laminite interval including one of the cross-sectioned sauropod tracks, and about 20 to 30 cm of each the under- and overlying limestone were subjected to microfacies analysis in order to detect potential small-scale vertical variations, which might indicate changes in the palaeoenvironment (Fig. 4.3, Annex 4.1). For this purpose, the distribution of the most common features and components in thin-sections were analysed in a quasi-consecutive way. The relative frequency of microfacies elements was estimated as:

Rare:	A few components per thin-section only (<1%)
Common:	A few components occur in the field of observation (~1-5%)
Abundant:	Components are abundant in the field of observation (~5-50%)
Dominant:	The component is the principal rock constituent (>50%)

Under the optical microscope, a magnification of 40x was used to estimate the frequency of elements with a diameter of more than 1 mm, and a magnification of 100x for elements smaller than 1 mm. Selected thin-sections were subjected to cathodoluminescence but did not reveal any additional information.

4.3 Descriptive part

4.3.1 Macroscopic description of the laminites, and underlying and overlying limestones

In the outcrop, the track-bearing laminites constitute a 60-70 cm thick interval of thinly-bedded, tabular and platy, marly limestones, which locally have a slightly stromatolitic appearance (Fig. 4.1, Plate 4.1). Generally, the interval is getting marlier and better laminated towards the top. The bottom of the interval is marked by the main track level (level 500). The lowermost 20-25 cm of the sequence (layers 501-520) consist of rather poorly-laminated, slightly marly, platy limestone with intercalations of thin layers of calcareous marls (layers 508, 511, 516). The middle part (layers 525-540) is built up of about 20-25 cm of more massive and slightly-laminated limestone with intercalated marly layers (layers 521, 528, 531, 532). Above this follow about 10-15 cm of calcareous marls (layers 542-546), which are characterized by finer lamination, intralaminar shrinkage cracks, and invertebrate burrows with a diameter of up to 1 cm. Finally, the interval is concluded with 10-15 cm of strongly-bioturbated, green-brown, mottled marls (layer 550) (Fig. 4.1). Screen-washing of these marls yielded scattered fragments of turtle carapaces, small gastropods, and ostracods. The latter are common in

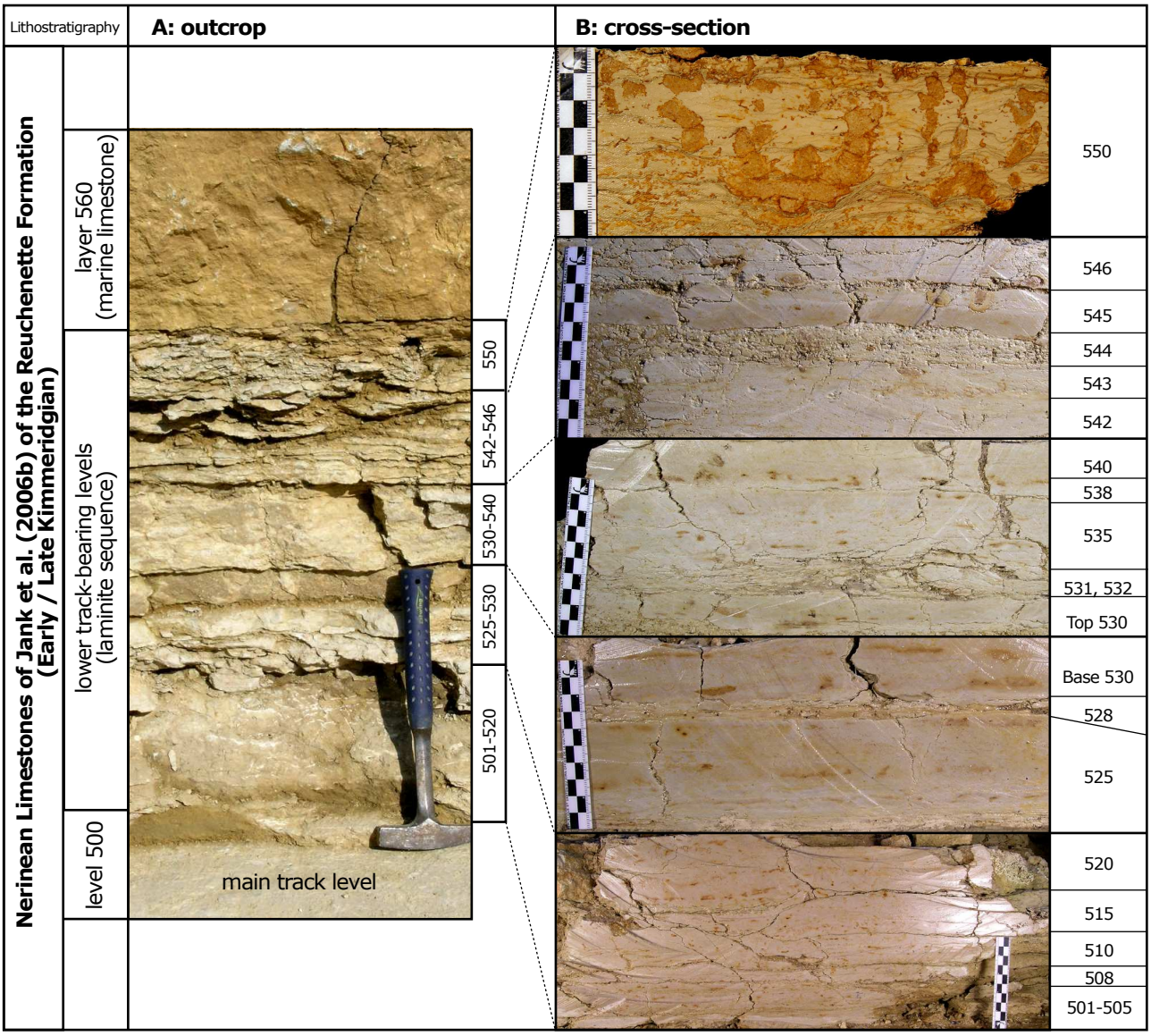


Fig. 4.1: Chevenez—Combe Ronde tracksite, excavation area 3: The dinosaur track-bearing calcareous laminites in outcrop (**A**, hammer for scale) and in a cross-section cut with a stone saw (**B**, scale bars are in 1 cm steps). Towards the top, the interval is becoming marlier, which is also expressed by thinner bedding (layers 542-546), and pronounced bioturbation (layer 550).

the screen-washed samples, but they are generally poorly preserved (internal molds) and could only tentatively be attributed to *Fabanella* sp., indicating a rather reduced salinity (U. Schudack, written comm., 2006). Some of the up to several mm large gastropods could be attributed to the family of the Procerithiidae, i.e., fully-marine gastropods (F.T. Fürsich, written comm., 2007).

Even though the laminites were excavated over large areas and considerable quantities of marls were screen-washed, vertebrate remains were rarely found. They are restricted to small remains of turtle carapaces (in layers 542, 550) and some teeth of pycnodontiform fishes (in layers 505, 510, 542, 550). On the main track level of excavation area 3 (Fig. 2.2C), a small, undetermined bone fragment was found within a shallow pes track of the sauropod trackway S2. More recently, at the Chevenez—Crat tracksite located about 1 km SE of the Combe Ronde site (Ayer & Iberg, 2004), a disarticulated, more or less complete turtle carapace was found in the same interval (layers 520-530) in very close proximity to deep sauropod footprints (pers. obs.). Because disarticulation and disintegration of recent turtle carapaces occur within short time periods (e.g., Meyer, 1991, 1995), the preservation of a turtle carapace in a subaerially-exposed tidal-flat environment can be explained by overgrowth and stabilization by microbial mats (pers. obs.).

Within the laminites, eight levels were uncovered laterally and documented. These exhibited variably preserved sauropod tracks, desiccation cracks, ripple marks (level 515) and wrinkle marks (level 540). The characteristic features of sauropod footprints are illustrated in Figure 4.12, other surface features in Figure 4.13, and Table 4.1 summarizes the observations made.

The laminites are interbedded between thinly bedded limestones (layers 430-495) below and massively bedded, about 1,6 m thick limestones (layers 560-570) above. With the exception of the uppermost 1-2 m, the underlying limestones bear a rich marine, mollusc-dominated macrofauna (bivalves and in particular nerineid gastropods). The same applies to the overlying limestones, of which the lower 20 to 30 cm (layer 560) is particularly fossiliferous. Here, internal molds of endobenthic bivalves (*Homomya* sp., *Ceratomya* sp., *Protocardia* sp.) are commonly found in life position, and eunerineid gastropods are numerous. The transition from the underlying limestone to the laminites is gradational, whereas the contact between the top of the laminite interval (the green-brown marls, layer 550) and the overlying limestone (layer 560) is very sharp and well defined, coupled with a conspicuous change in lithology, and a *Palaeophycus* burrow system with a marked positive hyporelief at the lower bedding plane of layer 560 (see also chap. 4.3.3.4)

4.3.2 Microfacies analysis

Facies is the sum of all organic and inorganic characteristics of sediment including colour, composition, texture, and sedimentary structures (Tucker & Wright, 1990). Microfacies encompasses all constituents and features visible in thin-section or on polished or etched slabs. The microfacies reveals important information about the depositional environment and its ecological conditions (Wilson, 1975; Scholle & Ulmer-Scholle, 2003; Flügel, 2004).

4.3.2.1 Microfacies features and components

In the following part, the most important features and components of the laminites and the under- and overlying limestones are described:

Brecciation

Description: Mainly observed in thin marly layers on top (layers 511, 516, 521) or below (528) track-bearing surfaces. These brecciated layers can be described as fracture to mosaic breccia (Fritz et al., 1993), characterized by minor clast rotation and fitted angular clasts. In association with dinosaur tracks, more heavily brecciated zones (matrix-supported breccia) have also been observed (Plate 4.7). The clasts are commonly micritized and darker than the surrounding matrix. Brecciation was sometimes also observed in more calcareous layers, where it is characterized by rounded to angular, micritic (coated) nodules or intraclasts, associated with circumgranular cracks.

Interpretation: Brecciation in tidal-flat environments occurs during periods of emersion, when drying of cohesive carbonate mud creates vertical and horizontal desiccation cracks. During subsequent flooding, fissures and cavities may be partially filled with fine carbonate material. Such brecciation has been described from modern supratidal settings (Kendall & Warren, 1987), and also from palustrine carbonates of semi-arid climates (e.g., Platt & Wright, 1992;

Marty & Meyer, 2006). Brecciation may also indicate the initial formation of a palaeosol (e.g., layer 528). In the present case, brecciation is also commonly associated with track formation: mechanical breaking of (semi-) consolidated sediment underneath sauropod tracks.

(Circumgranular) cracks

Description: Cracks include vertical (vertical joint planes), horizontal (horizontal joint planes, sheet cracks), planar horizontal, and oblique (skew planes) cracks (for terminology see Freytet & Plaziat, 1982). Curved or circumgranular cracks (craze planes) induce micronodulization and the formation of nodules (glaebules in soil nomenclature) with a subspherical shape, with no internal fabric, and which often look darker than the surrounding matrix. In the studied samples they are commonly associated with brecciation within the marly layers, but also within more calcareous layers.

Interpretation: Cracking may reflect minor pedogenic modification of the original carbonate texture, and is commonly associated with roots or induced by desiccation (e.g., Platt, 1989). Circumgranular cracking (and nodule formation) is believed to be the result of repeated wetting (expansion) and drying (shrinkage) (Bain & Foos, 1993). Desiccation can also lead to the formation of horizontal sheet-cracks (e.g., Hardie & Ginsburg, 1977), which can be mistaken for laminoid fenestrae (see below).

(Cryptmicrobial) lamination

Description: Planar or crinkled (undulated to curly) cryptmicrobial lamination is common throughout the laminites. It can be observed in weathered hand specimens as well as in thin-section. In thin-section it is commonly an alternation of bright and dark planar or wavy (curled) laminae, locally in association with coarser and finer laminae, or in association with laterally continuous laminoid fenestrae (Fig. 4.2). Well-defined microbial lamination is commonly present on top, within, or above layers with dinosaur tracks, and it is always associated with internal overtracks and overtracks with flat and broad displacement rims (e.g., on top of layer 520). In the upper part of the laminites (layers 542-546), lamination is alternating with thin (ostracod) shellbeds.

Interpretation: Lamination in tidal-flat environments is mainly the result of growth of microbial mats. Microbial mats are usually dominated by photosynthetic prokaryotes, particularly cyanobacteria and photosynthetic bacteria, and occasionally by eukaryotic microalgae such as diatoms (e.g., Walter, 1976; Awramik, 1984; Bauld, 1984; Cohen et al., 1984; Krumbein et al., 2003; Levit & Krumbein, 2003). They can either agglutinate sediment particles onto their sticky mucilaginous sheaths or act as bafflers that trap sediment washed into the tangle of filaments (Demicco & Hardie, 1994). Trapping and binding is regulated by microbial activity which, in turn, may be stimulated when the mat is covered by a thin sediment layer (Burne & Moore, 1987). Additionally, some microbial mats may quickly lithify by the precipitation of calcium carbonate (e.g., Krumbein & Cohen, 1977; Chafetz & Buczynski, 1992; Dupraz et al., 2004; Dupraz & Visscher, 2005) and consequently enhance the preservation potential of tracks (see also chap. 3) and other surface features such as desiccation cracks and ripple marks. The preservation of microbial laminations further indicates reduced bioturbation and grazing in restricted environments (e.g., hypersaline waters, frequent exposure) where sediments are moist and the substrate is stable (e.g., Garrett, 1970; Logan et al., 1974). On the supratidal flats and marshes of Andros Island (Bahamas), alternations of lamination and shellbeds either indicate storm or hurricane events that periodically imported the shells, or eventually blooms of ostracods during the wet season when the supratidal marsh is covered with freshwater (e.g., Monty, 1972, 1976; Hardie, 1977a).

Fenestrae (birdseyes, laminoid fenestrae)

Description: Fenestrae are mm-scale, irregular, either elongated (laminoid fenestrae) or spherical (birdseyes) cavities. They are always parallel to bedding, tubular fenestrae are absent. Laminoid fenestrae are locally laterally continuous. These may be irregular or regular (with matching roofs and floors). Fenestrae are always associated with lamination, but lamination on the other hand not always with fenestrae.

Interpretation: Fenestrae are characteristic features of tidal flat deposits, and they are generally interpreted as the product of trapped gases deriving from the decomposition of organic matter (e.g., Shinn, 1968a; Logan, 1974a; Grover & Read, 1978; Shinn, 1983a, b; Gerdes, 2007). Laterally continuous, regular laminoid fenestrae commonly form by decay of microbial mats in well-laminated sediments, and they may mark intralaminar boundaries formerly occupied by microbial mats (e.g., Logan, 1974a). However, irregular fenestrae ("shrinkage pores") may also form by desiccation (Fischer, 1964; Shinn, 1968a). Laminoid

fenestrae with matching roofs and floors may also be desiccation cracks (Hardie & Ginsburg, 1977).

Rhizoliths

No structures could unambiguously be identified as rhizoliths. Some structures resemble rhizoliths (e.g., Klappa, 1980; Bain & Foos, 1993), but most of these are probably completely pyritized invertebrate burrows (see above). The scarcity or absence of rhizoliths points either to an arid climate or a palaeoenvironment unsuitable for the growth of plants.

Organic matter

Small fragments of organic matter are common in all layers, but most abundant in the marly layers. Some of this organic matter may reflect the former presence of microbial mats.

(Framboidal) pyrite

Description: Completely opaque, black aggregates with diffuse boundaries and a maximum diameter of about 0,2 mm. It is generally rare but common in burrows, where locally almost the complete fill may be pyritized.

Interpretation: The presence of pyrite indicates bacterially decomposed organic matter and iron in the sediment. Its abundance within burrows suggests primary enrichment of organic matter within these systems. The framboidal texture results from rapid nucleation (e.g., Butler & Rickard, 2000). Completely pyritized burrows strongly resemble rhizoliths.

(Blackened, coated) intraclasts

Description: Angular to slightly rounded mudclasts

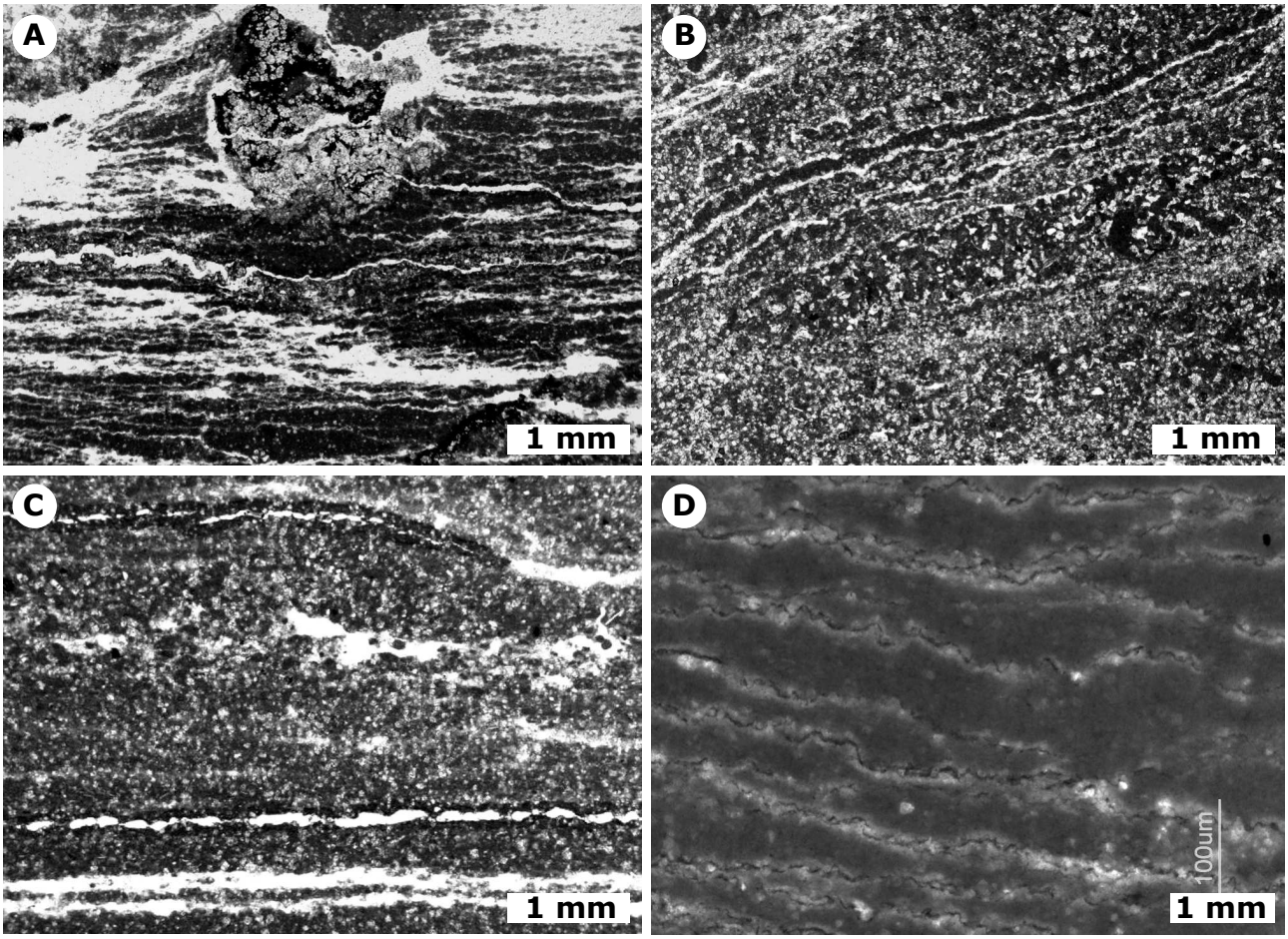


Fig 4.2: Chevenez—Combe Ronde tracksite: Cryptmicrobial lamination and fenestrae in thin-section. **A:** Layer 545, thin-section CRO004-132b: planar to slightly crinkled lamination. Alternation of laminae of clotted micrite and concordant, laterally continuous laminoid fenestrae. Note the small, dolomitized burrow in the upper middle part, which destroys the lamination. **B:** Layer 525, thin-section CRO004-190b: oblique planar lamination, characterized by an alternation of interlaminated dolomite-bearing layers and layers of clotted micrite, separated by laterally continuous, quite regular fenestrae. **C:** Layer 531, thin-section CRO004-3a: planar lamination, characterized by an alternation of interlaminated dolomite-bearing layers and layers of clotted micrite, separated by laterally continuous, regular fenestrae with matching floors and roofs. **D:** Layer 545, thin-section CRO004-132a: crinkled lamination, characterized by an alternation of clotted micrite and irregular seams enriched in organic matter.

or nodules with no internal structure and commonly a dark grey colour. Some are coated with dark, iron-rich clays. Blackened mudclasts and nodules exhibit a dark grey staining and they are, together with blackened foraminifers and peloids, common in invertebrate burrows. They also occur in association with (circumgranular) cracking and brecciation, notably in the marly layers.

Interpretation: Generally, mudclasts indicate early solidification of the sediment by desiccation or early lithification and reworking by subsequent flooding. Iron-coatings generally result from remobilization of iron-rich clays, which were carried by colloidal suspension into the depositional environment (Bain & Foos, 1993). The blackened intraclasts can be considered as black pebbles *sensu* Strasser & Davaud (1983) and Strasser (1984), who explained their blackening by impregnation of the sediment by dissolved, colloidal, or finely particulate organic substances in an anoxic and alkaline environment or microenvironment in the shallow subtidal to supratidal realm. Blackening or melanization only occurs in environments where the pH is high enough and the Eh is low enough to create the conditions necessary for the preservation of organic matter accompanied by the deposition of secondary calcite (e.g., Buol et al., 1980; Ettensohn et al., 1988; Martín-Chivelet & Giménez, 1992).

Dolomite

Description: The dolomite texture descriptions follow Sibley & Gregg (1986) and Tucker & Wright (1990, p. 365 ff.). Over the whole laminite sequence, dolomite is always abundant to dominant. Dolomite crystals range in size from 0,05 to 0,5 mm, but most crystals are small and have irregular and diffuse boundaries, giving it a rather subhedral to anhedral appearance. However, euhedral rhombs are also present. Some rhombs are zoned, some have cloudy centres. In places, incorporation of amorphous organic material gives dolomite rhombs a dark colour. Commonly, amorphous material also lines or sheaths dolomite crystals, which have irregular boundaries. The dolomite rhombs mostly float in the matrix and are only rarely packed. Accumulations of dolomite or dolomite halos occur in and around most invertebrate burrows in the form of a crystal-supported hypidiotopic dolomite texture. Most of this "burrow dolomite" is subhedral to anhedral with very diffuse boundaries.

Interpretation: In tidal-flat environments of arid to semi-arid climates, dolomitization is frequently explained by the sabkha model (e.g., Zenger et al., 1980; Patterson & Kinsman, 1982; Hardie, 1987; Baltzer et al., 1994), even if evaporite minerals or casts are lacking (Muir et al., 1980). However, early dolomitization, often in association with microbial mats, is also widespread in modern supratidal environments (beach ridge, levee, marsh) and has been described from Florida (Multer & Hoffmeister, 1968; Shinn, 1968b; Carballo et al., 1987), Andros Island, and the Bahamas (Shinn et al., 1965, 1969; Gebelein et al., 1980), Bonaire Island (Lucia, 1968), Baja California in Mexico (Pierre et al., 1984), and Ambergris Caye in Belize (Mazzullo & Reid, 1985; 1988; Mazzullo et al., 1987; Gregg et al., 1992, see also chap. 3). Such dolomite is of penecontemporaneous origin, with a dolomite precipitation linked to evaporation on tidal flats, involving strong recharge and/or tidal pumping (Patterson & Kinsman, 1982), and has been called "tidal flat dolomite" by Rameil (2005, 2006). Accumulations of dolomite in and around burrows may have precipitated from dolomitizing fluids during shallow burial under anaerobic conditions (e.g., Rameil, 2005, 2006). This may be mediated locally by enhanced porosity and permeability and/or the presence of organic matter and sulfate-reducing bacteria (Shukla & Friedman, 1983). Zoned crystals may indicate a later reflux-type dolomitization mechanism, allowing continued growth of the rhombs. Lining or sheathing of dolomite crystals could result from growing dolomite rhombs pushing aside amorphous material (Shukla & Friedman, 1983).

Quartz

Description: Angular quartz grains are the only detritic particles found apart from clays. Their diameter ranges around 50 μm. Quartz has been observed in all thin-sections, but it is generally rare (below 1%), and does not show any noticeable change in vertical distribution.

Interpretation: In the Late Jurassic of NW Switzerland, quartz is generally detritic. It may be of aeolian origin (e.g., Bolliger & Buri, 1967, 1970; Péwé, 1981; Hug, 2003), and/or was transported by rivers (Gygi & Persoz, 1986) and was redistributed by currents and tides (Hug, 2003). However, an authigenic origin for some of the quartz can not be ruled out as well (e.g., Chilingarian & Wolf, 1988).

Peloids

Description: Mostly spherical to ellipsoidal grains formed of cryptocrystalline carbonate without any internal structure. Generally, in the matrix their sizes are smaller than 1 mm. Within invertebrate burrows, peloids are clearly larger (around 1 mm or larger)

and commonly blackened. Micropeloids smaller than 100 μm (e.g., Chafetz, 1986; Tribovillard, 1998) were not observed. Peloids were seldom found in the matrix, but are common within the burrows, where they make up the greatest part of the fill (Plate 4.4).

Interpretation: Peloids are ubiquitous components of carbonates and may have different origins (e.g., MacIntyre, 1985; Scholle & Ulmer-Scholle, 2003; Flügel, 2004; Samankassou et al., 2005). The ones found in the burrows represent most probably fecal pellets.

Dasycladacean algae

Remains of dasycladacean algae are rare and restricted to small fragments. They are calcifying green algae, most frequent in shallow, protected lagoonal environments (Flügel, 1977). Small-sized fragments may easily be transported onto tidal flats.

Echinoderms

Description: Small unidentified fragments of echinoderms or fragments of echinoid spines are generally rare, but present in most layers. They show a similar distribution as the mollusc fragments, but are slightly rarer.

Interpretation: Echinoderms are restricted to the open-marine realm with a normal (stenohaline) salinity (e.g., Durham, 1966; Müller, 1989; Ziegler, 1998). However, due to their porous internal structure, they are easily displaced and transported by currents and storms onto tidal flats.

(Benthic) foraminifers

Description: Foraminifers were observed in both the matrix and burrows. Within the matrix, foraminifers are generally rare and clearly less common than ostracods, but they are the dominate element in the burrows. In both the matrix and burrows, miliolid foraminifers were most commonly encountered. Most of these can tentatively be attributed to *Quinqueloculina* sp. and a few to *Nautiloculina* sp. Other foraminifers include *Lenticulina* sp., *Everticyclammina* sp., *Pseudocyclammina* sp., *Alveosepta* sp., and other unidentified agglutinating forms. These non-miliolid foraminifers are rare.

Interpretation: Miliolid foraminifers such as *Quinqueloculina* sp. or *Nautiloculina* sp. indicate rather restricted environments, the other encountered foraminifers rather normal, open marine conditions (e.g., Tschudin, 2001). Due to their great porosity, benthic foraminifers are easily transported onto tidal flats by storms, where they may also form accumulations (e.g., Davaud & Septfontaine, 1995). Their concentration in burrows may be explained by tubular tempestites, i.e., infilling of the empty galleries by lagoonal sediment during storms (Wanless et al., 1988a, see also chap. 4.3.3.1).

(Fragments of unidentified) molluscs

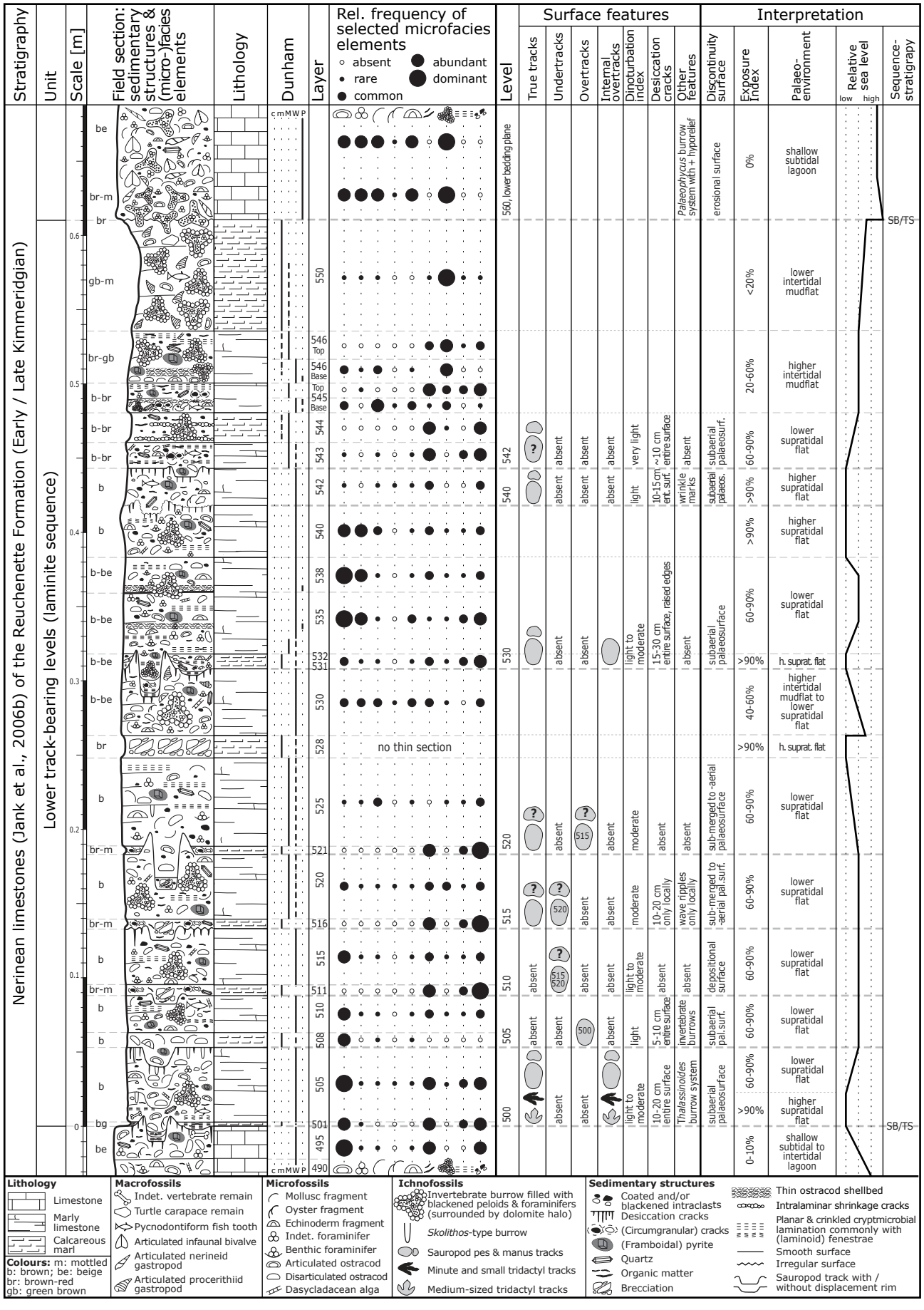
Description: Up to several mm large, mostly indeterminable fragments are present in most layers, and common in ostracod shellbeds. Locally, oyster shell fragments can be identified.

Interpretation: Oyster fragments may indicate a restricted environment with highly variable (euryhaline) conditions (e.g., Hudson & Palmer, 1976; Fürsich & Oschmann, 1986; Fürsich & Werner, 1986), while the unidentified fragments indicate normal marine to restricted environments. All these fragments may have been displaced, fragmented, and transported by currents or storms onto the tidal flats (e.g., Schäfer, 1972; Schopf, 1978; Fürsich & Flessa, 1987).

(Benthic) ostracods

Description: Both, thick- and thin-shelled ostracods are present. These are preserved articulated (2 valves), disarticulated (1 valve), or as fragments. The latter two are most frequent, but accumulations and thin horizons of articulated ostracods also exist. Ostracods are omnipresent with a relative frequency, which varies from rare to abundant. In a general way, ostracods are most abundant at the base and in the middle part of the laminites, and they are less common in the upper, marlier part. Locally, up to several millimetre thick ostracod shellbeds with scattered fragments of molluscs do occur. Even if ostracods are omnipresent in the thin-sections of the laminites, only few could be isolated from screen-washed samples of the marly layers. However, it is impossible to say whether these are the same species as those observed in the thin-sections or not.

Fig. 4.3 (opposite page): Chevenez—Combe Ronde tracksite: Log of the laminite interval and the under- and overlying limestones, coupled with an estimation of the relative abundance of selected microfacies elements (see also Annex 4.1). In the middle, the typical surface features of the excavated levels, highlighted by the thicker dashed lines, are shown. To the right the interpretation of the surfaces, exposure index, palaeoenvironment, evolution of the relative sea level and of sequence stratigraphy is summarized. SB: sequence boundary; TS: transgressive surface.


Stratigraphy
Unit
Scale [m]
Field section: sedimentary structures & (micro-)facies elements
Lithology
Dunham
Layer
Rel. frequency of selected microfacies elements
absent
rare
common
abundant
dominant
Level
Surface features
True tracks
Undertracks
Overtracks
Internal overtracks
Dinoturbation index
Desiccation cracks
Other features
Interpretation
Discontinuity surface
Exposure index
Palaeo-environment
Relative sea level
low
high
Sequence-stratigrapy
Nerinean limestones (Jank et al., 2006b) of the Reuchenette Formation (Early / Late Kimmeridgian)
Lower track-bearing levels (laminite sequence)
no thin section
SB/TS
SB/TS
Lithology
Limestone
Marly limestone
Calcareous marl
Colours: m: mottled b: brown; be: beige br: brown-red gb: green brown
Macrofossils
Indet. vertebrate remain
Turtle carapace remain
Pycnodontiform fish tooth
Articulated infaunal bivalve
Articulated nerineid gastropod
Articulated procerithiid gastropod
Microfossils
Mollusc fragment
Oyster fragment
Echinoderm fragment
Indet. foraminifer
Benthic foraminifer
Articulated ostracod
Disarticulated ostracod
Dasycladacean alga
Ichnofossils
Invertebrate burrow filled with blackened peloids & foraminifers (surrounded by dolomite halo)
Skolithos-type burrow
Sauropod pes & manus tracks
Minute and small tridactyl tracks
Medium-sized tridactyl tracks
Sedimentary structures
Coated and/or blackened intraclasts
Desiccation cracks
(Circumgranular) cracks
(Framboidal) pyrite
Quartz
Organic matter
Brecciation
Thin ostracod shellbed
Intralaminar shrinkage cracks
Planar & crinkled cryptmicrobial lamination commonly with (laminoid) fenestrae
Smooth surface
Irregular surface
Sauropod track with / without displacement rim

Interpretation: Ostracods live in fully marine, brackish, or freshwater environments (e.g., Schudack, 1993, 1999; Schudack & Schudack, 2000). Today, freshwater ostracods are also found in supratidal environments, i.e., in ponds and small lakes of Andros Island, Bahamas (Monty, 1972). Accumulations of articulated, closed carapaces indicate live burial, probably related to storms. Because ostracods are in the matrix clearly more abundant than foraminifers but almost absent in burrow fills where foraminifers are commonly found, it is suggested that accumulations of articulated ostracods indicate rather a restricted than a fully marine environment.

4.3.2.2 Microfacies type

Generally, the microfacies of the laminites is quite homogeneous and can be described as mudstone to wackestone *sensu* Dunham (1962), or dolo-biopelmicrite *sensu* Folk (1962). Only the thin shellbeds within some layers and the fills of invertebrate burrows can be described as packstones or grainstones. The most common biogenic sedimentary structures are (microbial) lamination and invertebrate burrows.

Only a few components show vertical variations in frequency, suggesting storm events or subtle changes of the palaeoenvironment, probably due to small changes in the environment related to fluctuations in sea level. Ostracods and foraminifers show the most pronounced vertical changes in frequency (Fig. 4.3), whereas foraminifers are, except in the burrow fills, clearly scarcer than ostracods. Dolomite and peloids are abundant but do not show any pronounced vertical change in relative frequency. Invertebrate burrows filled with coarse-grained (blackened) peloids, intraclasts, and foraminifers are also common and mostly surrounded by a dolomite halo. The marly layers (e.g., layers 511, 516, 521, 528) are strongly brecciated, and they are made up of about 50% of blackened intraclasts, which float or jigsaw fit in a marly, ferruginous matrix. Well-marked, thin layers of ostracod shellbeds occur only in the upper part of the laminites (layers 535, 538, base 545, base 546), and can be interpreted as storm layers.

The underlying thinly bedded limestone (layers 490, 495) is an ostracod-bearing wackestone, with a microfacies very similar to the base of the laminites. The overlying massively bedded limestone (layer 560) is clearly different and can be described as a packstone composed of abundant peloids, abundant foraminifers and other marine bioclasts.

4.3.3 Invertebrate ichnology

Even though distinct invertebrate burrows were commonly observed in thin-sections, they are comparatively rarely seen on a macroscopic scale. They are most frequent at the base (layers & levels 501 and 505) and at the top of the laminites (layer 550 and lower bedding plane of layer 560) but were also sporadically found in between (e.g., layer 525).

4.3.3.1 Burrows in thin-section (Plate 4.4)

Description: Burrows are always filled with coarse, unsorted sediment, which is clearly different from the surrounding sediment. Their pack- to grainstone fill consists of dolomite, (blackened) peloids and mudclasts, (blackened) foraminifers, and other marine bioclasts such as mollusc and echinoderm fragments, which are scarcer or not found in the surrounding sediment. Some burrows are completely pyritized in a way that the components of the fill cannot be recognized anymore. The boundaries of most burrows are blurred by accumulations or halos of dolomite, which may reach as far as twice the diameter of the burrows into the surrounding matrix.

Interpretation: On modern tidal flats of carbonate platforms such as the Bahamas, burrows are most commonly made by (decapod) crustaceans (e.g., *Psilonichnus*, *Thalassinoides-Ophiomorpha-Spongeliomorpha* burrows) or polychaetes (e.g., *Skolithos*-type burrows), which indicate lower intertidal to shallow subtidal environments (e.g., Curran & White, 1991; Curran, 1994, 2007). In higher, supratidal environments insects are important burrowers (e.g., Curran & White, 1991; Martin, 2006). Coarse burrow fills, unsorted and compositionally different from the matrix are interpreted as storm infill rather than backfill (Bromley, 1990; Tedesco & Wanless, 1991). The fills resemble tubular tempestites, which have been described as coarse burrow fills of recent *Callianassa* burrows with a mixture of coarse shells, grapestones, or peloids and very fluid carbonate mud (Wanless et al., 1988a). Within the same burrows, these authors also observed blackened foraminifers, whilst they were never found in the host sediment.

4.3.3.2 Burrows in cross-section

Description: At the base of layer 505, simple, non-branching, straight or gently-curved, shaft-like burrows, generally orientated perpendicular or oblique to bedding plane, have been observed (Fig. 4.4F).

They have a more or less sharp outline, a diameter of 2-4 mm, and are up to 2-3 cm in length. They are distinguished from the surrounding matrix by their darker colour. Burrow linings are not present.

Interpretation: Based on their simple morphology and vertical orientation, these burrows are attributed to the ichnogenus *Skolithos* Haldeman 1840. The same tracemaker may also be responsible for the round holes and raised protuberances on top of the bedding planes (see below). In palaeoenvironmental reconstructions, *Skolithos* tracemakers are typically considered to be deep-tier, opportunistic, suspension-feeding vermiform marine invertebrates representative of mobile substrates and indicative of high energy, intertidal to near-shore and deltaic marine environments (e.g., Bromley, 1996). On tidal flats *Skolithos*-type burrows are commonly found in association with

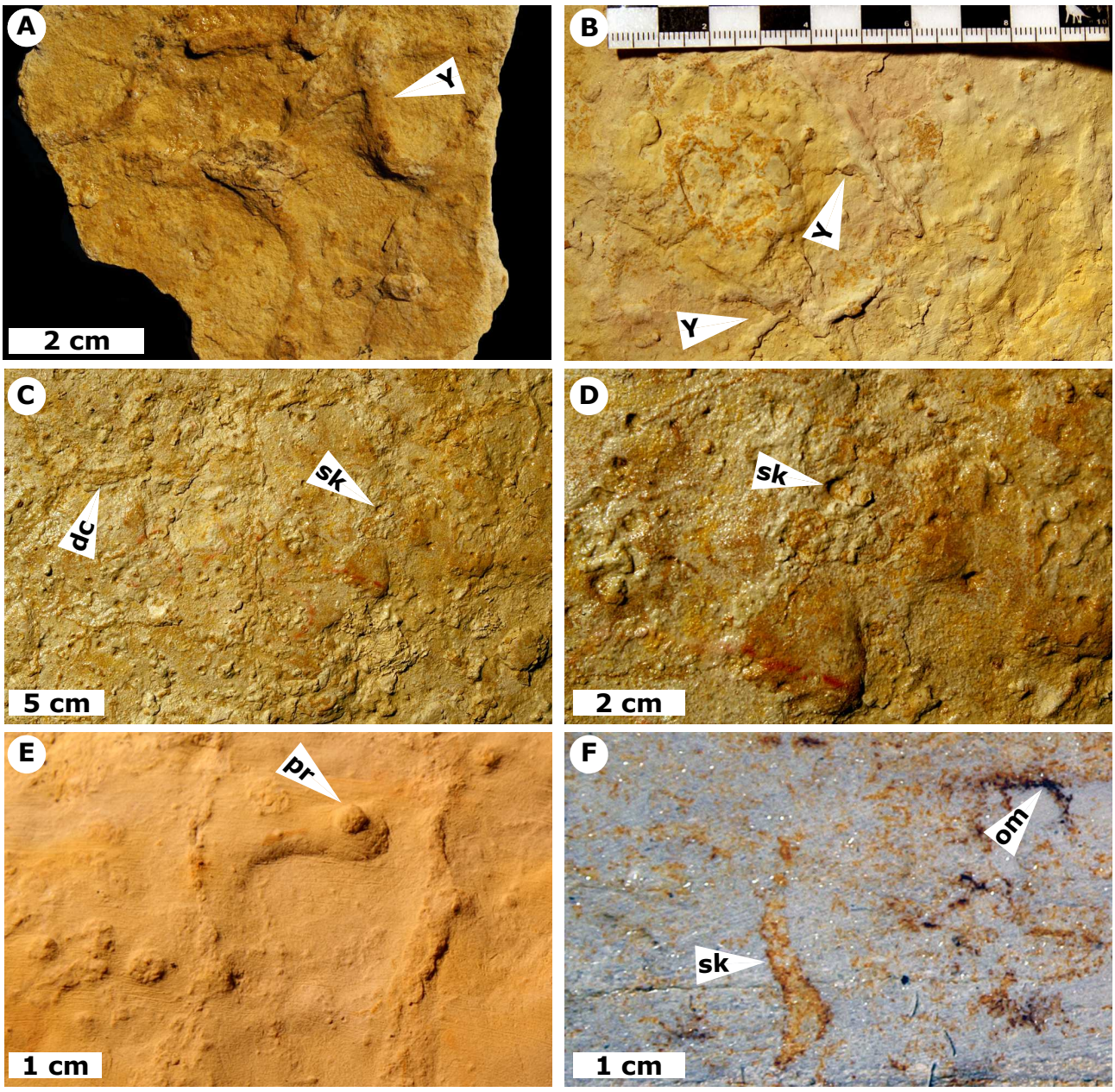


Fig. 4.4: Chevenez—Combe Ronde tracksite: Invertebrate burrows of the laminites. **A:** Lower bedding plane of layer 501, sample number CRO004-58: sinuous, Y-branching *Thalassinoides* burrows in positive hyporelief. **B:** Level 505, sample CRO004-221: straight, Y-branching *Thalassinoides* burrows, scale bar is 10 cm. **C & D:** Level 505, sample CRO004-72: desiccation cracks (dc) and small holes (sk, pointing to the same burrow in C and D), interpreted as *Skolithos*-type burrows. **E:** Level 505, sample CRO004-224: protuberance (pr), interpreted as a *Skolithos*-type burrow, on top of another, unidentified burrow. **F:** *Skolithos*-type burrow (sk) in a cross-section of the base of layer 505, sample CRO004-274: "om" points to organic matter, probably underlining cryptmicrobial lamination.

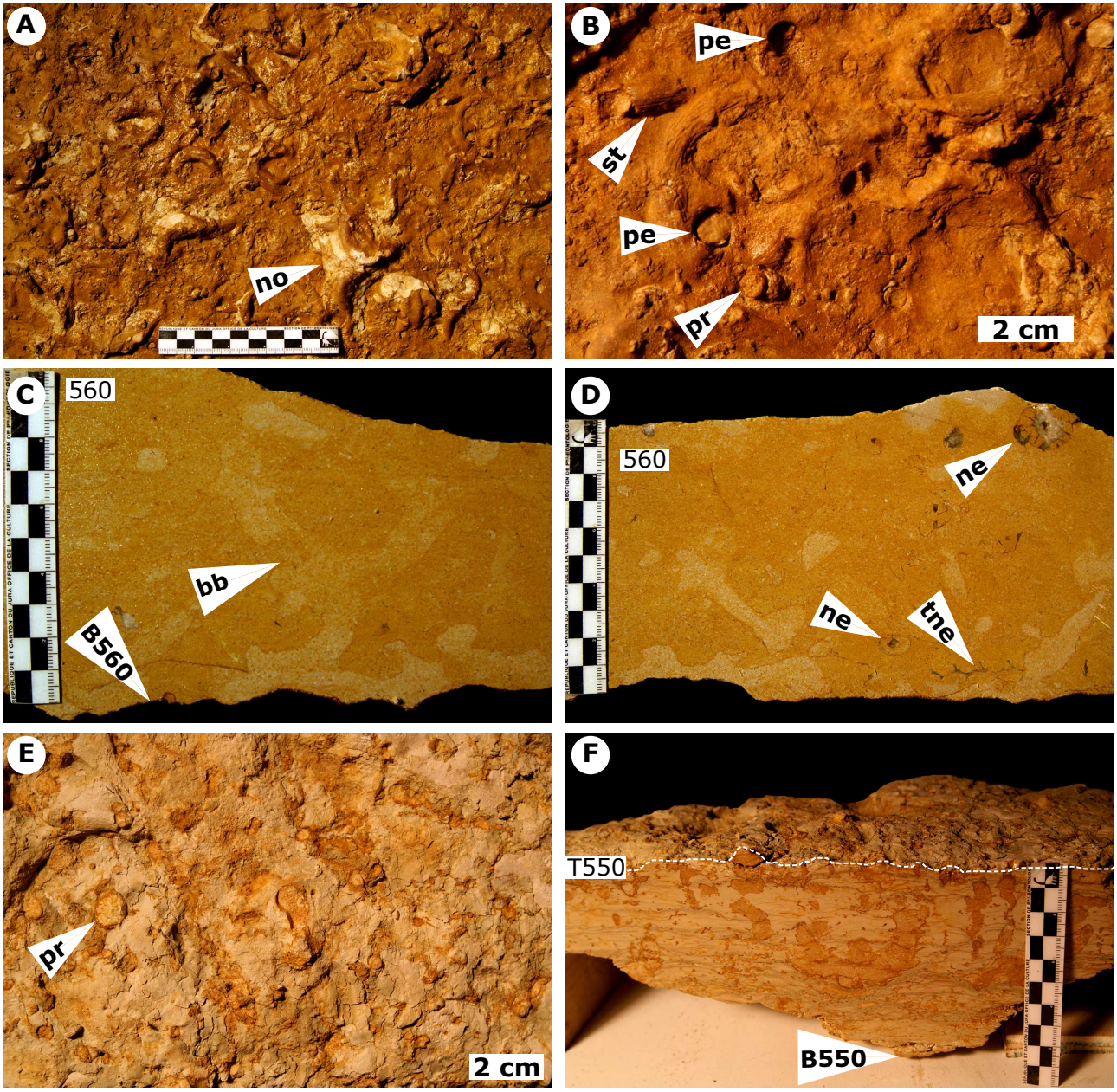


Fig. 4.5: Chevenez—Combe Ronde tracksite: *Palaeophycus* burrow system of the layers 550 and 560 in surface and cross-sectional view. **A & B:** Surface view of the lower bedding plane of layer 560 (sample CRO004-244), covered by a dense *Palaeophycus* network with varying burrow diameters. Note the thick nodes (no) due to crosscutting of burrows, and burrows exhibiting parallel, longitudinal striae (st). The latter is broken at its left end, strongly resembling perforations (pe). Note also perforations within other burrows (pe) and protuberances (pr), which is due to crosscutting by a smaller burrows and breaking off vertical burrows penetrating into the underlying layer 550. **C & D**: Cross-section of the base of layer 560 (sample CRO004-256). Note the branching burrow (lighter colour), which is clearly connected with the *Palaeophycus* burrows at the base. "ne" points to cross-sections and "tne" to transverse sections of eunerineid gastropods. **E:** Surface view of the top of layer 550 (sample CRO004-197): "pr" points to protuberance interpreted as a cross-section of a broken, vertical shaft. The pronounced relief is due to the *Palaeophycus* burrows at the base of layer 560. **F:** Cross-sectional view of layer 550 (sample CRO004-197), base and top are labelled: Note the strong bioturbation, which starts to destroy the well-pronounced lamination of layer 550. Scale bars in A, C, D, and F are 10 cm.

microbial mats and build-ups, where they keep, like the mats, up with sedimentation (Shinn, 1972; Gerdes et al., 2000). However, Gregory et al. (2006) suggested that in high intertidal and non-aquatic settings, the tracemaker of *Skolithos*-type burrows may also be a plant rather than an animal. This possibility cannot be ruled out in the present case, also because in thin-section pyritized burrows may resemble rhizoliths (Plate 4.4). Finally, insect burrows are also very common in recent supratidal microbially-colonized hypersaline settings (Gerdes & Krumbein, 1987; Gerdes et al., 2000), and such burrows may look similar to *Skolithos*-type burrows.

4.3.3.3 Burrows on bedding planes

Small holes and raised protuberances

Description: On level 505 small, round holes (negative epirelief) and raised protuberances (positive epirelief) with a diameter of less than 5 mm are common (Figs. 4.4C-E). Locally they are associated with bedding plane-parallel, slightly branching burrows (see below).

Interpretation: These structures resemble openings of *Steinichnus* isp. or *Cylindrichum* isp. in bedding plane view. Both these latter burrows are interpreted as stemming from beetles, constructed at or close to the water-air interface (e.g., Hasiotis, 2004). However, it is suggested that they are rather the openings or transverse sections of *Skolithos*-type burrows, which were observed in the cross-sections of layer 505.

Bedding plane-parallel burrows

Description: Bedding plane-parallel burrows are generally rare and were observed only on the lower bedding plane of layer 501 in positive hyporelief and on level 505 in positive epirelief (Figs. 4.4A & E). They are straight to slightly sinuous, have a maximum width of 5 mm, an elliptical (flattened) diameter, and exhibit a Y-shaped branching pattern without noticeably enlarged junctions. On level 505 they are associated with small round holes and protuberances.

Interpretation: These burrows are tentatively attributed to the ichnogenus *Thalassinoides* Ehrenberg 1944, which is characterized by a typical Y-shaped branching pattern. *Thalassinoides* usually is interpreted as a fodinichnial (combined feeding and dwelling) burrow. It is constructed by infaunal decapod crustaceans ("thalassinidean shrimps") or other kinds of arthropods, which are obligate or facultative deposit feeders (e.g., Fürsich, 1973; Ekdale, 1992; Nickell & Atkinson, 1995), since many taxa of deposit-feeding crabs, shrimps and lobsters are well known for creating extensive *Thalassinoides*-like burrow systems in modern shallow subtidal to intertidal environments (e.g., Miller & Curran, 2001; Curran & Martin, 2003; Ekdale & Bromley, 2003; Curran, 2007). Together with *Ophiomorpha* and *Spongeliomorpha*, *Thalassinoides* forms a compound trace fossil (Frey et al., 1978; Schlirf, 2000) that is two or more taxonomically distinct ichnofossils interacting with each other (Pickerill, 1994). *Thalassinoides* is often described from dinosaur track-bearing surfaces of tidal-flat settings (e.g., Fischer, 1998) and has often been observed on the other ichnoassemblages of the Ajoie (Marty, 2003b; Marty et al., 2003; pers. obs.). The rarity of *Thalassinoides* or other bedding plane-parallel burrows at the Combe Ronde site may indicate lower burrow densities due to an inhospitable substrate or palaeoenvironment.

4.3.3.4 Invertebrate traces at the top of the laminites

Description: The contact between the top of the laminite sequence (the green-brown marls, layer 550) and the overlying limestone (layer 560) is sharp. The lower bedding plane of layer 560 is highly ferruginous and irregular due to a noosed system of invertebrate burrows exhibiting a very pronounced positive hyporelief (Fig. 4.5A), which expands up to 3 cm into the underlying marls. The orientation of the burrows to the bedding plane ranges from horizontal to oblique. Burrow diameters are elliptical to round, range from several mm up to 1-2 cm, and they cover up to 50% of the lower bedding plane of layer 560. In places, the burrows exhibit fine, continuous, parallel, longitudinal striae (Fig. 4.5B). Systematic branching is absent, but the burrows are commonly crosscutting and interpenetrating each other, which leads to the formation of thicker nods (Fig. 4.5A). The burrows are filled with a relatively coarse-grained pack- to grainstone, rich in marine bioclasts, and similar to the facies of layer 560. Cross-sections of layer 560 show that this burrow system is connected with a bifurcating system of vertical to oblique burrows of a diameter of 1-2 cm (Figs. 4.5C & D). Additionally, the lower bedding plane of layer 560, including many of its burrows, and the top of the green-brown marls are covered by small, vertical and round holes and protuberances with a diameter of less than 5 mm (Fig. 4.5E). Cross-sections of layer 550 show that it is also heavily burrowed, and that these burrows destroy the initial, fine lamination of layer 550 and are connected with the top of layer 550 (Fig. 4.5F).

Interpretation: The burrow system on the lower bedding plane of layer 560 is assigned to the ichnogenus *Palaeophycus* Hall 1847, which is suggested to represent an open dwelling burrow constructed by predaceous or suspension feeding organisms, predominantly annelids (Pemberton & Frey, 1982). The formation of the striae may be the result of interior scraping or digging by the bristles or setae of a vermiform tracemaker (Pemberton & Frey, 1982). Osgood (1970) suggested predaceous polychaetes as a modern analog of the tracemaker of *Palaeophycus*. In addition to occurring in normal marine environments, *Palaeophycus* has also been reported from marginal marine and tidal-flat environments (Mángano et al., 2002). The small holes and protuberances are "counterparts" due to breaking of vertical to oblique shafts, which penetrate from layer 560 down into layer 550 to form the burrow system of layer 550. Thus, the burrows at the top of the laminite sequence (layers 544 to 550 and maybe even down to layer 530) were clearly made during the sedimentation of layer 560, after the deposition of the laminites. This is also the reason why within the laminites their fill is clearly different (more marine) from the surrounding matrix, which is not the case within layer 560, where the fill is similar to the surrounding matrix. Finally, the lower bedding plane of layer 560 is a good example of an erosional surface cutting primary structures (*sensu* Hillgärtner, 1998) and an excellent marker of a discontinuity surface with sequence stratigraphic- significance, here interpreted as a transgressive surface.

4.3.3.5 Invertebrate ichnofacies

The invertebrate ichnocoenosis of the laminites is not very diverse, dominated by burrows of *Skolithos* and *Thalassinoides*. The *Palaeophycus* burrow system clearly was constructed later, after deposition of the laminites.

Because vertebrate (dinosaur) tracks are abundant, the laminites are attributed to the *Psilonichnus*, rather than to the *Skolithos* ichnofacies. The latter indicates high-energy littoral to nearshore, marginal-marine environments, where organisms have to be able to respond rapidly to stressful conditions (e.g., Seilacher, 1967; Ekdale et al., 1984; Pemberton & MacEachern, 1995; Seilacher, 2007).

The archetypal *Psilonichnus* ichnofacies indicates a semi-terrestrial setting in upper beaches to backshore, coastal plain, higher intertidal to supratidal flat, and dune environments that are adjacent to fully marine environments (e.g., Frey et al., 1984; Curran, 2007). It is characterized by extreme variation in energy conditions, marked variations in sediment calibre, and periods of subaerial exposure, and it shows a low diversity and low abundance assemblage of small vertical burrows, narrow sloping T-shaped and Y-shaped burrows (*Psilonichnus*), root traces, and vertebrate tracks (Frey & Pemberton, 1987; Martin, 2006; MacEachern et al., 2007).

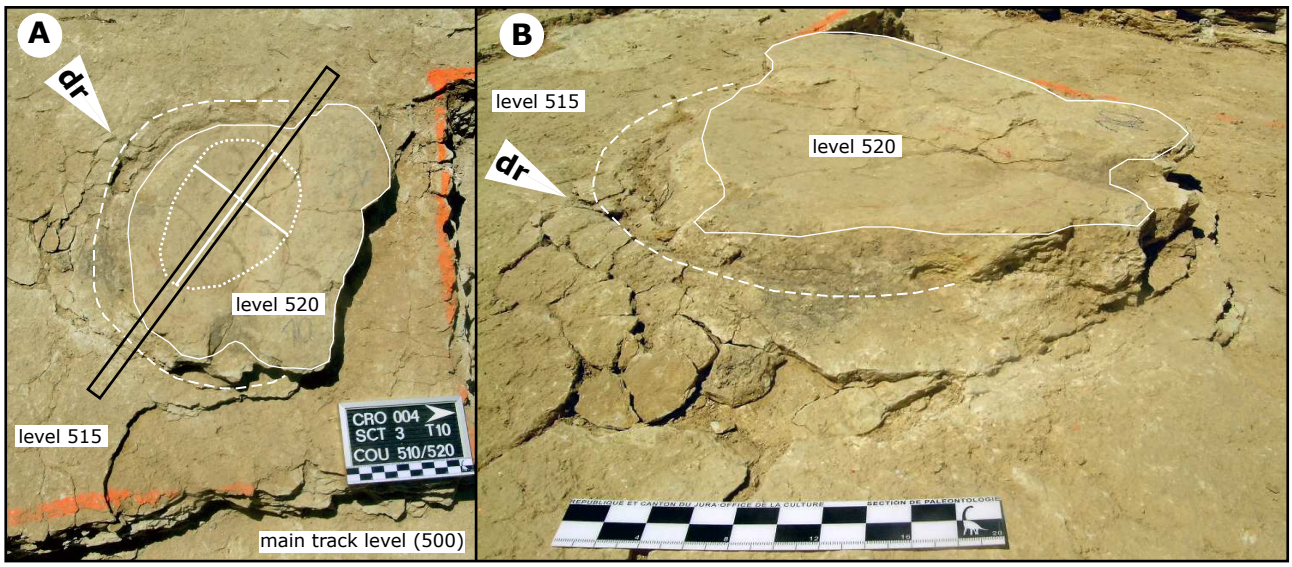


Fig. 4.6: Chevenez—Combe Ronde tracksite, excavation area 3. Surficial view of the track-bearing bloc (CRO004-44) prior to its extraction. **A:** The continuous line marks the outer limit of level 520, on which the sauropod pes track T10 is indicated with its long and short axis. Progression is towards the NW. A part of the track has been excavated down to level 515, and the dashed line marks the displacement rim on level 515. The rectangular marks the approximate position of the slab of Figure 4.7. **B:** Note the well-defined displacement rim (dr) on level 515 and the rather shallow and poorly-defined track on level 520. Scale bars are 20 cm, arrow on slate points north.

4.3.4 Description and interpretation of sauropod track (fill) cross-sections

4.3.4.1 Sauropod track T10 of level 520

Surficial morphology

On level 520 this was a reasonably-defined, isolated (not attributed to a trackway), shallow sauropod pes track with a length of 40 cm, width of 22 cm, and depth of 3 cm, entirely surrounded by small and broad (flat), poorly-defined displacement rims. A part of this track was excavated down to level 515, which revealed better-defined (steeper and narrower) and larger displacement rims as those on level 520 (Fig. 4.6). The interior of the track on level 515 could not be observed.

Even though this track can not be attributed to a trackway, the suggested direction of progression is towards the NW, because of the typical oval sauropod pes track outline (Fig. 4.6A) where the maximum width is located in the anterior part of the track (e.g., Farlow et al., 1989; Farlow, 1992; Lockley et al., 1994b). This track was extracted in a bloc (sample CRO004-44) and cut vertically, approximately along the longitudinal axis of the track into 16 serial-sections. Here, serial-section no. 6 (located approximately in the middle, parallel to the long axis of the track), which is believed to be the most representative, is described in detail and figured.

Cross-section

The section has a maximum thickness of 15 cm and comprises the layers 505 (top only), 510, 515, 516, and 520 (track fill). Layer 515 is strongly affected by the track formation. In the middle part of the print, it is fractured and compacted to about half of its lateral thickness. In the area of the displacement rims, it is slightly thicker than initially. Layer 511 is a thin marly joint on top of level 510, which is clearly thickened underneath the displacement rims. Layer 510 is slightly fractured in the middle part of the track, but no clear undertrack is visible on level 510. Layer 505 is unaffected by the track formation. Layer 520 has a uniform thickness over the whole width and a faint track with a broad and flat displacement rim is visible on top (Fig. 4.7).

Interpretation

Because layer 515 is affected by the most pronounced deformation (fracture, compaction, well-developed displacement rim), the true track was left on level 515. Consequently, the track on level 520 is believed to be an overtrack. This is confirmed by the uniform thickness of layer 520, which is best explained by a regular sedimentation, most probably due to the growth of microbial mats on top of level 515. During track formation, level 515 was likely a water-unsaturated, well-laminated sediment (biolaminite covered by a thick microbial mat) on top of the marly layer 511, whilst layer 510 was already (partially) consolidated. Consequently, layer 510 is only slightly fractured but not compacted. During track formation, the marly layer 511 acted as a detachement horizon on top of level 510 and was squeezed into the core of the displacement rims. A similar formation of displacement rims was observed leaving footprints in a water-unsaturated, thick microbial mat on top of water-saturated, coarse, bioclastic sand. Doing so, the bioclastic sand acted as a detachement horizon and was folded into the core of the displacement rim (Fig. 4.8, see also chap. 3).

The absence of displaced discs, bound by thrust faults, indicates that the dinosaur put the feet in a pronounced plantigrade way onto the sediment, that during the weight-bearing phase the force was primarily exerted vertically onto the sediment, and that the kick-off phase did not result in a transfer of the weight of the dinosaur towards the anterior part of the foot.

4.3.4.2 Sauropod track T16 of level 520

Surficial morphology

On level 520 this was a reasonably- to well-defined, isolated, deep sauropod pes track, with a length of 43 cm, width of 35 cm, and a depth of 8-9 cm (Plate 4.5C). Even though several similar pes tracks were found in close proximity, it could not clearly be attributed to a trackway. A large, well-defined displacement rim was present only on the northern side of the track, which is suggested to be the anterior part of the track. This is further supported by the typical oval sauropod pes outline with the maximum track width located in the anterior part of the footprint, and in this case close to the displacement rim. The track fill (layer 525) was uncased during excavation, but it has been replaced prior to the extraction of the track-bearing slab. This slab (sample CRO004-48) was then cut vertically, approximately along the longitudinal axis of the track into 2 sections (samples CRO004-185 & 186), one of which (sample CRO004-185) was used to fabricate thin-sections.

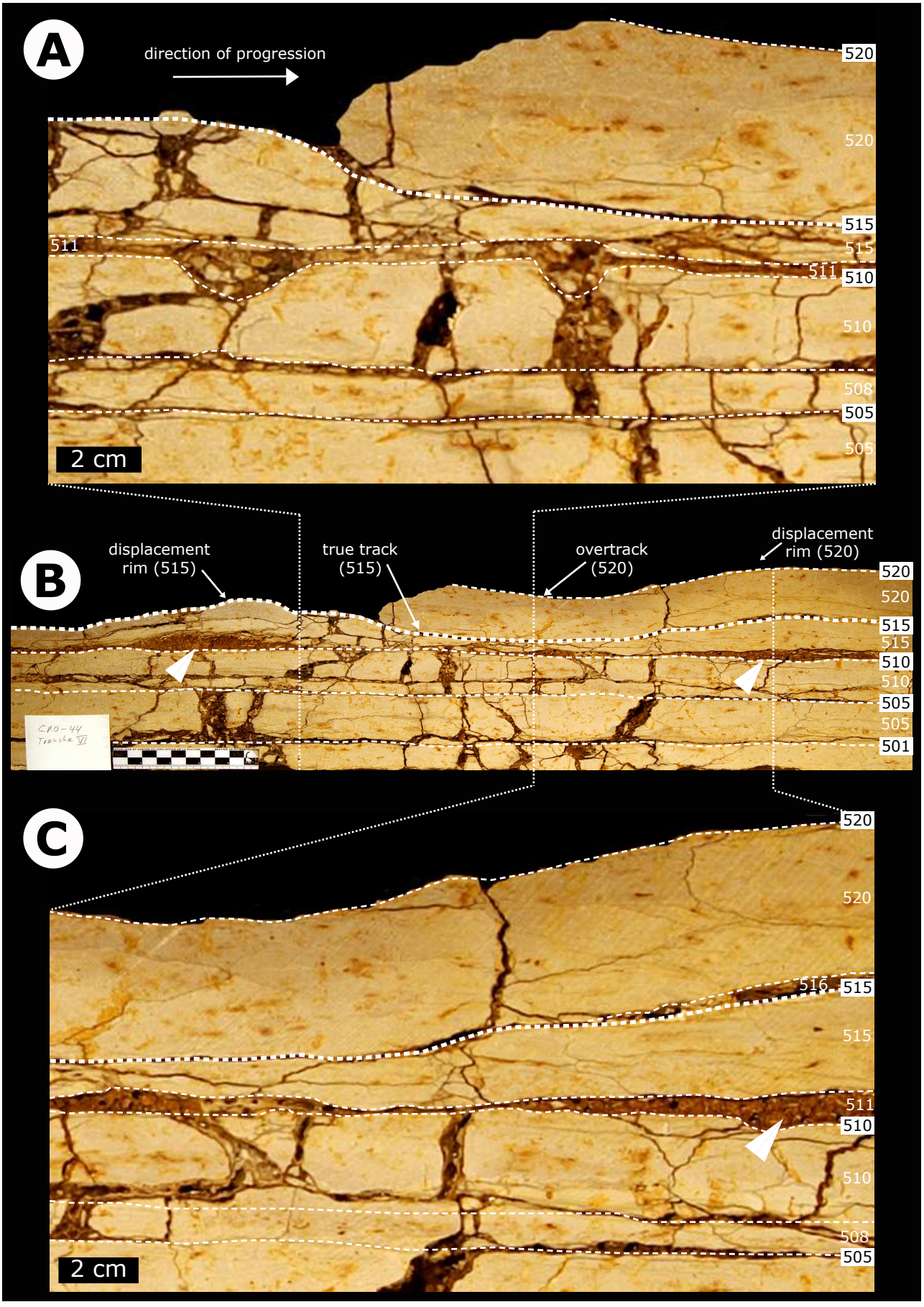

A
direction of progression
520
520
515
511
515
511
510
510
508
505
505
2 cm
B
displacement rim (515)
true track (515)
overtrack (520)
displacement rim (520)
520
520
515
515
510
510
505
505
501
C
520
520
516
515
515
511
510
510
508
505
2 cm

Fig. 4.7 (opposite page): Chevenez—Combe Ronde tracksite, excavation area 3, sauropod pes track T10 of level 520, section no. 6 of the serially sectioned bloc CRO004-44. **A:** Note the displacement rim (layer 515), which is progressively increasing in thickness towards the left. **B:** General view of the whole section. Arrows point to the thickened marly layer 511 underneath the displacement rims of layer 515. Even if layer 510 is slightly fractured underneath the print, an undertrack is not discernible on level 510. **C:** The displacement rim of level 515 is progressively getting thicker towards the right and the left, whilst layer 520 has the same thickness over the whole width. This suggests that the true track, left on level 515, was gradually covered by repeated growth of microbial mats, forming an overtrack with flat and broad displacement rims on level 520.

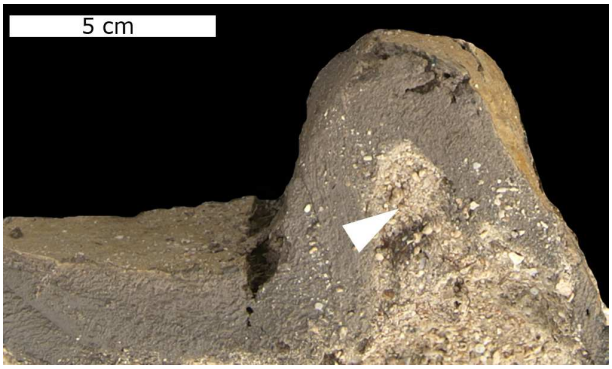


Fig. 4.8: Supratidal flat in the N of San Pedro Town (Ambergris Caye, Belize; see also chap. 3): Vertical cross-section of a displacement rim of a human footprint left in a water-unsaturated, thick microbial mat (dark grey layer). The inside of the print is to the right of the displacement rim. Underlying bioclastic carbonate sand (arrow) acted as a detachement horizon for the mat and was squeezed into the core of the displacement rim. Note cracking on top of the displacement rim and compare with Figure 4.7 and Figure 4.22.

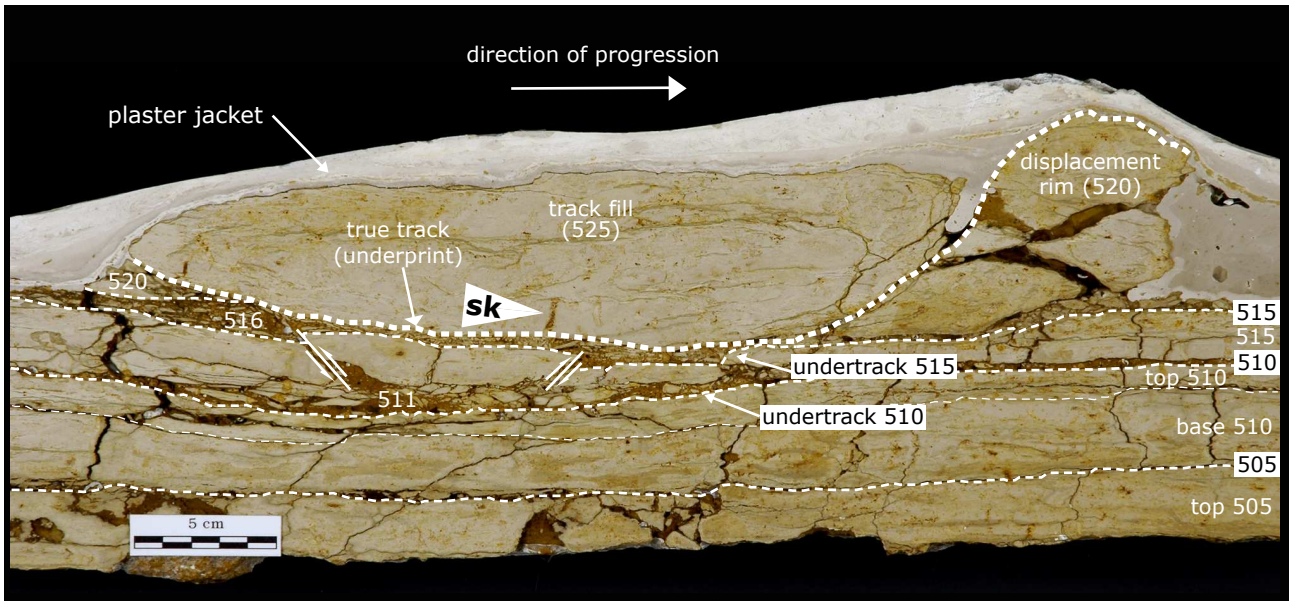


Fig. 4.9: Chevenez—Combe Ronde tracksite, excavation area 3: Cross-section of sauropod pes track T16 of level 520. The track is clearly marked by the large, homogeneous displacement rim to the right, and the fractured and compacted zone underneath the homogenous track fill in the centre of the picture. In the middle of the track fill, "sk" points to a *Skolithos*-type burrow. Faint undertracks without displacement rims are discernible on levels 515 and 510. Layer 505 is unaffected by the track formation, either due to earlier consolidation or due to insufficient track penetration depth. Track penetration depth amounts to about 6-9 cm. Layer 520 is compacted and completely thinned out in the middle of the print, in a way that an underprint is formed on top of layer 516. Note the uplifted bloc of layer 515 in the middle part of the track, between the two thrust faults. This bloc can also be described as a displaced disc or a pressure release structure *sensu* Brown (1999). Layer 510 is less fractured but at the top significantly compacted, especially at the rear of the print. This may indicate that the sauropod track maker put more weight on the posterior part of the hindfoot (pes) than on the anterior part. For further details refer to Plate 4.6 and Plate 4.7.

Cross-section (Plate 4.6, Plate 4.7)

The section (sample CRO004-186) has a maximum thickness of 15 cm and comprises the layers 505 (top only), 510, 511, 515, 516, 520, and 525 (track fill). Layers 511 and 516 are the thin, marly layers on top of levels 510 and 515 (Fig. 4.9).

The large displacement rim (layer 520) is homogeneous without any internal structures (e.g., flow or squeeze structures), equally when seen in thin-section. Layer 520 is completely thinned out in the middle of the track. The track formation clearly affected layers 520, 515 and 510 producing faint undertracks without displacement rims on levels 515 and 510. Layer 505 shows very minor distortion and is virtually unaffected. The layers 515 and 520 are affected by brittle deformation (shear zone with normal faults, thrust faults, rotated clasts) and by compaction, but not by ductile formation of the sediment. Right underneath the track, layer 515 is strongly fractured, partially displaced, and compacted. In the anterior part of the track, layer 515 is compacted to about half of its adjacent lateral thickness. Layer 510 is still fractured and compacted, but clearly less distorted when compared with layer 515. The base of layer 510 is undisturbed and only slightly compacted. The cavities caused by the fracturing and displacement of layers 515 and partially 510 are filled with brownish, strongly brecciated marls, stemming from layers 511 and 516. Underneath the track, these layers are thicker than beside the track. They contain rounded to angular, subspherical to elongated carbonate nodules and intraclasts, which have diffuse or sharp boundaries and the same texture as layers 515 and 510. These clasts and nodules either still fit together and form a mosaic breccia or they are rotated and float in the matrix.

In thin-section, the marly layers 511 and 516 are brecciated, and intraclasts and nodules are commonly outlined by circumgranular cracks and locally coated. The matrix is fine-grained, contains dolomite and is strongly ferruginous and mottled. Mottled areas are irregular, dark zones of varying intensity with diffuse or rarely sharp boundaries. Within these mottled areas, a network of anastomosing, fine, dark micritic filaments surrounding irregular, locally cylindrical calcite spar-filled voids and vugs can also be observed. Similar features are commonly described as alveolar texture. In thin-section, no evidence for the compaction in layers 515 and 510 was observed, and the microfacies is similar to that in thin-sections made at undeformed places.

Interpretation

Because the strongest deformation occurs in layer 520, which is squeezed into the displacement rim and completely thinned out (virtually absent) in the middle part of the track, and because the deformation diminishes and is partially brittle in the layers below, this track is believed to be a true track left on level 520. This is also supported by the absence of any better-defined track on the level above. The track was probably left in water-saturated, well-laminated sediment (microbial mat on top of a biolaminite; layer 520) on top of well-laminated and partially consolidated sediment (biolaminites; layers 515, 510). During track formation, layer 520 was squeezed outwards and formed the large displacement rim.

The maximal track penetration depth is about 6-9 cm, and the pressure of the foot fractured and compacted layers 515 and 510 to different degrees and slightly compacted layer 510. This led to the formation of faint, poorly-defined undertracks without displacement rims on levels 515 and 510. These undertracks would probably have been identified as very faint tracks on the levels 515 and 510.

The marly layer 516 on top of layer 515 is believed to have acted as a detachement horizon for layer 520 during track formation. In the middle part of the track, the true track *sensu stricto* is left on top of layer 516 and can thus be considered as an underprint. Subsequently, layer 516 filled the underlying cavities created by the fracturing of layers 515 and 510. Angular intraclasts with jigsaw fit indicate *in situ* genesis without significant mechanical reworking (e.g., Marty & Meyer, 2006). Fissures and cavities may be filled with finer carbonate material, resulting in pseudo-microkarst-like structures (e.g., Plaziat & Freytet, 1978; Freytet & Plaziat, 1982). This has also been called “autobrecciation”, resulting in “pseudoclast”-containing “pseudobreccia” (Armenteros et al., 1997). The alveolar texture is commonly interpreted to be the product of mm-sized organic filaments related to roots leading to the formation of discrete channelways and diagenetic alteration within the sediment (Steinen, 1974; Klappa, 1978; Esteban & Klappa, 1983; Bain & Foos, 1993).

The displaced disc in the middle of the track and the fact that the track is deeper in the anterior part, indicate that the dinosaur during the kick-off phase did slightly transfer the weight towards the anterior part of the foot, which resulted in a backward component of the foot movement. However, this

backward component is minor, when compared with displaced discs (imbricated fold-thrust systems) described from theropod tracks, which indicate a pronounced shift in the force exerted by the foot (Graversen et al., 2007).

4.3.4.3 Sauropod track S2-RP2 of level 530

Surficial morphology

On level 530, this was the right sauropod pes track RP2 of the pes-only trackway S2. The track was well-defined and entirely surrounded by a large displacement rim. The track fill (layers 535-540) was not removed, and the track length is estimated at about 55 cm and width at 35 cm. This track was cut *in situ* vertically along the short axis of the pes (perpendicular to the longitudinal axis) into a slab (CRO004-52), which was then extracted, solidified and cut into two sections (Plate 4.5B).

Cross-section

The section (CRO004-52, section 3) comprises about 25 cm of the laminite interval, including layers 520, 525, 528, 530, and a part of the track fill (layers 535 & 538) (Fig. 4.10). The formation of the track only affected layer 530, which was penetrated and squeezed outwards forming a relatively deep track (about 8-9 cm), surrounded by large and homogeneous displacement rims. Layers 520 and 525 are completely undeformed, and the marly layer 528 shows only very minor distortion in the middle part of the track. There is no evidence for any brittle deformation as observed in the sections of level 520. The track fill is very homogeneous, unlike the fill of the antecedent track LP2, described below.

Interpretation

This track is a good example of an underprint. This means that at the time when the sauropod was passing, layer 530 was a subaerially-exposed, unlaminated, water-saturated carbonate mud, through which the foot penetrated easily and squeezed it outwards. This led to the formation of large displacement rims, and the true track was actually left on level 528, which was located within the sediment prior to track formation. Because layer 528 and the sediment below is not affected by the track formation, it must have been consolidated (or even lithified) prior to track formation.

The large displacement rims surrounding the entire track indicate that the dinosaur put the feet in a pronounced plantigrade way, vertically onto the sediment, and that during the take-off phase the animal took off the foot vertically as well, because otherwise the displacement rims are likely to be affected by dragging of the foot. This is supported by the equal depth of the track and the absence of displaced discs. However, this may also be related to the presence of the early consolidated layer 528 below, which was not susceptible to record changes in the weight distribution of the foot.

4.3.4.4 Track fill of sauropod track S2-LP2 of level 530

Surficial morphology

On level 530, this was the left sauropod pes track LP2 with a length of 46 cm, a width of 34 cm, and a depth of 10 cm, of the pes-only trackway S2 (Fig. 4.12F). The track was very similar to its subsequent print RP2, described above: well-defined and entirely surrounded by a large displacement rim. From this track, only the fill (CRO004-30) comprising layers 531 to 538 was removed and cut vertically along the short axis of the pes (perpendicular to the longitudinal axis) into several serial-sections, of which the most representative one is described and figured here.

Cross-section

The cross-section comprises the track fill only, which is composed of the layers 531, 532, 535 and 538. Microbial lamination, underlined by higher contents of organic matter, reveals internal overtracks, of which the most pronounced are located within layer 535 (Fig. 4.11). During excavation, these overtracks were not detected because the track fills were always amalgamated.

Interpretation

The revealed structures are interpreted as internal overtracks, due to the growth of microbial mats. The presence of several increasingly ill-defined internal overtracks suggests that the track was filled subsequently, and that it was finally covered by layer 538, on top of which no overtrack is discernible anymore. The presence of several, thin ostracod shellbeds alternating with well-defined lamination in thin-sections of layers 535 and 538 also suggests a subsequent filing of the track by growing microbial mats and occasional sedimentation due to storms. Because layer 538 covers the track, despite the large displacement rims, without leaving a clear overtrack (see also Figs. 4.15D & F), it is suggested that microbial mats preferentially grew within the (moister) track interior, and that layer 538 was deposited quite rapidly, interrupting the microbial growth.

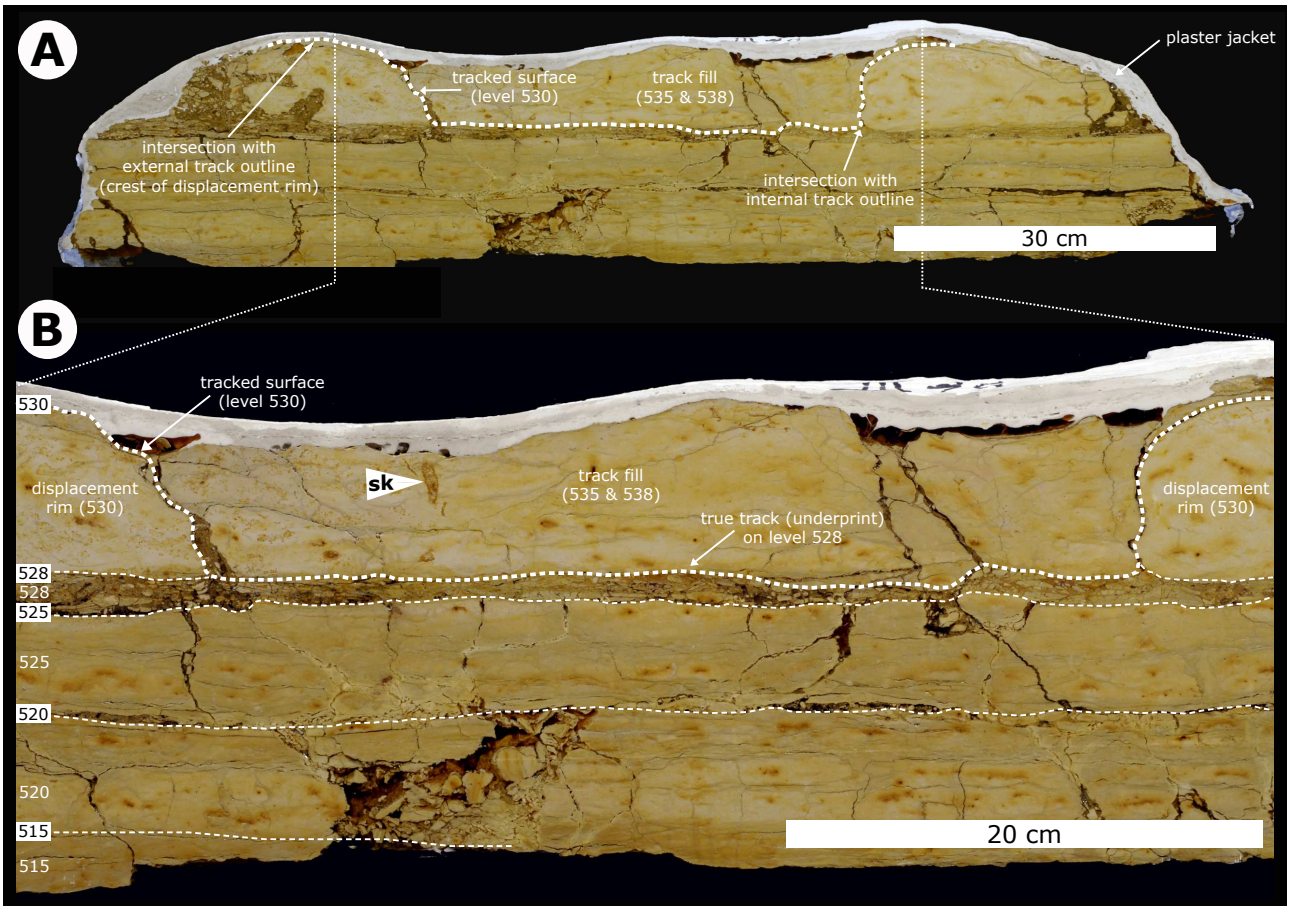


Fig. 4.10: Chevenez—Combe Ronde tracksite, excavation area 3: Cross-section of sauropod pes track RP2 of the pes-only trackway S2 of level 530; cut vertically along the short axis of the pes (perpendicular to the longitudinal axis). **A:** The cross-section comprises about 25 cm of the laminites, including layers 515 (top only), 520, 525, 528, 530, and the track fill (layers 531, 532, 535 and the base of 538). **B:** Detail of A: note the homogeneous displacement rims at the right and left and the slightly less homogenous track fill in between. "sk" points to a *Skolithos*-type burrow. The sediment below the true track (layers 525, 528) is undeformed because it has been consolidated prior to track formation. The true track was left on level 528 and hence is an underprint.



Fig. 4.11: Chevenez—Combe Ronde tracksite, excavation area 3: Cross-section of the track fill (CRO004-30) of sauropod pes print LP2 of the pes-only trackway S2 of level 530; cut vertically along the short axis of the pes (perpendicular to the longitudinal axis). Microbial laminations, underlined by dark bands of probably higher contents of organic matter, reveal internal overtracks, of which the most pronounced are located at the top of layer 535.

4.3.5 Description and interpretation of excavated levels: sauropod tracks and macrosedimentary surface features

4.3.5.1 Level 500 (main track level)

Description

This smooth surface is the only level with tracks of both sauropods and bipedal, tridactyl dinosaurs. The dinoturbation index varies from very light to moderate (Fig. 4.14B). Generally, the tracks are well defined and almost all are organized in trackways, even though a few isolated tracks were also found. In the excavation areas 1 and 2 twelve sauropod trackways (S3-S14) consist of relatively deep (up to 10 cm) tracks with a well-defined overall outline and large displacement rims, but without showing anatomical details such as digit or claw impressions (Fig. 4.12A and Fig. 5.1). However, this was also difficult to observe as the fills (layers 501 and 505) of most of the deep sauropod tracks were amalgamated within the tracks. Once the fills are removed, these tracks will likely reveal more details. Excavation area 3 is marked by two sauropod trackways (S1, S2) with shallow (up to 5 cm deep) and poorly-defined tracks without displacement rims (see also Fig. 5.2). In total, 43 trackways with well-defined tracks of minute to medium-sized bipedal, tridactyl dinosaurs were identified. Generally, trackways of both bipedal dinosaurs and sauropods show minor variation in track preservation along their trackway course, and this is more pronounced in some of the bipedal trackways than in the sauropod trackways. Additionally, the whole surface is covered with slightly sinuous desiccation cracks with a polygon diameter ranging between 10-20 cm, forming an orthogonal to curved mostly triradiate ("triple junction") crack pattern (Fig. 4.13A). Layer 501, an up to 2 cm thick, well-laminated calcareous marl, covered the main track level without a pronounced increase in thickness within the tracks and other depressions, and on top of layer 501 the same desiccation crack pattern as on level 500 was observed.

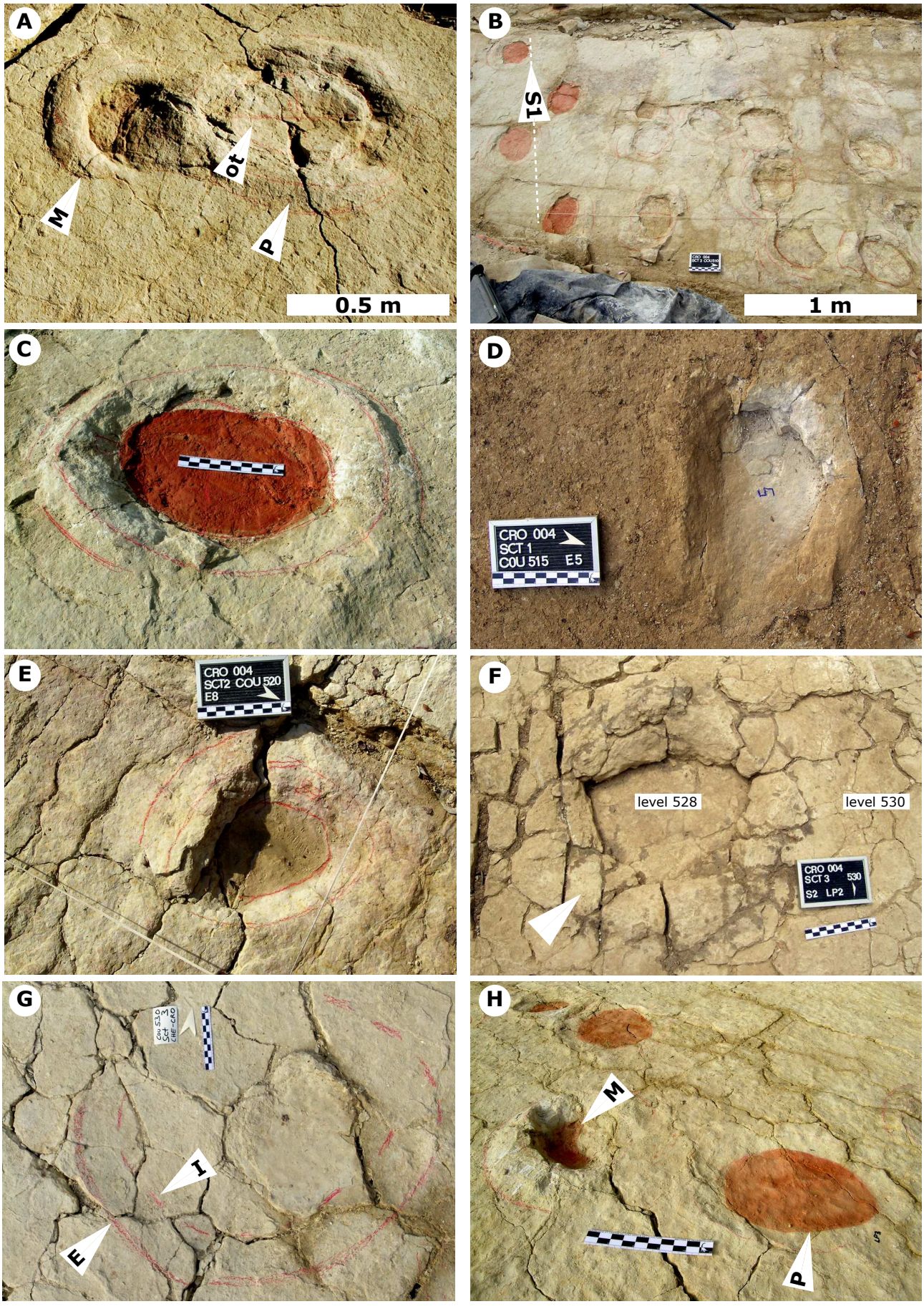
Interpretation

The generally good preservation of the tracks, the presence of minute tridactyl tracks, and the presence of sauropod overtracks on level 505 (see below) suggest that all tracks of level 500 are true tracks. Interferences between desiccation cracks and tracks indicate that the tracks have been left prior to desiccation, or approximately at the same time. Thereby, some tracks may have acted as a localizing agent for desiccation cracks (e.g., Smith, 1993; Thulborn, 1990; Billon-Bruyat, 2003; Billon-Bruyat & Mazin, 2003), but the desiccation pattern is generally not particularly footprint-controlled. The joint presence of deep and shallow sauropod tracks indicates that the surface had been crossed by the animals at two different time moments, first when the sediment was water unsaturated, and later when it was more or less dry and already quite firm. Both these sediment consistencies are not ideal to preserve fine anatomical details of the foot morphology (see also chap. 3). This hypothesis is supported by the presence of trackway T10 of a minute, bipedal dinosaur, which crosses the areas with the deep and the shallow sauropod tracks (see also chap. 5.4.7.3). As the tracks of T10 all show a very similar preservation, a lateral variation in substrate consistency can be excluded. Moreover, the right pes track R25 of T10 is overprinted by the right pes track RP4 of sauropod trackway S2, which also indicates that the shallow sauropod tracks were left later on the same surface (assuming that overprinting by undertracks is not possible), when the sediment was drier. After that, the surface was probably overgrown by microbial mats (layer 501), which stabilized and preserved the tracks, before it was again subjected to desiccation. The same desiccation crack pattern on level 500 and on the top of layer 501 suggests that the pattern of level 500 figured as a localizing agent for those on level 501, probably by continuing growth of a microbial mat. However, it can not be excluded that the desiccation cracks on level 500 are prism cracks, which means they are downward continuations of those of level 501. This would then imply that they had been formed after the deposition of layer 501. In any case, the top of layer 501 was subjected to subaerial exposure and desiccation, even though no tracks were revealed on this level.

4.3.5.2 Level 505

Description

This smooth, slightly reddish surface exhibited shallow and poorly-defined sauropod pes tracks without displacement rims (Fig. 4.15A-B), which are cut by slightly sinuous desiccation cracks with a polygon diameter ranging from 5-10 cm (Fig. 4.13B). The dinoturbation is very light. In places small, round holes and protuberances, interpreted as *Skolithos*-type burrows (see also chap. 4.3.3.3 and Figs. 4.4C & E), were observed.


A
M
ot
P
0.5 m
B
S1
1 m
C
D
CRO 004
SCT 1
COU 515 E5
E
CRO 004
SCT2 COU 520
E8
F
level 528
level 530
CRO 004
SCT 3 530
S2 LP2
G
I
E
H
M
P

Interpretation

As all tracks of this level were located precisely above sauropod tracks of level 500, they are clearly identified as overtracks. However, only the deepest sauropod tracks of level 500 also caused an overtrack on level 505. It is suggested that level 500 had first been covered by the continuous growth of microbial mats (layers 501 and base 505; Fig. 4.15C), and then by rapidly deposited sediment (top of layer 505), producing only slight overtracks on top of the deepest sauropod tracks of level 500. Level 505 was then subjected to burrowing and a short phase of desiccation.

4.3.5.3 Level 510

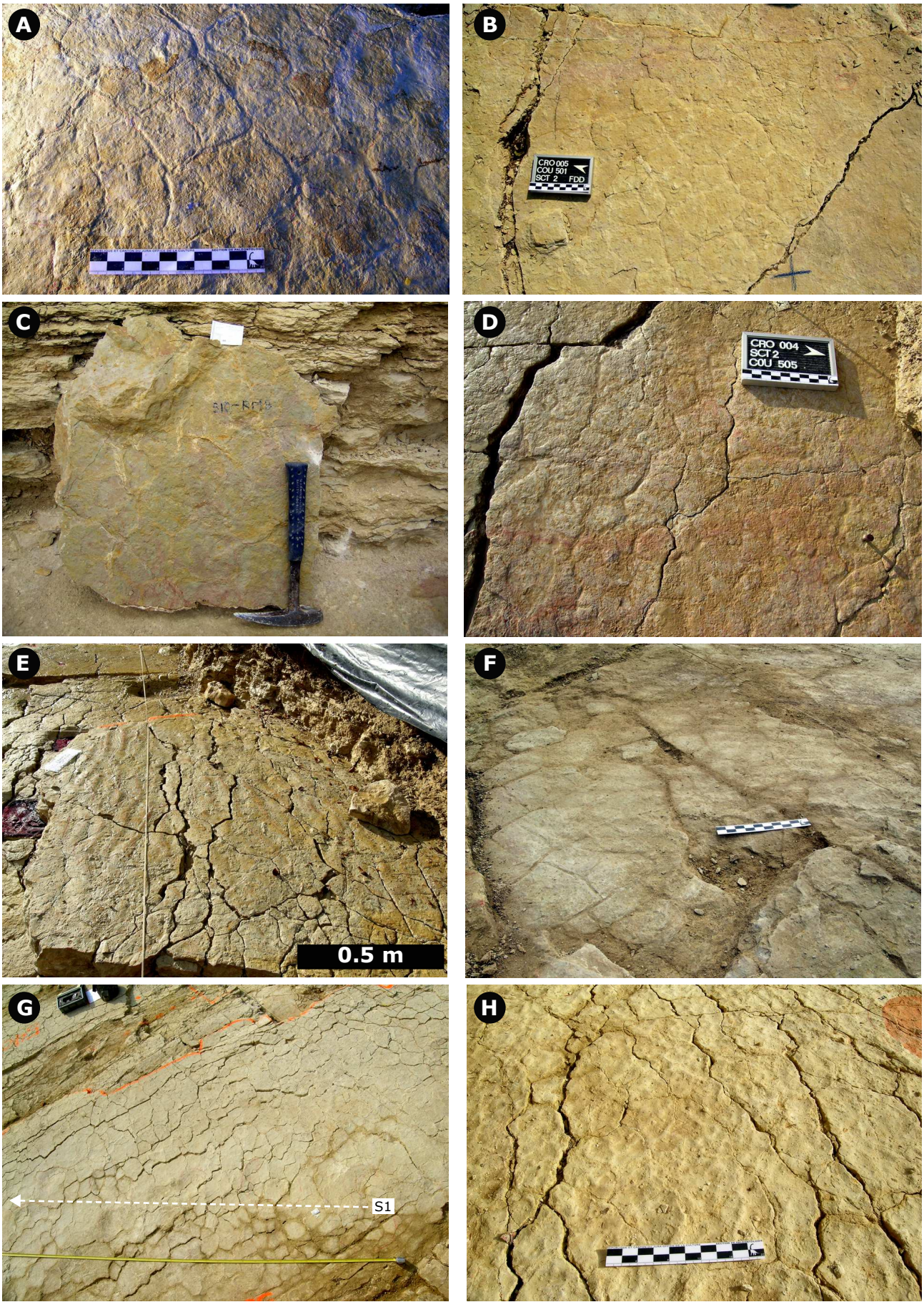
Description

Slightly irregular and uneven surface with generally shallow and poorly- to reasonably-defined sauropod pes tracks with small and narrow, weakly-developed displacement rims (Figs. 4.12B & C). Some tracks resembled manus tracks but could not unambiguously be identified as such. Further, no signs of desiccation cracks or ripple marks were observed. This is the surface with the highest (moderate to heavy) dinoturbation index (Fig. 4.14C).

Interpretation

Almost all tracks of level 510 have also been documented either on level 515 or 520. Because the relief of the tracks is inferior when compared with their counterparts on the overlying levels 515 and 520 (Figs. 4.17C & D), all tracks of level 510 are considered to represent undertracks. The few tracks, which have only been documented on level 510 (Fig. 4.16, Fig. 4.17A) are probably due to an excavation bias, because layer 515 was here and there amalgamated with layer 520. The undertrack interpretation is supported by a comparison between tracks found on both levels 510 and 520 (Fig. 4.17B), which shows that the tracks on level 510 are with a few exceptions clearly larger and shallower than their counterparts on level 520. An increase in horizontal dimensions and decrease in vertical topography has also been observed in experimental ichnology, where an emu produced true tracks and undertracks in layered sediment (Milàn & Bromley, 2006). Level 510 can be interpreted as a bedding plane preserving primary structures with undertracks of levels 520 and 515.

Fig. 4.12 (opposite page): Chevenez—Combe Ronde tracksite: Typical sauropod pes track morphologies of the different excavated levels. **A:** Level 500 (main track level), excavation area 2: deep, well-defined pes (P) – manus (M) pair (RP1-RM1 of trackway S9), surrounded by large and well-defined displacement rims. Note the well-defined internal morphology of the manus print whilst the pes print still carries the track fill, on top of which (=level 505) the overtrack ("ot") can still be seen. The tracks are cut by desiccation cracks. These tracks are interpreted as true tracks, left in a moist to water-unsaturated carbonate mud, probably covered with a thick microbial mat. **B:** Level 510, excavation area 3: moderately to heavy dinoturbated level with shallow, reasonably-defined pes tracks, surrounded by small and narrow displacement rims. Note the pes-only trackway on the left (S1, coloured tracks). All these tracks are interpreted as undertracks of levels 515 and 520. **C:** Level 510, excavation area 3: Detail of a shallow pes undertrack (coloured), characterized by a small and narrow displacement rim and a reasonably-defined internal outline. Note the irregular surface of this level. **D:** Level 515, excavation area 1: reasonably-defined, moderately deep pes track E5 with small and narrow displacement rims and a poorly-defined internal morphology; probably an undertrack of level 520. **E:** Level 520, excavation area 2: well-defined, deep pes track E8 (coloured), characterized by large and broad, well-defined displacement rims and a reasonably-defined internal outline. This track is interpreted as a true track left in a water-unsaturated to water–saturated biolaminite. **F:** Level 530, excavation area 3: deep pes track (LP2) of trackway S2. This pes-only trackway is characterized by deep tracks with a reasonably-defined internal outline, surrounded by large and broad displacement rims (arrow). This track is interpreted as a true track (underprint) left in water-saturated, unlaminated carbonate mud. The tracked surface was level 530, whilst the true track (underprint) was left on level 528. A cross-section of the track fill is illustrated in Figure 4.11. **G:** Level 530, excavation area 3: a very shallow, poorly-defined pes track of trackway S1, cut by desiccation cracks with slightly raised edges. Arrows point to the external (E) and internal (I) track outline. This track is interpreted as a true track left on an almost dry, thick microbial mat or carbonate mud. This trackway was found only a few metres beside trackway S2 with the deep tracks (figured in F). **H:** Level 540, excavation area 2: pes (P) – manus (M) pair (LP3-LM3, coloured) of the manus-dominated trackway S1. The manus track is characterized by a well-defined internal outline, anteriorly surrounded by a well-defined displacement rim, whilst the pes track is very shallow and exhibits a poorly-defined internal and external outline without any displacement rims. These tracks are interpreted as true tracks left on a moist, thick microbial mat on top of biolaminated sediment. Scale bars in C, D, E, F and H are 20 cm and 10 cm in G.


A
B
CRO 005
COU 501
SCT 2 FDD
C
D
CRO 004
SCT 2
COU 505
E
0.5 m
F
G
S1
H

4.3.5.4 Level 515

Description

Smooth surface with, in places, ripple marks and desiccation cracks. Sauropod pes tracks are reasonably to well defined, mostly surrounded by small to medium-sized, well-defined displacement rims and up to 10 cm deep (Fig. 4.12D, Fig. 4.6). Manus tracks were not unequivocally identified, and the dinoturbation index is moderate. In excavation area 1, slightly sinuous, bifurcated, symmetrical, and relatively large ripple marks but no desiccation cracks were found (Fig. 4.13E). In excavation area 3, symmetrical, small ripple marks are cut by slightly sinuous desiccation cracks (Fig. 4.13F). These cracks have a polygon diameter ranging from 10-20 cm, and are healed. Here and there and in almost the whole excavation area 2, layer 515 was amalgamated with layer 520 and could thus not be excavated. Most of the tracks of level 515 correspond to tracks on level 520 or 510, or on both. Several tracks were found exclusively on level 515 (Fig. 4.16D).

Interpretation

Because the deeper tracks were either not encountered on level 520 or they were shallower on level 520, these deeper tracks on level 515 can be considered as the true tracks. They often caused the

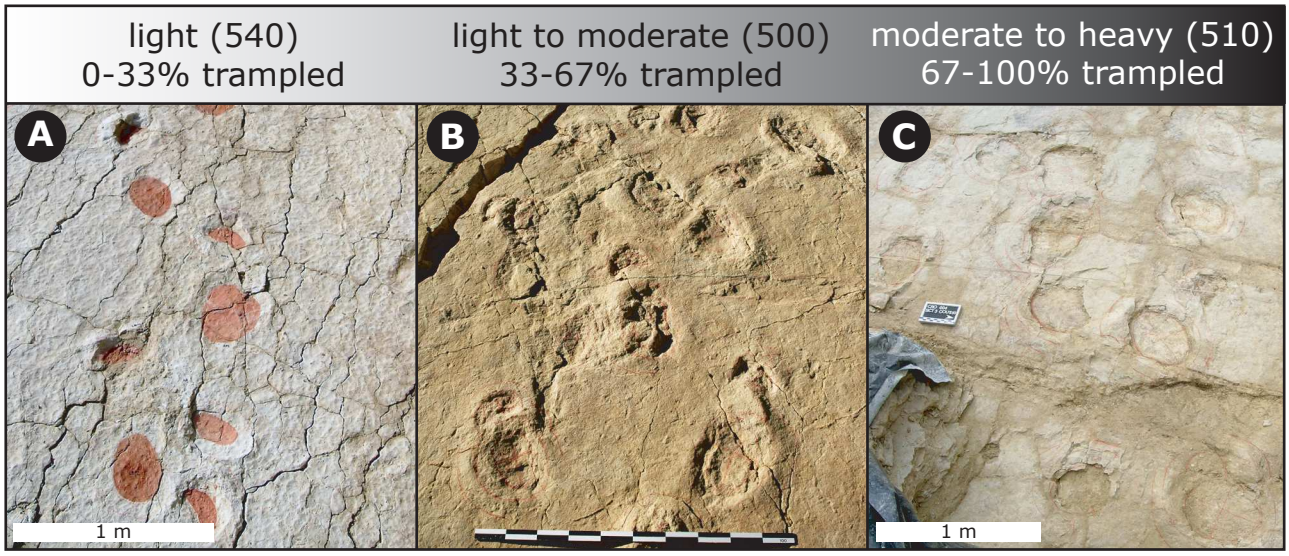


Fig. 4.14: Chevenez—Combe Ronde tracksite: Assignation of the dinoturbation index following Lockley & Conrad (1989, Fig. 14.2). **A:** Manus-dominated sauropod trackway S1 of level 540, excavation area 2, tracks are coloured. **B:** Two parallel trackways (S12 and S13) of tiny sauropods heading to the top, crossed in the upper right by trackway S11 of a small sauropod heading to the lower right, excavation area 2, scale bar is 1 m. **C:** Isolated sauropod pes tracks on level 510, excavation area 3. Note that this figure is not schematic and shows the most typical examples for the different dinoturbation ranges at the Combe Ronde site.

Fig 4.13 (opposite page): Chevenez—Combe Ronde tracksite: Macrosedimentary surface features of the excavated levels. **A:** Level 500, main track level, excavation area 3: slightly sinuous desiccation cracks with a polygon diameter ranging between 10-20 cm. Scale bar is 20 cm. **B:** Level 501, 1 cm above the main track level, excavation area 2: same desiccation crack pattern as on level 500. Scale bar is 20 cm. **C:** Base of level 505, excavation area 2: same desiccation crack pattern as on levels 500 and 501. This desiccation crack pattern is clearly larger than the one on top of layer 505 (figured in D). Note the track fill of a manus print (S10-RM9) of the main track level, which is also cut by the desiccation cracks (upper left of the slab). Hammer for scale. **D:** Level 505, excavation area 1: slightly sinuous desiccation cracks with a polygon diameter ranging from 5-10 cm. On this level, poorly-defined overtracks of deep pes footprints of the main track level were frequently found, and are cut by the desiccation cracks (compare with Fig. 4.18). These are the smallest desiccation cracks of all uncovered levels. **E:** Level 515, excavation area 1: in the upper left slightly sinuous, bifurcated wave ripples, presumably preserved by a microbial mat cover. On the lower right healed desiccation cracks, but no wave ripples. **F:** Level 515, excavation area 3: symmetrical wave ripples (upper right), presumably preserved as a ripple patch and cut by slightly sinuous, healed desiccation cracks (lower left) with a polygon diameter ranging from 10-20 cm. Scale bar is 20 cm. **G:** Level 530, excavation area 3: desiccation cracks with slightly raised (upturned) edges and a polygon diameter ranging from 15-30 cm. These are the largest desiccation cracks of all uncovered levels. The dashed line marks the hypothetical midline of sauropod trackway S1 with the very shallow tracks. The length of the scale bar is 3 m. **H:** Level 540, excavation area 2, with wrinkle marks. Scale bar is 20 cm.

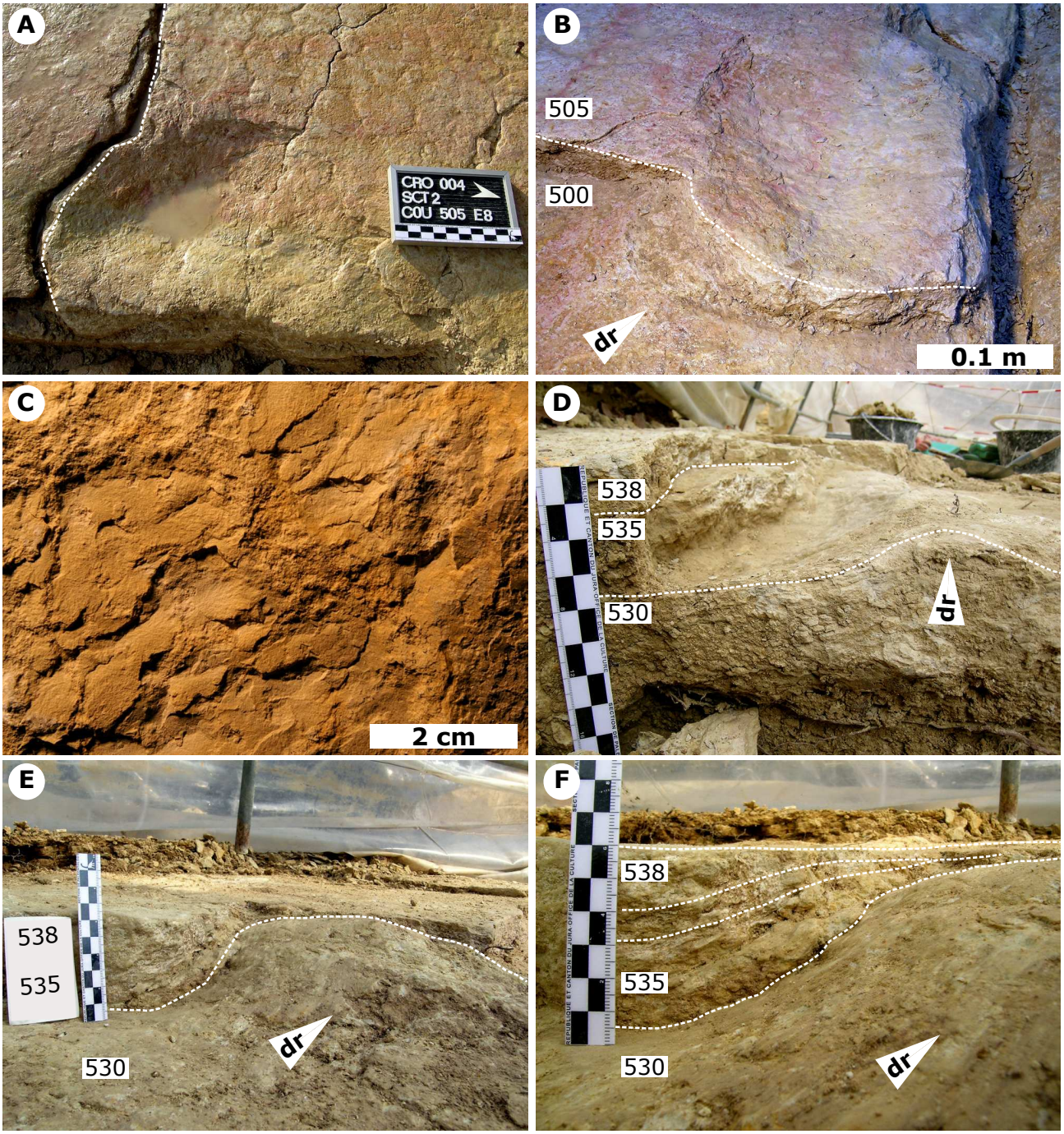


Fig. 4.15: Chevenez—Combe Ronde tracksite: Track burial and formation of overtracks. **A:** Level 505, track E8, excavation area 2: overtrack of the pes track S9-LP3 of the main track level (500). There is no displacement rim visible and the internal and external outline of the track is poorly defined. **B:** Level 505, track E8, excavation area 2: same overtrack as in A, but here the true track on level 500 has been excavated up to the white dashed line (also indicated in A). The displacement rim on the main track level (500) becomes visible. **C:** Lower bedding plane of layer 505, excavation area 2, track fill (CRO004-228) of S11-RM3 of the main track level: oblique, thin laminae at the base of the track fill due to repeated growth of microbial mats within the track, leading to the formation of internal overtracks and an amalgamation of the track fill. **D:** Level 530, sauropod pes track E3 in cross-sectional view, excavation area 2: this track was buried by levels 535 and 538, without forming an overtrack on level 538. **E:** Level 530, sauropod pes track S2-RP2, excavation area 3: the large displacement rim was covered without forming an overtrack. A cross-section of this print is illustrated in Figure 4.10. **F:** Detail of E: note how layer 535 is thinning out towards the displacement rim. Scale bars in A and D are 20 cm; in E and F 10 cm; "dr" = displacement rim.

formation of overtracks on level 520, which is also disclosed by the section of track T10 of level 520 (see also chap. 4.3.4.1), probably by repeated growth of microbial mats. They also induced the formation of undertracks on level 510. The shallower tracks, i.e., those with a reduced vertical topography and narrow displacement rims, on the other hand, are suggested to be undertracks of level 520 because they were mostly better defined and deeper their counterparts on level 520. Many of these were equally reported on level 510 (Fig. 4.16D). Level 515 had a comparatively high dinoturbation index because it bore both true tracks and undertracks. From a purely morphological point of view, it would not be possible to distinguish between the true tracks and undertracks. This is possible only with the surface data from the over- and underlying levels, and still an unequivocal identification of each single track is impossible. This is the reason, why an identification of trackways was difficult. The symmetrical ripple marks are interpreted as wave ripples left in very shallow (probably not deeper than a few cm) water before the surface was subjected to desiccation. As the wave ripples occur only locally, they may be explained as ripple patches in erosion pockets on a microbial-mat-covered surface (Schieber, 2007; Gerdes et al., 2000). The healed desiccation cracks indicate a renewed growth of a microbial mat after a phase of desiccation.

4.3.5.5 Level 520

Description

Smooth and flat surface without desiccation cracks. Sauropod pes tracks were either well-defined, up to 10 cm deep, and surrounded by large displacement rims (Fig. 4.12E), or they were rather shallow with flat and broad displacement rims (Fig. 4.6). Some tracks resembled manus tracks, but clear manus tracks were not identified. About half of the tracks of level 520 were also encountered on the underlying levels 515 and 510 (Fig. 4.16D). The dinoturbation index is moderate. No evidence for ripple marks or desiccation cracks was found.

Interpretation

The deep tracks with the large displacement rims are believed to be true tracks, because their counterparts on levels 515 and 510 are shallower and larger (Fig. 4.17). Not all true tracks of level 520 caused the formation of undertracks on the underlying levels, which was probably related to lateral changes in the consolidation state of the sediment. This is also disclosed by the cross-section of track T16, which reveals only faint undertracks without displacement rims (see also chap. 4.3.4.2), difficult to identify in a surficial view. Many of the shallower tracks with broad and flat displacement rims, on the other hand, are probably overtracks of level 515, which is also suggested by the cross-section of the track T10 (see also chap. 4.3.4.1). The absence of desiccation cracks suggests that surface 520 has not been subjected to subaerial exposure prior to burial, either because of a higher water table, a very short period of emersion, and/or the presence of a coherent microbial mat not susceptible for crack formation by desiccation. The absence of overtracks (even above the deepest tracks) in cross-sections of track fills and on level 525 can be explained by rapid deposition of layer 525, which prevented the growth of microbial mats and peneplained the area.

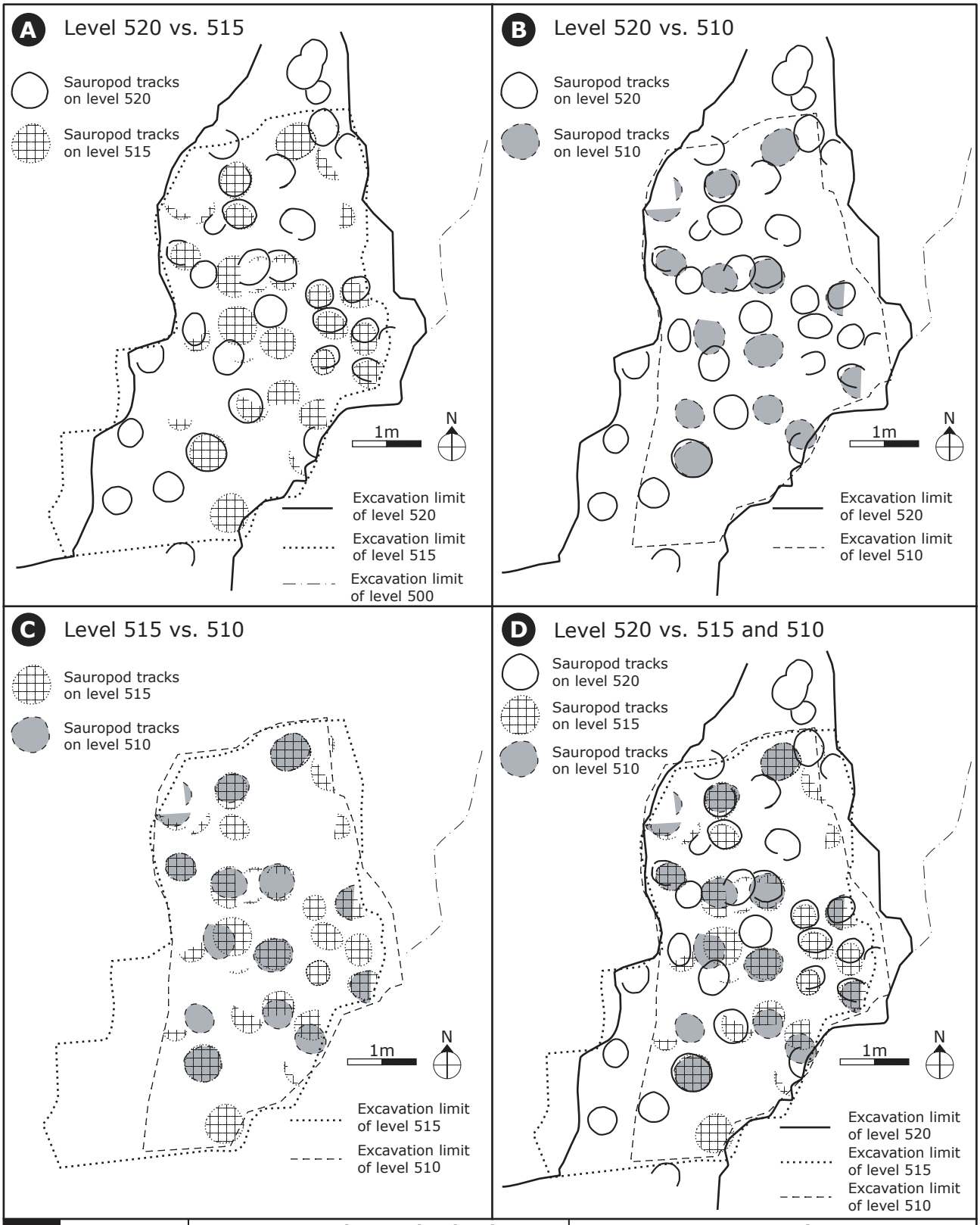
4.3.5.6 Level 530

Description

This surface exhibited both deep (up to 10 cm), well-defined sauropod tracks with large displacement rims (Fig. 4.12F, Figs. 4.15D & F), and very shallow (up to 2 cm), almost indiscernible, poorly-defined tracks without any displacement rims (Fig. 4.12G). This surface was characterized by comparatively large, slightly sinuous desiccation cracks with a polygon diameter ranging from 15-30 cm. The desiccation cracks were further characterized by slightly raised edges and they had a healed aspect (Fig. 4.13G). The deep tracks formed a pes-only trackway (S2), whereas the shallow tracks were organized in a quadrupedal trackway (S1). The dinoturbation index was light to moderate.

Interpretation

The well-defined tracks on level 530 and the absence of tracks on levels below or above indicate true tracks. The deep and shallow tracks are in very close proximity, suggesting that they were left during two different time intervals. The deep tracks were probably left in a water-saturated, unlaminated carbonate mud, which was subsequently covered by a microbial mat (layer 531) and afterwards subjected to a relatively long period of desiccation, as indicated by the largest desiccation cracks of the studied interval. This led to the growth of a thick microbial mat and the formation of desiccation cracks with slightly raised edges, which typically form when a thick microbial mats is subjected to desiccation during the dry season or a period of drought (e.g., Hardie & Garrett, 1977; Demicco & Hardie, 1994; pers. obs.): The upper surface dries more quickly than the base



E		**Same tracks on other levels**			**Interpretation**		
Level		520	515	510	true tracks	undertracks	overtracks
520	top (youngest)		about 50%	about 50%	in part	none	of 515
515	intermediate	about 50%		about 50%	in part	of 520	none
510	base (oldest)	about 50%	almost 100%		none	of 515 & 520	none

(Kendall & Skipwith, 1969), resulting in differential capillary contraction that breaks the mat free of the substrate (Bradley, 1933). The shallow tracks were left in this microbial mat when it was almost dry, probably during or after the formation of the desiccation cracks. Wetting of the surface led to renewed growth of a microbial mat and to the healing of the desiccation cracks.

4.3.5.7 Level 540

Description

This surface was characterized by shallow and poorly-defined as well as by relatively deep, well-defined sauropod tracks within a single trackway (trackway S1). This trackway was manus-dominated, i.e., the manus tracks were much deeper than the shallow pes tracks. Manus tracks were well-defined and surrounded by medium-sized, broad displacement rims in the anterior part of the track. Pes tracks were poorly-defined and lacked displacement rims (Fig. 4.12G). Further, the surface was covered with wrinkle marks and desiccation cracks with a polygon diameter ranging from 10-15 cm (Fig. 4.13H). The desiccation cracks cut through the sauropod tracks and wrinkle marks and are healed. The dinoturbation index was light (Fig. 4.14A).

Interpretation

Well-defined tracks together with an absence of tracks on levels below and above indicate true tracks. This is supported by the presence of healed desiccation cracks cutting wrinkle marks. Wrinkle marks were originally named *Runzelmarken* (Häntschel & Reineck, 1968; Reineck, 1969), they are generally related to the former presence of a microbial mat (for reviews see Porada & Bouougri, 2007a, b), and they are most commonly found in the intertidal zone of coastal plains (Eriksson et al., 2007a).

Subjected to a couple of years of weathering, this trackway would possibly have resulted in a manus-only trackway with pes tracks not discernible anymore, due to the relatively marly and not very hard sediment. Accordingly, manus-only trackways are not always undertracks or underprints (e.g., Lockley & Rice, 1990; Vila et al., 2005), but can also be explained as weathered "true trackways".

4.3.5.8 Level 542

Description

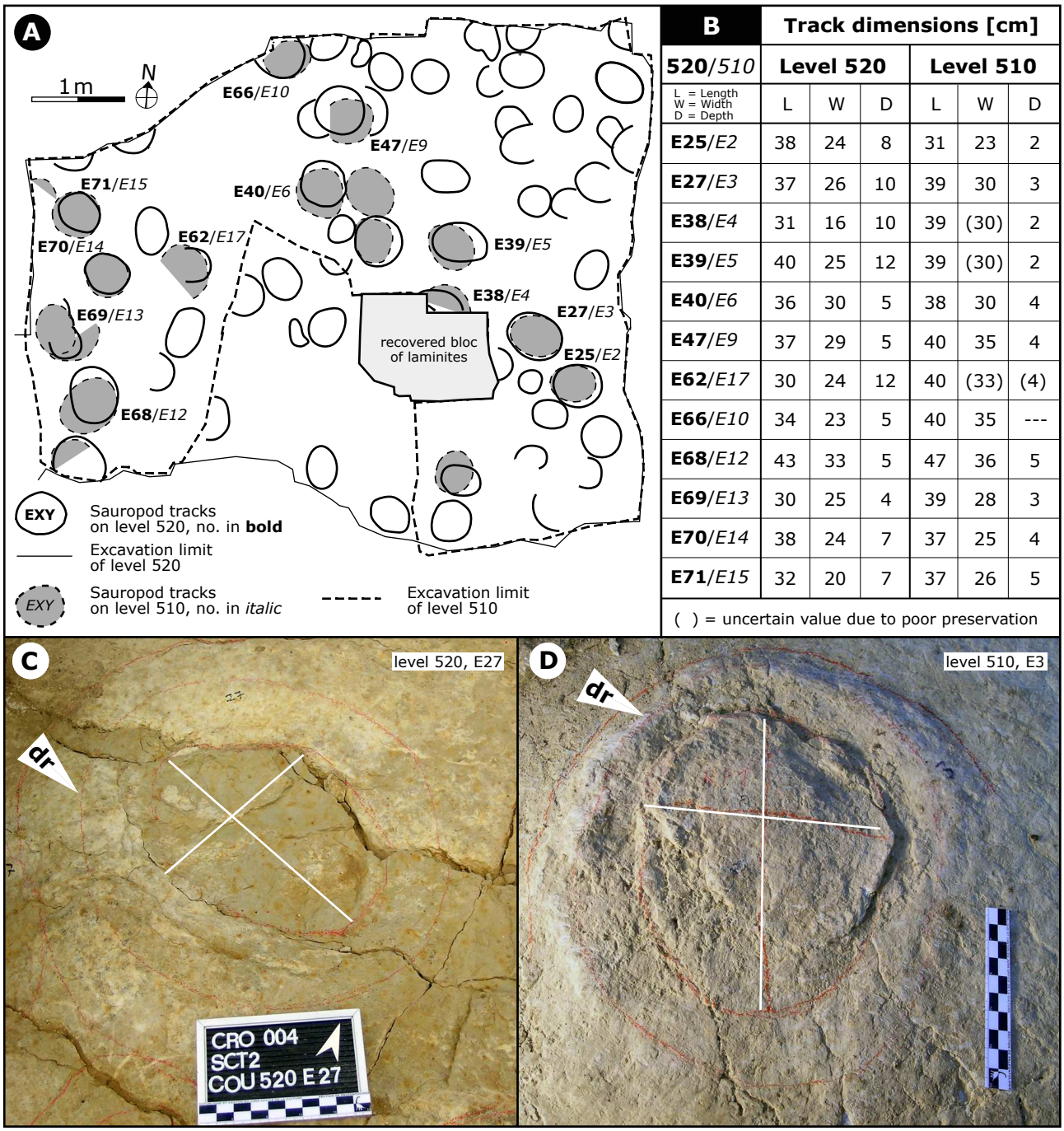
This level had an irregular surface and was uncovered only in excavation area 3 on a small surface, where it yielded some poorly-defined sauropod tracks with small or no displacement rims, most of which resembled manus tracks. The surface was covered with small desiccation cracks with a polygon diameter of about 10 cm. The dinoturbation index was very light.

Interpretation

Even if no trackways could have been identified, the tracks are considered as true tracks because no counterparts were found on the over- and underlying levels. As the excavated surface is located far away from the excavated surface of level 540 in excavation area 2, a precise correlation of the levels at the thinly-bedded top of the laminites was not possible. It can not be excluded that this may be the same horizon as level 540 in excavation area 2, also because the tracks rather resemble manus than pes tracks.

Fig. 4.16 (opposite page): Chevenez—Combe Ronde tracksite, excavation area 3. **A-D:** Comparison of the tracks of the three levels 520 (youngest), 515 (intermediate), and 510 (oldest) by superimposition of the maps. For location of the levels within the laminites refer to Figs. 4.1 and 4.3. **E:** Table outlining and interpreting the comparison:

Level 520 vs. level 515 (**A**):	About half of the tracks of each level were found on the other level.
Level 520 vs. level 510 (**B**):	About half of the tracks of each level were found on the other level.
Level 515 vs. level 510 (**C**):	All except one track of level 510 were found on level 515, about half of the tracks of level 515 were found on level 510.
Level 520 vs. levels 515 and 510 (**D**):	Just a few tracks were only found on a single level. Those only found on level 520 are true tracks without undertracks. Tracks only found on levels 515 or 510 were located in areas, where the interval between levels 510 to 520 was amalgamated and where the three levels could thus not be properly excavated.



B

520/510	Track dimensions [cm]					
	Level 520			Level 510		
L = Length W = Width D = Depth	L	W	D	L	W	D
E25/*E2*	38	24	8	31	23	2
E27/*E3*	37	26	10	39	30	3
E38/*E4*	31	16	10	39	(30)	2
E39/*E5*	40	25	12	39	(30)	2
E40/*E6*	36	30	5	38	30	4
E47/*E9*	37	29	5	40	35	4
E62/*E17*	30	24	12	40	(33)	(4)
E66/*E10*	34	23	5	40	35	---
E68/*E12*	43	33	5	47	36	5
E69/*E13*	30	25	4	39	28	3
E70/*E14*	38	24	7	37	25	4
E71/*E15*	32	20	7	37	26	5

( ) = uncertain value due to poor preservation

Fig. 4.17: Chevenez—Combe Ronde tracksite, excavation area 2: Comparison of the excavated levels 510 and 520. **A:** Superimposition of the maps. About half of the tracks of level 520 were not found on level 510. Almost all tracks of level 510 were also found on level 520, and the congruence is very good. Those tracks of level 510, which were not found on level 520 are probably undertracks from level 515, which was not excavated in this area because it was amalgamated with layer 520. **B:** Table showing the track dimensions of measured tracks, occurring on both levels. Note that almost all tracks of level 520 are clearly smaller and deeper than those of level 510, which are comparatively larger and shallower. **C:** Level 520, track E27: moderately deep true track with a large and broad displacement rim ("dr"). **D:** Level 510, track E3: shallow undertrack of the true track shown in C. Note the smaller and narrower, weakly-developed displacement rim when compared with C. Scale bars in C and D are 20 cm, long and wide axes are indicated.

Table 4.1 (opposite page): Chevenez—Combe Ronde tracksite: Characteristics of macrosedimentary surface features and sauropod tracks and trackways, and interpretation of the tracks, the sediment in which the tracks were left, and the surfaces. Note the rareness of manus tracks on levels 505, 510, 515, and 520. These are also the only levels with undertracks and overtracks, suggesting that manus tracks were either frequently overprinted or that they were smaller and less deeper and thus less susceptible to form undertracks and overtracks than the pes tracks.

Level		500	505	510	515	520	530	540	542
Total excavated surface [m²]		~600	~30	~50	~30	~100	~50	~15	~5
Macro-sedimentary surface structures	Desiccation cracks: 1. Distribution 2. Diameter [cm] 3. Interferences and other particularities	entire surface 10 - 20 cut tracks	entire surface 5 - 10 cut tracks *Skolithos* burrows	absent	not entire surface 10 - 20 healed, cut tracks and wave ripples	absent	entire surface 15 - 30 healed, cut tracks, raised edges	entire surface 10 - 15 healed, cut tracks and wrinkle marks	entire surface ~10 cut tracks
	Ripple marks	absent	absent	absent	wave ripples not on entire surface	absent	absent	wrinkle marks on entire surface	absent
Sauropod tracks & trackways	Total amount of pes and manus tracks	264	26	74	40	137	38	22	6
	Presence of manus tracks	frequently present	always absent	a few isolated tracks resemble manus tracks	a few isolated tracks resemble manus tracks	a few isolated tracks resemble manus tracks	only present on trackway S1	frequently present	most tracks resemble manus tracks
	Pes length size range [cm]	17 - 57	27 - 43	~20 - 58	27 - 40	~20 - 43	~29 - 56	17 - 35	no clear pes tracks
	Pes depth size range [cm]	1 - 9	90	1 - 9	3 - 9	1 - 12	1 - 10	2 - 3	1 - 2 (manus-like tracks)
	Definition of external outline	reasonable to good	90	good	reasonable to good	reasonable to good	poor to good	reasonable to good	poorly to reasonable
	Definition of internal morphology	reasonable to very good	very poor	poor to reasonable	poor to good	poor to good	very poor to good	poor to good	poor
	Size & definition of displacement rims	1. large, high, well defined (S3-S17) 2. absent (S1-S2	always absent	small, flat, narrow, well defined	1. small, flat, narrow, poorly defined 2. large, high well defined	1. large, high, well defined 2. large, flat, broad, poorly defined	1. large, high, well defined (S2) 2. absent (S1)	1. absent (pes) 2. large, high, well defined (manus)	1. small, poorly-defined 2. absent
	Particularities	best-defined tracks, deep & shallow tracks	(very) shallow and poorly defined pes prints	shallow prints with small & narrow displacement rims	shallow & deep tracks, often amalgamated with layer 520	shallow & deep tracks, deepest tracks of all levels	very deep (S2) and very faint (S1) tracks	best-defined tracks besides level 500, deep & shallow tracks	most structures no clear tracks, rather manus than pes tracks
	Tracks attributed to trackways	by the majority	all	exceptional case	exceptional case	exceptional case	by the majority	by the majority	none
	Number of trackways	15	4	3	2	3	2	1	none
	Trackway patterns	quadrupedal and pes-dominated	pes-only	pes-only	pes-only	pes-only	quadrupedal and pes-only	manus-dominated	---
	Dinoturbation index	very light to moderate	very light	moderate to here and there heavy	moderate	moderate	light to moderate	light	very light
Same tracks on other excavated levels (A=All, NA= Not all, none)		505 / NA	500 / A	515 / NA 520 / NA	510 / NA 520 / NA	515 / NA 510 / NA	none	none	none
Interpretation	True tracks	all	none	none	in parts	in parts	all	all	all
	Underprints	none	none	none	none	in parts on top of layer 516	trackway S2 on top of layer 528	none	none
	Undertracks	none	none	all of levels 515 and 520	in parts of level 520	none	none	none	none
	Overtracks	none	all of level 500	none	none	in parts of level 515	none	none	none
	Internal overtracks	commonly present	absent	absent	absent	absent	in deep pes tracks	absent	absent
	Sediment properties during track formation	unlaminated carbonate mud, probably covered by a microbial mat	biolaminite at the base, unlaminated carbonate mud at the top	(partially) consolidated biolaminite covered by a microbial mat	biolaminite covered by a (thick) microbial mat	biolaminite probably covered by a microbial mat	unlaminated carbonate mud later overgrown by thick microbial mat	biolaminite covered by a microbial mat	biolaminite probably covered by a microbial mat
	Sediment water content during track formation	1. water unsaturated to moist 2. moist to dry	?moist to water saturated	dry to water saturated	water unsaturated	water unsaturated to saturated	1. water unsaturated to saturated 2. almost dry	moist to dry	water unsaturated to moist
	Surface	subaerial palaeosurface with 2 generations of true tracks	subaerial palaeosurface with shallow overtracks of level 500	bedding plane (depositional surface) with undertracks of levels 515 and 520	subaerial palaeo-surface with true tracks & undertracks of level 520	palaeosurface with true tracks and overtracks of level 515	subaerial palaeo-surface with 2 generation of tracks (true tracks and underprints)	subaerial palaeosurface with true tracks	subaerial palaeosurface with true tracks

4.4 Discussion

4.4.1 Sauropod true tracks, undertracks, and overtracks

It has long been understood that a correct identification of true tracks and undertracks is crucial in ichnotaxonomy and for palaeoecological and palaeoenvironmental interpretations (e.g., Hitchcock, 1858; Manning, 2004; Milàn & Bromley, 2006). As highlighted in Chapter 3, the distinction is furthermore complicated by the presence of poorly-preserved true tracks, true tracks with extramorphological features, modified true tracks, internal overtracks, and overtracks. This suggests that only a very small proportion of the tracks in a given area are well-defined, unmodified true tracks, capable of yielding reliable taxonomic information about the animals that made them (Allen, 1997).

Most dinosaur tracksites are natural sites that have not been excavated, and many are protected *in situ* as they are considered geotopes or geosites (e.g., Marty & Hug, 2003; Thüring et al., 2003, 2007; Marty et al., 2004; Breithaupt et al., 2006; Meyer & Thüring, 2006; Milner et al., 2006; Bates et al., 2008). Thus, they are often weathered and/or not susceptible for excavation revealing underlying

Water content		**dry (low or negligible)**	**moist (moderate)**	**water unsaturated (high)**	**water saturated (very high)**
Mud properties Allen, 1997	consistency	firm and hard	stiff	soft	semi liquid
	characteristics	desiccation cracks	readily moulded, tends to adhere to surfaces, tracks may serve to localize desiccation cracks	little tendency to flow and collapse, tends to adhere to surfaces, no desiccation cracks	ability when disturbed to flow and/or collapse, no desiccation cracks
	yield strength	high	moderate	low	very low
General morphology of (sub-)recent tracks left in mud Scrivner & Bottjer, 1986 Allen, 1997		almost no deformation, shallow prints with no displacement rims, crinkled edges, preservation of finest anatomical details (skin impressions) is possible in firm mud	best-defined tracks with high resolution of substantial anatomical details, no or weakly-developed displacement rims	no grosser anatomical features, sometimes impression of pad, toe and interdigital ridge structure, well-developed displacement rims	mostly collapsed, poorly-developed displacement rims, lack of internal structure such as toe outline and pad or interdigital ridges, very low preservation potential
General morphology of human tracks left in microbial mats (Chapter 3)		poorly-defined, cracked surface, only gross foot outline, formation of underprints if mat is broken and pushed into underlying not dry sediment	shallow and well-defined with anatomical details of the toes, small, poorly-defined displacement rims or no displacement rim	great variability of footprint morphology depending on the underlying sediment, generally well-defined but seldom with anatomical details, surrounded by large and well-defined displacement rims	only poorly-defined tracks, deep tracks and underprints frequently formed
Morphology of sauropod true tracks at the Chevenez—Combe Ronde tracksite		(very) shallow poorly-defined tracks, gross internal outline without anatomical details, no displacement rims, always associated with desiccation cracks (sometimes with raised edges)	shallow to moderately deep, well-defined tracks, well-defined internal outline sometimes with anatomical details of the toes, small and rather narrow, weakly-developed displacement rims,	deep, reasonably- to well-defined tracks, reasonably-defined internal outline without anatomical details of the toes, large and broad, well-defined displacement rims	**water unsaturated to water saturated:** very deep, reasonably-defined tracks, poorly-defined internal outline, large and broad poorly-defined displacement rims ► No deep tracks at the Combe Ronde site
Levels at the Chevenez—Combe Ronde tracksite		500 (shallow tracks) 530 (shallow tracks) 540 (shallow pes tracks)	500 (deep tracks 540 (deep manus tracks) 542	500 (deep tracks) 515 520 530 (deep tracks) 542	520 (deep true tracks) 530 (deep true tracks)

Table 4.2: Relationships between water content, sediment (mud) properties and the morphology of recent tracks and comparison with the sauropod tracks unearthed at the Chevenez—Combe Ronde tracksite.

surfaces and providing more detailed sedimentological data. In this sense, the Combe Ronde tracksite is an exception because, threatened by destruction due to the construction of the highway, it had to be excavated systematically level-by-level. This revealed eight superimposed, track-bearing levels, unmodified by recent weathering.

4.4.1.1 True tracks

At the Combe Ronde tracksite, true tracks of sauropods make up the majority of the tracks and were identified on all excavated levels, except on level 505 revealing overtracks only, and on level 510 revealing undertracks only. Besides a few tridactyl tracks with impressions of phalanges and claws on level 500, none of the excavated levels revealed tracks of sauropods with fine anatomical details, which would have readily identified them as true tracks. This absence of fine anatomical details is explained by the kinematics of the trackmakers, by improper sediment properties (namely the water content and/or the presence of a microbial mat), and also by modification after track formation or the presence of internal overtracks (amalgamated track fills).

That the water content of the sediment at the time of track formation is crucial and most strongly controls track morphology is commonly recognized (e.g., Soergel, 1925; Allen, 1997; Diedrich, 2002a, b; Billon-Bruyat & Mazin, 2003; Mazin et al., 2003; Manning, 2004; Milàn, 2006), and also confirmed by the study of human footprints in Chapter 3. Scrivner & Bottjer (1986), based on recent observations, and Allen (1997), based on experimental ichnology, classified footprint morphologies as a function of water (moisture) content, and Allen (1997) additionally as a function of the yield strength of the mud. In Table 4.2 the classification of these authors is summarized and compared with the human footprints in Chapter 3, and the sauropod true tracks from the Combe Ronde site.

This comparison suggests that the sauropod tracks were left in dry, moist and water-unsaturated sediment, and only exceptionally in water-saturated sediment. Deep tracks, which are typically formed in water-saturated, semi-liquid mud, were not found at all. Well-defined underprints typically forming in a thin layer of water-saturated mud on top of a consolidated layer were only detected on level 530, even though some of the tracks of level 520 may also be considered as underprints.

The best-defined tracks were left on levels 500 and 540, in moist sediment. They are generally not very deep, characterized by a well-defined internal outline and well-developed, rather narrow displacement rims. However, most of the excavated levels bore tracks left in moist to water-unsaturated sediment. These are deep, reasonably-defined to well-defined tracks surrounded by large and broad, well-defined displacement rims and an internal outline without anatomical details of the digits or the claws. Tracks left in quasi-dry sediment are only reported on levels 500 and 530, where they coexist with tracks left in moist to water-saturated sediment. Tracks left in dry sediment are very shallow, exhibit only the gross internal and external outline and lack displacement rims. As they do not show evidence for internal cracking, it is suggested that they were left in a thick, plastic and coherent microbial mat.

The majority of the tracks are surrounded by well-defined displacement rims because they were left in moist to water-saturated sediment. When subjected to destructive taphonomic processes (Fig. 3.11), the elevated displacement rims are likely the first part of a track that would be disintegrated, leading to the formation of modified (weathered) true track. However, as the displacement rims are generally well-preserved and never show evidence for disintegration, the tracks were never seriously affected by such processes. This suggests that most tracks were left in a low-energy, stable environment at the end or shortly after a period of rain or wetting, and that they were rapidly consolidated by desiccation and/or lithification (see below).

However, the track bottom, which contains the direct impression of the trackmaker's foot (the true track *sensu stricto*), was often difficult to precisely locate because track fills (internal overtracks) were frequently amalgamated within the overall track. This is presumably due to renewed growth of microbial mats, covering the bottom of the tracks and forming modified true tracks and/or internal overtracks. Such tracks are still termed true tracks (*sensu lato*), even if they rather are "true overall tracks" with a modified track bottom or with a track bottom covered by internal overtracks. Thus, the term true track is used here in the sense of an overall track, which is located on the tracked surface.

A true track *sensu stricto* is only the bottom of an overall track, which contains the direct impression of the trackmaker's foot. Accordingly, impressions

of fine anatomical details such as digits, foot pads, phalanges, claws, or skin (e.g., Currie et al., 1991; Gatesy, 2001; Currie et al., 2003; Lockley et al., 2003; Platt & Hasiotis, 2006; Milàn & Loope, 2007) readily identify true tracks. However, such fine details are absent in the majority of true tracks, which can sometimes be barely recognizable as tracks at all (see also chap. 3 and Fig. 3.5). This is related to improper physicochemical factors of the palaeoenvironment (e.g., substrate or preservation conditions), to covering of the foot by mud from a previous step, to the trackmaker's behaviour (e.g., Cohen et al., 1991, 1993; Nadon, 2001; Milàn, 2006), and/or because of taphonomic processes acting after track formation (Fig. 3.11). Besides, true tracks may also be recognized by the presence of recognizable track fills unconformably resting on the track bottom and the tracked surface (Tunis & Venturini, 2000). True tracks may be affected by recent subaerial erosion, once they are exposed in a natural outcrop (e.g., Milàn & Loope, 2007), even though Henderson (2006a) suggested that such weathered tracks could still be distinguished from undertracks.

At the Combe Ronde site, most tracks were only identified as true tracks through the level-by-level excavation and the superimposition and comparison of the documentation of the levels. This disclosed if better defined track-counterparts were present on levels above and/or below the excavated surface or not.

4.4.1.2 Undertracks

Undertracks were only found on two of eight excavated levels (levels 510 and 515). This suggests that their formation is not so common and necessitates particular conditions, even in (bio) laminated sediment.

Most of the undertracks are pes tracks and only a few resemble manus tracks. Level 510 is the only surface with undertracks only, stemming from two different levels (levels 515 and 520), and this explains why this is the surface with the highest dinoturbation index, despite that it is not a palaeosurface. Level 515 is a surface with true tracks and undertracks stemming from level 520. The true tracks of level 515 look quite similar to the undertracks. Many but not all of the undertracks of level 515 were also found on level 510, forming a stack of undertracks below the true tracks on level 520. Undertracks were never found more than 10-15 cm below the tracked surface of the true track. This corresponds also to the maximum track penetration.

Generally, the identified undertracks were increasingly worse defined, i.e., shallower (decrease in vertical topography), larger (increase in horizontal dimensions), and had narrower and smaller (weakly-developed) displacement rims than their corresponding true tracks (Fig. 4.19). Nevertheless, an unambiguous identification from a purely morphological point of view was very difficult and only possible by means of the superimposition of the level-by-level documentation.

Undertracks shallower, larger, and less detailed than their true tracks were produced in experimental ichnology with an emu (Milàn & Bromley, 2006). This can also be deduced from a stack of undertracks figured in Pittman & Gillette (1989; Fig. 34.10) from the Early Cretaceous of Arkansas, which was probably formed in a supratidal biolaminite with a high yield strength, because the laminae are bent but not broken. That the horizontal dimensions (length and width) are larger than in the true track can be explained because the pressure from the foot is transferred radially outwards (Allen, 1997).

The examined track cross-sections of the true tracks T16 of level 520 and T10 of level 515 reveal a more brittle deformation of layers 515 and 510 with a stack of faint, poorly-defined undertracks without displacement rims or no undertracks at all. This indicates lateral differences in sediment properties, such as already (partially) consolidated areas at the time of track formation, or maybe that not all tracks of level 520 were left at the same time.

Since the "dinostatic pressure" exerted by large sauropods on the substrate is very high (up to 30-40 metric tons/m^2; Lockley, 1991b), the formation of well-defined undertracks with displacement rims on levels 510 and 515 necessitated very particular sediment properties at the time of track formation on levels 515 and 520, that is a well-laminated, unconsolidated, moist to water-unsaturated biolaminite with high yield strength and a pronounced plastic behaviour. This sediment was deformed and compacted, but not penetrated by the foot. On recent tidal flats, moist to water-saturated sediment with such a pronounced lamination coupled with high yield strength and plasticity typically forms by repeated growth of smooth microbial mats, for instance on higher intertidal to supratidal, restricted flats or marshes, where microbial mats are generally not subjected to grazing and/or bioturbation. Consequently, undertracks offer important clues for the interpretation of the consolidation history of the sediment and the reconstruction of the palaeoenvironment. A similar

plastic deformation of microbial mats with a stack of undertracks has also been described by Avanzini et al. (1997) from sauropod tracks with displacement rims from the Early Liassic of Northern Italy.

The high resemblance between sauropod true tracks and undertracks has to be kept in mind when analysing vertebrate tracks. Even an excavated, well-defined track without any better-defined track on the overlying levels could be an undertrack, considering that the overlying sediment, in which the true track was left, may have been eroded after track formation. Lockley (1991b) suggested that this might be a common mechanism of track preservation, and that for this reason undertracks might be more easily preserved and more commonly found than true tracks.

4.4.1.3 Overtracks

Overtracks occur on levels 505 and 520, and they are clearly less frequent than true tracks and undertracks. They were never found more than 5-7 cm above the tracked surface of the true tracks. Overtracks on level 505 and on level 520 clearly differ from each other.

The overtracks on level 505 are rather shallow, poorly-defined tracks without displacement rims and a poorly-defined internal outline. They are found only on top of the larger, deep sauropod pes tracks of level 500, and are organized in pes-only trackways (Fig 4.18).

Track numbers		Track dimensions [cm]					
500	505	Level 500			Level 505		
	L = Length W = Width D = Depth	L	W	D	L	W	D
S8-LP2	E5	30	20	---	32	26	7
S8-RP2	E6	31	21	4	---	29	4
S9-LP3	E8	25	15	5,5	42	23	5
S9-RP3	E9	26	18	9	38	26	3
S10-LP4	E11	30	20	4	30	20	1
S10-RP4	E12	32	20	6	30	22	1
S10-RP5	E14	30	19	4	37	22	1
S10-RP6	E16	30	21	---	35	24	3
S11-LP4	E19	27	17	5	29	18	2
S11-RP4	E20	31	18	6,5	27	18	5
S11-LP7	E23	29	18	5	31	21	2
S11-LP5	E25	26	17	5,5	31	21	2

Table 4.3: Chevenez—Combe Ronde tracksite, excavation area 2: Track dimensions of true tracks of level 500 and their corresponding overtracks on level 505. Most of the overtracks are slightly larger and shallower than the true tracks. Only tracks measured on both levels are shown; the depth of some tracks of level 500 could not be measured because of the amalgamated track fill. Compare with Figure 4.18.

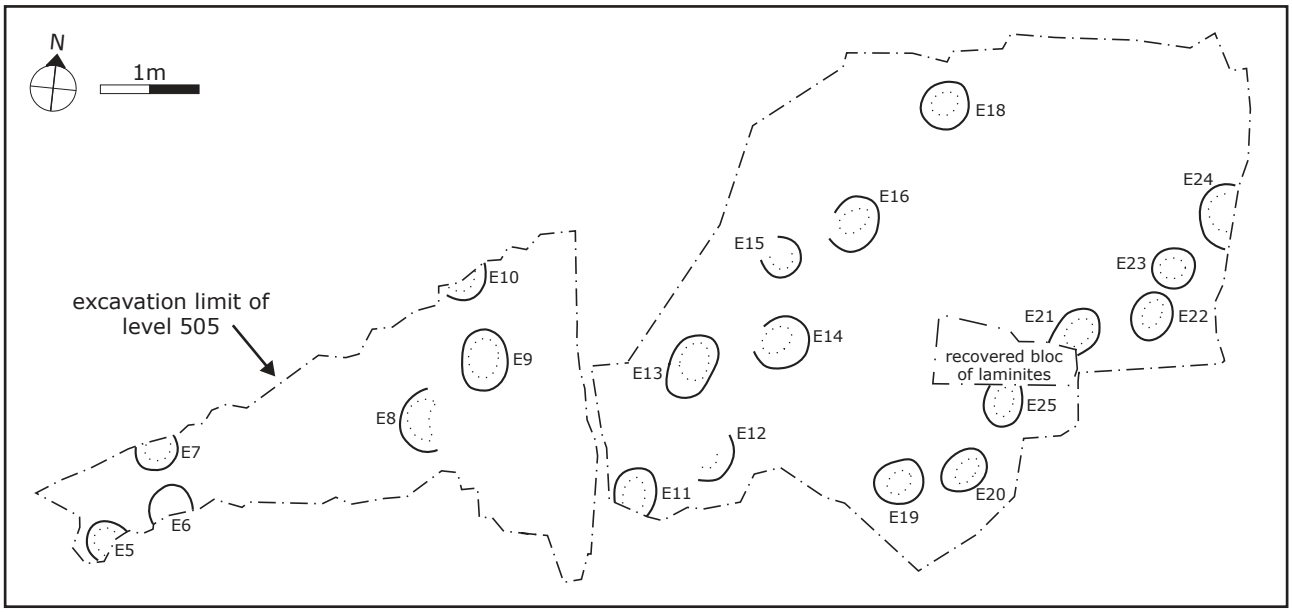


Fig. 4.18: Chevenez—Combe Ronde tracksite, excavation area 2, level 505: Overtracks of larger and deep pes tracks of the main track level are organized in parallel, pes-only trackways, difficult to interpret without uncovering of the underlying level. The overtrack E8 is shown in Figures 4.15A and B, and the dimensions of selected tracks are given in Table 4.3.

These overtracks are shallower and most but not all are also slightly larger than their true counterparts on level 500 (Table 4.3).

The overtracks on level 520 are reasonably-defined, surrounded by broad and flat displacement rims, and they are associated with similar deep true tracks surrounded by larger displacement rims. Thus, an unambiguous distinction from the true tracks is only possible in cross-section, where they display a consistent thickness on top of the true track of level 515. Most of the overtracks of level 520 are pes tracks, and only a few resemble manus tracks.

As a general rule, overtracks were shallower but rather larger than their true counterparts. The internal outline was always poorly defined, and if present, displacement rims were broader and flatter when compared with those of the true tracks. In comparison to the identified undertracks, overtracks are worse-defined (Fig. 4.19). However, an unambiguous identification from a morphological point of view, without the superimposition of the level-by-level documentation and cross-sections, was mostly not possible, because overtracks may be mistaken for true tracks left in a relatively dry, well-laminated sediment covered by a thick coherent microbial mat with high yield strength. Consequently, the overtracks on level 520 would not have been identified as such without excavation and without the analysis of the cross-sectioned tracks. The overtracks of level 505, on the other hand, may likely have been misinterpreted as parallel, either pes-only or manus-only trackways of sauropods.

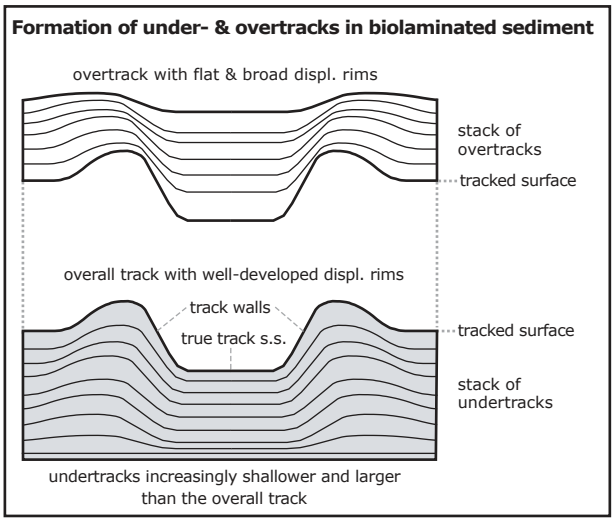


Fig. 4.19: Schematic figure for the formation of undertacks and overtracks at the Combe Ronde site. **Bottom:** Formation of a stack of undertracks in biolaminated sediment, which are increasingly shallower and larger than the true overall track. **Top:** Formation of a stack of overtracks with broad & flat displacement rims, and a poorly-defined internal outline due to the repeated covering of the whole tracked surface with microbial mats. These overtracks are increasingly shallower and slightly larger than the true overall track.

So far, the existence of overtracks was only briefly mentioned (e.g., Langston, 1986, 1987; Farlow, 1987; Pitman & Gillette, 1989; Paik et al., 2001), and their importance in ichnological and sedimentological studies was not fully recognized. However, because they tell us how a true track was incorporated into the sedimentary record, they provide an exceptional insight into the sedimentary regime of the palaeoenvironment. Absence of overtracks or faint overtracks without displacement rims indicate rapid covering of the true track by sediment. Overtracks with displacement rims, on the other hand, indicate a slow, continuous sedimentation, most probably by growth of microbial mats. Unlike undertracks, overtracks are easily identified by continuative excavation, if the level with the true track is not amalgamated within a thicker layer of sediment.

4.4.1.4 Internal overtracks

Internal overtracks were identified within shallow and deep sauropod pes and manus tracks of level 500 (layer 501, base of layer 505) and within deep sauropod pes tracks of level 530 (layers 531, 532, 535).

Internal overtracks are either formed by simple trapping of sediment within the track (e.g., Paik et al., 2001), by continuing growth of microbial mats, or by both processes alternating (Fig. 4.20). Internal overtracks cover the bottom of the track, i.e., the true track *sensu stricto*. At the same time, the rest of the track (track walls and displacement rims) can remain unmodified because trapping of sediment and growth of microbial mats preferentially take place in depressions, in occurrence, the track interior. Here, the growth of microbial mats is further stimulated because, after wetting, depressions remain moist longer than their surroundings. If the whole surface remains moist, microbial mats grow over the entire surface and overtracks tend to form instead of internal overtracks. The presence of stacks of internal overtracks within tracks left in a supratidal environment indicates that the given track or palaeosurface was consolidated but not covered up rapidly. If trapping of sediment was involved in the formation of internal overtracks, the lack

of extraclasts (e.g., coarser marine bioclastic material) at the track bottom implies that the palaeoenvironment was located relatively far from the coastline towards the marine realm, a lagoon, or a pond. The absence of intraclasts (e.g., mudclasts) further indicates that the surfaces were consolidated rapidly, preventing the formation of intraclasts by desiccation and reworking.

The well-defined lamination in the studied cross-sections and the absence of coarse track fills suggest that these internal overtracks were mainly formed by the growth of microbial mats, in an environment not located in (very) close proximity to the marine realm.

4.4.1.5 Relative frequency of true tracks, undertracks, and overtracks

Controversial opinions exist about the relative frequency of true tracks and undertracks in the vertebrate track record. Thulborn (1990) suggested that many dinosaur tracks described in the literature are undertracks rather than true tracks. Nadon (2001), on the other hand, claimed that the vast majority of tracks are true tracks. Lockley (1991b) stated that undertracks may be common in the fossil record because they are already within the sediment at the time of track formation, whilst the true track is more readily eroded.

At the Combe Ronde site, 967 identified true tracks account for the major part of the 1167 excavated tracks, even if the approximately 550 minute and small tridactyl tracks of the main track level are deduced from this number, resulting in over 400 true sauropod tracks. About 100 sauropod tracks were clearly identified as undertracks, and about 70 as overtracks (Fig. 4.21). The term true track is used in this comparison in the sense of a track, which is located on the tracked surface. It includes modified true tracks and tracks with internal overtracks, which probably make up most of the true tracks. True tracks *sensu stricto*, exhibiting the sediment, which was touched by the foot and hence anatomical details of the foot, were only exceptionally found on levels 500 and 540. Also, not all levels were excavated over the same surface and this is not considered in Figure 4.21. Thus, the frequency of true tracks may be over-represented judging from the analysed sample, because the main track level yielding most of the true tracks was by far excavated over the largest surface (Table 4.1).

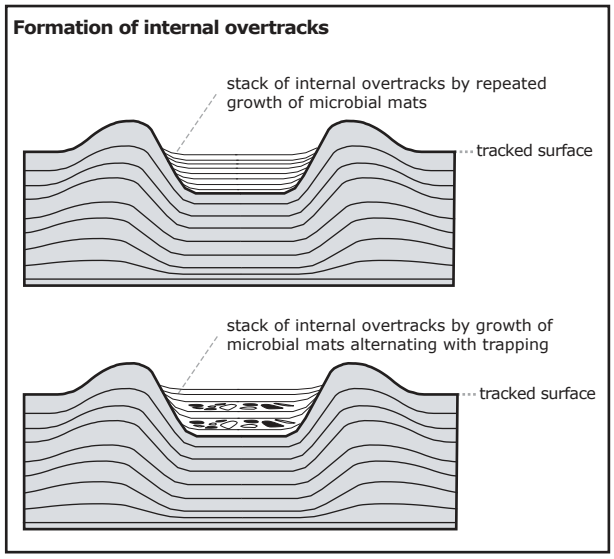


Fig. 4.20: Schematic figure showing the formation of internal overtracks by repeated growth of microbial mats (**top**), and growth of microbial mats alternating with trapping of sediment, e.g., due to storm sedimentation (**bottom**).

Overtracks and undertracks are nearly exclusively made up of pes tracks; no clear manus undertracks or overtracks were ever identified. Moreover, pes-only trackways were identified in the form of "under-" and "over-trackways". For the undertracks this is surprising, because in sauropod trackways manus tracks are often deeper than pes tracks, and manus-only trackways are commonly interpreted as undertracks (e.g., Lockley & Rice, 1990; Lockley et al., 1994b, Vila et al., 2005). Accordingly, manus tracks should at least as likely as pes tracks lead to the formation of undertracks. In the present case, the absence of manus undertracks can be explained by the predominance of pes-only trackways.

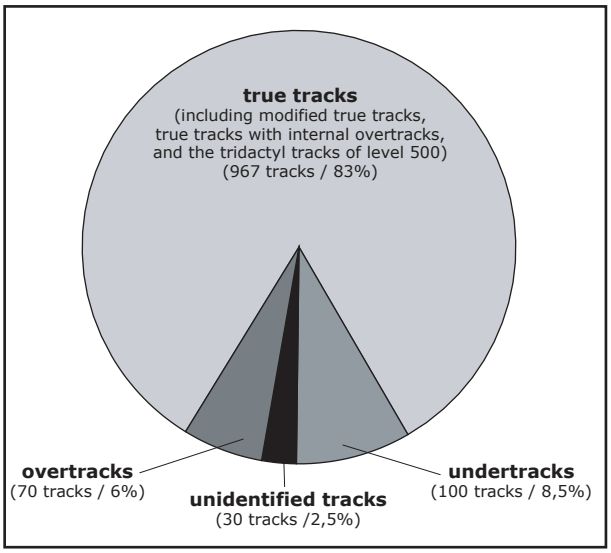


Fig. 4.21: Chevenez—Combe Ronde tracksite: Relative frequency of true tracks, undertracks, and overtracks of all excavated levels. Only the data of the systematic excavations (by the end of the year 2005) are included. Not all levels were excavated over the same surface and the main track level, yielding the majority of the true tracks, was excavated over the largest surface.

4.4.2 Palaeosurfaces

In peritidal environments on shallow carbonate platforms, only minimal accommodation space is available. Consequently, the sedimentary record represents only a small part of the geological time (Strasser et al., 1999, 2006). Because much of this missing time is spent in discontinuity surfaces during (subaerial) exposure, their analysis is important and can reveal information about depositional processes not necessarily indicated by the sedimentary facies alone (Hillgärtner, 1998, 1999). Discontinuity surfaces represent the time periods with the highest dynamics in environmental change (changes in energy regime, relative sea level, accumulation rate, and sediment type) during platform evolution, and they often mark a transition from shallower to deeper water facies (Hillgärtner, 1998, 1999).

Subaerial palaeosurfaces are recognized by emersion features such as desiccation cracks, rain drop marks, particular invertebrate and insect burrows, and true tracks of terrestrial vertebrates. As palaeosurfaces are always *in situ*, they occupy a key position in the reconstruction of terrestrial palaeoenvironments and ecosystems on carbonate platforms, which are otherwise not or only indirectly documented. Moreover, they are important for the reconstruction of sea-level changes, platform evolution, and palaeogeography. Finally, the understanding of processes that form and affect these surfaces leads to reliable outcrop correlations and an improved sequence-stratigraphic interpretation (e.g., Sattler et al., 2005).

At the Combe Ronde site, based on macrosedimentary features and the identification of true tracks and associated track features of sauropods (Table 4.1), seven out of eight excavated levels were identified as palaeosurfaces (levels 500, 505, 515, 520, 530, 540, 542), and only one level as bedding plane (level 510). Ongoing excavations of the PAL A16 suggest that several of these surfaces can be correlated with levels currently being excavated at the Courtedoux—Béchat Bovais tracksite located about 2 km to the north and the Chevenez—Crat site located 0,5 km to the east of Combe Ronde site (pers. obs.).

All identified palaeosurfaces are considered as subaerial, even though this does not exclude that they were never submerged (e.g., due to a surge of water after an exceptionally high tide, a heavy storm, or during a rainy period), and that some tracks were not left in a substrate that was covered by a few centimetres of water. On modern tidal flats, it is frequently observed that after heavy rainfall water may briefly cover subaerially formed tracks but does not alter their morphology.

All palaeosurfaces exhibited minor lateral variations, some were similar, but none was identical with another. The most common features of the palaeosurfaces are true tracks of sauropods and desiccation cracks. The general morphology of these true tracks varies between the palaeosurfaces and on levels 500 and 530 also over a single palaeosurface. This provides clues about the sediment properties and the water content of the sediment at the time of track formation. The presence of true tracks does not exclude the presence of undertracks (level 515) or overtracks (level 520) on the same surface, and a palaeosurface may bear overtracks without true tracks (level 505). The morphology of the true tracks indicates that all palaeosurfaces were moist to water-saturated, at least for a short period. This implies an environment affected by tides or spring-tides (e.g., tidal flat), or a supratidal environment (e.g., a supratidal flat or marsh), where wetting occurs during the rainy season, or due to sporadic storms in a more arid climate.

4.4.2.1 Desiccation cracks

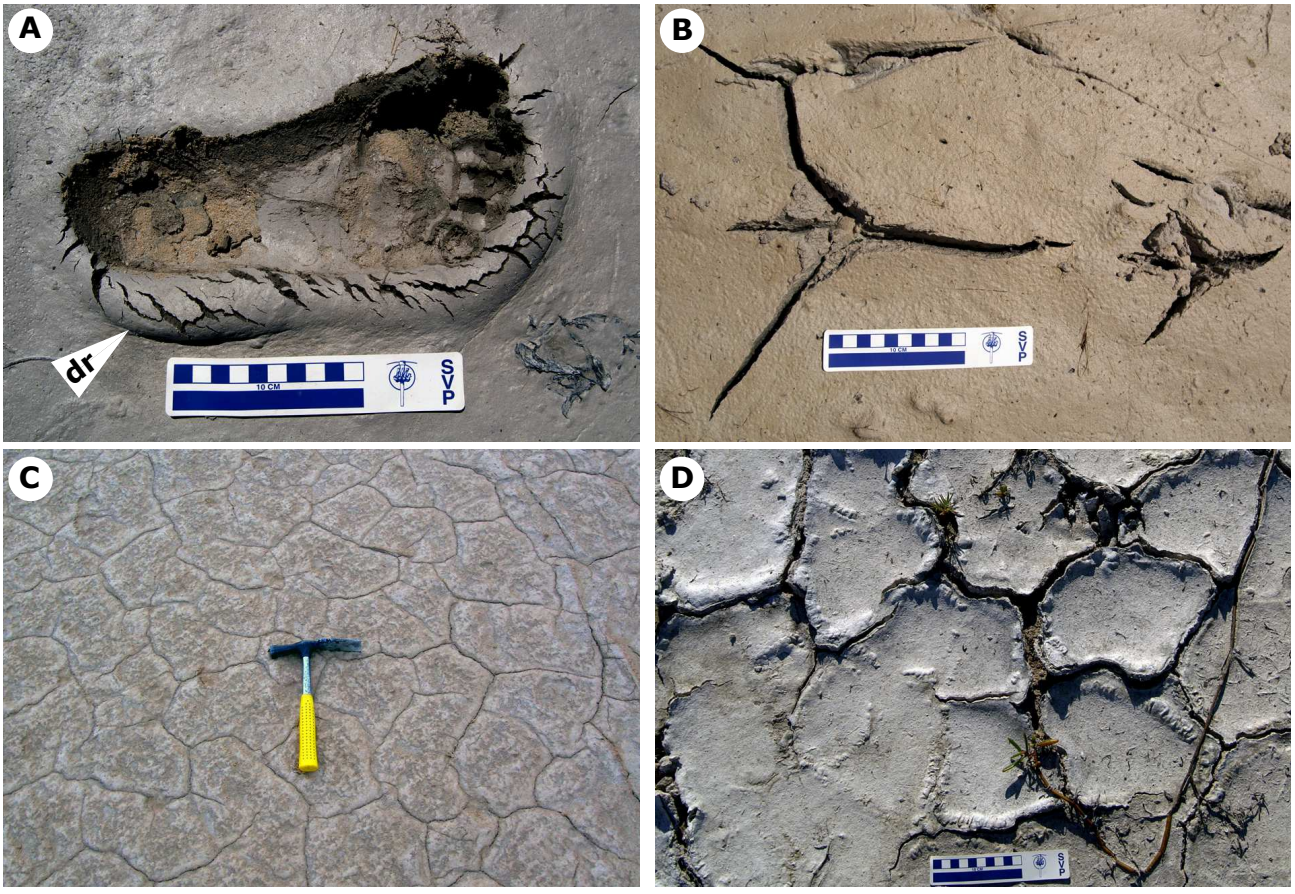
Desiccation cracks occur on all palaeosurfaces except on level 520, and they mostly formed after track formation. Only on levels 500 and 530 were tracks also left during or after the formation of desiccation cracks, when the sediment was almost dry as indicated by the shallowness of the tracks and the absence of displacement rims. On level 500, the distal ends of tridactyl tracks have here and there acted as a localizing agent for desiccation cracks (Fig. 4.22 and Fig. 4.23B), indicating that the tracks were made first. The displacement rims of sauropod tracks may have acted similarly, because in thick microbial mats or cohesive mud they are frequently cracked during track formation. This is due to the bending of the sediment, causing differential tensions at the base and the top of the layer (Fig. 4.23A).

Generally, all desiccation crack patterns are similar and characterized by an orthogonal to slightly curved, mostly triradiate ("triple junction"), polygonal crack pattern. Only on level 530 desiccation cracks with slightly raised edges were encountered. On levels 515, 530, and 540 healed desiccation cracks were observed, but weathered desiccation cracks do not occur. Only first order crack patterns were observed,



Fig. 4.22: Chevenez—Combe Ronde tracksite, natural cast of a small tridactyl track of the main track level (sample CRO004-273): Digits II and IV (white arrows) acted as localizing agents for desiccation cracks, "T" points to a *Thalassinoides*-type burrow. Compare with Figure 4.23B.

Fig. 4.23: Cracks and desiccation cracks in microbial mats of recent supratidal environments. A, B and D are from the supratidal flats of Ambergris Caye (Belize), C is from the supratidal flats of Sabkha Bou Jemel (southern Tunisia), scale bars are 10 cm. **A:** Cracking of the displacement rim due to the bending of the mat, causing differential tensions at the base and at the top of the mat. **B:** Tracks of a shorebird left in a thick water-saturated, gelatinous microbial mat on top of non-laminated, water-saturated carbonate mud. The track on the left acted as localizing agent for desiccation cracks. This enlarged and considerably modified the true track, when compared to the unmodified true track to the right. **C:** Orthogonal to slightly curved, mostly triradiate ("triple junction"), polygonal crack pattern. The cracks are healed by renewed growth of the microbial mat. This crack pattern is very similar to most of the patterns observed on the palaeosurfaces of the Chevenez—Combe Ronde tracksite (see also Figs. 4.14A, B & D). **D:** Slightly curved, mostly triradiate polygonal crack pattern with raised edges, similar to the desiccation crack pattern of level 530 shown in Figure 4.13G and Figure 4.12G.



and the fills of the cracks are always very similar to the surrounding sediment. Cross-sections of layers 542 to 546 reveal intralaminar shrinkage cracks, which indicate *in situ* fracturing of a consolidated layer (e.g., Shinn, 1968b).

On recent tidal flats desiccation cracks are a very common feature, which can take a variety of forms and sizes depending on the presence and nature of a microbial mat, the underlying sediment, the rate of draining, and exposure time (e.g., Kendall & Skipwith, 1968, 1969; Hardie, 1977a; Shinn, 1983b; pers. obs.). Generally, desiccation cracks are classified as mudcracks, prism cracks, or sheet-cracks, of which only mudcracks and prism cracks form subaerially (Demicco & Hardie, 1994). Sheet cracks form within the sediment (Hardie & Ginsburg, 1977). Prism cracks are a polygonal network of vertical cracks that break the sediment into vertical prisms (Fischer, 1964).

Generally, the desiccation cracks of all palaeosurfaces can be considered as mudcracks. Initial prism cracks were observed only on top of layer 501 and at the base of layer 505, which both reveal about the same crack pattern as the main track level, located 1-3 cm below. Some of the laminoid fenestrae may actually have been induced by desiccation rather than decay of microbial mats and may be considered as sheet-cracks.

It has been suggested that it may be possible to interpret minimum periods of subaerial exposure of palaeosurfaces from the distribution of mudcracks (Smith, 1993), and Shinn (1983b) assumed that mudcracks are generally best preserved in the supratidal and possibly the upper part of the intertidal zones. However, it is not so easy to correlate the size and morphology of desiccation cracks with the period of exposure and the palaeoenvironment because the sediment may consolidate or lithify rapidly. Moreover, thin layers generally form smaller polygons than thick layers (Shinn, 1983b), but the maximum diameter of mudcracks also depends on factors such as grain size (Demicco & Hardie, 1994), the presence and thickness of microbial mats, and the relation between submersion and exposure of the mat (Kendall & Skipwith, 1968). By the presence of a microbial mat, mudcracks may also perpetuate upwards with continuing growth of the mat, forming prism cracks. However, mudcracks do not necessarily form, even in microbial mats subaerially exposed for as much as 90% of the time, because the binding of the surface sediment by a thick and coherent mat frequently may prevent cracking (Demicco & Hardie, 1994; pers. obs.). This was also observed on supratidal flats of the Hassi Jerbi tidal flat (southern Tunisia), where coherent and completely dry mats are not cracked (Fig. 3.8) but consolidated in a way that they could only be disintegrated by cutting with a knife. The lack of mat desiccation features has also been described as a typical feature of subaerial laminated crusts of the Florida Keys (Multer & Hoffmeister, 1968). Thus, the absence of desiccation cracks does not indicate that a given palaeosurface was never emerged and dry.

Nonetheless, the crack patterns of all studied palaeosurfaces look similar to recent shrinkage cracks in coherent microbial mats of subtropical supratidal flats and marshes, which are characterized by a relatively small, shallow, mostly triradiate, polygonal network, which sometimes has raised edges and is often healed (Figs. 4.23C & D; Kendall & Skipwith, 1968; Monty & Hardie, 1976; Hardie & Garrett, 1977; Shinn, 1983b; Gaillard et al., 1994; Gerdes, 2007; Eriksson et al., 2007a, b). In these environments, polygonal cracking of the mat is believed to record extensive periods of exposure (Hardie & Garrett, 1977).

The generally small size of the desiccation cracks at the Combe Ronde site may be due to the relatively thin layers, which were probably originally covered by a thick and coherent microbial mat not susceptible for the formation of larger mudcracks. This may have been coupled with a fast consolidation and/or burial of the surface. This is also supported by the rarity of desiccation cracks with raised edges, and the general absence of rounded edges and higher order crack patterns.

4.4.2.2 Ripple and wrinkle marks

Wave ripple marks were only found on level 515, where they are cut by desiccation cracks. Wave ripples commonly form on intertidal flats, but they may also form in a supratidal setting, during the rainy season or after a major storm, when water is ponded on supratidal flats and marshes. Wave ripples and current lineations have frequently been reported from recent supratidal marshes (e.g., Hardie & Garrett, 1977; pers. obs.). In the supratidal realm, a preservation of wave ripples through overgrowth of microbial mats seems more likely than in the intertidal zone where the sediment surface is frequently subjected to levelling and erosion by tidal currents.

The wrinkle marks of level 540 are the only direct surface evidence for the former presence of microbial mats (e.g., Porada & Bouougri, 2007a, b). This is also

suggested by cryptmicrobial lamination seen in thin-sections (Fig. 4.2). Several samples of the laminites interval are currently analysed by Muriel Pacton (University of Geneva) for the PAL A16, in order to determine the nature of the organic matter (see Pacton et al., 2008 for methodology), and first results confirm a bacterial or microbial origin (M. Pacton, written comm., 2007).

4.4.2.3 Track taphonomy and consolidation of palaeosurfaces

The preservation of recent vertebrate tracks necessitates particular conditions, as footprints tend not to survive significant disturbance and as exposed tracks degrade rapidly after formation (e.g., Laporte & Behrensmeyer, 1980; Cohen et al., 1991, 1993), due to physico-chemical and biological processes (Fig. 3.11). A track can also be, on several occasions, partly filled, partly or wholly emptied, and its upper part erosively be modified (Allen, 1997; Fornós et al., 2002). However, other taphonomic processes may also favour track preservation (Fig. 3.11). In tidal-flat environments such processes are consolidation by desiccation, lithification by early cementation, or overgrowth by a microbial mat.

Within the laminites, the generally good preservation of true tracks suggests that the palaeosurfaces were consolidated shortly after their formation by comparatively rapid drying of the sediment or the microbial mat, in which they were left. This may have been aided by early cementation within microbial mats (e.g., Hardie, 1977b; Krumbein & Cohen, 1977; Pratt, 1979; Keller et al., 2000; Noffke et al., 2001b) or by dolomitization (Fig. 3.2A; Lucia, 1968; Shinn, 1968b; Gebelein et al., 1980; Gregg et al., 1992), which resulted in a rapid lithification of the surface.

An early consolidation is also implied by the presence of relatively small desiccation cracks, which are sometimes healed and show no evidence for prolonged desiccation (curled edges) or weathering (e.g., rounded edges, overturning, formation of mudchips). Early consolidation protected the palaeosurfaces and tracks from further taphonomic processes (physical & biological disturbance, Fig. 3.11), even during prolonged periods of subaerial exposure, and ensured that time averaging of the ichnoassemblage is negligible. However, a preservation of true tracks was also possible without previous significant consolidation, as disclosed on level 515, where true tracks and undertracks coexist (see also chap. 4.3.5.4).

4.4.3 Duration of subaerial exposure and covering up

The duration of subaerial exposure mainly depends on the location on the carbonate platform and climate, because even supratidal flats and marshes may remain submerged for longer periods under a humid climate. The presence of tracks may help to estimate this time period because the amount of time between track formation and burial is an important factor for their preservation (Laporte & Behrensmeyer, 1980). Nevertheless, over a period of subaerial exposure the track record may be wiped out several times, before consolidation and/or incorporation of the surface into the sedimentary record takes places. Consequently, a fossil ichnoassemblage is only a snapshot of the vertebrate activity on a given palaeosurface during a given time period; it is not necessarily representative for the vertebrate activity during the entire period of subaerial exposure.

The best preservation potential for tracks is given in a transgressive context without major erosion due to sea-level fall. Tracks are commonly preserved in environments that experience periodic or cyclic accumulation of sediments (Thulborn, 1990). More stable environments are less susceptible to track preservation than unstable, rapidly changing environments (Scrivner & Bottjer, 1986), and desiccation, short subaerial exposure and high accumulation rate of the capping sediments are important factors for footprint preservation (Tunis & Venturini, 2000). Thus, the probability of track preservation is minimal during long lasting periods of exposure.

In the recent, sub-tropical, supratidal environments of different climatic settings described in Chapter 3, consolidated surfaces with (modified) human (Fig. 3.8 and Fig. 3.9) and other vertebrate footprints were frequently met. Most of these surfaces were covered with a thick, coherent, and consolidated microbial mat, which was extremely hard to disintegrate. Such surfaces including tracks were sometimes even found submerged in hypersaline ponds, and they likely withstand significant modification by heavy rain or vertebrate trampling for years (Fig. 3.9B). This is also suggested by the study of Neumann et al. (1970), who showed that subtidal microbial mats could withstand direct current velocities three to nine times as high as the maximum tidal currents (13 cm/s) recorded in the mat environment.

4.4.3.1 Covering up by microbial mats

After wetting of a surface, renewed growth of a microbial mat may stabilize but also considerably modify a surface and lead to the formation of modified true tracks, internal overtracks or, if the whole surface is overgrown, overtracks (Fig. 4.19 and Fig. 4.20). Repeated growth may form stacks of internal overtracks or stacks of increasingly shallower overtracks with broad and flat displacement rims. This process is generally slow, particularly in arid settings. Growth rates of living mats are typically in the order of 2,0 to 2,5 mm per year, after desiccation and compaction, the accretion rate is around 0,2 mm per year (e.g., Tucker & Wright, 1990; Sanchez-Cabeza et al., 1999). Consequently, covering up by microbial mats indicates a slow, continuous process in a stable environment.

Within the studied laminite interval, evidence for covering up by microbial mats are stacks of internal overtracks within fills of deep tracks of levels 500 (layer 501 and base of layer 505) and 530 (layers 531, 532, 535), and well-defined overtracks with broad and flat displacement rims of level 515 on level 520.

The presence of overtracks on level 520 suggests that level 515, where the true tracks were left, was covered up slowly in a stable environment by the repeated growth of microbial mats, leading to the formation of a biolaminite and a stack of overtracks. On the other hand, true tracks left on level 520 still produced well-defined undertracks with displacement rims on level 515 and locally even down to level 510. Hence, the succession between layers 510 and 520 is the only place within the studied interval, where the sediment was not, or at least not everywhere, (significantly) consolidated prior to burial. This may indicate the presence of a thick, coherent microbial mat, which prevented the underlying biolaminated sediment from desiccation, a high water table, a humid period, and/or an environment with a relatively low exposure index. At the time of track formation on level 520, the underlying sediment from the bottom of layer 510 upwards was made up of a well-laminated, at least in places unconsolidated, coherent biolaminite with a high yield strength, which was easily deformed in a plastic way. Repeated growth of microbial mats is further supported by well-pronounced cryptmicrobial lamination and the absence of shellbeds in the numerous thin-sections of layers 510 to 520 analyzed.

Levels 500 and 530 are the only palaeosurfaces with two clearly different track generations left during the gradual drying of the substrate: deep tracks with displacement rims, and very shallow tracks without displacement rims. On these two levels the presence of (stacks of) internal overtracks can be explained by the growth of microbial mats essentially within the (deep) tracks. This is indicated on top of level 500 by layer 501 with well-defined cryptmicrobial laminations, and oblique, fine laminae at the base of layer 505. On level 530, stacks of overtracks within track fills of the deep tracks, and the well-laminated layers 531 and 532 on top of level 530 equally suggest the growth of microbial mats covering up level 530. This is also indicated by the amalgamated track fills. Because the filling of a track by the growth of microbial mats is a slow process, it is suggested that these two palaeosurfaces experienced the longest periods of subaerial exposure.

4.4.3.2 Covering up by rapid sedimentation

Many previous studies have suggested that spring tides, storms, and hurricanes have significant geomorphic and sedimentologic effects on coastal systems (Aigner, 1985). It has also been suggested that the geologic evolution of ancient tidal-flat successions may have been shaped by mega-storms of an intensity and duration not physically possible today (Rankey et al., 2004). However, today hurricanes do not always cause major changes such as shoreline erosion or channel migration within these environments (e.g., Boss & Neumann, 1993; Rankey et al., 2004).

In supratidal environments such as the freshwater marshes of Andros Island (Bahamas), important and fast sedimentation takes place only during periodical flooding due to exceptionally high (spring) tides, seasonal storms, and/or hurricanes (e.g., Monty, 1972, 1976; Demicco & Hardie, 1994). In such a sedimentation regime, the surface tends to be peneplained even over obstacles, due to a sudden and brutal influx of sediment-laden waters. A large sediment load is discharged, and the finest or lightest material is carried farthest inland from the intertidal zone, and this may disrupt the unprotected or weakly lithified surfaces in the supratidal zones and gradual reduction of sheet flow and current velocity may then result in deposition of graded beds (e.g., Ball et al., 1967; Roehl, 1967; Perkins & Enos, 1968; Monty, 1972; Wanless et al., 1988a, b; Rankey, 2002; Bourrouilh-Le Jan, 2007).

At the Combe Ronde site, rapid sedimentation is indicated by faint overtracks without displacement rims located near the true track, or the absence

of overtracks near to a high displacement rim. A major peneplanation event occurred on top of level 530, where levels 538 to 540 show no evidence for deformation not even on top of the deepest tracks with the large and high displacement rims. The fact that the tracks on level 530 are still well-defined clearly shows that they were consolidated if not lithified prior to this event, because otherwise they would likely have been eroded.

Deep sauropod tracks as natural sediment traps may be important structures to reveal the presence and frequency of storm sedimentation. Breccia fills of footprints were for instance described by Tunis & Venturini (2000) and interpreted as storm layers. However, at the Combe Ronde site there is no evidence that even the deepest tracks ever acted as traps for coarser sediment reworked during the rainy season (e.g., flat pebbles) or storms (e.g., coarser marine bioclasts). This may indicate a low-energy palaeoenvironment or a location far away from any coastline. This is supported by the presence of only thin layers of ostracod shellbeds, and the absence of any larger marine bioclasts or mollusc shells such as gastropods or bivalves on the studied palaeosurfaces, which are found on the palaeosurfaces of the intermediate track-bearing levels of the Courtedoux—Tachâfouè and Courtedoux—Bois de Sylleux sites (pers. obs.).

An alternation of thin ostracod shellbeds with pronounced cryptmicrobial lamination was observed in layers 542-546. Often this was coupled with a higher fraction of marine bioclasts such as foraminifers or fragments of echinoderms and molluscs. Such alternations are best explained by the growth of microbial mats, occasionally interrupted by the influx of sediment-laden waters due to high-energy events. Similar alternations are described from the supratidal marshes of Andros Island, Bahamas (Shinn et al., 1969; Hardie, 1977a) and supratidal environments at Shark Bay in Western Australia (Davies, 1970).

4.4.3.3 Sedimentation rates and frequency of the presence of sauropods

Knowledge of sedimentation rates is of great importance for the understanding of sedimentary systems (Strasser & Samankassou, 2003) and might in the present case allow making an assumption about the frequency of the presence of sauropods that walked on the tidal flats of the Combe Ronde site. The general timing for the deposition of the laminite interval (lower levels) is given by the cyclostratigraphical frame, suggesting that it was deposited during one elementary sequence (unpublished data of the PAL A16; Keller et al., 2006; Colombié & Rameil, 2007; Strasser, 2007), corresponding to the 20 kyr precession cycle of the equinoxes (Strasser et al., 1999).

In tidal-flat environments, depositional sequences may also be autocyclic, created by progradation of tidal flats or lateral migration of tidal channels, without being related to sea-level changes (e.g., Osleger, 1991; Strasser, 1991; Strasser et al., 1999; Burgess, 2001). However, an autocyclic origin of the laminite interval is not very probable, since this sequence shows a high lateral continuity in the order of several square kilometres, within which several of the described palaeosurfaces can be correlated (pers. obs.).

Mechanical reorganization of grains and dewatering in carbonate mud leads to a porosity loss of about 10-30%, and with deeper burial, chemical compaction through pressure solution at grain contacts become important. Thus, the sediments have to be decompacted to estimate the original sediment thickness. Here, a decompaction factor of 2,5 is used, which has been applied by Strasser & Samankassou (2003) for lagoonal mudstones of the Kimmeridgian Reuchenette Formation deposited in a shallow subtidal to intertidal environment.

Within the time period of 20 kyr represented by the laminites, six palaeosurfaces with true tracks of sauropod dinosaurs were encountered (Table 4.1). Most of the time the sediment was not susceptible for track recording and thus the preservation of sauropod tracks occurred only sporadically. In order to make any estimation about the frequency of presence of the sauropods, a package of sediment is needed, which is supposed to have been susceptible for continuous track recording for most of the time.

Such an interval may be provided by the 10 cm of sediment between the base of layer 515 and the top of layer 520. This interval corresponds to about 25 cm of uncompacted sediment and includes the three levels with the highest dinoturbation index of the laminites (levels 510, 515, and 520). The existence on level 510 of undertracks from levels 515 and 520, the coexistence on level 510 of true tracks and undertracks from level 520, and the presence on level 520 of true tracks and overtracks from level 515 suggest that this interval was a biolaminite not (significantly) consolidated prior to burial and was thus continuously susceptible for track recording.

Figure 4.24 compares different sedimentation rates and the time required for the accretion of 25 cm of uncompacted sediment. Assuming that this interval was essentially formed by microbial mats, which grow typically in the order of 2,0 mm/a (e.g., Tucker & Wright, 1990; Sanchez-Cabeza et al., 1999) a time period of 125 years would be expected. If the typical rate of 0,2 mm/a for accretion by microbial mats after desiccation and compaction (e.g., Tucker & Wright, 1990) is taken, the time period is ten times as high (1250 years). Strasser & Samankassou (2003) found by comparison with the Holocene that for lagoonal to intertidal mud facies of the Kimmeridgian Reuchenette Formation typical sedimentation rates may vary between 0,07 and 0,6 mm/a. This would result in time periods between 3570 and 417 years for the deposition of the considered interval. A high value of 3086 years results if the mean sedimentation rate of 0,081 mm/a of the laminites is used (calculated on a time period of 20 kyr and 1,625 m of decompacted laminites, using a decompaction factor of 2,5). However, this latter value may not be realistic because considerable time was certainly spent during the subaerial exposure of the palaeosurfaces.

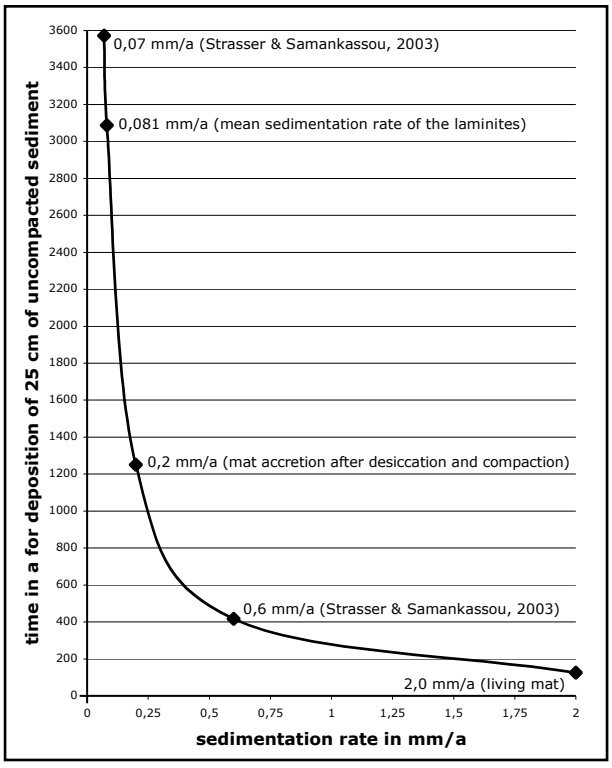


Fig. 4.24: Time (in years), based on different sedimentation rates (in mm/a), required for the sedimentation of the 10 cm thick (corresponding to 25 cm of uncompacted sediment) interval captured between levels 510 and 520.

Based on these calculated time values, different hypotheses about the frequency of the presence of sauropod dinosaurs can be inferred:

1. Assuming that this interval formed during a long time period, the presence of only two palaeosurfaces with true tracks would imply that sauropods were only rarely present. If sauropods were frequently present, the incomplete dinoturbation of the examined interval could be explained by important sedimentation events and subsequent rapid lithification (for short time periods) or by improper track formation and preservation conditions such as early lithification, or wiping out of the tracks by weathering.
2. Assuming that this interval formed during a short time period by the growth of microbial mats and that sauropods were frequently present, it would have been exposed to a high and constant pressure of sauropod dinoturbation. This would have afffected the sediment in a way that distinct tracks probably could not be recognized anymore. Heavily dinoturbated surfaces could even have been preserved as undertracks if the true tracks were eroded and never incorporated into the sedimentary record.

For the interval between levels 510 and 520 input of large amounts of sediment due to storm sedimentation can be excluded because of the lack of any coarser material, and early lithification because of the presence of undertracks on levels 510 and 515. The high dinoturbation of the levels 510, 515, and 520 can be explained by the association of true tracks with undertracks or overtracks, even though this does not exclude that the palaeosurfaces were unsusceptible for track recording during most of the time because of early consolidation or for other reasons. However, the existing evidence suggests that sauropods were occasionally rather than regularly (e.g., seasonally) present in the palaeoenvironment and during the time period represented by the interval between levels 510 and 520.

4.4.4 Reconstruction of the tidal-flat palaeoenvironment

Tidal flats represent dynamic geomorphic, sedimentologic, and ecologic systems, and are subject to the widest spectrum of environmental conditions. Despite little topographic relief they are highly structured and characterized (depending on the climate) by subenvironments such as microbial tidal flats, mudflats, tidal channels, beach ridges, levees,

tidal ponds, hypersaline ponds, tidal salt marshes, freshwater marshes, mangrove swamps, or supratidal flats and marshes (e.g., Ginsburg, 1975; Hardie, 1977a, Shinn, 1983b; Hardie & Shinn, 1986; Rankey, 2002). Andros Island is one of the sedimentologically best-described examples of a modern tidal-flat environment (e.g., Black, 1933; Shinn et al., 1969; Hardie, 1977a), and it was frequently cited as an analogue for ancient tidal-flat deposits and for biolaminites (e.g., Laporte, 1967; Roehl, 1967, Eriksson & Truswell, 1974). Besides Andros Island, other modern examples of tidal flats of different climatic setting are found at Shark Bay in Western Australia (arid climate; e.g., Davies, 1970; Logan, 1974b), along the Trucial Coast of the Persian Gulf (fully arid climate; e.g., Kendall & Skipwith, 1968, 1969; Bathurst, 1971; Purser, 1973; Kinsmann & Park, 1976), in southern Tunisia (arid, subtropical to Mediterranean climate), southern Sinai in Egypt (fully arid, subtropical climate), or in Belize (humid, tropical climate). Shinn (1983b) suggested that the zone that is most extensive and most likely to be preserved is the supratidal marsh in semi-arid to humid settings, and the sabkha in arid settings.

Tidal deposits are very sensitive to record small differences in environmental conditions such as sea-level fluctuations, circulation changes, variations in sediment supply, or major storm events. Very small surface elevation differences (measured in cm) across the tidal flat result in major differences in frequency of subaerial exposure and in sedimentary structures (Hardie, 1977a; Wright, 1984; Tucker & Wright, 1990).

Meyer & Pittman (1994) showed that coeval dinosaur tracksites of the (Upper) Reuchenette Formation of Switzerland were left in several subenvironments ranging from lower to higher intertidal to supratidal pond and marsh, and they speculated whether sauropod dinosaurs were frequent visitors in such marginal marine environments or chance visitors only. The recurrent presence of sauropod tracks in such marginal marine environments has also been referred to as the *Brontopodus* ichnofacies (Lockley et al., 1994a), or as the *Brontopodus* ichnocoenoses of the *Brontopodus* ichnofacies (Hunt & Lucas, 2006, 2007).

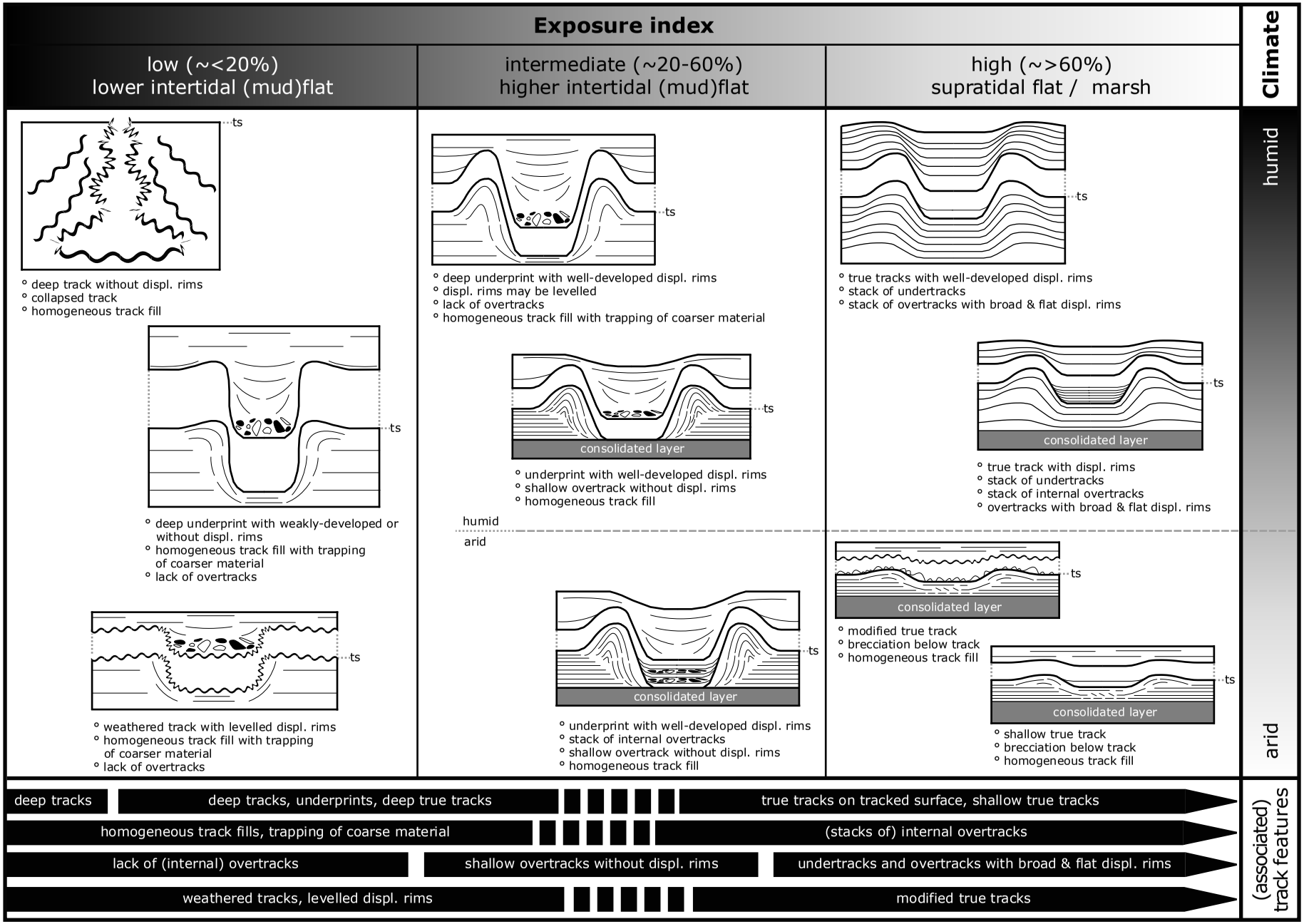
4.4.4.1 Utility of vertebrate tracks for identification of the exposure index

The exposure index was originally introduced to enhance the classification of tidal-flat environments, based on observations made on the tidal flats of Andros Island (Bahamas), which are subjected to a semi-arid and subtropical climate (Ginsburg & Hardie, 1975; Ginsburg et al., 1977). Smosna & Warshauer (1981) developed the rank exposure index for the classification of a Silurian tidal flat, and more recently a freshwater exposure index concept was conceived to characterize palustrine carbonates (Platt & Wright, 1992; Marty & Meyer, 2006). The exposure index links characteristic sedimentary and organic features to the hydroperiod, which is defined as the mean number of days per year on which the ground surface at a given site is covered with water (Ginsburg & Hardie, 1975; Ginsburg et al., 1977; Platt & Wright, 1992). Thereby, a hydroperiod of zero is equivalent to an exposure index of 100%.

Since water content is the most crucial factor for vertebrate track morphology (see also chap. 3), tracks can be used to make conclusions about the sediment consistency at the time they were left. If it is assumed that trackmakers are frequently present and that surfaces are only susceptible for track recording when they are not completely dry and (early) consolidated, tracks tend to record the moistest conditions to which a given surface was subjected to.

For example, in an arid climate on a supratidal flat with an exposure index >90%, an environment which is most of the time dry and its surface consolidated and not susceptible for track recording, a track indicating water-unsaturated substrate may be formed in a microbial mat during or shortly after a period of submersion or heavy rain. However, a deep track indicating a thick layer of water-saturated sediment is not likely to form on a supratidal flat, because biolaminated sediment covered by a thick microbial mat dominates in this environment and is commonly deformed in a plastic way.

Besides the water content, the presence of a microbial mat or biolaminated sediment is also important for track morphology and the formation of undertracks (Marty, 2007; Marty et al., 2007b). Once formed, taphonomic processes and the sedimentary regime preserving the tracks lead to the formation of further associated track features such as unweathered true tracks, weathered true tracks, levelled displacement rims, modified true tracks and internal overtracks by renewed growth of a microbial mat, overtracks with flat and broad displacement rims by repeated growth of microbial mats, homogeneous track fills, or shallow overtracks without displacement rims. These associated track features provide even more valuable information about the exposure index and the palaeoenvironment


Exposure index
low (~<20%)
lower intertidal (mud)flat
intermediate (~20-60%)
higher intertidal (mud)flat
high (~>60%)
supratidal flat / marsh
Climate
humid
arid
ts
° deep track without displ. rims
° collapsed track
° homogeneous track fill
° deep underprint with weakly-developed or without displ. rims
° homogeneous track fill with trapping of coarser material
° lack of overtracks
° weathered track with levelled displ. rims
° homogeneous track fill with trapping of coarser material
° lack of overtracks
° deep underprint with well-developed displ. rims
° displ. rims may be levelled
° lack of overtracks
° homogeneous track fill with trapping of coarser material
consolidated layer
° underprint with well-developed displ. rims
° shallow overtrack without displ. rims
° homogeneous track fill
humid
arid
° underprint with well-developed displ. rims
° stack of internal overtracks
° shallow overtrack without displ. rims
° homogeneous track fill
° true tracks with well-developed displ. rims
° stack of undertracks
° stack of overtracks with broad & flat displ. rims
° true track with displ. rims
° stack of undertracks
° stack of internal overtracks
° overtracks with broad & flat displ. rims
° modified true track
° brecciation below track
° homogeneous track fill
° shallow true track
° brecciation below track
° homogeneous track fill
(associated) track features
deep tracks
deep tracks, underprints, deep true tracks
true tracks on tracked surface, shallow true tracks
homogeneous track fills, trapping of coarse material
(stacks of) internal overtracks
lack of (internal) overtracks
shallow overtracks without displ. rims
undertracks and overtracks with broad & flat displ. rims
weathered tracks, levelled displ. rims
modified true tracks

Exposure index Ginsburg et al., 1977	**~ 90 -100% (high)**	**~ 60 - 90%**	**~ 20 - 60%**	**~ 0 - 20% (low)**
Typical tidal range Ginsburg et al., 1977	lower to higher supratidal	higher intertidal to lower supratidal	lower to higher intertidal	subtidal to lower intertidal
Typical water content of the substrate	dry (low or negligible)	moist (moderate)	water unsaturated (high)	water saturated (very high)
Typical mud consistency	firm and hard	stiff	soft	semi-liquid
Typical tidal-flat environments	°supratidal flat °high algal marsh °inland algal marsh °levee crest °levee backslope °beach ridge hummocks	°low algal marsh °high algal marsh °channel bank °beach ridge washover	°higher intertidal (mud)flat °beach °beach terrace °channel bank °mangrove pond °mangrove swamp	°lower intertidal (mud)flat °shallow lagoon °tidal pond °tidal channel (floor) °mangrove swamp
Typical distinctive features of Andros Isl. tidal flat Bahamas, semi-arid subtropical climate Ginsburg & Hardie, 1975; Ginsburg et al., 1977; Hardie, 1977a; Hardie & Ginsburg, 1977	°smooth & disrupted flat lamination °wavy fenestral lamination °small mudcracks °festooned skeletal sands °oligochaete worm burrows °halophyte grasses	°crinkled fenestral lamination °disrupted fenestral bedding °flat-pebble gravels °*Scytonema* microbial mats °halophyte grasses °mangroves	°crinkled fenestral lamination °deep prism cracks °round-pebble gravels °*Schizothrix* microbial mats °mangroves	°bioturbated mud, no lamination °deep prism cracks °flat-pebble gravels °round-pebble gravels °rippled skeletal sands °*Callianassa* burrows °sea-grasses °green algae
Typical track morphologies Based on observations made on human footprints (chap. 2)	°rather shallow, reasonably- to well-defined true tracks with weakly-developed or without displ. rims °lack of deep tracks & underprints	°rather deep, well-defined true tracks with displ. rims °deep tracks & underprints rare	°deep, reasonably-defined tracks with large, well-defined displ. rims °deep tracks & underprints common	°poorly-defined, deep tracks without displ. rims, often collapsed °deep tracks °underprints
(Suggested) typical associated track features Based on observations made on sauropod tracks at the Combe Ronde tracksite in comparison with observations made in recent tidal-flat environments (chap. 2)	°formation of undertracks in bio-laminated sediment °formation of modified true tracks by renewed growth of microbial mats °common formation of internal overtracks °formation of overtracks with broad & flat displacement rims by repeated growth of microbial mats °weathered tracks rare due to early consolidation	°common formation of undertracks in bio-laminated sediment °formation of modified true tracks by renewed growth of microbial mats °formation of internal overtracks °common formation of overtracks with broad & flat displacement rims by repeated growth of microbial mats °weathered tracks not common due to early consolidation	°weathered (eroded) tracks common °homogeneous track fills °trapping of coarse material °internal overtracks not common °shallow overtracks without displacement rims °undertracks not common	°weathered (eroded) tracks common °homogeneous track fills common °trapping of coarse material common °no undertracks °no overtracks

Table 4.4: Suggested relationships between exposure index and environment and typical distinctive features, track morphologies, and associated track features. The latter have been classified comparing recent features of human footprints with the sauropod tracks of the Combe Ronde site. During the rainy season or in a humid climate, the typical track features of environments with a low exposure index (~<60%) may also be found in environments, which are normally characterized by a higher exposure index (~>60%). Contrarily, track features typical of environments with a high exposure index are not likely to be found in environments with a low exposure index.

Fig. 4.25 (opposite page): Suggested relationships between exposure index and track morphology and associated track features of large, plantigrade vertebrates in a tidal-flat environment, which is by the majority covered with microbial mats. This figure is based on observations made on human footprints left in recent, tropical tidal-flat environments, as well as on the sauropod tracks of the Combe Ronde site. Besides the exposure index the climatic and the energy regime to which a given track is subjected are important factors as well. "ts" is the tracking surface. This figure should be seen as a first assessment, stimulating further research and discussion.

than the morphology of the overall true track. Many of these associated track features are closely linked to the growth of microbial mats, which are themselves very sensitive to the hydrological, climatological, and depositional conditions, and have been suggested to be very facies-specific within modern tidal-flat environments (e.g., Gerdes et al., 2000; Noffke et al., 2001a; Noffke et al., 2008).

Nonetheless, there are also a few precautions that have to be considered, because tracks can only be recorded if the substrate is not completely dry or consolidated, because tracks can be left at any time during subaerial exposure, and because the longer the exposure the higher the amount of tracks left and of associated features formed. Moreover, as regards the trackmakers, it is usually unknown whether they were frequently or only occasionally present. Finally, as stated Schieber et al. (2007) "in the Recent it is relatively easy to establish a relationship between a given feature and its environment, but elucidation of palaeoenvironments from rocks is almost always a much greater challenge with a less certain result".

Based on observations made on human footprints, Table 4.4 links typical track morphologies with the exposure index and tidal-flat environments, and this is further illustrated in Figure 4.25. The suggested typical associated track features are based on observations made on sauropod tracks of the Combe Ronde site in comparison with observations made in recent tidal-flat environments. Even though many diagnostic criteria, including sedimentological features and associated track features, are not restricted to specific tidal zones, they may still provide an approximate assessment of the exposure index and, consequently, a way towards a better understanding of the palaeoenvironment. These aspects of track preservation may then even be used to refine the vertebrate ichnofacies concepts (see also chap. 5.7.8), because they may be more closely linked to a given environment than the trackmaker itself, the latter who may leave its tracks in a number of different environments.

4.4.4.2 Benefits of sauropod tracks for the reconstruction of the tidal-flat palaeoenvironment

The few distinctive tidal-flat features of the laminites such as the desiccation cracks or the cryptmicrobial laminations have, on its own, a limited use to evaluate the exposure index and the precise position within the tidal-flat palaeoenvironments of the Jura carbonate platform. On the other hand, the sauropod tracks and the associated features are very diverse and frequently found. This is probably due to the fact that sauropods as large animals were relatively insensitive to microhabitat differences and left tracks in a wide range of tidal-flat environments.

The comparison of the sauropod tracks with human footprints left in tidal-flat environments suggests that the observed range of sauropod track morphologies is a reflection of (mostly biolaminated) sediment covered with a smooth, flat microbial mat of different water content, and that these circumstances can be linked with the exposure index (Marty et al., 2008b). The presence of biolaminated sediment is disclosed by well-defined undertracks on levels 515 and 510, and overtracks on level 520, even though the deep underprints of level 530 indicate an unlaminated carbonate mud. Today, strongly biolaminated sediment is typically found in higher intertidal to supratidal, restricted and low-energy environments (supratidal flat, marsh) with an exposure index between 60% and 90% or higher than 90%. This is also suggested by the general absence of deep tracks and the rarity of underprints, which both indicate environments (e.g., intertidal flat, swamp, tidal pond) with a low exposure index (<60%), characterized by thick layers of water-saturated mud and the absence of biolaminated sediment due to bioturbation or grazing, even though a mat is commonly present on the surface.

The presence of internal overtracks and overtracks with broad and flat displacement rims is also evidence for slow covering up and a restricted, hostile environment with a high exposure index (>90%), which is favourable to the growth of microbial mats because burrowers and grazers are absent or rare.

Besides, a high exposure index is indicated by the generally good preservation of tracks or the lack of weathered tracks (e.g., levelling of displacement rims by tidal currents) or significantly modified tracks. This indicates a fast consolidation or lithification of the sediment, which generally takes place in supratidal environments. A high exposure index is further suggested by a generally shallow track penetration depth, i.e., layers located more than 10-15 cm below the tracked surface are unaffected by track formation.

Evidence for a slightly lower exposure index are the interval between levels 510 and 520, shallow overtracks without displacement rims on level 505, deep underprints on level 530 left in unlaminated carbonate mud, wave ripple marks on level 515, and

the absence of any overtracks on top of several track-bearing palaeosurfaces. A lower exposure index is also suggested by alternations of ostracod shellbeds with cryptmicrobial lamination and by bioturbated marls with occasional teeth of pycnodontiform fishes and small turtle bone fragments at the top of the laminite sequence coupled with a lack of dinosaur tracks.

4.4.5 Reconstruction of the palaeoclimate

In the reflections made so far on the exposure index and the palaeoenvironment, the influence of the palaeoclimate has not been discussed, even though the climate is one of the controlling factors for the morphology of modern tidal flats.

The Late Jurassic has been considered to lie in the Mesozoic "cool" mode, leading to elevated evaporation rates accelerating the global water cycle (Frakes et al., 1992; Husinec & Read, 2007). During the Kimmeridgian, the structurally complex Jura carbonate platform occupied a low-latitude, subtropical position (e.g., Thierry, 2000a, b), and the palaeoclimate is considered as semi-arid to arid (e.g., Hallam, 1984, 1985; Moore et al., 1992; Ross et al., 1992; Moore & Ross, 1994; Weissert & Mohr, 1996; Bertling & Insalaco, 1998; Rees et al., 2004; review in Rameil, 2005). However, for the short time period during which the studied laminites were deposited, it is difficult to estimate the pluviometrical regime, which might have been ruled by micro-climatic factors and influenced by repeated emersions of the Jura carbonate platform during that period.

4.4.5.1 Evidence from sedimentological analyses

The repeated presence of dinosaur tracks left in water-unsaturated to moist sediment and/or microbial mats indicate that wetting of the substrate occurred at least occasionally. In a supratidal environment, wetting is either related to storms or to a rainy season. The generally good preservation of these tracks and the presence of relatively small, non-weathered desiccation cracks on the other hand suggest that they were rapidly consolidated after they were left and not significantly affected by weathering. This is evidence for prolonged, quiet and dry periods (droughts), or at least a pronounced dry season. The formation of internal overtracks also suggests that the environment was not subjected to significant changes during longer periods, when renewed or repeated growth of microbial mats occurred after wetting. All this is in favour of a semi-arid climate.

A fully arid climate can be excluded because of the general lack of evaporites. A humid climate is neither likely because of the absence of rooting, charophytes, palaeosols, extensive burrowing, detritic sliciclastics, and coal. Also, vertebrate tracks are normally best preserved in zones free of vegetation (Cohen et al., 1991).

4.4.5.2 Evidence from clay mineral analysis

Compared with the underlying and overlying limestone, the laminites are marked by an important increase in clay minerals, as expressed by the marly facies. The clay minerals of several, selected samples of the laminites and the under- and overlying limestone have been analysed by J.-F. Deconinck from the University of Dijon. The overall evolution of the clay mineralogy between the Banné Member and the Marnes à *virgula* is shown in Figure 2.5. It exhibits two peaks with higher fractions of kaolinite located above the lower and the intermediate track-bearing levels. Levels indicating emersion generally lack kaolinite, even if in the laminite interval (lower levels) of the Combe Ronde site some kaolinite was detected. However, over the studied laminite interval, no pronounced change in the relative abundance of the clay minerals can be observed. Detrital illite is most frequent (55%–70%), followed by illite/smectite mixed-layers (30%–45%). Kaolinite is generally rare, and in most samples analysed, only traces of it were found. Kaolinite was not detected in the green-brown marls (layer 550) at the top of the laminites (Table 4.5).

Layer	Sample No.	Illite	I/S	Kln
450	CRO005-42	70	30	0
490	CRO005-24	65	30	5
501	CRO004-122	60	35	5
520	CRO004-130	60	40	traces
528	CRO004-139	60	40	traces
530	CRO004-128	60	35	5
532	CRO004-105	70	30	traces
535	CRO004-95	60	40	traces
542	CRO004-88	65	35	traces
544	CRO004-126	55	40	5
546	CRO004-125	60	40	traces
550	CRO004-199	55	45	0
560	TCH005-761	65	30	0
600	TCH005-787	60	35	0

Table 4.5: Clay mineral assemblage within the laminite sequence (layers 501-550) and the underlying (layers 450 and 490) and overlying (layers 560 and 600) shallow marine limestones. I/S is illite/smectite mixed layers, Kln is kaolinite. Data are courtesy of the PAL A16 and have been gathered by J.-F. Deconinck (University of Dijon, France). Compare with Figure 2.5.

On the Jura carbonate platform, clays are often associated with the shallowest and/or most restricted facies. This is explained by an increased erosional potential in the hinterland following a rapid fall of relative sea level, possibly in combination with increased rainfall in the hinterland due to climatic changes depending on atmospheric circulation patterns (e.g., Mouchet, 1995, 1998; Strasser & Hillgärtner, 1998; Strasser et al., 1999; Hug, 2003). If the clay minerals were formed and/or eroded in the hinterland (i.e., in the Rhenish Massif and the London-Brabant Massif to the N-NW, the Bohemian Massif to the NE, or the Massif Central to the SW) they were transported from the parent rocks in the continental source area to the Jura carbonate platform by water currents or by wind, as it has been suggested for the detrital quartz (see also chap. 4.3.2.1). Probably, also immature palaeosols in the platform interior were a source for the clay minerals and may explain the low kaolinite/illite ratio. This, in combination with reduced accommodation space and hence reduced carbonate production and lower sedimentation rates, would have led to a preferential accumulation of clay minerals within the laminite sequence when compared with the under- and overlying limestones. Since the increase in kaolinite is associated with the most normal marine conditions and the highest generation in accommodation space, it is suggested that the kaolinite was reworked from the hinterland and did not form on the Jura carbonate platform at that time.

The formation of clay minerals strongly depends on the weathering environment, which is mainly controlled by the climatic setting (e.g., Singer, 1980; Sladen, 1983; Singer, 1984; Chamley, 1989). Illite and illite/smectite mixed layers commonly form under temperate conditions, low annual precipitations, or limited time for soil development, and they are dominant in immature palaeosols subjected to a weak chemical weathering (e.g., Chamley, 1989; Curtis, 1990; Robert & Kennet, 1994; Thiry, 2000). Smectite commonly forms under warm, subtropical to tropical conditions that are characterized by an elevated seasonality of alternating wet and dry periods (e.g., Deconinck, 1993). Kaolinite typically forms in humid climates in palaeosols with deep weathering associated with perennial precipitation (e.g., Chamley, 1989; Curtis, 1990). Consequently, the very low kaolinite/illite ratio suggests a clay formation in immature palaeosols subjected to a weak chemical weathering in a semi-arid to arid climate. Nonetheless, it has to be considered that the climate in the source area may not have been the same as on the platform, and that clay minerals may have been stored temporarily before having been reworked again (e.g., Pittet & Strasser, 1998; Hug, 2003).

4.4.6 Vertical evolution of the palaeoenvironment

At the Combe Ronde tracksite, the marly laminite sequence is cooped between shallow marine limestones (Fig. 2.5). The thinly-bedded limestone below is a wacke- to packstone with marine macrofossils such as bivalves or gastropods (nerineans) frequently found up to 1 m below the laminites. The last metre below the laminites is thinly bedded and almost devoid of marine macrofossils. The ostracod-bearing wackestone microfacies at the top of the limestones (i.e., layers 495, 500) is similar to that of the base of the laminites, but with a slightly higher percentage of bioclasts. On the Jura carbonate platform, similar ostracod-dominated wackestones are typical for the intertidal to supratidal facies zone (e.g., Hillgärtner, 1999; Colombié, 2002; Hug, 2003; Tresch, 2007). It is suggested that the limestone just below the laminites was deposited in a very shallow, intertidal, semi-open lagoon with intermittent, low to moderate energy, and that the palaeoenvironment was already subjected to a sea-level fall and confinement prior to the formation of the first subaerial palaeosurface, the main track level (500), at the base of the laminite sequence.

The main track level marks a significant fall in sea level and is interpreted as a sequence boundary (Fig. 4.3). This supratidal palaeosurface was subjected to prolonged exposure, which led to the formation of two generations of tracks. After desiccation and consolidation, internal overtracks formed by growth of microbial mats, leading to an amalgamation of track fills, before it was finally covered up by high-energy sedimentation coupled with the formation of shallow overtracks without displacement rims on level 505.

Because of the smallest desiccation cracks of all surfaces and the lack of true tracks, level 505 was probably only subjected to a short period of subaerial exposure, and rapidly covered up by high-energy sedimentation. High-energy sedimentation rather than accretion by the growth of microbial mats is also suggested by an increased presence of marine bioclasts and the absence of cryptmicrobial lamination between the middle of layer 505 and the middle of layer 510. This may indicate a small rise in sea level coupled with an opening of the palaeoenvironment, or simply a stormy period.

About from the middle of layer 510 to the top of layer 520 there is evidence for a higher water table probably due to a rise in sea level and/or an opening of the environment. This is also suggested by the discovery of a disarticulated carapace of a marine turtle at the nearby Chevenez—Crat site. Well-defined undertracks with displacement rims identified on levels 515 and 510 and overtracks of level 515 on level 520 indicate that this interval was a biolaminite, which was not completely consolidated until tracks were made on level 520. Moreover, wave ripple marks were found on level 515, even though healed mudcracks are present as well. Similar sediments susceptible for the formation of undertracks form today on higher intertidal flats and supratidal flats and marshes with a relative high exposure index (60% to 90%, or >90%).

As the deep, large tracks of level 530 had no impact on the underlying sediment it must have been consolidated prior to the deposition of layer 530 and the formation of the tracks. The top of layer 528 may also have been subjected to prolonged subaerial exposure, which could explain the brecciation of layer 528 by the initial formation of a palaeosol, even though no dinosaur tracks are reported from level 528. This, together with the fact that layers 525 and 528 have the least marine bioclasts of the studied laminite interval and that layer 525 exhibits cryptmicrobial lamination and is a mud- rather than a wackestone, is evidence for a palaeoenvironment with a high exposure index (>90%).

The palaeosurface 530 is the only place where underprints with large and homogeneous displacement rims formed. This indicates that at the time of track formation the sediment was a water-unsaturated to water-saturated, unlaminated carbonate mud. Because deep underprints are not typical for environments with a high exposure index, the palaeoenvironment had a somewhat lower exposure index (~60-90%), probably due to a small fall in relative sea level. However, it was rapidly subjected to the growth of microbial mats forming internal overtracks and to a prolonged period of desiccation, during which a second generation of shallow tracks was left. This desiccation also led to the formation of cracks with slightly raised edges. Finally, palaeosurface 530 was covered up by high-energy sedimentation, which is expressed by the lack of overtracks on level 538, even on top of the deepest tracks. This comes along with the first thin ostracod shellbeds alternating with cryptmicrobial lamination, increased bioturbation, and a high percentage of marine bioclasts. This implies a minor transgressive pulse.

Besides palaeosurface 500, palaeosurface 540 exhibits the best-defined sauropod tracks of the sequence. Wrinkle marks on top and well-developed cryptmicrobial lamination and absence of ostracod shellbeds within layer 540 is evidence for biolaminated sediment, even though layer 540 still has a relatively high percentage of marine bioclasts. This indicates a supratidal flat with a high exposure index (>90%). The tracks are filled with homogeneous track fills and internal overtracks or overtracks on level 542 are absent. However, a few true tracks were also encountered on palaeosurface 542, which is the uppermost level of the sequence with tracks. This surface is also covered without (internal) overtracks by layers 543 and 544, which are both marked by a small percentage of marine bioclasts and invertebrate burrows. Layer 544 exhibits intralaminar shrinkage cracks and is the uppermost layer with evidence for prolonged subaerial exposure. Above the base of layer 545, a change in the sedimentary regime is indicated by a pronounced alternation of cryptmicrobial lamination with few marine bioclasts and ostracod shellbeds with more marine bioclasts. Moreover, invertebrate burrows become increasingly abundant.

Finally, the laminite sequence is concluded by green-brown marls without dinosaur tracks or other evidence for subaerial exposure, but which are clearly more affected by bioturbation than the rest of the sequence and also yielded scattered teeth of pycnodontiform fishes and fragments of turtle carapaces. Similar illite-dominated green marls commonly occur at the top of small-scale shallowing-upward sequences, and have been interpreted as having been formed during cyclic wetting and drying of a shallow carbonate platform (Deconinck & Strasser, 1987; Strasser, 1988; Hillgärtner, 1999). This, together with the absence of tracks or other features of subaerial exposure, indicates a rise in relative sea level and a palaeoenvironment with an increasingly lower exposure index.

On top of the laminite sequence, the large thickness of the massively-bedded limestones and its marine facies is evidence for the creation of new accommodation space during a period of rising sea level. The ferrugineous lower bedding plane exhibits a pronounced relief due to the *Palaeophycus* burrow system. This transgressive surface overlies the upper sequence boundary of the elementary sequence of the laminite interval.

The lowermost 20-30 cm of the overlying limestones (layer 560) are characterized by a high

percentage of marine invertebrate macrofossils and a well-developed burrow system. This indicates some condensation, which is typical after a rapid deepening following emersion, when carbonate production is reduced because the carbonate factory has to start up again (e.g., Kendall & Schlager, 1981; Wright & Burgess, 2005). Normal carbonate production is indicated by the upper part of the limestone bed, where marine macrofossils are less frequent but mud-dwelling bivalves commonly preserved in life position, indicating less bioturbation, increased sedimentation rates, and relative rapid filling up of the newly created accommodation space.

The evolution of the tidal-flat palaeoenvironment suggests that it was affected by (sub-Milankovitch) high-frequency accomodation changes, most probably resulting from a combination of changes in eustatic sea level, subsidence, and platform morphology.

4.5 Conclusions

The systematic level-by-level excavation of a 0,65 m thick Kimmeridgian laminite interval, representing an elementary sequence, revealed six palaeosurfaces with true tracks, one palaeosurface with overtracks, and one bedding plane with undertracks. This indicates that discontinuity surfaces are more frequent than bedding plane within the laminite interval.

On these surfaces, the sauropod tracks and their associated track features are the most diverse and most frequently found macrosedimentary structures. Their analysis discloses the sediment properties at the time of track formation and the consolidation history prior to track formation, and reveals processes that form, modify, and preserve palaeosurfaces. Many of these processes can not be inferred from other macrosedimentary features such as desiccation cracks or ripple marks, or from the microfacies analysis.

An unambiguous identification of true tracks without anatomical details is a difficult task. An identification is facilitated by systematic level-by-level excavations coupled with sedimentological analyses.

The level-by-level superimposition of the surface documentations, coupled with the sedimentological analyses allowed for identifying true tracks and for distinguishing them from undertracks and overtracks. This would often not have been possible from a purely morphological point of view. At the Combe Ronde site, true tracks are most common, even though many of these are true overall tracks, in which the track bottom (the true track *sensu stricto*) is not discernible due to the presence of internal overtracks and/or amalgamated track fills.

The studied cross-sections of sauropod pes tracks provide insight into the walking dynamics of dinosaurs from the touch-down phase until the kick-off phase and confirm that sauropods put their hindfeet in a pronounced plantigrade way on the bottom, while during the kick-off phase the weight may have been transferred forward to the anterior part of the foot, occasionally resulting in the formation of displaced discs, which are bound by thrust faults.

The comparison of the sauropod tracks of the Combe Ronde site with footprints of recent tidal-flat environments suggests that microbial mats may have played an important role in the formation and preservation of sauropod tracks, and that these mats are highly facies sensitive. This helps to link track morphology and the associated track features with the exposure index, important for the characterization of the tidal-flat palaeoenvironment.

It is assumed that, in a semi-arid climate, unweathered tracks coupled with the presence of internal overtracks, and in a humid climate, stacks of undertracks in biolaminated sediment and overtracks with broad and flat displacement rims due to the repeated growth of microbial mats, are good evidence for supratidal palaeosurfaces with a high exposure index. If the exposure index is intermediate, underprints and/or shallow overtracks without displacement rims are common. Environments with a low exposure index are characterized by underprints and deep tracks with homogeneous track fills.

This evidence, together with the analysis of the palaeosurfaces, the sauropod tracks, and microfacies and facies of the encasing sediment results in a better understanding of the tidal-flat palaeoenvironment and its evolution, and of the palaeoclimate. The latter was likely semi-arid with prolonged droughts.

At the Combe Ronde site, the sauropods generally left their tracks in a stable supratidal flat or marsh environment, characterized by an exposure index higher than 90%. Only the middle and uppermost part of the laminite interval is characterized by an exposure index of around 60% or lower, typically found on higher intertidal flats or around supratidal ponds, either due to an opening of the palaeoenvironment or to a small transgressive pulse.

This supratidal-flat palaeoenvironment was not located in close proximity (i.e., > several 100 m) to a coastline towards the open marine realm or an internal lagoon. For most of the time, it was characterized by restricted and hostile conditions, which may have been interrupted by occasional wetting due to periods of rain or storm surges, which also imported the small marine bioclasts. During or rather at the end of such periods of wetting, tracks were recorded.

Vertebrate tracks are generally best preserved where the exposure index is low, by prompt deposition of a covering layer. Environments with a high exposure index, as represented by the laminites of the Combe Ronde site, have so far not been considered to be very susceptible for track preservation because of long periods of subaerial exposure without significant sedimentation, and during which tracks are subject to weathering and disintegration (e.g., Cohen et al., 1991, 1993; Platt & Meyer, 1991).

The common presence of well-defined, unmodified sauropod tracks in a palaeoenvironment with a high exposure index is evidence that dinosaur tracks are, contrary to the general assumption, likely to be preserved in such environments. This can be explained by a fast consolidation or lithification of the ground, and/or due to renewed growth of a microbial mat. Both processes are common in modern environments and prevent surfaces from complete trampling and other disintegration, for example during periods of heavy rain.

The frequency of the presence of sauropods in tidal-flat environments of the Jura carbonate platform is difficult to assess. If the supratidal flats consolidated early and were not susceptible for track recording during most of the time, sauropod tracks may only exceptionally have been registered and incorporated into the sedimentary record. Accordingly, the presence of six palaeosurfaces with sauropod tracks within an elementary sequence (20 kyr) would suggest that sauropods were regular rather than chance visitors. However, if the supratidal flats were susceptible for track recording during longer periods, an occasional presence of sauropods would rather be suggested, as is also indicated by the absence of completely dinoturbated levels.

The sharp upper boundary of the laminite interval, marked by the *Palaeophycus* burrow system at the base of the overlying marine limestones, suggests that this surface is a transgressive surface.

4.6 Outlook and perspectives

The analysis of processes involved during the formation, the taphonomic history, and the preservation of sauropod tracks offers interesting benefits for the reconstruction of a tidal-flat palaeoenvironment and the sedimentary processes acting within, for the interpretation of palaeosurfaces, and for sequence stratigraphy. This approach was facilitated by systematic level-by-level excavations and documentations, which was, however, expensive and time-consuming and can thus not always be applied in vertebrate ichnology.

The observations made on human footprints left in microbial mats proofed to be very helpful for the interpretation of the fossil sauropod tracks. It is recognized that microbial mats occupy a key position in the formation and preservation of vertebrate tracks and associated track features, but these processes are not yet fully understood. Consequently, surveys of the formation and preservation of recent vertebrate tracks left in carbonate and siliciclastic tidal-flat environments, similar to the approaches of Cohen et al. (1991, 1993) and Scott et al. (2008), will help to better understand the processes that are involved in the making of fossil tracks. This will lead to a better understanding of fossil ichnoassemblages, and improve the use of the preservational state of vertebrate tracks in the exposure index concept, and even in vertebrate ichnofacies.

The laminite interval studied here was and still is excavated by the PAL A16 at several nearby tracksites (Chevenez—Crat, Courtedoux—Béchat Bovais, and Chevenez—La Combe). Several palaeosurfaces can be correlated between the different tracksites, and similar analyses as performed in this work will provide a better insight into the lateral variability of the state of preservation of sauropod tracks and the different tidal-flat palaeoenvironments.

In this work, only selected cross-sections of serially-sectioned sauropod tracks were analysed and notably in terms of sedimentology. Ongoing work should focus on the systematic analysis (e.g., digital imaging) of serially-sectioned sauropod and tridactyl tracks, which may provide a better insight into the walking dynamics (kinematics) of the trackmakers (see also Graversen et al., 2007; Milàn et al., 2006).

* * *

5 - Ichnology of the Chevenez—Combe Ronde tracksite: implications for dinosaur diversity, locomotion, and palaeoecology on the Jura carbonate platform

5.1 Introduction

The sedimentological and taphonomical analyses of sauropod tracks and the encasing sediment (chap. 4) and their comparison with recent tracks (chap. 3) facilitated interpreting the sediment properties at the time of track formation, the sedimentary processes acting within and preserving the tracks, and the palaeoenvironment. With this evidence at hand, ichnotaxonomy, the anatomy of the feet of the trackmakers and the behaviour of the trackmakers in that given environment can now better be analysed and interpreted.

This chapter focuses on the palaeoichnology of the dinosaur tracks and trackways of the Chevenez—Combe Ronde tracksite. This includes the identification of well-defined tracks and the definition of anatomical morphotypes, which can be compared with known dinosaur ichnotaxa, and afterwards enables one to make assumptions about possible trackmakers and hence the composition of the dinosaur community, part of the terrestrial palaeoecosystem of the Jura carbonate platform, which is otherwise not or poorly bequeathed. Further emphasis is put on the analysis of trackway patterns, configurations, and parameters (notably trackway gauge), which allows to make some preliminary conclusions about the locomotion capabilities of the trackmakers, and which has important implications for the understanding of the trackways. Finally, the general analysis of the trackway orientation pattern provides insight into the behaviour of the dinosaurs.

Particular emphasis is put on the tracks and trackways of the main track level (level 500), as this is the largest excavated surface with the best-defined tracks and the most diversified ichnoassemblage. Additionally, selected important sauropod trackways of overlying levels are studied.

On the main track level both sauropod and tridactyl tracks are fairly well defined with the internal and external outlines clearly marked, even though imprints of anatomical details are rare (e.g., digits, claws, phalangeal pads) or not preserved (e.g., skin). All tracks of the main track level are preserved as negative epichnia and they are all identified as true tracks. The trackways are characterized by different patterns and configurations. Most of the trackways are less than 10 m long, and a few are between 10 and 20 m long. With a total length of almost 60 m, the bipedal trackway T10 and its continuation T41 in excavation area 2 is the longest trackway of the site. It crosses excavation areas 3 and 2 approximately from SSW to N, and it is composed of over 80 single, minute tracks. This trackway exhibits the smallest tridactyl tracks of the site and is one of the longest trackways of a minute bipedal dinosaur worldwide.

The majority of the tracks is unaffected by faults and/or erosion, but a few tracks located at the external borders of the site and in close proximity to faults, are affected by epikarstification and associated enlargement of faults. Consequently, some tracks are cut and trackways slightly displaced by faults, which had to be considered when measuring their parameters.

5.2 Sauropod tracks and trackways of the main track level

By the end of 2005, 14 sauropod trackways were uncovered on the main track level, and there were no clear isolated sauropod tracks identified that could not be attributed to trackways. The mean pes track length of the trackways varies between 19,6 cm (S12) and 39 cm (S2), which are rather small dimensions for sauropod pes tracks.

5.2.1 Track preservation

All sauropod tracks are preserved as negative epirelief. Preservation and imprint depth does not significantly vary along single trackways, which is evidence for homogeneous substrate conditions over the tracksite. However, the track morphology varies between the sauropod trackways left in excavation areas 1 and 2 and those left in excavation area 3. Two track generations can clearly be distinguished:

5.2.1.1 Deep, well-defined tracks with large displacement rims

Description

These are the tracks of trackways S3 to S14, located in the northern part of the site in the excavation areas 1 and 2. All these trackways exhibit tracks with a very similar preservation, independently of their mean size. The tracks are always surrounded by large and well-defined displacement rims, which mark well their external outlines (Fig. 5.1). In many of the deep tracks, the track fill or parts of the track fill were amalgamated with the main track level, and could not have been removed without partial destruction of the tracks. Because it was decided that the site will be protected *in situ*, these track fills were not yet removed. Thus, the internal outline of the tracks was often not very well-defined and anatomical details such as impressions of the digits, claws (ungual phalanges), or foot pads were not reported from any track. This also somewhat hampered the measuring of the track dimensions of the concerned tracks. However, it may be possible that in a couple of years these tracks will reveal further details, when the fills will detach due to ongoing erosion, or when the tracks may be mechanically prepared, once the site is made accessible for the public.

Interpretation

Because all deep tracks are well-preserved, exhibit well-defined displacement rims, and the pes tracks caused faint overtracks on level 505, they are believed to be true tracks. They were left in a moist to water-unsaturated carbonate mud, which was probably covered by a microbial mat. After the tracks were left, the mud desiccated, as indicated by the desiccation cracks, which penetrate into the tracks. Later, renewed and repeated growth of microbial mats within the deep tracks led to the formation of stacks of internal overtracks and an amalgamation of the track fill.



Fig. 5.1: Chevenez—Combe Ronde tracksite, excavation area 2, main track level: Typical deep right pes (RP1) and manus (RM1) tracks of the trackway S9. Direction of displacement is towards the top. Note the well-defined displacement rims surrounding the tracks. The manus track is slightly deformed in its posterior part by the displacement rim of the pes track. Both pes and manus tracks still bear parts of their track fill. The desiccation cracks clearly formed after the tracks were left, because they penetrate into the displacement rims and the tracks. Scale bar is 40 cm, rising sunlight from the lower right, photo by B. Migy (SAP).

5.2.1.2 Shallow, poorly-defined tracks without displacement rims

Description

These are the shallow, poorly-defined tracks without displacement rims of the trackways S1 and S2 of excavation area 3. Trackway S1, oriented northwest, is located in the southern part of the site and S2, oriented northeast, in the middle part. In both trackways the gross external track outline is well defined, but it was difficult to precisely define the internal outline, which lies somewhere within the track (Fig. 5.2). Hence, the internal outline was defined as a limit where the track wall slightly ascends. However, this line is tentative as the changes in slope are subtle. Thus, the mean track dimensions (pes length and width) of S1 and S2 rather should be seen as an order of magnitude, and these tracks are not used to describe the general sauropod track morphology of the site. Nevertheless, the trackmakers of S1 and S2 are clearly larger than those of the other trackways of the main track level. Contrary to the deep tracks, their fills (layers 501 and 505) always easily detached from the main track level.

Interpretation

Shallow tracks with a poorly-defined outline and without displacement rims are often considered as undertracks (e.g., Milàn & Bromley, 2006, 2008). However, in Chapter 4.3.5.1 the tracks of the trackways S1 and S2 were clearly identified as true tracks by means of the level-by-level excavation and documentation. It is also implausible that the original true tracks were eroded and never incorporated into the sedimentary record, because some of the tracks overprint tridactyl tracks. For instance is the right pes track R25 of the bipedal trackway T10 overprinted by the right pes track RP4 of the sauropod trackway S2. This implies that the shallow sauropod tracks were left on the same surface but clearly later than the deep tracks and theropod tracks, when the sediment was drier. From the comparison with modern vertebrate tracks it is assumed that such shallow and faint tracks of large plantigrade animals are most likely left in a thick and coherent, moist to dry microbial mat, which deformed in a plastic way, and that the sediment below had not a high water content or was even (partially) consolidated (see also chap. 3).

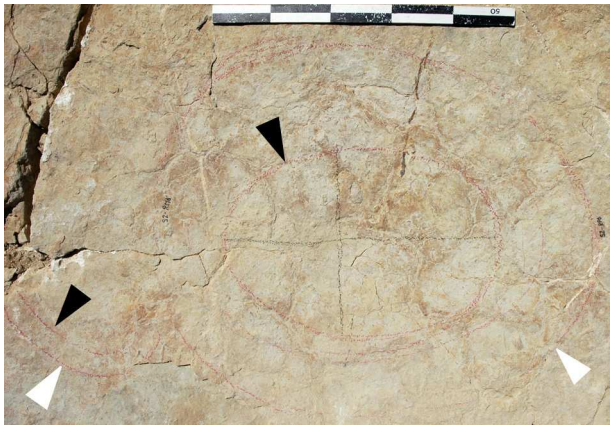


Fig. 5.2: Chevenez—Combe Ronde tracksite, excavation area 3, main track level: Typical shallow right pes (RP6) and manus (RM6) tracks of trackway S2, without displacement rims and cut by desiccation cracks. Direction of displacement is towards the left. The black arrows mark the approximate internal outlines, the white arrows the exterior outlines, both underlined with chalk. Scale bar is 50 cm, photo by Y. Marti (PAL A16).

5.2.2 Track morphology

The following descriptions of the general track morphology are mainly based on the best-defined tracks of the trackways S9 to S13, even though many of their track fills were amalgamated with the tracks and have yet not been removed. This somewhat hampers the description of the internal track morphology, as anatomical details such as digit and claw imprints, which were not discernible at the time when this study was carried out, may still be exhibited once the track fills will detach or be mechanically removed.

5.2.2.1 Pes (hindfoot) tracks

The pes tracks are subcircular to oval in shape (Fig. 5.3). The shallow tracks of the trackways S1 and S2 are clearly more elongated than the pes tracks of the other trackways, probably because the substrate was drier and firmer at the time they were left. Generally, the maximum width is located in the middle, or slightly towards the anterior part of the track with respect to a line perpendicularly intersecting the pes length axis at its midpoint (Figs. 5.3B & C). It is only exceptionally located slightly in the posterior part of the pes track (Fig. 5.3A). Pes prints are always considerably longer than wide, with a mean size ranging from 19,6 cm (S12) to 39 cm (S2) in length and from 12,3 cm (S12) to 28,8 cm (S6) in width. There is no evidence for longitudinal grooves anteriorly or laterally, along the inner margins of the tracks, nor for imprints of the digits or claws (ungual phalanges). Deep pes tracks are generally surrounded by a more or less continuous, large and broad displacement rim (Fig. 5.1 and Fig. 5.3). The displacement rim may be absent or weakly-developed in the posterior part of the tracks (Figs. 5.3A & B), and it is often more pronounced along the anterior and exterior lateral side of the track (Figs. 5.3A & B).

5.2.2.2 Manus (hand) tracks

Manus tracks are generally about twice as wide as long, with a mean size ranging from 4,4 (S12) to 12,6 cm (S1) in length and from 11,8 cm (S12) to 20,4 cm (S1) in width. The internal outline of manus tracks, undeformed by the proceeding pes track, is semicircular (D-shaped) to slightly crescent-shaped (horseshoe-shaped), always convex forward (in the direction of progression) (Fig. 5.4). They are typically deepest in the anterior part, and become increasingly shallower towards the posterior end of the track. Generally, they are only anteriorly surrounded by a displacement rim, which may be well-developed and as large as the displacement rim of the corresponding pes (Fig. 5.4A). Deeper manus tracks show a more pronounced crescent-shaped form and are steeper inclined towards the anterior part (Fig. 5.4B) when compared with shallower tracks, which have a more semicircular shape, and which are only slightly deeper in their anterior part than at their posterior end (Fig. 5.4C). The best-defined manus tracks, which are believed to be those of the trackways S12 and S13 with the smallest tracks, are slightly asymmetric. Their interior half is broader than their exterior, and the bulge at the interior, posterior end is clearly larger than the one at the exterior, posterior end of the track. Between these two bulges a shallow, more or less well-defined indentation is visible (Fig. 5.6B).

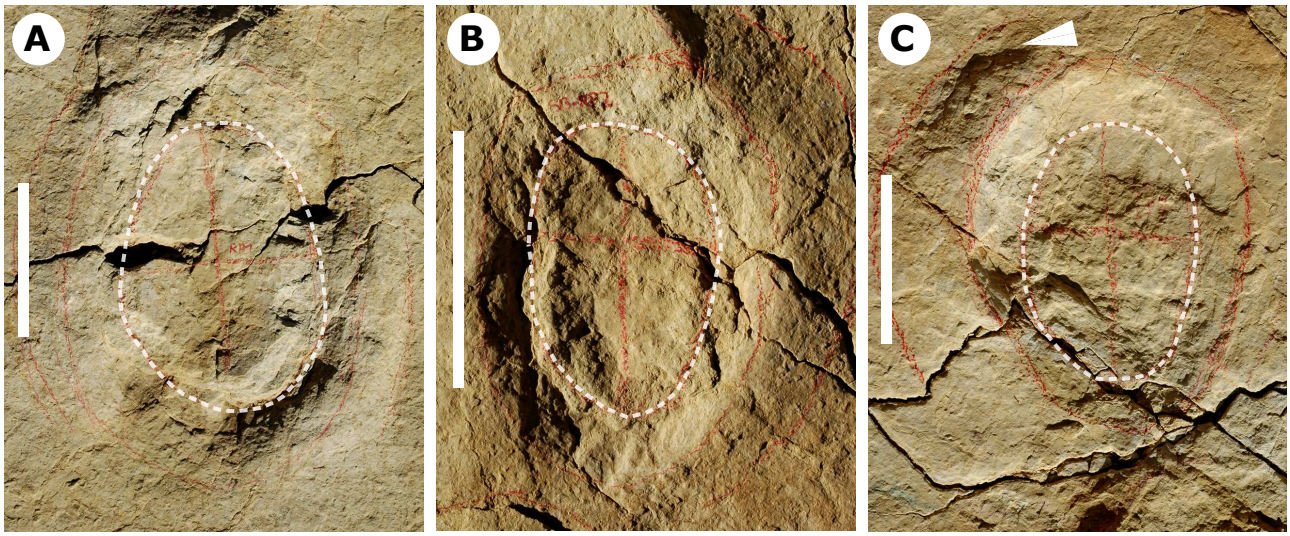


Fig. 5.3: Chevenez—Combe Ronde tracksite, excavation area 2, main track level: Typical sauropod pes tracks. The approximate internal outline is marked by the dashed white line, and the direction of progression is upwards. All prints still (partially) bear their fills, and are cut by desiccation cracks. **A:** S9-RP1 with the maximum width located slightly in the posterior part of the track. **B:** S13-RP2 with the maximum width located in the anterior part of the track. **C:** S11-LP7, with the maximum width located in the anterior part of the track. Arrow points to the manus track S11-LM7, which is located in close proximity to the pes track and which is deformed by partial overprinting by the pes. All scale bars are 20 cm, photos by B. Migy (SAP).

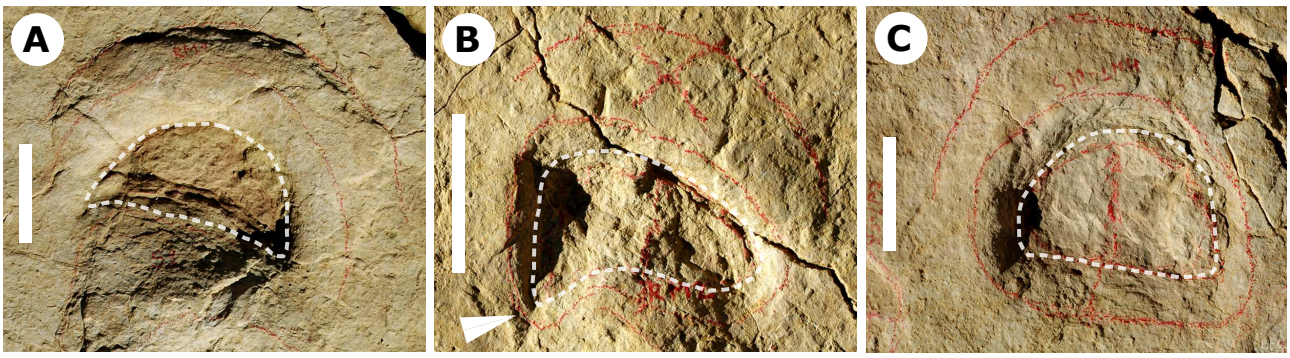


Fig. 5.4: Chevenez—Combe Ronde, excavation area 2, main track level: Typical sauropod manus tracks, which are unaffected by the proceeding pes tracks. All tracks still (partially) bear their fills, and are cut by desiccation cracks. The approximate internal track outline is marked by the white, dashed line. Direction of progression is upwards. **A:** S9-RM1 with a broad & large, well-defined displacement rim in the anterior part. **B:** S13-RM2, the arrow indicates the bulge at the interior, posterior end, which may correspond to the impression of digit I. **C:** S10-LM4, entirely surrounded by a broad and flat displacement rim. All scale bars are 10 cm, photos by B. Migy (SAP).

5.2.3 Size classes and correlations of track parameters

5.2.3.1 Size classes

The mean track parameters of all trackways are shown in Table 5.1. The histograms in Figure 5.5 and in Figure 5.6 exhibit the frequency of the size classes of the mean pes and manus track parameters (track length, width, and the index of track size) of the trackways. Note that due to a lack of manus tracks in the pes-only trackways S4 and S5, the manus sample is smaller (N=12 trackways) than the pes sample (N=14 trackways), and the mean values of the manus parameters are with the exception of the quadrupedal trackways S1 and S2 generally based on fewer tracks than the mean values of the pes parameters.

The mean pes length of the trackways ranges between 19,6 cm (S12) and 39 cm (S2), their width between 12,3 cm (S12) and 28,8 cm (S6). The mean values are 30,2 cm for the length and 20,3 cm for the width. The size classes of the pes width are more widely distributed than those of the length. The latter show a concentration around the mean value, which is less pronounced in the width, where fewer trackways are located around the mean value.

Sauropod trackway number				**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**	**S13**	**S14**	**530-S1**	**530-S2**	**540-S1**
Level			[ ]	Main track level (level 500)														530	530	540
Excavation area			[ ]	3	3	1	1	1	1	1	2	2	2	2	2	2	2	3	3	2
Number of pes tracks			[ ]	14	11	4	6	9	11	8	5	5	12	15	18	15	7	7	3	7
Number of manus tracks			[ ]	14	7	1	0	0	2	1	2	3	9	4	10	9	4	8	0	8
Trackway pattern (q=quadrupedal, p-d=pes-dominated; p-o=pes-only; m-d=manus-dominated)			[ ]	q	q	p-d	p-o	p-o	p-d	p-d	p-d	p-d to q	p-d to q	p-d	p-d to q	p-d to q	p-d to q	q	p-o	q m-d
Approximate trackway length			[m]	13	10	2	3	5	7	4	3	5	9	9	11	9	7	6	3	8
Approximate trackway orientation			[°]	328	56	16	26	23	27	13	23	12	25	25	279	280	279	206	84	256
Track parameters	Pes tracks	length (PL)	[cm]	37,5	39,0	35,0	30,2	29,4	34,7	27,7	31,3	29,6	30,0	28,3	19,6	22,1	28,7	38,8	48,0	25,7
		width	[cm]	25,3	26,1	21,8	22,7	22,7	28,8	16,0	20,3	19,0	19,0	17,5	12,3	14,2	19,0	30,3	34,7	19,1
		index of track size (IPS)*	[cm]	30,8	31,9	27,6	26,2	25,8	31,6	21,1	25,2	23,7	23,9	22,3	15,5	17,7	23,3	34,3	40,8	22,2
		depth	[cm]	3,5	3,6	7,5	3,2	5,3	6,3	7,7	4,0	5,9	4,3	4,5	3,5	3,5	4,4	1,7	10,0	2,6
		left rotation	[°]	40,6	6,2	40,0	32,3	11,0	8,5	20,3	5,0	20,0	8,8	8,5	16,0	18,0	21,0	-10,0	22,0	25,3
		right rotation	[°]	3,7	8,3	21,5	7,3	19,5	-10,0	23,5	36,5	28,3	30,5	20,1	22,1	20,0	29,0	31,7	8,5	21,0
	Manus tracks	length	[cm]	12,5	10,5	9,0	no manus tracks	no manus tracks	10,0	6,0	6,0	9,3	9,6	5,5	4,4	6,3	8,7	11,0	no manus tracks	6,8
		width (MW)	[cm]	20,4	20,2	17,0			20,0	15,0	12,5	19,3	19,1	12,7	11,8	14,6	15,7	22,9		14,7
		index of track size (IMS)*	[cm]	16,0	14,6	12,4			14,1	9,5	8,7	13,4	13,5	8,3	7,2	9,6	11,7	15,9		10,0
		depth	[cm]	2,5	2,6	3,0			4,0	0,6	1,8	4,3	3,3	1,3	2,4	2,3	3,0	1,6		4,4
		left rotation	[°]	22,5	38,4								29,7		52,7	19,0	21,5	25,8		50,8
		right rotation	[°]	28,0	31,0								29,0		72,5	32,0	35,0	38,5		38,6
Trackway parameters	Pes tracks	stride	[cm]	154,8	182,3	129,0	106,0	107,4	106,0	109,5	115,0	159,3	137,0	121,3	115,1	112,6	162,8	149,8	141,5	136,3
		width angulation pattern (WAP)	[cm]	54,6	50,0	53,5	31,0	46,5	54,4	49,3	45,7	57,3	68,9	37,8	25,7	27,0	46,7	43,8	64,0	34,4
		left pace	[cm]	97,0	113,0	90,0	57,0	70,3	72,5	77,3	77,0	95,5	98,0	76,9	60,8	63,8	78,0	86,0	1,3	78,0
		left progression*	[cm]	80,1	96,3	70,5	49,0	51,2	59,9	55,4	62,5	77,9	69,0	67,0	55,2	57,7		74,4		70,2
		right pace	[cm]	90,5	101,2	82,0	65,5	71,3	85,0	69,3	71,0	92,5	91,7	67,2	66,9	62,2	98,0	90,0	1,4	74,0
		right progression*	[cm]	71,0	86,5		58,2	55,2	68,7	49,0	58,7	79,7	61,2	55,9	62,3	54,5	86,0	76,5		65,3
		pace angulation	[°]	109,6	123,3	98,0	116,8	101,0	91,0	95,5	101,5	106,0	87,7	114,3	128,0	120,7	127,0	117,2	115,0	126,0
	Manus tracks	stride	[cm]	150,0	179,5	insufficient number of manus tracks	no manus tracks	no manus tracks	insufficient number of manus tracks	insufficient number of manus tracks			141,3	116,0	113,3	103,0	165,0	152,2	no manus tracks	137,7
		width angulation pattern (WAM)	[cm]	68,1	67,9								76,2			39,2	70,0	68,4		42,0
		left pace	[cm]	108,0	110,2						86,0	105,0	107,0			71,0	99,0	91,7		80,0
		left progression*	[cm]	78,4	106,2								73,0			59,5		66,2		68,8
		right pace	[cm]	102,3	108,5							94,0	112,0		80,0	61,0		81,5		79,0
		right progression*	[cm]	75,7	84,9								83,9			29,7		51,0		71,2
		pace angulation	[°]	96,3	109,3								83,0			90,6		122,5		116,0
	gleno-acetabular distance		[cm]	134,3	137,0						80,0	93,0	98,3		56,5	66,8		140,2		104,8
Trackway gauge	Pes tracks	pes trackway ratio*	[%]	37,0	35,5	39,1	29,2	45,0	34,7	42,6	30,9	32,5	27,3	32,7	33,0	34,7	34,1	45,4	32,4	34,3
		gauge cf. Romano et al. (2007)		M	M	M	W	M	W	M	W	W	W	W	W	W	W	M	W	W
		[WAP/PL]-ratio*	[ ]	1,46	1,28	1,53	1,03	1,58	1,57	1,78	1,46	1,94	2,30	1,34	1,31	1,22	1,63	1,13	1,33	1,34
		[WAP/IPS]-ratio*	[ ]	1,77	1,57	1,94	1,18	1,80	1,72	2,34	1,81	2,42	2,88	1,70	1,65	1,53	2,00	1,28	1,57	1,55
	Manus tracks	[WAM/MW]-ratio*	[ ]	3,34	3,37								3,98			2,68	4,47	2,99		2,86
		[WAM/IMS]-ratio*	[ ]	4,26	4,67								5,63			4,10	6,01	4,31		4,20
	([WAP/PL]-ratio) / ([WAM/MW]-ratio)*		[ ]	0,44	0,38								0,58			0,46	0,36	0,38		0,47

Table 5.1: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 (without the enlargement of 2006), main track level and levels 530 and 540: Mean parameters of the sauropod tracks and trackways. Note that due to the (partial) absence of manus tracks not all parameters were obtained for all trackways (crossed-out cells). Asterisks mark parameters, which were not measured in the field but calculated based on other parameters. The pes trackway ratio was obtained from measurements on magnifications of outline drawings.

The mean manus length of the trackways ranges between 4,4 cm (S12) and 12,6 cm (S1), their width between 11,8 cm (S12) and 20,4 cm (S1). The mean values are 8,2 cm for the length and 16,5 cm for the width (Fig. 5.6). The distributions of the manus parameters all show two peaks at the lowers and higher values, with the mean value located in between.

Generally the distributions of the pes and manus parameters do not closely match. The comparison of the indices of track size shows that the range of distribution for the manus is about half of the range of the pes. However, trackway S12 clearly has the smallest tracks, followed by trackway S13, even though the latter has a longer manus than S7, S8, and S11 (which all lack undeformed manus tracks). The trackways S1 and S2 form the upper limit of the distributions, but the difference with the other trackways is small, especially regarding the manus tracks.

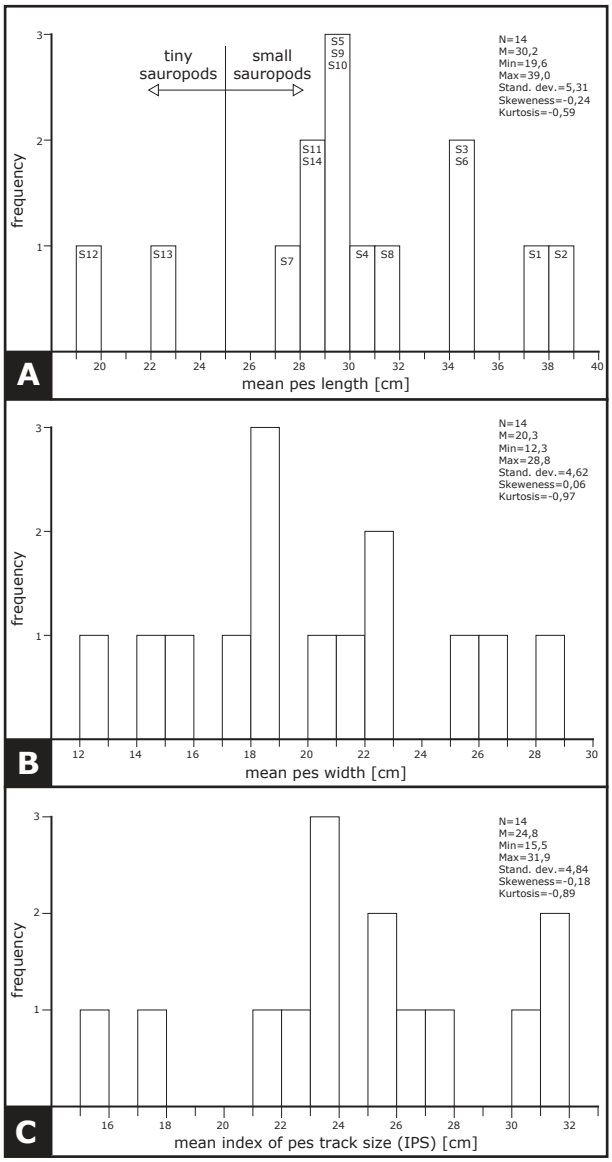


Fig. 5.5: Chevenez—Combe Ronde tracksite, main track level, sauropod trackways. **A-C:** Size-frequency distributions of pes length, width, and mean index of pes track size (IPS). In A, the boundary (25 cm) between tiny and small sauropods is indicated.

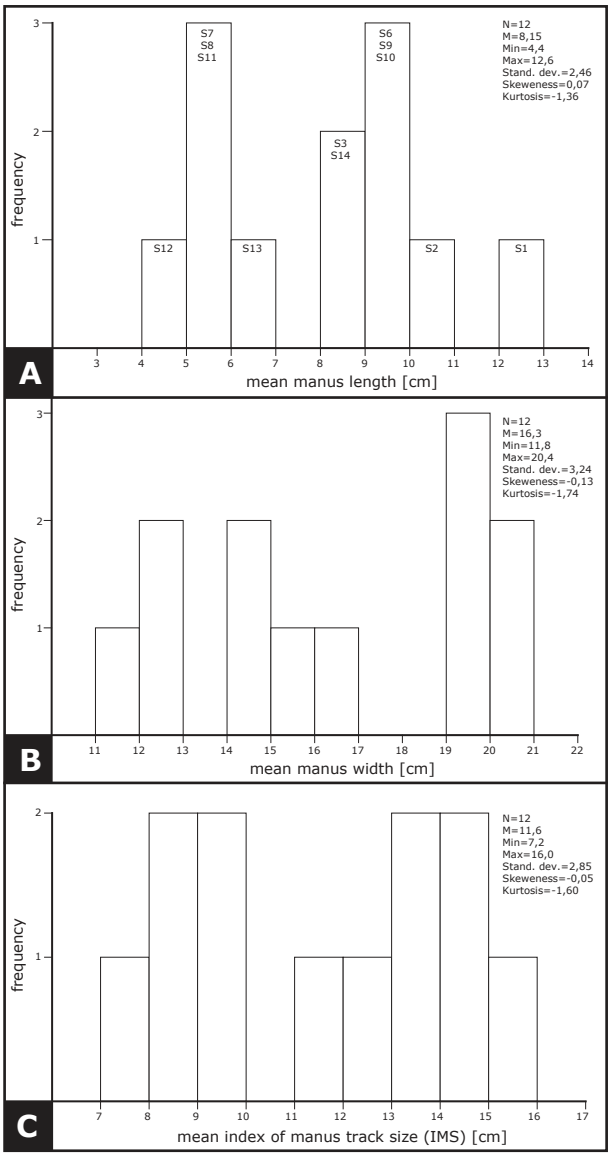


Fig. 5.6: Chevenez—Combe Ronde tracksite, main track level, sauropod trackways. **A-C:** Size-frequency distributions of manus length, width, and mean index of manus track size (IMS).

5.2.3.2 Length-width correlation

Figure 5.7 shows a plot of the mean pes length against mean pes width, and Figure 5.8 a plot of the mean manus length against mean manus width. Both plots exhibit quite a good correlation between track length and width.

In the pes length-width plot, the outliers (S3-S7) are the trackways in excavation area 1, whose tracks are partially displaced by normal faults and affected by epikarstification. However, the two trackways with the smallest pes tracks (S12 and S13) show a very good correlation with the two trackways with the largest pes tracks (S1 and S2), even though the latter exhibit shallow tracks. In the manus width-length plot, the outliers are rather related due to different degrees of manus overprinting than to preservation. An exception is trackway S1, which shows variably preserved manus tracks. Apart from trackway S1, there is still a good correlation between the trackways with small and those with larger tracks.

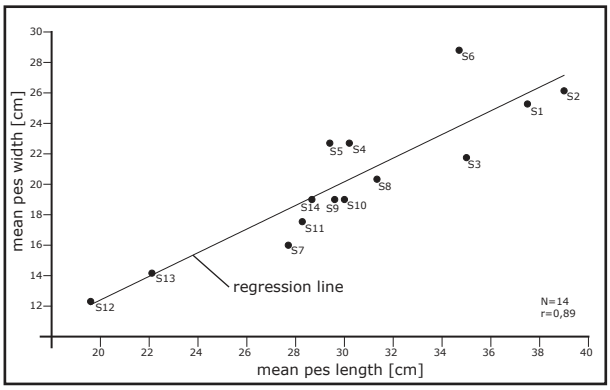


Fig. 5.7: Chevenez—Combe Ronde tracksite, main track level, sauropod trackways: Plot of mean pes length against mean pes width with trackway numbers.

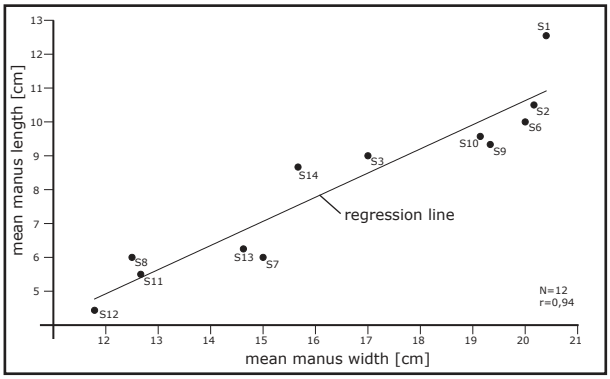


Fig. 5.8: Chevenez—Combe Ronde tracksite, main track level, sauropod trackways: Plot of mean manus width against mean manus length with trackway numbers.

5.2.4 Trackway configuration

The "normal" configuration of quadrupedal sauropod trackways on the main track level is characterized by a pronounced heteropody between pes and manus tracks, outward rotated pes and manus tracks, pes and manus tracks well away from the trackway midline, and manus tracks located in front of the subsequent pes track and slightly farther away from the trackway midline than the pes (Fig. 5.3 and Figs. 5.9D & G-I). The outward (positive) rotation is generally higher for the manus than for the pes tracks.

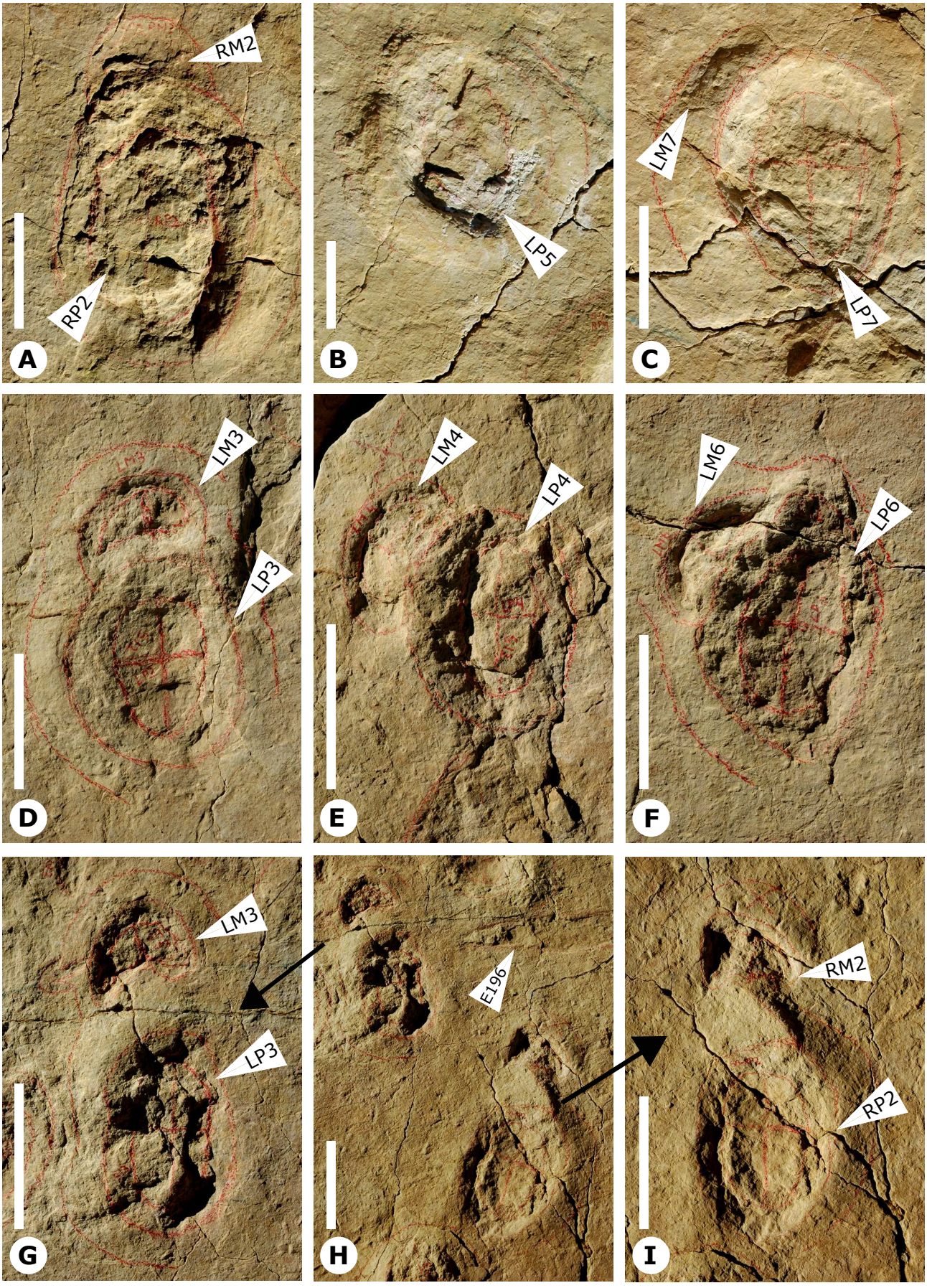
However, at the Combe Ronde site quadrupedal trackways are rare and the "normal" trackway configuration is only occasionally found. Variations concern notably trackway gauge, the rotation of pes and manus tracks, and the relative position of pes and manus tracks. Most of the manus tracks are partially or completely overprinted by the pes. If they are present, their position with respect to the pes is highly variable between trackways and also along single trackways (Figs. 5.9D-F). Following, these variations are first described in a general way, succeeded by a more detailed description of selected peculiar trackways.

5.2.4.1 Heteropody

All trackways are characterized by a pronounced heteropody between the pes and manus tracks, i.e., pes tracks are always clearly larger than the manus tracks. The (pes/manus)-ratio lies between 1:2 (for shallower, more semicircular manus tracks as illustrated in Fig. 5.3C) and 1:3 (for manus tracks with a rather horseshoe-shape as illustrated in Fig. 5.3B), when estimated from manus tracks not deformed by the following pes impact (Figs. 5.9D & G).

However, another indication about the (pes/manus)-ratio and whether it is related to the size classes of the trackways or not, may be provided by the relation between the index of pes and manus size. This ratio shows a relatively small variation, and most trackways are located near the mean value of the ratio, which is 2,16. The outliers are the pes-dominated trackways S8 and S11, both lacking undeformed, well-preserved manus tracks, which may explain the higher ratios (Fig. 5.10A).

The mean indices of pes and manus track size show a good correlation, whereas the plot of the mean index of pes track size against the ratio of the indices


RM2
RP2
A
LP5
B
LM7
LP7
C
LM3
LP3
D
LM4
LP4
E
LM6
LP6
F
LM3
LP3
G
E196
H
RM2
RP2
I

of pes and manus track size is widely scattered and poorly correlated (Figs. 5.10B & C). This indicates that the (pes/manus)-ratio and hence heteropody is independent of the trackway size classes. This is also suggested by the parallel trackways S8 and S10, which show the highest difference in the ratio of the indices of pes to manus track size, but which have a similar pes length.

5.2.4.2 Pes and manus track rotation

With the exception of the right rotation of the pes-dominated trackway S6, the mean pes rotation of all trackways is positive (outward rotated). However, in trackway S6 only a few measures were obtained due to the poor preservation of the tracks and the strong karstification in that area. Trackways S2, S6, S7, and S13 show a similar mean outward rotation of the left and the right pes with a difference of less than 5°, whereas the other trackways are characterized by higher differences, the highest difference occurring in trackway S1 (3,7° of the right against 40,7° of the left pes).

Reliable values for the rotation of the manus tracks were obtained only in six trackways. Thereby, the mean manus rotation is always positive (outward rotated). Except in trackway S10, the mean left and right rotation vary considerably with a difference of nearly 20° in trackway S12, which is also the trackway with the most pronounced manus outward rotation.

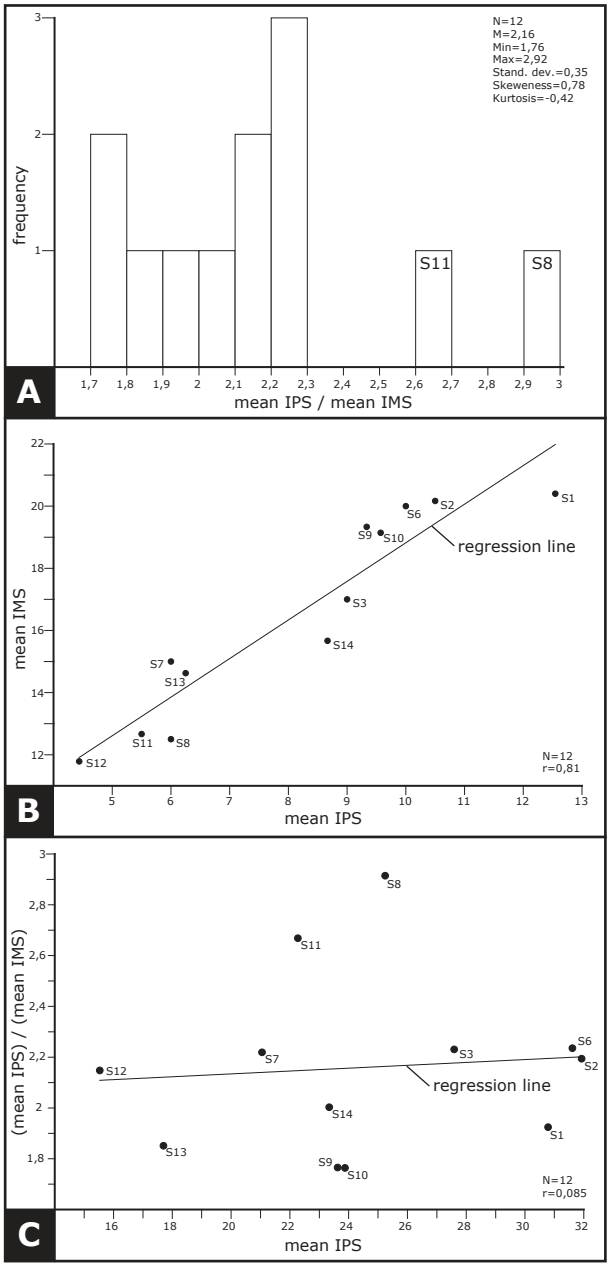


Fig. 5.10: Chevenez—Combe Ronde tracksite, main track level, mean indices of pes (IPS) and manus (IMS) track size of the sauropod trackways. **A:** Size-frequency distribution of the ratio of the indices of pes to manus track size. **B:** Plot of the mean index of pes track size against the mean index of manus track size. **C:** Plot of the mean index of pes track size against the ratio of the mean index of pes to manus track size.

Fig. 5.9 (opposite page): Chevenez—Combe Ronde tracksite, excavation area 2, main track level: Different pes – manus positions and degrees of overprinting within the sauropod trackways S11 (A-C), S12 (D-F), and S13 (G-I). The normal pes – manus position is characterized by a manus track located in front of the pes track, approximately in the extension of the long axis of the pes, and by a slightly higher outward rotation for the manus than for the pes. **A:** S11-LP2 and LM2, manus track partially overprinted by the pes, and with a similar outward rotation than the pes. **B:** S11-LP5, manus track completely overprinted by the pes. **C**: S11-LP7 and LM7, manus track with an anterior-lateral position, a high outward rotation, almost completely overprinted by the pes. **D:** S12-LP3 and LM3, manus track unaffected by the pes and with a similar outward rotation than the pes. **E:** S12-LP4 and LM4, manus track with a striking lateral exterior position and a very high outward rotation, partially deformed by the pes. **F**: S12-LP6 and LM6, manus track with a striking lateral exterior position and a very high outward rotation, heavily deformed by the pes. **G:** S13-LP3 and LM3, detail of H, manus track unaffected by the pes and with a slightly higher outward rotation than the pes. **H:** S13-RP2 and RM2 (lower right) followed by S13-LP3 and LM3 (upper left), E196 is an elongated enigmatic trace (groove). Note the bulge on the inner, posterior side of the manus tracks. **I:** S13-RP2 and RM2, detail of H, manus track unaffected by the pes and with a similar outward rotation than the pes. All scale bars are 20 cm, rising sunlight from the lower right in A-C, and from the upper left in D-I, all photos by B. Migy (SAP).

Apart from the left manus rotation in trackway S1 and the right manus rotation in S10, the left and right outward manus rotation is always greater than the pes outward rotation. However, these differences are mostly not very pronounced, with exception of the trackway S12, where the manus shows an extremely high outward rotation in comparison with the pes, and also in comparison with the other trackways (Figs. 5.9E & F).

The differences between the left and right rotation are generally more pronounced in the pes than in the manus tracks, and the correlation between the degree of the outward rotation of the pes and the subsequent manus is poor (Fig. 5.11).

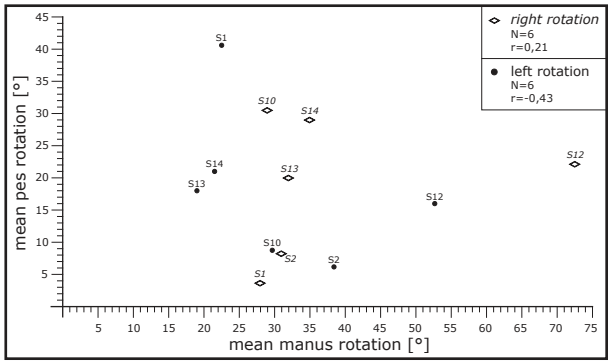


Fig. 5.11: Chevenez—Combe Ronde tracksite, main track level, sauropod trackways with pes and manus tracks: Plot of manus rotation against pes rotation for right and left tracks, respectively.

5.2.4.3 Relative position of pes and manus tracks

The "normal" manus position is in front of the anterior part of the pes track, with the centre (i.e., the intersection of the long and wide axis) of the manus track approximately located on the extension of the pes long axis (Figs. 5.9D & G-I). However, the manus may occupy many different positions farther outward, and may even be located antero-laterally, at the exterior side of the pes track (Figs. 5.9C & E-F). Exceptionally, it may also be located as close or slightly closer to the trackway midline as the pes (e.g., the right manus tracks in S1, Fig. 5.12A).

Partially or completely overprinted manus tracks are more common than undeformed manus tracks. The latter are generally located in the "normal" manus position described above and may be very close (a few cm) to or up to 20 cm in front of the pes track (Figs. 5.9D & G-I). Manus tracks located in a very lateral, exterior position beside the pes, are always partially overprinted. The position of completely overprinted manus tracks can not be identified because the pes tracks do not show any significant deformation (i.e., larger displacement rims) due to the overprinting. This indicates moist to water-unsaturated sediment with low yield strength (see also chap. 4).

5.2.4.4 Trackway gauge (width)

After the analysis of the trackways in the field and from their outline drawings, it was clear that none of the trackways is narrow gauge in the sense that the pes tracks touch or intersect the trackway midline, and it was also recognized that the trackway S10 clearly has the widest gauge of all trackways and classifies as a medium- to wide-gauge "*Brontopodus*-type" trackway (Marty, 2004c).

The pes trackway ratio of Romano et al. (2007) was calculated for all trackways of the Combe Ronde site from magnifications of the outline drawings. Applying the provisional trackway ratio boundaries of 35% (wide-medium gauge) and 50% (medium-narrow gauge) of these authors, nine trackways are wide-gauge and five trackways are medium-gauge.

None of the sauropod trackways of the main track level actually is narrow gauge, and only for the trackways S5 and S7 a pes trackway ratio larger than 40% was calculated. All the other trackways are characterized by a pes trackway ratio of less than 40%. The trackways S4 and S10 even feature a ratio of less than 30%. This revises Marty et al. (2006b) who suggested that the Combe Ronde trackways are rather narrow-gauge.

As the pes trackway ratios were not directly measured on the trackways, ratios between the width of the angulation pattern and the track size expressed by the mean length (for the pes) and width (for the manus), and track size index were calculated. For pes tracks these ratios are (WAP/PL) and (WAP/SIP), and for manus tracks (WAM/MW) and (WAM/SIM) (Table 5.1). Apart from trackway S4, these ratios are always clearly larger than 1, which indicates that the trackways are not narrow-gauge.

5.2.5 Trackway patterns

The sauropod trackways of the main track level are quadrupedal, pes-only, or pes-dominated trackways (Fig. 5.12); manus-dominated and manus-only trackways are absent.

Trackways S1 and S2 with the shallow tracks in excavation area 3 are quadrupedal trackways with a quite regular configuration along the whole trackway. Some manus tracks are lacking because of fracturing around normal faults or because they were too shallow to be clearly identified, but clearly not because of overprinting by the pes. Manus tracks are only exceptionally deformed by the pes.

The trackways with the deeper tracks in excavation areas 1 and 2 are either pes-only (S4, S5) or pes-dominated (S3, S6-S8, S11, S12, S14). Trackways S9, S10, and S13 are described as pes-dominated to quadrupedal because they exhibit at least three consecutive pes-manus pairs. Manus tracks are lacking due to overprinting by the pes. In the pes-dominated trackways, on the other hand, manus tracks occur occasionally but never three in a row, and they also tend to be partially overprinted by the pes. In pes-dominated to quadrupedal trackways, undeformed manus tracks are clearly more common than in the pes-dominated trackways. In the pes-dominated trackways S11, S12, and S14, manus tracks occur frequently and are better preserved than in the rest of the pes-dominated trackways. However, this may also be related to the fact that the other pes-dominated trackways are considerably shorter and those in excavation area 1 are generally highly affected by karstification and normal faults. It can also not be excluded that these are also the reasons for the absence of the manus tracks in the pes-only trackways S4 and S5 in excavation area 1.

5.2.6 Description and interpretation of selected trackways

This chapter describes some of the most striking trackway peculiarities of the main track level and their relationships with trackway parameters.

5.2.6.1 Trackways S1 and S2

Description

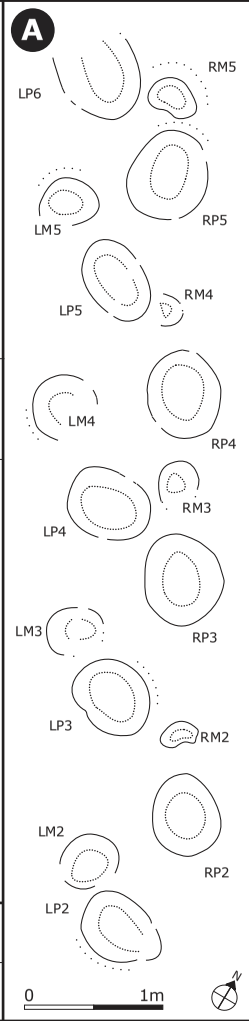
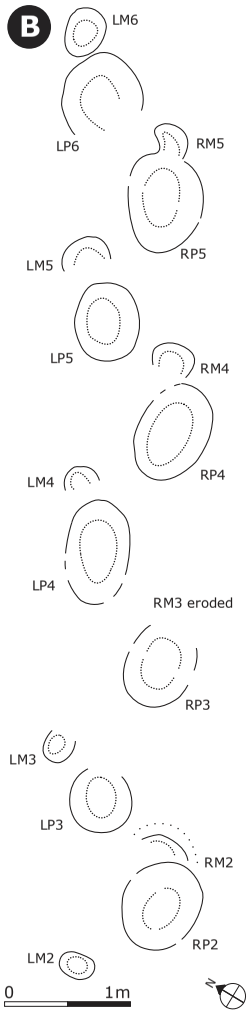
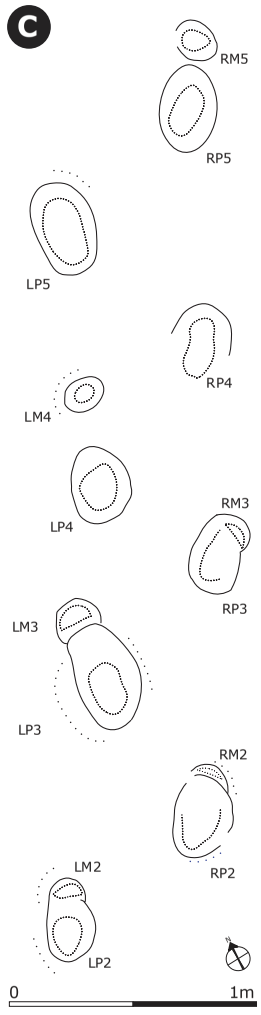
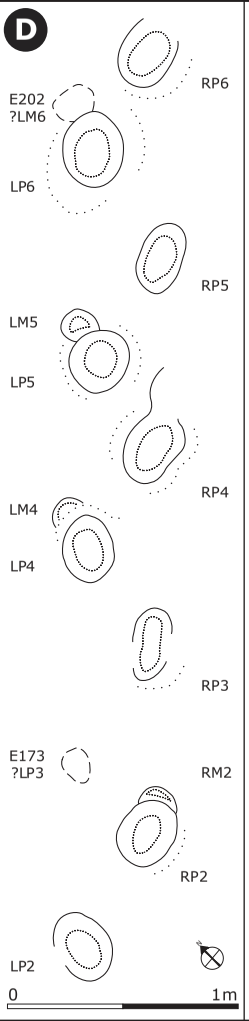
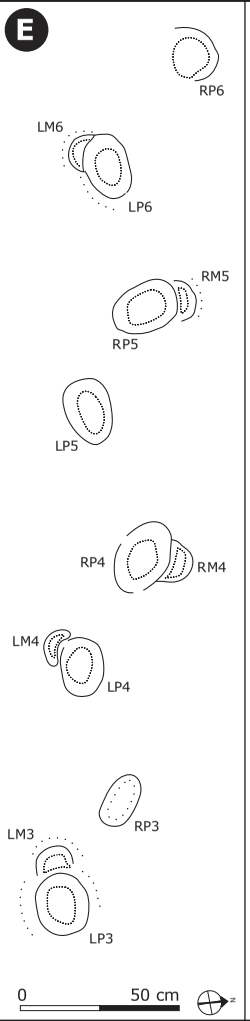
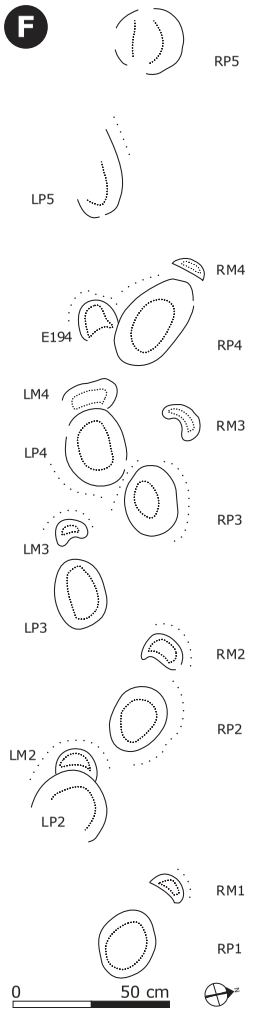
Trackway S1 is characterized by a striking exterior position of the left manus tracks and a very interior position of the right manus tracks. This is coupled with a pronounced outward rotation of the left pes tracks (mean rotation of 40,6°), whilst the right pes tracks are almost angled in the direction of progression (mean rotation of 3,7°) (Fig. 5.12A). However, there is no correlation between the peculiar position of the manus tracks and the pace distances of the manus and pes tracks. Neither is there any evidence for systematically alternating short-long steps in both pes and manus tracks.

In trackway S2, the right manus tracks are also located close to the trackway midline, similar to trackway S1. The left manus tracks still occupy an exterior position, but this is less pronounced than in trackway S1 (Fig. 5.12B). Moreover, left and right pes tracks are both angled in the direction of progression. Unlike S1, trackway S2 shows some evidence for short-long steps. For the manus tracks the left pace (that is the distance between the left and right track) is always larger than the right pace, but the differences (7-9 cm) are not very pronounced. For the pes the difference may be as high as 35 cm, but two out of five measured subsequent left-right/right-left pace pairs show almost equal values.

Interpretation

Trackways with alternating long and short steps were interpreted to be related to limping due to an injury of the trackmaker or to some other unusual gait (changes in speed, substrate) (e.g., Dantas et al., 1994; Lockley et al., 1994d). However, in the present case, there is little evidence that the peculiar position of the left and right manus tracks is related to systematical short-long steps (pace distances), even though this atypical configuration could reflect an usual gait. In trackway S1, the very exterior position of the manus could for example be linked to a turning of the head to the left side or simply to an individual walking style.

It can not be excluded that both trackways were left by the same trackmaker either traversing the area twice or by making a 90° turn coupled with a slight acceleration just outside (to the W) of excavation area 3. The latter scenario might explain the slightly different configuration, notably the less exterior left manus position of S2 when compared with S1. More evidence may be provided by the analysis of trackway S2 in the enlargement of excavation area 3, where this trackway can be followed over another 20 m.

Trackway (speed) trackway pattern	S1 (3,6 km/h) quadrupedal			S2 (4,6 km/h) quadrupedal			S10 (3,9 km/h) pes-dominated to quadr.			S11 (3,4 km/h) pes-dominated			S12 (4,7 km/h) pes-dominated			S13 (4,0 km/h) pes-dominated to quadr.		
Trackway outline drawings exterior limit of the displacement rim external track outline or crest of the displacement rim internal track outline or true track *sensu stricto*																		
LP = left pes LM = left manus RP = right pes RM = right manus																		
S10 and S11 are parallel, located side by side, and are part of sauropod group 1 heading N-NNE S12 and S13 are parallel, located side by side, and are part of sauropod group 2 heading W S1 and S2 feature shallow tracks generally without displacement rims; S10-S13 deeper tracks mostly with displ. rims S1 & S2; S10 & S11; and S12 & 13 are drawn to approximately the same scale																		
mean track and trackway parameters																		
calculated ratios and trackway gauge																		
pes length (PL) [cm]	left pes rotation [°]	right pes rotation [°]	37,5	40,6	3,7	39,0	6,2	8,3	30,0	8,8	30,5	28,3	8,5	20,1	19,6	16,0	22,1	22,1	18,0	20,0
manus width (MW) [cm]	left manus rotation [°]	right manus rotation [°]	20,4	22,5	28,0	20,2	38,4	31,0	19,1	29,7	29,0	12,7	no value	no value	11,8	52,7	72,5	14,6	19,0	32,0
width of the angulation pattern [cm] pes (WAP) / manus (WAM)			WAP=54,6 / WAM=68,1			WAP=50,0 / WAM=67,9			WAP=68,9 / WAM=76,2			WAP=37,8 / WAM=no value			WAP=25,7 / WAM=no value			WAP=27,0 / WAM=39,2		
[WAP/PL]-ratio [ ]	[WAM/MW]-ratio [ ]	[WAP/PL]-ratio [WAM/MW]-ratio	1,46	3,34	0,44	1,28	3,37	0,38	2,30	3,98	0,58	1,34	no value	no value	1,31	no value	no value	1,22	2,68	0,46
calculated pes trackway ratio [%] pes trackway gauge *cf.* Romano et al. (2007)			37,0 medium-gauge			35,5 medium-gauge			27,3 wide-gauge			32,7 wide-gauge			33,0 wide-gauge			34,7 wide-gauge		

5.2.6.2 Trackway S6

Description

Trackway S6 is remarkable because it is first a pes-only trackway with pes tracks in close proximity to each other, but at the end of the trackway it looks like a "normal" quadrupedal trackway, even though a third pes-manus pair was not revealed because the trackway was not further excavated (Fig. 5.29). For the first part of the trackway (between RP2 and LP4) a locomotion speed of 1,77 km/h can be calculated (using eq. 2 and ha; chap. 2.7.6), and at the end of the trackway (from RP4 to RP5) of 3,3 km/h.

Interpretation

Generally, pes-only trackways produced by overprinting of the manus by the pes assuming a footfall pattern of LM-LP-RM-RP, are believed to be related to high locomotion speed. However, in trackway S6, the complete overprinting of the manus tracks at the beginning of the trackway is associated with a decrease in locomotion speed. This may indicate that the trackmaker was slowing down or standing still for a moment overprinting the manus tracks.

5.2.6.3 Trackway S10

Description

Trackway S10 is, with respect to track morphology, track and trackway parameters, the general trackway configuration (pes – manus position, heteropody), and locomotion speed (chap. 5.5), similar to the other trackways of the main track level. S10 is a pes-dominated to quadrupedal trackway and the lacking manus tracks are absent because of overprinting by other trackways rather the pes tracks (Fig. 5.12C).

S10 is striking because it is clearly wider than all other trackways. The pes trackway ratio and the [WAP/PL]-ratio indicate that S10 is very wide gauge (Fig. 5.38).

Interpretation

The similar track morphology of S10 and the other trackways suggests that S10 was left by the same trackmaker species. The clearly wider gauge of S10 can be explained by an individual walking style or an unusual gait reflecting a special behaviour, a different trackmaker species, or eventually sexual dimorphism.

5.2.6.4 Trackways S12 and S13

Description

These two trackways feature the smallest tracks of the main track level. They are parallel, side-by-side in very close proximity one to each other.

In the middle of trackway S12, between LP4 and LP6, a striking exterior manus position coupled with a very high manus outward rotation occurs in both left and right manus tracks (Fig. 5.12E), whilst at the

Fig. 5.12: Chevenez—Combe Ronde tracksite, main track level, excavation areas 2 and 3: Outline drawings (not to scale) of representative parts of selected trackways and indication of some mean track and trackway parameters. Note that trackway S10 (**C**) has the widest gauge, which is confirmed by the pes trackway ratio and the [WAP/PL]-ratio. Note also the striking exterior position of the left manus tracks, and the interior position of the right manus tracks in trackway S1 (**A**) and in a similar way but less pronounced in S2 (**B**). Trackway S12 (**E**) with the smallest tracks features a striking lateral and exterior position of some manus tracks with regard to the pes, and the most pronounced manus outward rotation of all trackways. In trackway S13 (**F**) the track E194 in front of LM4 is one of the best preserved manus tracks of the main track level. It is most probably a double imprint of the left manus, because an affiliation with the trackway S11, which is in close proximity but heading in an other direction, is unlikely. For the original position of the trackways with respect to each other refer to Figures 5.30 and 5.32.

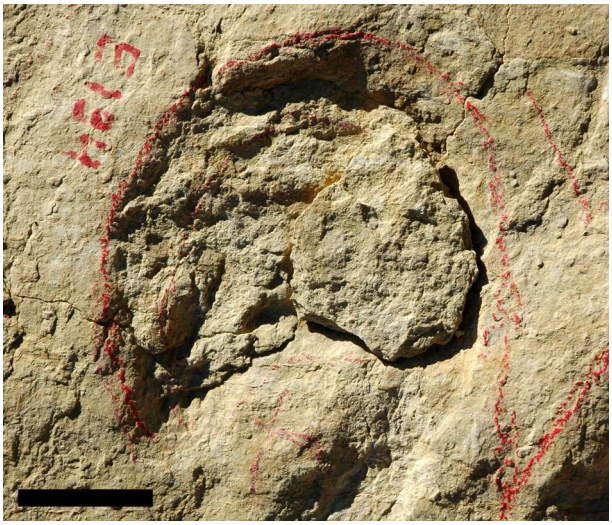


Fig. 5.13: Chevenez—Combe Ronde tracksite, main track level, excavation area 2: The isolated manus track E194 in front of LM4 of trackway S13, interpreted as a double step of the left manus due to decelerating. Track still carries the fill, but note the well-defined exterior track outline with a horseshoed, crescent shape, very similar to the other well-preserved manus tracks of trackway S13 (compare with Figs. 5.9G-I). Scale bar is 5 cm, rising sunlight from the upper left, photo by B. Migy (SAP).

beginning and at the end of the trackway manus tracks occupy a normal position in front of the pes tracks with a clearly lower outward rotation.

In the same area, trackway S13 is characterized by well-defined and undeformed manus tracks well in front of the pes tracks, a probable double step (E194) of the left manus after LM4 (Fig. 5.13), and pes tracks located closer together (shorter pace) than in the rest of the trackway (Fig. 5.12F). This comes along with clearly reduced pace lengths. For the corresponding stride length of 0,71 m a locomotion speed of 1,85 km/h results, which is clearly lower than the mean speed of the trackway (4 km/h). In trackway S12, pace and stride length tend to increase towards the end of the trackway, but there is no marked change associated with the peculiar manus positions.

Interpretation

Trackways S12 and S13 are so close to each other that the two trackmakers most probably were not walking side-by-side but one behind the other. This is also indicated by RP2 of trackway S12, which overprints LP2 of trackway S13. In S12, the unusual exterior position of the manus and associated high outward rotation is not related to the small size of the trackmaker, because it does not systematically occur along the entire trackway course and neither so in trackway S13, which has tracks almost as small. It is best explained by an atypical gait due to an unusual behaviour such as alternately turning the neck to the left and right side. Maybe there was an interaction between the two trackmakers, for example when the animal in front decelerated. However, it can not be proven whether these two animals were really travelling one behind each other at the same time, but it is likely that the well-defined quadrupedal trackway pattern with undeformed manus tracks well in front of the pes in the middle part of S13 and the associated double step of the left manus (E194) is linked to deceleration. This is in contrast to trackway S6 where deceleration probably resulted in a pes-only trackway pattern.

5.3 Sauropod tracks and trackways of the overlying levels

The systematic excavation of the 0,65 m thick laminite sequence above the main track level in excavation areas 1, 2 and 3 yielded seven levels with sauropod tracks, but no tracks of bipedal, tridactyl dinosaurs were unearthed.

Totally, 347 sauropod tracks were excavated and 11 sauropod trackways identified. However, only the levels 530 and 540 yielded well-preserved tracks and well-defined trackways, which will be described in greater detail hereafter. On the highly dinoturbated levels 510, 515, and 520 several trackways were identified and measured during the excavation. However, the subsequent analysis including the superimposition of the maps with the track outline drawings revealed that this high dinoturbation is mainly related to track interference of tracks from different levels. Consequently, most of the initially identified trackways can not unambiguously be confirmed, even though some look quite realistic (see Annex 5.1). These trackways are considered as invalid and not subjected to further analyses here.

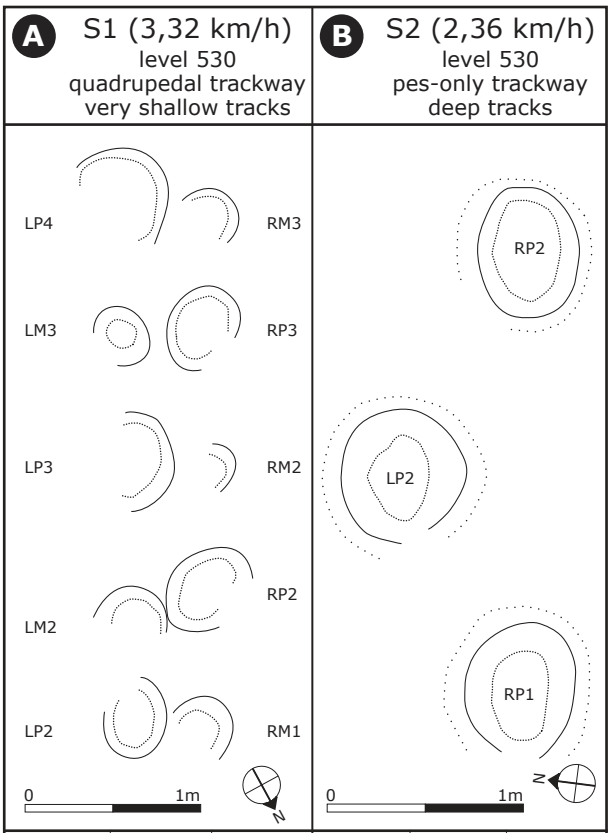
5.3.1 Trackways of level 530

Level 530 exhibited two generations of tracks, as observed on the main track level, and it is the level with the largest sauropod tracks.

5.3.1.1 Shallow quadrupedal trackway S1

Trackway S1 is characterized by the shallowest and faintest tracks of all excavated tracks, which were only discernible under oblique light. These were left in almost dry sediment, probably covered by a thick microbial mat. Consequently, the external and internal track outlines are very poorly defined and the track and trackway measurements are subjected to a relatively high margin of error. It is also not possible to describe the track morphology in greater detail than that the pes is oval, longer than wide, and the manus semicircular.

The trackway is quadrupedal and characterized by a “normal” configuration with manus tracks in front of the pes tracks and with a higher outward rotation than the pes. The right pes shows a pronounced outward rotation, whilst the rotation of the left pes is negative, which might however, also be related to the poorer preservation of the left pes tracks.



38,8	-10,0	31,7	48,0	22,0	8,5
22,9	25,8	38,5	no manus tracks		
WAP=43,8 / WAM=68,4			WAP=64,0 / WAM=no value		
1,13	2,99	0,38	1,33	no value	no value
45,4 / medium-gauge			32,4 / wide-gauge		

Fig. 5.14: Chevenez—Combe Ronde tracksite, level 530, excavation area 3: Outline drawings of trackways S1 (**A**) and S2 (**B**). Note that S1 is narrower than S2. For the legend of the table at the bottom see Figure 5.12.



Fig. 5.15: Chevenez—Combe Ronde tracksite, level 530, excavation area 3: LP2 of the pes-only trackway S2. The dashed line marks the approximate position of the crest of the large and broad displacement rim, the dotted, fine line the suggested internal track outline with long and wide axes indicated. Scale bar is 20 cm, picture taken in the shadow.

The trackway outline drawing suggests that this trackway has a quite narrow gauge, even though the pes tracks do not touch the trackway midline, and the manus tracks are located closer to the trackway midline than in any other of the described trackways (Fig 5.14A). This is also expressed by the highest pes trackway ratio (45,4%) of all trackways and a low [WAP/ PL]-ratio (1,13).

5.3.1.2 Deep pes-only trackway S2

Trackway S2 exhibits the deepest and largest of all excavated tracks, entirely surrounded by large displacement rims (Fig 5.15). Some of the pes tracks of this trackway were recovered and cut into serial-sections (Fig. 4.10). This shows that the tracks are underprints left in water-unsaturated to saturated sediment (layer 530), which was penetrated and pushed besides by the foot in a way that the true track *sensu stricto* was left on top of, at that time already consolidated, layer 528 (see chap. 4). The cross-section of a track fill (Fig. 4.11) further reveals the presence of internal overtracks, which blur the track morphology and do not allow a detailed description of the original track morphology. However, the general oval internal outline of the pes tracks is similar to those of the main track level, with the maximum width located in the middle, or slightly towards the anterior part of the track.

The trackway is pes-only without any evidence for manus tracks, implying that these were completely overprinted by the subsequent pes track. The pes tracks do not show a very pronounced outward rotation and are located well away from the trackway midline, giving this trackway a wide-gauge appearance (Fig. 5.14B). This is confirmed by the pes trackway ratio (32,4) and the [WAP/ PL]-ratio (1,33).

5.3.2 Trackway S1 of level 540

This level could only be excavated in excavation area 2 over a comparatively small area and no further trackways were discovered. However, a cast of the first part of trackway S1 including the well-defined manus tracks LM2 and RM3 was made and is available for further studies.

5.3.2.1 Pes and manus track morphology

The external and internal outline of the pes tracks is poorly-defined. The pes tracks are subcircular to oval in shape with the maximum width approximately located in the middle of the long axis or slightly towards the anterior part of the tracks. They are longer (mean pes length of 25,7 cm) than wide (mean pes width of 19,1 cm), have a flat internal morphology and lack anatomical details (Figs. 5.16A & D). They are very shallow, almost indiscernible tracks.

Generally, the manus tracks are semicircular to circular in shape with the maximum width located at the rear in the semicircular tracks and in the middle in the more circular ones. They are wider (mean manus width 14,7 cm) than long (mean pes length 6,8 cm) and inclined and deeper towards the anterior part of the track, which is characterized by a crescent-shape, convex-forward groove and surrounded by a well-defined displacement rim (Fig. 5.16). At the rear of the manus tracks, the displacement rim is, if present, small and rather poorly-defined (Fig. 5.16E). Manus tracks LM2 and RM3 are amongst the best-defined of all manus tracks excavated at the Combe Ronde site. These tracks are particular because the rear of the foot is also impressed, giving them a rather circular, slightly U-form shape. They further exhibit small lateral indentations at both sides in the middle of the track (i.e., approximately at the intersection with the maximum manus width), whereas the indentation on the internal side is better developed (Figs. 5.16B & E).

5.3.2.2 Trackway configuration and gauge (width)

The manus tracks are always located in front of the anterior part of the pes track and have an outward rotation almost twice as high as the pes (mean pes rotation 23,2° vs. 44,7° of the manus). Similarly to trackway S1 on the main track level 500, this trackway is characterized by left manus tracks located

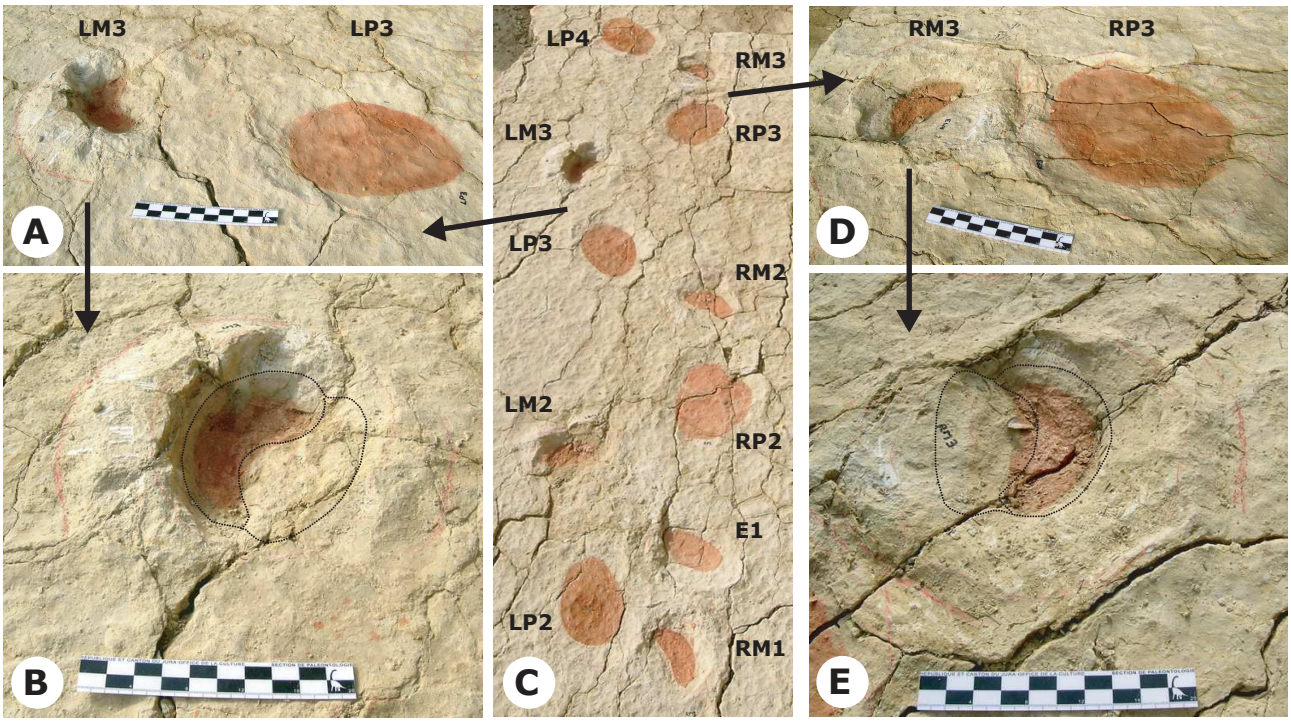


Fig. 5.16: Chevenez—Combe Ronde tracksite, level 540, excavation area 2: Manus-dominated sauropod trackway S1 in overview (**C**), and details of LP3 and LM3 (**A-B**) and of RP3 and RM3 (**D-E**). Note the well-defined displacement rims in the anterior part of the manus tracks. The dotted lines in B and E mark the approximate internal track outline and the pronounced groove in the anterior part of the tracks. This crescent-shaped groove probably corresponds to digits II, III, and IV, which are bound together in a pad. All scale bars are 20 cm, tracks are coloured with water colour; in E rising sunlight from the top in all others from the left.

farther outside with respect to the antecedent pes track and the trackway midline than the right manus tracks (Fig. 5.17). The latter are located almost as closely to the trackway midline as the right pes tracks and also have a smaller outward rotation (mean left manus rotation 50,8° vs. 38,6° of the right manus). The heteropody is similar as on the main track level, about 1:2 for the semicircular manus tracks.

The pes tracks are located well away from the trackway midline. The calculated pes trackway ratio (34,3%) as well as the [WAP/PL]-ratio (1,34) suggest that this trackway is wide-gauge.

5.3.2.3 Trackway pattern

Despite similar track morphology, trackway configuration and gauge as the other so far described trackways, this trackway is different because it systematically exhibits much deeper manus than pes tracks. Most manus tracks are surrounded by large displacement rims whereas many pes prints are very shallow and almost not discernible. This trackway is thus described as a manus-dominated trackway.

At the beginning of the trackway, the trace E1 probably represents a double step of the right manus and E4 of the left pes. Contrary to the trackways S6 and S13 of the main track level where double steps are associated with deceleration, there is no obvious change in pace and stride length in trackway 540-S1. Hence, it may have resulted from a different behaviour of the trackmaker.



pes length (PL) [cm]	left pes rotation [°]	right pes rotation [°]	25,7	25,3	21,0
manus width (MW) [cm]	left manus rotation [°]	right manus rotation [°]	14,7	50,8	38,6
width of the angulation pattern [cm] pes (WAP) / manus (WAM)			WAP=34,4 / WAM=42		
[WAP/PL]-ratio [ ]	[WAM/MW]-ratio [ ]	[WAP/PL]-ratio / [WAM/MW]-ratio	1,34	2,86	0,47
calculated pes trackway ratio [%] pes trackway gauge cf. Romano et al. (2007)			34,3 wide-gauge		

Fig. 5.17: Chevenez—Combe Ronde tracksite, level 540, excavation area 2: Outline drawings of trackway 540-S1. Compare LM3 and RM3 with Figures 5.16B & E. For the legend of the table at the bottom see Figure 5.12.

5.4 Tracks and trackways of bipedal dinosaurs of the main track level

5.4.1 Introduction

Unlike the sauropod tracks, tridactyl tracks occur exclusively on the main track level 500. On this level, they are clearly more abundant than the sauropod tracks, and by the end of 2005 nearly 400 tridactyl tracks were documented in all three excavation areas. Thereof, 362 tracks can be attributed to 43 trackways, and about 40 tracks are isolated. Exceptionally, suites of two tracks were also labelled as trackways if they are aligned in an eye-catching way in areas without any other similar tracks in proximity (e.g., T31, T35). Isolated tridactyl tracks are comparatively rare and generally poorly-defined, even though a few are well-preserved (e.g. E38). These isolated tracks are likely to reveal further trackways in the future because amalgamated track fills may slowly detach due to weathering. The study of the enlargement of excavation area 3 is also likely to allow attributing some of the isolated tracks to trackways. In this chapter emphasis is put on the distinction of preservational and anatomical morphotypes, notably amongst the dominant, minute and small tridactyl tracks.

5.4.2 Track preservation

Track morphology not only depends on the foot anatomy of the trackmaker but also on its limb kinematics and the substrate competency (e.g., Padian & Olsen, 1984). Evidently, this is even more important when dealing with tracks of (semi-) digitigrade than plantigrade animals. Their feet and toes are likely to interact with the sediment in many different ways, depending on the behaviour (e.g., stand, walk, run) of the trackmaker, as was shown by Thulborn & Wade (1989) on the base of tridactyl tracks of the dinosaur "stampede" of Lark Quarry. This can also readily be experienced ourselves when walking in mud at different speeds or moving the toes. Such interactions may be expressed by a variety of extramorphologic ("ichnodynamic") features but may also result in morphological differences in the divarication angle between the digits, or the general track morphology (e.g., presence or absence of a heel or metatarsal imprint). Thus, as Mazin et al. (2003) stated, "it is necessary to accurately discriminate between "ichnoanatomic" characters and "ichnodynamic" features".

At the Combe Ronde tracksite, such discrimination may be corroborated by the great number of specimens available for study. Despite their scarcity and rather poor preservation, the medium-sized tracks (tracks of T11 and T43 with a mean pes length >20 cm) are morphologically different from the smaller tracks (isolated tracks and tracks of the other trackways all characterized by a mean pes length <20 cm). The majority of the minute and small tridactyl tracks are poorly-to reasonably-defined, and only a few exhibit anatomical details of the foot such as well-defined toes with phalanges discernible and claw impressions. These well-defined small tracks are rather randomly distributed along the course of a trackway and also amongst trackways, even though there are a few trackways showing a trend towards better-defined tracks than others. The small tracks can be attributed to several preservational morphotypes.

Fig. 5.18 (opposite page): Chevenez—Combe Ronde tracksite, excavation area 3, main track level: Range of observed morphologies of minute and small tridactyl tracks, which reflects how the feet behaved under particular kinematics as they interacted with substrate of different properties. The ternary diagram is after Padian & Olsen (1984), and the classification of the tracks within this diagram is tentative. Note that it is not assumed that all figured tracks were left by a single trackmaker species, and that it is not the purpose of this figure to provide the most typical examples of tridactyl tracks particularly affected by kinematics, anatomy, or the substrate. In photos, the tips of the digits are indicated with white arrows; artificial illumination from the upper left; all scale bars are 20 cm apart from the black scale bars in B, F, and H, which are 10 cm. **A:** T20-R1, poorly-defined track probably related to unsuitable substrate properties and because parts of the foot penetrated relatively deep into the sediment. Note the narrowness of digit III, which indicates that at least digit III is a deep track. **B:** T30-R2, reasonably-defined track reflecting the anatomy of the foot and how the foot was placed (MT points to the imprint of the metatarsal). This is one of the few tracks with small displacement rims between the digits, probably related to a pronounced weight-bearing phase. **C**: T28-R3, well-defined print with phalanges of digit III discernable, digits II and IV are poorly-defined, probably because the trackmaker did not place its entire foot on the ground. **D:** T21-R6, poorly-defined track with digits II and IV fused in a broad heel. **E:** T24-L2, well-defined track with isolated digits and most phalanges discernible. **F:** T12-R4, poorly-to reasonably-defined track with a well-defined digit III, and with digits II and IV fused in a broad heel. **G:** Isolated track E8, Reasonably-defined track with a well-defined digit III, well-separated from the heel, digits II and IV fused in a narrow heel, and evidence for claw imprints on digits III and IV. **H:** T16-R4, Well-defined track with three isolated digits all exhibiting the outlines of the phalanges and claw impressions because the foot was placed in an ideal way in a well-suited substrate.

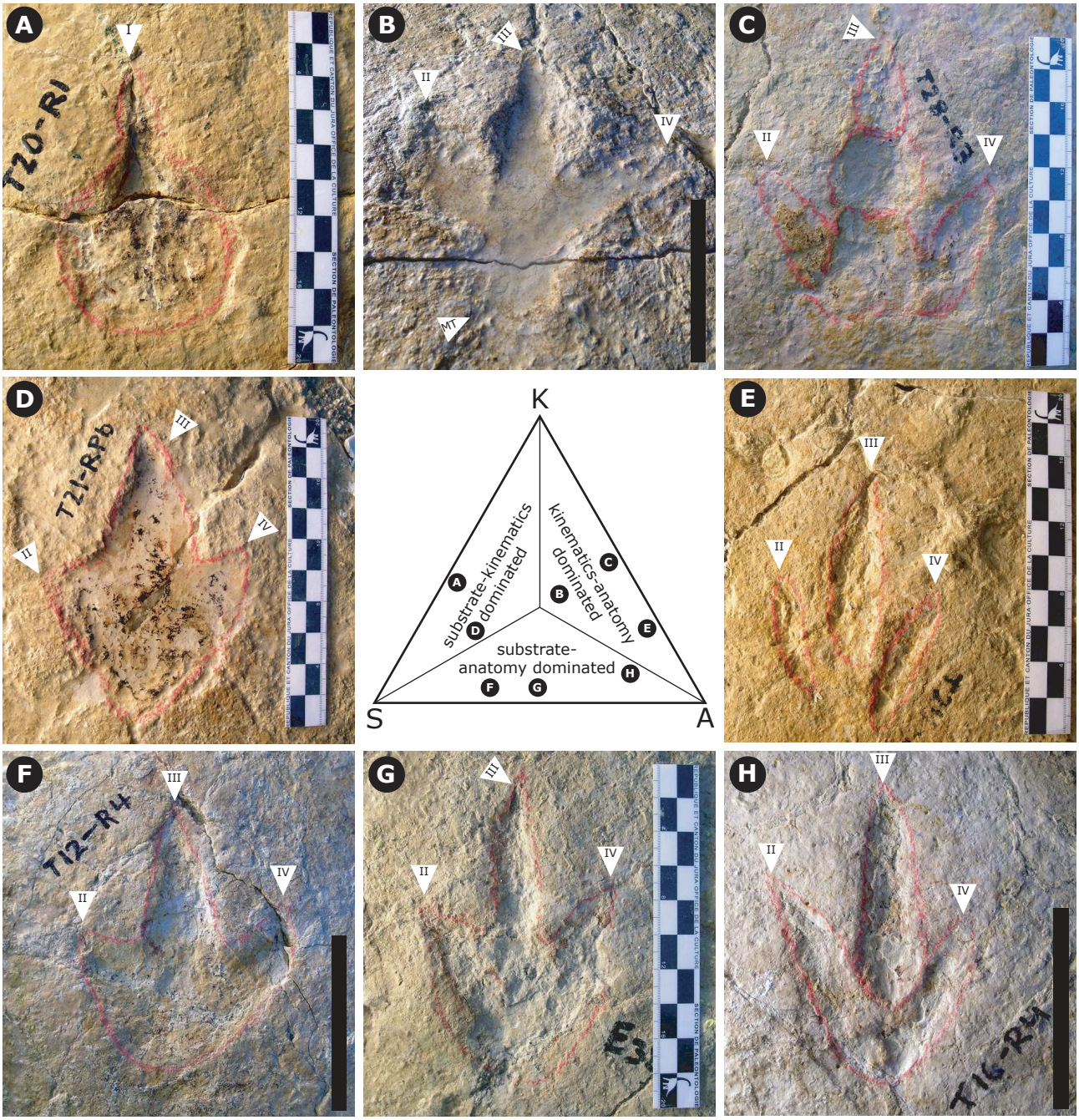
5.4.2.1 Tracks of minute and small, bipedal dinosaurs

The preservational variability of the minute and small tracks is illustrated in Figure 5.18, which is an attempt at classification of the observed preservational morphotypes using the ternary diagram of Padian & Olsen (1984). The transitions between these morphotypes are fluent. Generally, the minute and small tracks are not surrounded by displacement rims, which occur only occasionally laterally of digit III (e.g., T18-L4, T30-R2). In some tracks, (parts of) the fill or internal overtracks were amalgamated and only exceptionally removed.

Well-defined tracks with isolated digits and impressions of phalangeal pads

Description: These tracks exhibit isolated toes, not connected in the heel region, with well-defined internal outlines sometimes exhibiting the outline of the phalanges, and rarely of the claws (Figs. 5.18 E & H). These tracks are used for the general description of the anatomical morphotype of the tracks of the minute and small bipedal dinosaurs (see also chap. 5.7.2.1).

Interpretation: Well-defined tracks with isolated digits most probably formed in a moist carbonate mud or microbial mat, when the foot was placed in



an ideal way and was not covered with mud from a previous step. Under these substrate conditions, incomplete tracks with details only of digit III may also have formed, if the foot was placed in an exceptionally digitigrade way, probably related to a faster gait (Fig. 5.18C).

Reasonably-defined tracks with digits II and IV merged in a narrow heel

Description: Such tracks generally have a well-defined and isolated digit III, rarely with impressions of the phalanges and exceptionally of the claw, while digits II and IV are less well defined, and merge in a narrow heel (Figs. 5.18G & F). Exceptionally, an imprint of the metatarsal is visible if the trackmaker walked in a more semi-digitigrade way (Fig. 5.18B).

Interpretation: These tracks probably formed in a moist to water-unsaturated carbonate mud or microbial mat when the foot sank slightly deeper into the sediment and/or was placed in a slightly less digitigrade way than in the well-defined tracks.

Poorly-defined tracks with digits II and IV merged in a broad heel

Description: Tracks with tapered digits, a poorly-defined internal outline and without any anatomical details of the digits. Digit III often has a pronounced angular shape, the digits II and IV are merely discernible, and all three digits are merged in a broad and blunt, rounded heel with a triangular shape (Fig. 5.18D).

Interpretation: The formation of these tracks is not easy to explain. Maybe the foot was covered with mud from a previous step, the digits moved laterally when in contact with the substrate, or the track was left in an almost dry microbial mat with high yield strength superimposed on still moist or water-saturated sediment. In the latter case, the foot could have pushed the mat into the underlying sediment similarly to the tracks illustrated in Figure 3.5B. Or, these tracks are deep tracks, because such tracks sometimes also show a very angular shape (e.g., Gatesy et al., 1999). However, it can be excluded that these tracks mirror a particular foot anatomy, because they do not occur systematically along any of the trackways.

Poorly-defined tracks with digit III merged in a round heel

Description: Tracks with a poorly-defined and narrow, tapered digit III connected with a round and not very large heel, in which digits II and IV can not be differentiated (Fig. 5.18A). These tracks were rarely found, and they resemble deep tracks (cf. Gatesy et al., 1999).

Interpretation: It is suggested that these tracks were left in a water-unsaturated carbonate mud or microbial mat, into which the foot or at least the third digit penetrated quite deeply and foot withdrawal induced partial collapse of the track.

General interpretation

Because no evidence for tridactyl tracks was found on the levels above (in particular on top of layer 501), and because of the presence of internal overtracks in some of the tracks, all tracks of small bipedal dinosaurs are believed to be true tracks. A few tracks can be considered as deep tracks in the sense that a part of the foot (normally digit III) was penetrating into the substrate, which slightly collapsed after foot withdrawal. The majority of the tracks, however, can be considered as true tracks *sensu stricto*.

The wide range in morphology is explained by the dynamic interaction of the foot with a substrate of different water contents, which was probably covered with a microbial mat. It is also possible that renewed growth of a microbial mat after track formation blurred the original track morphology, and led to the formation of modified true tracks or (internal) overtracks. This could also be an explanation for the poor preservation of some of the tracks. Note that the possibility of track modification after formation (see also Fig. 3.8 and Fig. 3.9) is not considered in the ternary diagram shown in Figure 5.18.

Trackway T10 in excavation area 3 and its continuation T41 in excavation area 2 is the longest bipedal trackway with the smallest tridactyl tracks (and hence of a very small and light trackmaker) of the site. It locally shows reasonably-defined to well-defined tracks of a similar imprint depth, even though some poorly-defined tracks also occur. This trackway is almost 60 m long indicating that the substrate was quite homogeneous over this distance.

Because several trackways with minute and small tridactyl tracks are dominated by tracks of a different, distinct preservational morphotypes, it is suggested that they were left at different moments during the desiccation and consolidation history of the main track level. Incomplete trackways may be explained by tracks not revealed because they still carry the fill. This also explains the presence of isolated, well-

defined tracks with impressions of the phalanges (Fig. 5.18G), even though these could also have been left later in slightly lower areas, which remained longer moist whilst the rest of the surface was already too dry and not susceptible for track recording.

The scenario of the gradual desiccation of the main track level would imply that first deep tracks and poorly-defined tracks were left in a water-saturated to water-unsaturated substrate. Later, when the substrate was moist, the well-defined tracks were left, and finally poorly-defined tracks (maybe those with the broad and blunt heel) were left when the sediment was less moist. Subsequent desiccation is also indicated by the desiccation cracks, which always cut the tracks in a similar way (Fig. 4.22). Exceptionally, tracks also acted as localizing agents for the desiccation cracks. The general shallowness of the tracks may further testify the presence of a surficial microbial mat, which prevented the trackmakers from sinking deeper into the sediment.

Several preservational morphotypes are related to locomotion speed. Tracks with a heel imprint (e.g., Fig. 5.18B) may have been left by dinosaurs walking slower, while tracks with isolated digits may have been left by faster moving trackmakers. Trackway T10 for instance, which most frequently shows tracks with isolated digits, is one of the faster trackways (see also chap. 5.5). Notwithstanding, there are also trackways with a high speed, having tracks with a broad heel. Thus, in order to make any better conclusion, the variations in track morphology, in speed, and in gauge needs to be analysed along single trackways. This is, however, not in the focus of this work.

5.4.2.2 Tracks of medium-sized, bipedal dinosaurs

These are the tracks of trackways T11 and T43, showing a similar preservation, even though all three tracks of T11 are disintegrated by normal faults and affected by epikarstification. The following description is only based on the tracks of T43.

Description

The preservation of the tracks of T43 is very similar to the surrounding deep sauropod tracks. They are clearly the deepest tridactyl tracks and exhibit well-defined displacement rims, notably between the digits and also around the heel region. In several tracks (notably T43-L1 & R2), the track fill or parts of the track fill were amalgamated with the main track level and could not have been removed without partial destruction of the tracks. This hampered the measuring of the track dimensions and the identification of the precise internal track outline. However, also in tracks without fill the internal outline, especially of digits II and IV, is rather poorly defined and the there are no impressions of the phalanges discernible. Around some of the tracks the main track level is characterized by internal overtracks in the form of fine and imbricated laminae, indicating the former presence of microbial mats.

Interpretation

Because these tracks are deep, fairly well-defined, and exhibit well-defined displacement rims they are believed to be true tracks. They were probably left in a moist to water-unsaturated carbonate mud, which was probably covered by a microbial mat. After the tracks were made, the mud desiccated, as indicated by the desiccation cracks, which penetrate into the tracks. Later, renewed and repeated growth of microbial mats within the tracks led to the formation of internal overtracks and an amalgamation of the track fill. In places, this may have blurred the original track morphology, which has to be considered in the description of morphotype II.

5.4.3 Track morphology

Based on the best-defined minute and small tracks and on the medium-sized tracks of T43, well-defined tridactyl tracks of the main track level can be assigned to two anatomical morphotypes: (1) minute and small, mesaxonic tridactyl tracks characterized by slender and isolated digits with claw impressions, and with a 2-3-3 phalangeal-pad impression formula; and (2) the medium-sized tridactyl tracks with blunt toes, a digit III with a trapezoidal form, a broad heel, and without impressions of phalangeal pads.

5.4.3.1 Morphotype I: minute and small mesaxonic tracks with a 2-3-3 phalangeal pad formula

The following description is based on the best-defined specimens, some of which are illustrated and interpreted with outline drawings in Figure 5.19.

Morphotype I is characterized by mesaxonic and elongate, slightly asymmetric tridactyl tracks, which are decidedly longer than wide. They have isolated, slender and tapering digits with distal claw impressions and a relatively low total divarication angle in well-defined specimens.

Digit IV lacks a fourth proximal phalangeal pad, and hence the tracks feature a 2-3-3 phalangeal-pad impression formula (for digits II, III, and IV, respectively) instead of the "normal grallatorid" 2-3-4 formula. This character can be observed only in the best-defined minute and small tracks. Nonetheless, it is suggested that the lack of the fourth proximal pad on digit IV is a primary feature reflecting the anatomy of the trackmaker (i.e., a short metatarsal IV), and is not related to peculiar substrate conditions or kinematics (e.g., a more pronounced digitigrade stance) of the trackmakers. This also suggests that the short metatarsal IV is independent of the ontogenetic stage (e.g., Lockley et al., 1998a).

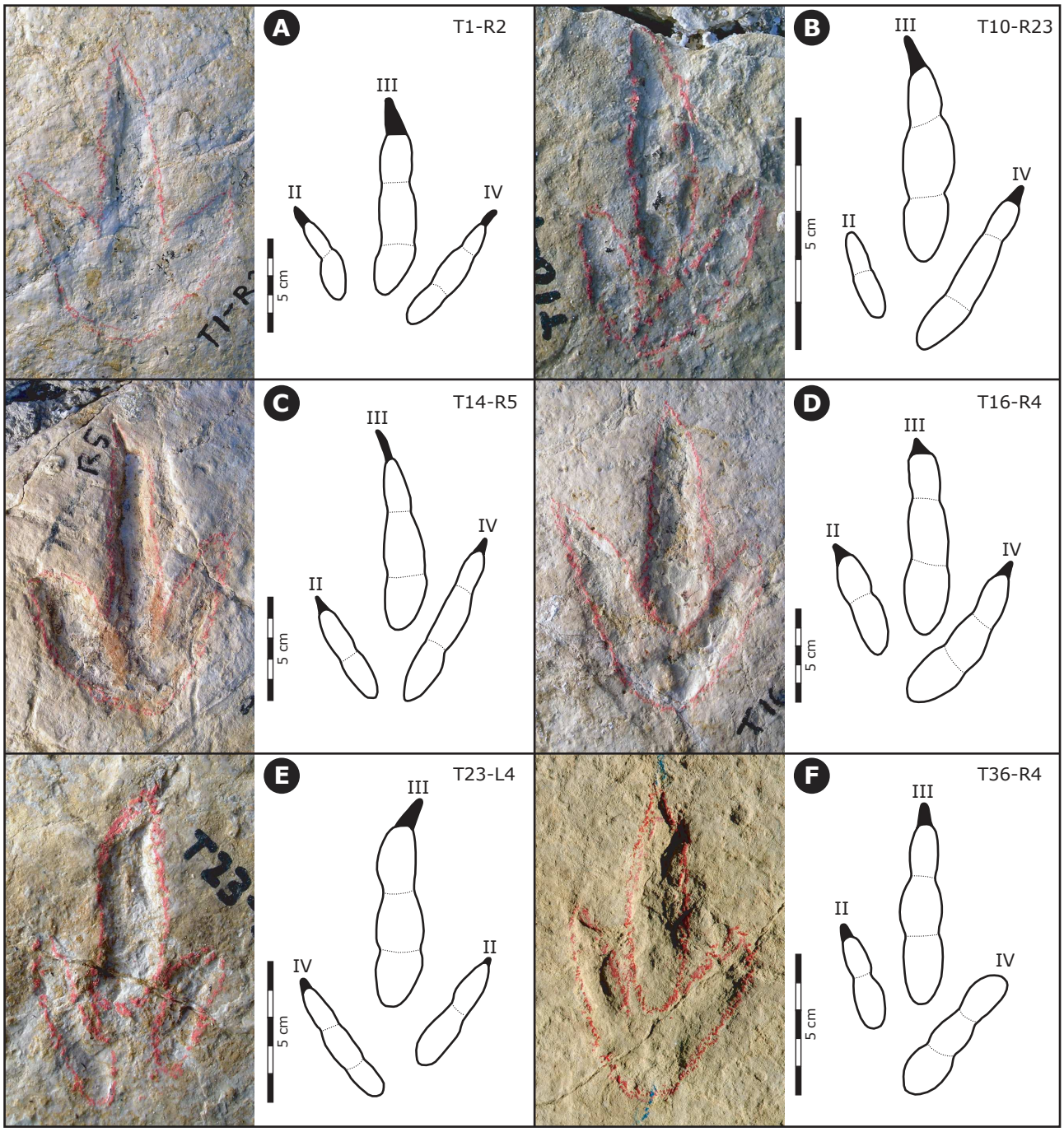


Fig. 5.19: Chevenez—Combe Ronde tracksite, excavation areas 2 and 3, main track level: Photos (left) and interpretative outline drawings (right) of some of the best-defined, small, mesaxonic tridactyl tracks characterized by a 2-3-3 phalangeal pad formula and attributed to morphotype I. Artificial illumination from the upper left in A-E, rising sunlight from the right in F; tracks partially outlined with chalk; photo in F by B. Migy (SAP).

Digit III is the longest and generally best-defined digit, followed by digit IV, which is clearly longer than digit II. Digits II and IV are similar in width, but digit II is shorter posteriorly than digit IV, which forms the rear of the tracks. The interdigital angles between II-III and III-IV are in the same order.

Because of inadequately-defined tracks, not all bipedal trackways with small tracks can unambiguously be attributed to morphotype I. However, at least the following reasonably well-defined tracks and trackways exhibit the typical features or at least some of the typical features, which suggest an attribution to morphotype I (track numbers followed by an asterisk are illustrated in the Figure indicated behind):

- E38*(isolated track) Fig. 5.18G
- T1 (R2*) Fig. 5.19A
- T3 (R2)
- T8 (L1, R1)
- T10 (R1, R4, R9, L10, L16, R23*, R32, L37, R37) Fig. 5.19B
- T14 (L4, R5*) Fig. 5.19C
- T15 (R2)
- T16 (R2, R4*) Figs. 5.18H, 5.19D
- T17 (R3)
- T18 (R2, L4)
- T21 (R4)
- T23 (R3, L4*, L2) Fig. 5.19E
- T24 (R1, L2*, R7) Fig. 5.18E
- T25 (R1, R3)
- T26 (R2)
- T28 (R3*) Fig. 5.18C
- T36 (R4*) Fig. 5.19F
- T38 (R6, R8)
- T39 (L6)
- T40 (R1)
- T41 (R1, L6, R7)
- T42 (R1)

The other bipedal trackways with minute and small tracks (T2, T4-T7, T9, T12, T13, T19, T20, T22, T27, T29-T35, and T37) generally exhibit rather poorly-defined tracks and can not unambiguously be attributed to morphotype I. Finally, the enlargement of the excavation area 3 considerably extended some of the trackways and its final study will allow characterizing some of the so far ambiguous trackways (e.g., T27, T29, T30, T31).

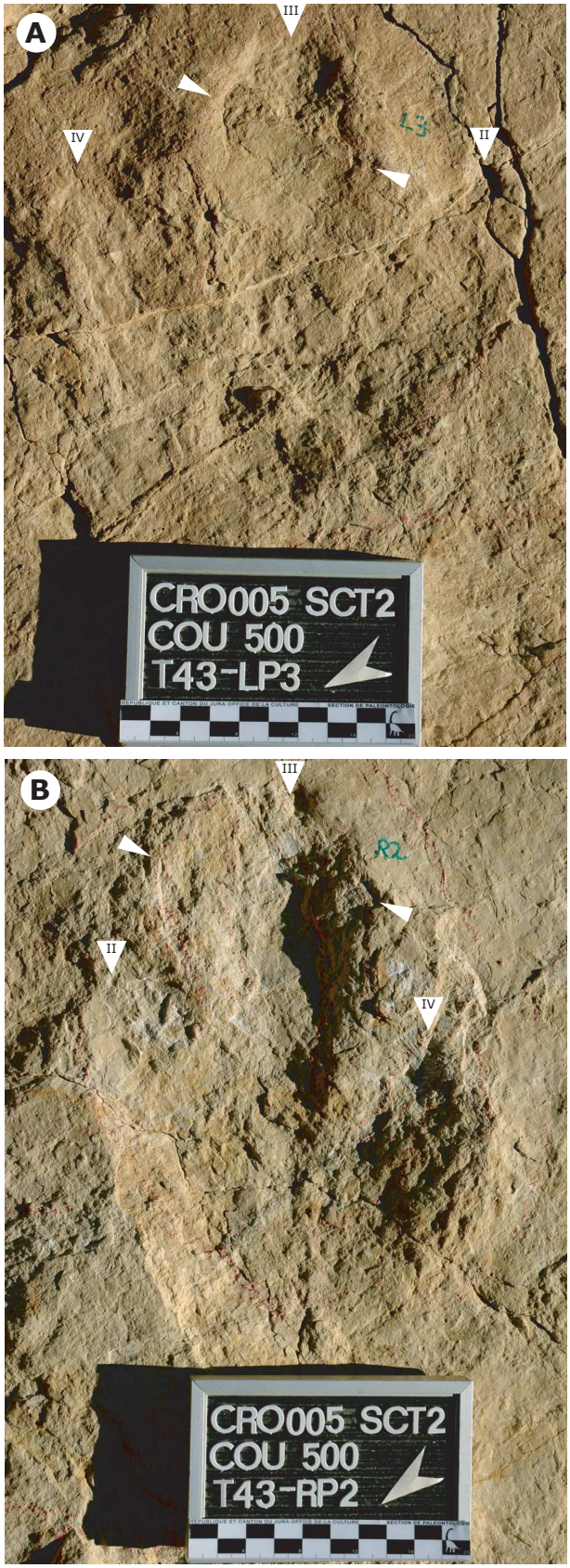
5.4.3.2 Morphotype II: medium-sized tracks with blunt toes without impressions of phalangeal pads

The description of this morphotype is based on trackway T43. The tracks of T11 are similar to those of T43, but as they are poorly preserved, they can not unambiguously be attributed to the same morphotype. It also has to be considered that some of the tracks of T43 bore parts of their fill and that those without track fills may have been affected by the growth of microbial mats after their formation. This may have blurred possible impressions of phalangeal pads or claws.

Morphotype II is characterized by subsymmetric slightly mesaxonic tracks almost as wide as long (width/length ratio of 0,9) with blunt toes and without evidence for impressions of discrete digital pads and claws. The only well-defined digit is digit III, which is separated from the other digits and has a slightly angular, trapezoidal shape with the maximum width located in the anterior part of the digit. Digits II and IV are less well-defined, more oval and more or less merged in a rather short, broad and round heel, without evidence for a postero-medial indentation on the heel (Fig. 5.20).

Digit III is longer (26,8 cm) than digit II (21 cm) and digit IV (19,5 cm). The best-preserved tracks have a slightly longer digit IV than digit II, which is, however, not expressed by their mean values shown in Table 5.2. Also, due to the narrow trackway with inward rotation of some of the tracks (Fig. 5.27), left and right tracks are identified tentatively. The mean pes length of T43 is 30 cm, the width 27 cm, the mean divarication angle is 39,8° between digits II and III, 42,3° between digits II and IV, and the mean total divarication angle is 84,3°. The (width/length)-ratio equals 0,9 indicating that the tracks are almost as wide as long. The best-defined track (L3) is also almost as wide (29 cm) as long (31 cm), and has a total divarication between digits II and IV of 90°.

It is suggested that morphotype II (T43) is not the ontogenetic suite of morphotype I, because the tracks are decidedly wider (less slender) and less mesaxonic, and because of the particular elongated trapezoidal shape of digit III and the oval and blunt digits II and IV without evidence for impressions of phalangeal pads and claws.



5.4.4 Acquisition of track and trackway data

The following chapters analyse and compare the mean values of the track and trackway parameters, shown in Table 5.2.

Apart from exceedingly poorly-defined tracks, the main track parameters (length, width, depth) were measured for all tracks, independent of their preservation. Digit length and width and the divarication angles between the digits were measured in well-defined tracks with isolated digits and, if possible, also in tracks where digits II and IV were merged in a narrow or broad heel. It has to be considered that the latter measurements are more inaccurate than those measured in the well-defined tracks with the isolated digits, even though it is considered that they do not significantly influence the mean values of the trackways.

There are some trackways with generally poorly-defined tracks for which not all track parameters were obtained. This is highlighted in Table 5.2 by crossed-out cells. The same is true for some of the trackway parameters, which could not always be obtained either because of incomplete trackways or because tracks were displaced by normal faults, making it impossible to acquire reliable data.

5.4.5 Size classes and correlation of track parameters

5.4.5.1 Size classes

The mean pes length of all trackways varies from 8,1 cm (T10) to 30 cm (T43), the mean width from 5 cm (T41) to 27 cm (T43), and the index of track size from 6,5 cm (T10) to 28,5 cm (T43) (Fig. 5.21). The mean values are 13,6 cm for the length, 9,5 cm for the width, and 11,4 cm for the index of track size.

Fig. 5.20: Chevenez—Combe Ronde tracksite, excavation area 2, main track level, best-defined, medium-sized tracks of the bipedal trackway T43. **A:** T43-L3 with pronounced angular, trapezoidal shape of digit III with the maximum width located in the anterior part of the digit (indicated by white arrows). The digits II and IV are fused in a broad and round heel and can not be clearly distinguished. **B:** T43-R2, slightly narrower than L3. Trapezoidal shape of digit III is less pronounced due to partially amalgamated track fill. Digit II is slightly longer than IV. Scale bars are 20 cm; rising sunlight from the right; photos by B. Migy (SAP).

The distribution of the pes length shows that the majority of the trackways can be attributed to small, several trackways to minute, and only two trackways to medium-sized bipedal, tridactyl dinosaurs. Trackways T11 (mean PL of 24 cm) and T43 (mean PL of 30 cm), both attributed to morphotype II, clearly have the largest tracks, and trackway T35 (mean PL of 18,5 cm, Fig. 5.21A) displays the largest tracks amongst the trackways of the minute and small bipedal dinosaurs. The distributions of pes length and of the index of track size show a second peak in the array of the minute trackways.

The size classes correlate well with the two morphotypes of tridactyl tracks revealed. Morphotype I is represented by minute and small tracks, and morphotype II by the medium-sized tracks.

The mean pes length of the trackways attributed to morphotype I varies from 8,1 cm (T10) to 15 cm (T3). Its length-frequency distribution is shown in Figure 5.22 and has two peaks, one within the tracks of minute and one within the tracks of small bipedal dinosaurs. This distribution is not significantly different from the distribution of all minute and small trackways shown in Figure 5.21A.

Trackway number	Generalities					Track parameters and ratios																	Trackway parameters and ratios								
											digit II		digit III		digit IV		divarications			rotation											
	excvation area	total no. of tracks	appr. TW length	appr. TW orientation	Morphotype	length (PL)	width	depth	index of track size (IPS)	width/length [W/L]-ratio	length	width	length	width	length	width	II-III	III-IV	total divarication II-IV	left rotation	right rotation	stride	(WAP) width of the angulation pattern	left pace	left progression	right pace	right progression	pace angulation	[WAP/PL]-ratio	[WAP/IPS]-ratio
	[ ]	[ ]	[m]	[ ]	[°]	[cm]	[cm]	[cm]	[cm]	[ ]	[cm]	[cm]	[cm]	[cm]	[cm]	[cm]	[°]	[°]	[°]	[°]	[°]	[cm]	[cm]	[cm]	[cm]	[cm]	[cm]	[°]	[ ]	[ ]
T1	3	4	3	81	I	13,5	9,1	1,0	11,1	0,68	9,0	1,3	9,3	1,3	7,5	1,8	33,3	39,5	72,8		3,5		12,50	74,00				164	0,93	1,13
T2	3	8	7	36		15,1	10,5	1,1	12,6	0,70	8,6	2,0	8,9	1,7	9,0	1,8	36,5	34,8	71,3	5,5	10,0	136,5	6,8	57,0	69,9	55,0	54,4	163	0,45	0,54
T3	3	7	4	270	I	15,0	8,3	1,0	11,1	0,55	8,8	1,4	10,2	1,5	8,1	1,2	34,0	27,6	61,6	4,0	8,3	137,3	6,6	72,5	72,1	63,0	-	167	0,44	0,60
T4	3	4	2	45		14,5	10,8	0,9	12,5	0,75	8,0	1,5	10,8	1,7	8,8	1,5	47,0	38,3	85,3		-8,0	80,0	3,0	43,0		36,0	35,9	169	0,21	0,24
T5	3	3	5	220		13,7	9,5	0,5	11,4	0,70	7,7	1,3	8,3	1,7	8,0	1,8	33,0	32,0	69,5					96,0						
T6	3	7	5	96		14,9	9,5	0,6	11,9	0,64	9,5	1,5	8,3	1,5	6,0	1,0	38,0	32,3	70,3	9,0	9,5	125,0	15,0	56,5	54,3	72,0		153	1,01	1,26
T7	3	6	5	101		13,6	10,4	0,8	11,9	0,76	8,0	2,0	9,8	1,8	8,0	1,9	42,0	43,7	85,7	0,5	1,0	148,0	9,5	58,5	57,6			165	0,70	0,80
T8	3	11	7	125	I	14,0	10,1	0,9	11,9	0,72	7,1	1,6	8,9	1,7	6,8	1,5	44,0	34,1	73,3	9,0	15,2	125,1	13,2	62,9	62,5	66,5	64,8	157	0,94	1,10
T9	3	7	4	48		15,6	10,0	0,7	12,5	0,64	8,7	2,2	11,3	2,3	9,3	2,0	35,3	30,0	65,3	4,0	9,5	136,0	4,8	69,0	69,7	67,5	67,4		0,31	0,39
T10	3	68	47	14	I	8,1	5,2	0,6	6,5	0,64	3,4	0,6	5,3	0,7	3,7	0,6	28,2	28,4	57,0	7,0	3,6	113,4	6,0	56,7	56,2	57,0	56,5	168	0,74	0,92
T11	3	3	3	73	II	24,0	21,0	1,3	22,4	0,88	15,0	4,5	15,0	3,7	10,0	4,5	45,0	47,5	95,0			220,0	0,1	100,0		110,0		175,0	0	0,00
T12	3	6	5	262		13,8	11,4	1,0	12,6	0,83	6,9	1,9	8,5	2,3	7,2	1,9	40,8	41,3	81,0	-4,0	-5,8	153,0	6,8	75,5	75,0	76,5	77,9	169	0,49	0,54
T13	3	7	5	278		13,7	10,2	0,8	11,8	0,75	7,1	2,1	9,6	2,1	6,9	1,6	45,4	44,0	90,3	0,5	-1,3	140,5	11,1	70,5	69,9	71,5	70,2	165	0,81	0,94
T14	3	7	7	100	I	13,9	9,2	0,8	11,3	0,66	6,9	1,4	8,3	1,7	6,8	1,4	38,2	33,5	71,7	5,7	3,3	125,5	6,3	61,0		66,5	68,4	161	0,46	0,56
T15	3	7	5	291	I	12,4	9,0	0,6	10,6	0,72	7,0	1,2	8,9	1,5	7,3	1,0	35,2	36,4	71,6	2,0	8,3	125,0	5,5	62,5	62,1	58,5	58,3	170	0,44	0,52
T16	3	11	9	54	I	14,3	9,0	0,9	11,4	0,63	8,3	1,5	10,4	1,8	7,3	1,4	33,0	34,6	63,2	7,2	1,5	132,6	4,6	66,0	63,6	64,3	64,2	169	0,32	0,41
T17	3	9	7	81	I	12,4	8,6	1,1	10,3	0,70	7,5	1,2	10,1	1,8	7,4	2,0	36,1	34,2	65,4	14,5	6,0	130,9	11,9	63,0	61,5	63,3	62,2	161	0,97	1,15
T18	3	6	5	282	I	11,9	8,5	0,5	10,0	0,72	5,3	1,3	7,1	1,6	5,0	1,4	36,3	39,3	75,5	14,0	1,0	154,7	2,8	82,5	76,5	74,0	73,5	175	0,23	0,27
T19	3	5	3	153		9,8	7,3	0,9	8,5	0,75			6,0	1,3			50,0	49,3	105,0	-3,0	2,7	165,2	5,3	74,8	74,6	73,5	73,5	172	0,54	0,63
T20	3	4	3	279		12,5	6,8	0,7	9,2	0,54										-4,0	1,0	149,5	11,0	77,0	76,2	73,5		166	0,88	1,20
T21	3	17	17	45	I	12,9	7,9	0,9	10,1	0,61	7,5	1,8	11,8	1,7	8,0	1,9	34,4	40,3	74,8	12,7	5,1	170,0	14,1	88,5	87,1	86,4	86,1	161	1,09	1,39
T22	3	4	5	324		11,9	6,8	0,6	9,0	0,58	7,5	1,5	10,5	1,6	7,8	1,5	38,0	26,0	64,0	4,0	10,0	147,5	6,5	72,0	74,7	72,0	71,7	170	0,55	0,72
T23	3	8	7	254	I	9,8	6,5	0,6	8,0	0,67	4,0	0,9	6,5	1,3	6,2	1,3	31,3	25,7	61,0	2,5	1,0	123,6	6,3	57,7	61,2	67,3	67,0	170	0,65	0,79
T24	3	17	15	45	I	10,9	8,1	0,7	9,4	0,74	4,8	1,3	6,6	1,6	4,7	1,3	26,6	30,5	56,7	9,3	1,4	141,2	4,5	70,3	70,6	70,5	69,0	174	0,41	0,48
T25	3	7	7	111	I	14,8	8,8	0,9	11,4	0,60	8,4	1,3	7,9	1,8	8,8	1,4	33,9	28,8	61,0	6,7	11,0	175,5	10,3	88,3	87,7	89,5	88,9	167	0,70	0,90
T26	3	8	5	76	I	13,4	9,2	0,9	11,1	0,68	7,5	1,4	9,7	1,5	6,9	1,2	31,8	29,6	58,2	17,0	2,0	134,8	14,0	68,7	65,7	66,0	66,0	162	1,04	1,26
T27	3	8	6	272		11,3	7,9	0,7	9,4	0,70	5,5	1,1	7,1	1,4	6,0	1,5	35,4	38,2	77,0	1,5	4,5	147,6	5,8	72,7	72,4	75,0	74,8	171	0,51	0,61
T28	3	6	5	256	I	14,8	11,1	1,2	12,8	0,75	8,3	2,3	11,7	2,7	6,3	2,1	28,5	35,0	70,0	11,3	-1,0	167,2	9,2	89,0	87,5	83,5	83,0	167	0,62	0,72
T29	3	4	3	299		14,2	8,8	1,1	11,1	0,62	6,7	1,2	9,4	2,2	6,5	1,9	27,0	33,0	56,0	10,0	8,0	189,5	9,8	94,0	93,5	94,0	94,5	168	0,69	0,88
T30	3	3	3	283		12,5	11,3	0,9	11,9	0,90	7,0	1,9	10,0	1,8	6,2	1,7	37,5	40,0	82,5		-8,0	115,0	2,0						0,16	0,17
T31	3	2	2	119		12,5	9,0	1,4	10,6	0,72	7,5	1,0	10,5	1,9	7,0	1,0	27,0	39,0	66,0							140,0				
T32	1	7	4	223		13,7	10,2	0,8	11,8	0,75	8,0	2,2	11,0	2,5	8,7	2,5	25,8	35,3	62,3	-3,7	-6,0	126,8	5,4	64,0	63,8	62,0	61,3	179	0,40	0,46
T33	1	4	2	83		9,8	5,8	0,5	7,5	0,60	4,8	1,3	8,3	1,3	5,1	1,1	33,0	33,0	65,3	9,0	6,0	129,5	4,5	65,5	67,8	66,0	65,9	171	0,46	0,60
T34	1	4	3	317		16,0	10,2	1,0	12,8	0,64	9,8	2,3	14,2	2,5	9,0	2,0	36,0	25,7	61,7	2,0	11,5	185,5	9,5	91,5	89,5	93,0	92,5	168	0,59	0,74
T35	2	2	1	36		18,5	10,5	0,6	13,9	0,57	8,5		18,3	3,0	11,5		36,0	37,5	81,0					92,0						
T36	2	12	9	131	I	10,9	7,6	0,5	9,1	0,70	6,1	1,3	9,2	1,7	5,8	1,3	38,0	39,0	75,7	2,8	0,8	121,8	3,2	57,1	60,1	62,4	62,6	175	0,29	0,35
T37	2	9	8	308		15,8	9,5	0,7	12,2	0,60	10,0	2,0	16,0	4,0	11,0	3,0				5,0	2,3	146,0	11,7	73,3	72,4	74,1	73,2	162	0,74	0,96
T38	2	11	9	325	I	12,0	7,8	0,6	9,7	0,65	6,2	1,4	10,5	1,9	6,9	1,5	27,2	32,8	58,1	3,6	4,0	130,1	4,5	70,7	64,8	66,2	65,3	169	0,38	0,47
T39	2	10	6	79	I	11,5	6,8	0,4	8,8	0,59	6,4	1,5	10,0	1,6	7,2	1,3	24,2	26,7	51,0	9,3	7,5	126,9	5,2	59,0	58,7	64,2	64,9	168	0,45	0,59
T40	2	5	4	58	I	14,3	10,6	0,6	12,3	0,74	8,2	2,3	10,0	2,3	8,0	1,8	33,3	31,6	65,0	5,0	4,0	144,0	11,5	72,0	67,8	73,0	72,3	162	0,80	0,93
T41	2	15	10	356	I	9,2	5,0	0,4	6,8	0,55	3,9	0,8	7,6	1,2	4,9	0,9	23,5	22,4	44,0	7,2	3,4	118,5	7,2	58,8	58,3	61,0	60,4	164	0,78	1,06
T42	2	4	2	155	I	9,6	7,0	0,5	8,2	0,73	5,5	0,9	8,1	1,2	4,5	0,8	34,3	33,3	67,3	4,5	3,5	132,0	8,8	64,0	63,5	69,0	68,3	164	0,92	1,07
T43	2	5	4	129	II	30,0	27,0	2,3	28,5	0,90	21,0	6,5	26,8	6,5	19,5	5,9	39,8	42,3	84,3	5,0	-5,0	207,3	5,2	96,5	93,8	112,0		171	0,17	0,18

Table 5.2: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 (without the enlargement of 2006), main track level: Mean parameters of the bipedal, tridactyl trackways. Note that due to the incomplete trackways or poor preservation not all parameters were obtained for all trackways (crossed-out cells). Note that trackways T31 and T35 are trackways with two steps only.

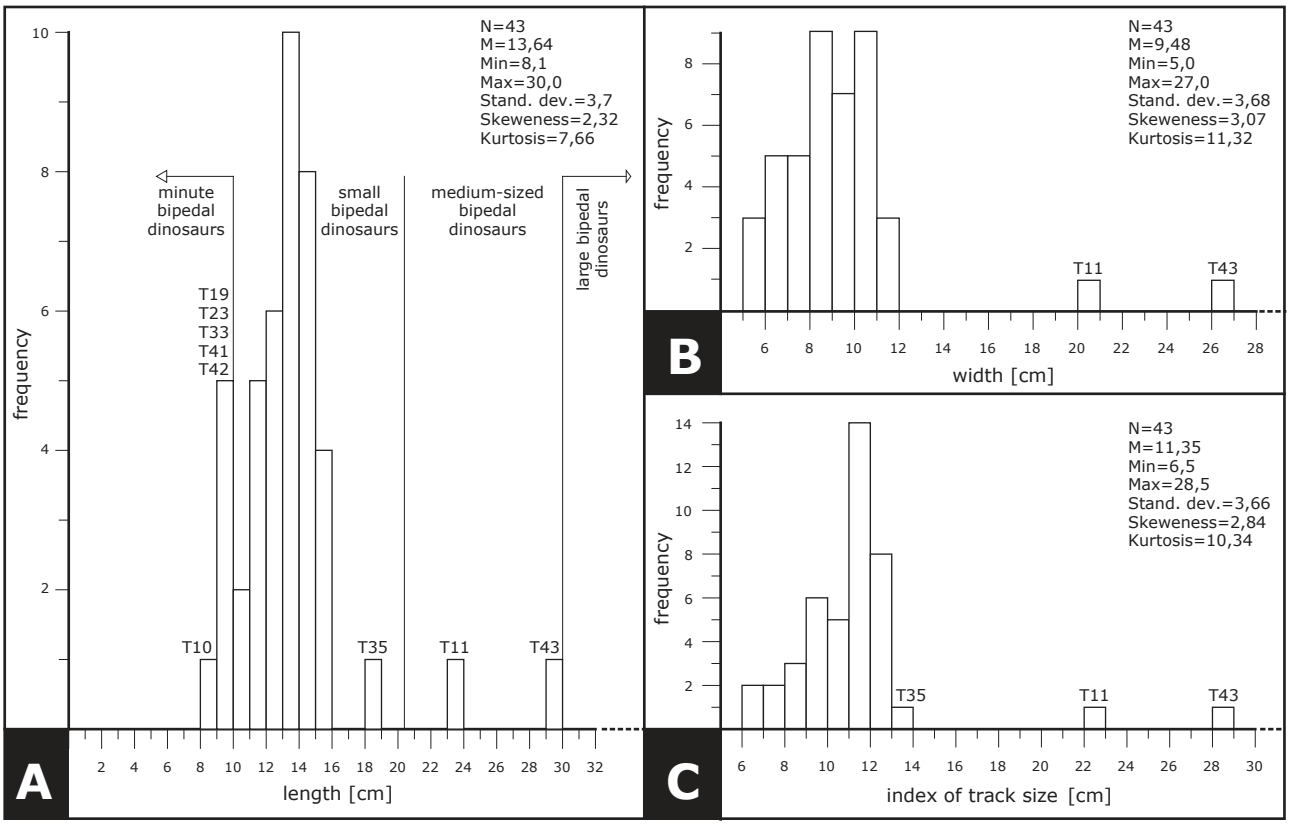


Fig. 5.21: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3, main track level: Histograms for some of the mean parameters of all bipedal trackways. **A:** Distribution of mean pes length with boundaries between minute, small, and medium-sized bipedal dinosaurs indicated. **B:** Distribution of mean pes width. **C:** Distribution of the index of track size.

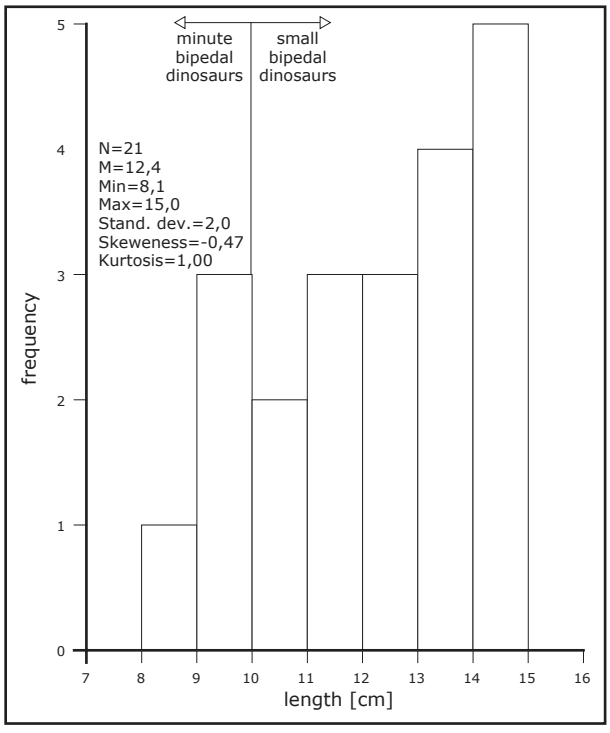


Fig. 5.22: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3, main track level: Length-frequency distribution of the trackways attributed to morphotype I.

5.4.5.2 Length vs. width correlation ([W/L]-ratio)

Description

Figure 5.23A shows a plot of the mean pes length against the mean pes width for all bipedal trackways. Four trackways, those of morphotype II (T11 and T43) and trackways T12 and T30, show a [W/L]-ratio higher than 0,8 indicating tracks almost as wide as long. In trackways T11 and T43, this is considered as one of the typical features of morphotype II. Trackways T12 and T30, on the other hand, are trackways of a small bipedal dinosaur. In T12, the high ratio can be explained by poorly-defined tracks, mostly cut or partially displaced by normal faults, and in T30 by particular kinematics of the trackmaker (i.e., a less digitigrade stance), leading to a higher total divarication angle and occasionally to the impression of the metatarsal of digit IV (Fig. 5.18B).

The other minute and small trackways are fairly well distributed between [W/L]-ratios ranging from 0,5 to 0,8. The trackways with lowest ratio (<0,55) are T41 and T20. In trackway T41 (continuation of T10),

this low total divarication angle is a morphological feature, while in T20 it results from poorly-defined tracks, in which digits II and IV are not discernible (Fig. 5.18A).

In Figure 5.23B only the minute and small trackways are shown. There is a slight trend to lower ratios in the trackways attributed to morphotype I, but there is no clear separation between these and the ones, which could not unambiguously be attributed. Trackway T40, for instance, even though attributed to morphotype I, is characterized by a relatively high [W/L]-ratio (0,74), which is the highest of all trackways attributed to morphotype I. The attribution of this trackway is based on track R1 with a [W/L]- ratio of 0,75, which is higher than the mean value of the trackway (0,74).

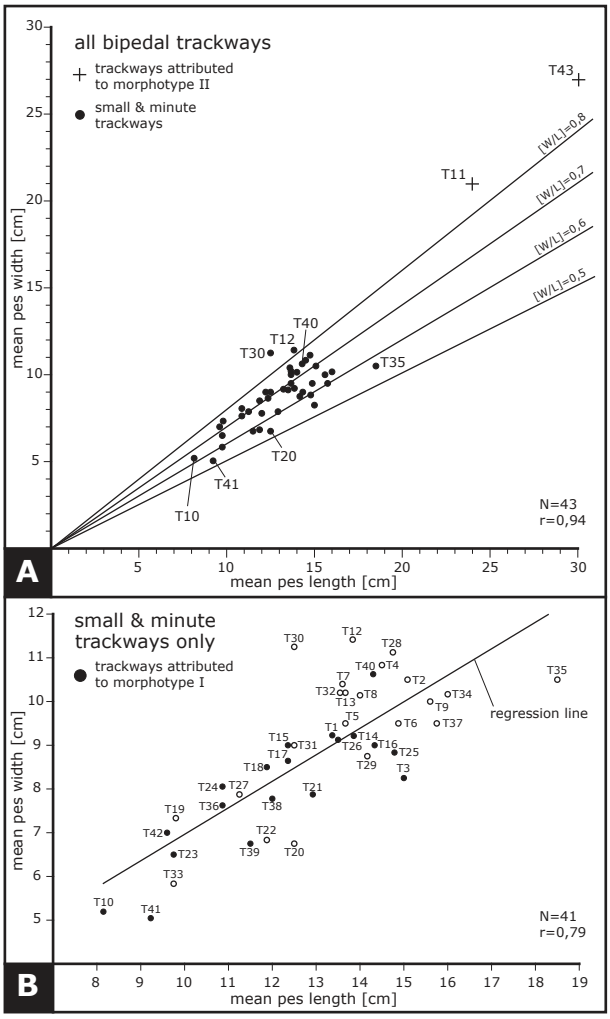


Fig. 5.23: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3, main track level, bipedal trackways: **A:** Plot of the mean pes length against mean pes width of all bipedal trackways of the main track level with [W/L]-ratios (width/length) indicated. **B:** Plot of mean pes length against the mean pes width of the minute and small bipedal trackways only. The trackways attributed to morphotype I are marked with black dots.

Interpretation

Morphotype II is characterized by a higher [W/L]-ratio than morphotype I and, apart from a few exceptions (T12, T30), than all minute and small tridactyl trackways. The variation in the [W/L]- ratio within the minute and small trackways is not considered to be of significance. There is, however, no evidence to suggest that T12 and T30 are younger ontogenetic stages of morphotype II, because their higher ratios can be explained by preservational and kinematical factors.

The poorly-defined separation of trackways attributed to morphotype I and the other minute and small trackways may indicate that all belong to the same morphotype. However, this may also be related to the fact that only the mean values of the trackways are plotted, and that different kinds of preservational morphotypes within a single trackway affect the [W/L]-ratio. Trackways T12 and T20 show that poorly-defined tracks or preservational variability can result in either a lower or a higher [W/L]-ratio. The example of T40, on the other hand, discloses that the best-defined tracks do not necessarily have a lower [W/L]-ratio than the poorly-defined tracks. The higher values in T40 are thus rather related to the kinematics of the trackmaker (e.g., movement of the toes resulting in greater track width) than to particular substrate properties. In order to confirm this hypothesis, more trackways need to be analysed in greater detail, including [W/L]-plots of well-defined tracks only. However, this is outside the scope of this work.

5.4.5.3 [W/L]-ratio vs. total divarication angle correlation

Description

Figure 5.24 plots the [W/L]-ratio against the mean total divarication angle for all bipedal trackways except T20 and T37, for which no precise values for the total divarication angle could be measured.

Even though the correlation is not very good, there is a trend towards higher divarication angles in the trackways with "wider" tracks, i.e., those with a higher [W/L]-ratio. Apart from a few exceptions, there is a clustering recognizable for the minute and small trackways including those of morphotype I. The two

trackways T11 and T43 of morphotype II plot well outside this cluster. They may form a second cluster, but more data is needed for confirmation.

In contradiction to the length vs. width plot, there is quite a high discrepancy between T10 and T41, which are supposed to be the same trackway: the tracks of T10 are wider and have a higher total divarication angle than T41.

Interpretation

It has to be considered that the total divarication angle is a highly variable parameter due to preservational and kinematical factors, and here only the mean values of the trackways are analysed. Nonetheless, the total divarication angle is often used for the characterization of tridactyl tracks (e.g., Thulborn, 1990) (Fig. 5.47B). Generally, the total divarication angle is strongly correlated with the track width because, assuming a similar track length, a higher divarication angle evidently results in a greater width and hence also a higher [W/L]-ratio.

The clustering of the minute and small trackways indicates that these trackways have similar tracks. The outliers are again the trackways T12 and T30 as already seen in the length vs. width plot, and this

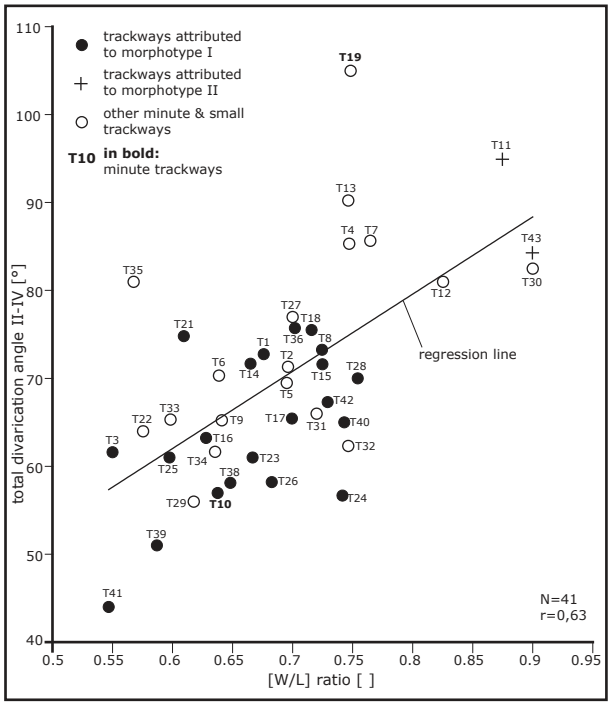


Fig. 5.24: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3, main track level, all bipedal trackways: Plot of the [W/L]-ratio (width/length) against the total divarication angle II-IV.

can be explained with the same reasons mentioned above. Trackways T4, T7, T13, and notably T19 show strikingly high total divarication angles. Trackway T4 is the trackway with the lowest locomotion speed (see also chap. 5.5), and hence the higher total divarication angle may have resulted from the kinematics of the trackmaker, i.e., a rather semi-digitigrade stance. Trackways T7, T13, and T19 are dominated by tracks with digits II and IV fused in a broad or narrow heel, resulting in higher divarication angles. Trackway T19 is probably the trackway with the worst-defined tracks of the site, and hence the high values of T19 are not representative. The discrepancy between trackways T10 and T41 may be related to the fact that T41 exhibits mainly well-defined tracks, whereas T10 crosses several normal faults, around which the tracks are not so well preserved.

The mean total divarication angle of T43 (84,3°) is at the higher end of all bipedal trackways, even though some of the small bipedal trackways also have similarly high or even slightly higher mean values. However, most of these are trackways with predominantly poorly-defined tracks, which could not unambiguously be attributed to morphotype I. Unless those poorly-defined small tracks with digits II and IV fused in a broad heel are actually not preservational morphotypes of morphotype I but represent the earlier ontogenetic stages of morphotype II. There is at the moment no clear evidence for this scenario, but it can not be definitely excluded as well.

5.4.6 Trackway configuration

Generally, the bipedal trackways are characterized by a small (<10°) outward rotation of digit III long axis of both left and right pes tracks. Only a few trackways show a negative rotation for either the left or the right pes, and only T12 is characterized by a slight inward rotation of both left and right pes tracks. The differences in mean rotation between the left and the right pes tracks are rather small and pronounced only in the trackways T18 (difference of 13°) and T26 (difference of 15°).

The same holds true for the mean left and right pace. Apart from a few trackways (e.g., T18, T23), they do not show pronounced differences for the longer minute and small trackways (i.e., more than 5 steps), whose tracks are not displaced by normal faults. However, different are the medium-sized trackways T11 and T43, which both show a large difference between the left and the right pace, indicating irregular trackways.

Almost all trackways exhibit a very narrow to narrow gauge. This is expressed by a mean pace angulation higher than 160° for most of the trackways and [WAP/PL]-ratios smaller than 1 for all trackways (except T6, T21, and T26). However, the most striking differences in trackway configuration are related to the trackway width.

5.4.6.1 Trackway gauge (width)

Description

At first glance, most bipedal trackways are characterized by a narrow gauge because pes tracks intersect or touch the trackway midline. However, several trackways (notably T6, T8, T17, T21, T26, T42) show a somewhat wider gauge with tracks aligned in a zig-zag fashion, in which the pes tracks do not touch the trackway midline.

In order to better distinguish these differences in trackway gauge, the [WAP/PL]-ratio and [WAP/IPS]-ratio were calculated (Table 5.2). The [WAP/IPS]-ratio is always larger than the [WAP/PL]-ratio, because all tracks are longer than wide, and hence the index of pes size (IPS) is always smaller than the mean pes length (PL).

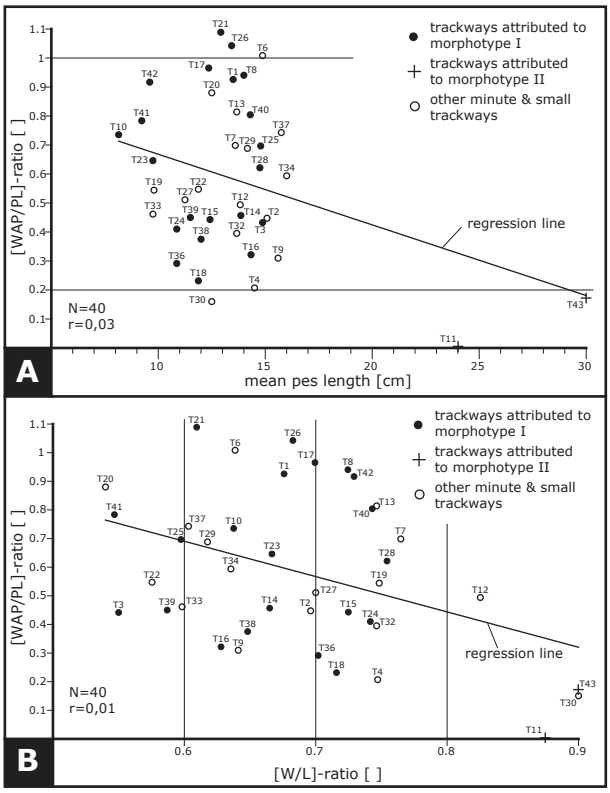


Fig. 5.25: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3, main track level, all bipedal trackways except T5, T31, and T35. **A:** Plot of mean pes length against [WAP/PL]-ratio. **B:** Plot of the (width/length)-ratio ([W/L]) against [WAP/PL]-ratio.

Figure 5.25A shows a plot of the mean pes length against the [WAP/PL]-ratio. Three trackways (T6, T21, and 26) have a [WAP/PL]-ratio higher than 1, and three trackways (T11, T30, T43) lower than 0,2. The other trackways, all of minute and small bipedal dinosaurs, are fairly equally distributed in between. Regarding the [WAP/IPS]-ratio, which is not plotted, in addition to T6, T21, and T26, trackways T1, T8, T17, T20, T41, T42 also have a ratio higher than 1, and several trackways (T10, T13, T37,T40) have a ratio higher than 0,9.

Figure 5.25B shows a plot of the [W/L]-ratio against the [WAP/PL]-ratio. Similarly to the plot of the [W/L]-ratio against the total divarication angle shown in Figure 5.24, the trackways of morphotype II plus T12 and T30 form a cluster outside the other minute and small trackways, which are rather widely distributed.

Interpretation

Both trackways attributed to morphotype II are characterized by a very narrow-gauge, and only trackway T30 with small tracks shows a similarly low value. Despite the small number of trackways attributed to morphotype II, which does not allow estimating the range of distribution of the [WAP/ PL]-ratio for morphotype II, it is suggested that morphotype II is characterized by a narrower gauge than morphotype I.

Most minute and small trackways, including those attributed to morphotype I, are as well narrow-gauge, even though they show generally a higher [WAP/PL]-ratio than the trackways of morphotype II. Only trackways T6, T21, and T26 have a [WAP/PL]-ratio higher than 1, indicating that their tracks do not intersect the trackway midline. These three trackways also show a similar [W/L]-ratio, but only T6 has a low locomotion speed, suggesting that this wide gauge is not necessarily related to a lower locomotion speed (see also chap. 5.5 and chap. 5.7.5).

The minute and small trackways feature a wide range of [WAP/PL]-ratios, which is independent of the mean pes length. Because the substrate was quite homogeneous all over the tracksite (see also chap. 4.3.5.1), and because trackways dominated by poorly-defined tracks, do not show a trend towards lower

or higher [WAP/PL]-ratios, it is suggested that the [WAP/PL]-ratio is not significantly influenced by poorly-defined tracks (preservational morphotypes). This wide range of values rather reflects differences in the stance of the trackmakers. Assuming that all minute and small trackways, or at least those attributed to morphotype I, were left by a single trackmaker species, these differences in gauge may be related to locomotion speed, a special behaviour, or they may simply be a reflection of individual stance or walking style. These relationships are further discussed in Chapter 5.7.5.

5.4.7 Description and interpretation of selected trackways

Following detailed descriptions of selected bipedal trackways, which are peculiar with respect to trackway gauge and/or other track and trackway parameters and ratios including their bivariate plots, are given, and some are illustrated in Figure 5.26.

5.4.7.1 Trackway T4

Description

The tracks of T4 are poorly-defined and can only be followed over three steps, with tracks located very close one to each other. This results in the lowest value for the relative stride length and hence also the lowest locomotion speed of all bipedal trackways.

Interpretation

T4 may be the trackway of a very slow animal, but because it is so short this trackway can be considered as tentative. This, has to be considered regarding the plots of speed and relative stride length, where T4 always plots well outside the other trackways.

5.4.7.2 Trackway T8 (morphotype I)

Description

This trackway is dominated by tracks where digits II and IV are fused in a broad heel, resulting in rather wide tracks (preservational morphotype). T8 is characterized by quite a wide-gauge, expressed by tracks aligned in a zig-zag fashion, a [WAP/PL]-ratio of nearly 1, and by one of the lowest values for the mean pace angulation of all trackways (Fig. 5.26A). Based on the well-defined track R1 with isolated digits, T8 is attributed to morphotype I.

Interpretation

T8 is one of several trackways attributed to morphotype I based on a single well-defined track only. The rather wide gauge of T8 is associated with one of the slowest locomotion speeds of all bipedal trackways. A less digitigrade stance related to the lower locomotion speed may also explain why this trackway is dominated by tracks where digits II and IV are merged in a broad heel. This also suggests that this preservational morphotype is influenced by substrate properties, as well as by the kinematics of the trackmaker (compare also with Fig. 5.18).

5.4.7.3 Trackways T10 and T41 (morphotype I)

Description

These are the trackways with the smallest tracks of the site, and T10 exhibits some of the best-defined tracks of morphotype I. Trackway T10 has 68 tracks, and only a few are missing due to karstification along normal faults and overprinting by sauropod tracks (of S2). Trackway T41 has 15 tracks and a few tracks are overprinted probably by the sauropod trackway S11 and S14. Both are characterized by a narrow-gauge and, in comparison with the other bipedal trackways, by a low [W/L]-ratio and a low total divarication angle (Figs. 5.26B & C).

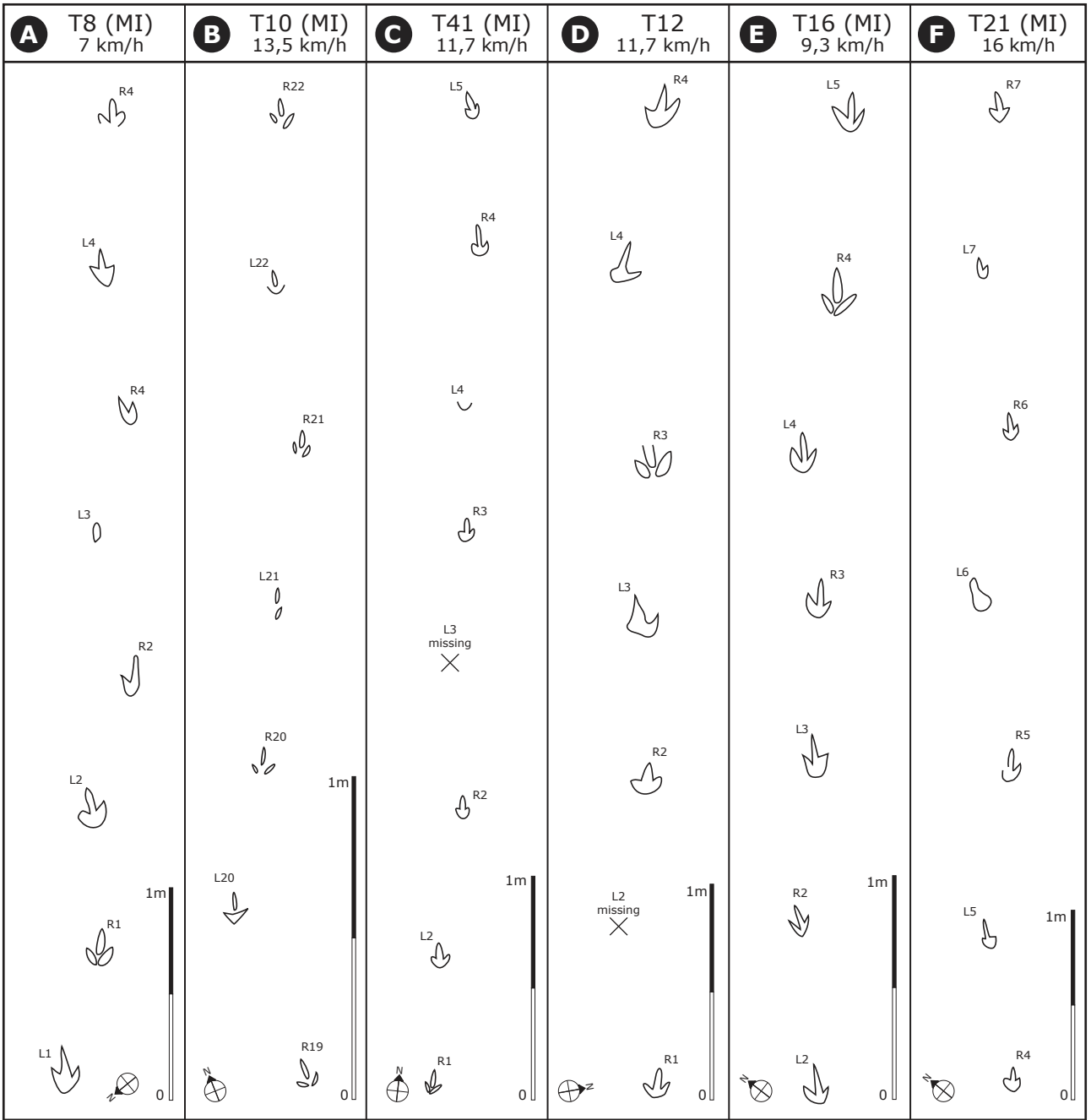
Interpretation

These two trackways located in excavation area 1 (T10) and 2 (T41) are supposed to have been left by the same trackmaker because T41 lies almost in the extension of T10, and because of the similarity in track morphology, and (apart from the [W/L]-ratio) similar mean track parameters. Despite of a slightly wider gauge at the end of T10 where the tracks are rather aligned in a zig-zag fashion (Fig. 5.34), both trackways do not show significant changes in their trackway parameters (pace length, stride length, pace angulation), and there is only a small change in orientation from NE at the beginning of T10 towards the N at the end of T41. This suggests that the trackmaker was consciously heading from A to B, and excludes a special behaviour such as foraging.

5.4.7.4 Trackway T11 (morphotype II)

Description

This trackway is characterized by a very narrow-gauge, expressed by a [WAP/PL]-ratio of almost 0, which indicates that the tracks follow a straight line. There is a difference of 10 cm between the left and the right pace. However, because it is poorly preserved and its tracks are partially displaced by normal faults, the measured trackway parameters are not very representative.



PL	PW	W/L	PL	PW	W/L	PL	PW	W/L	PL	PW	W/L	PL	PW	W/L	PL	PW	W/L
14,0 cm	10,1 cm	0,72	8,1 cm	5,2 cm	0,64	9,2 cm	5,0 cm	0,55	13,8 cm	11,4 cm	0,83	14,3 cm	9,0 cm	0,63	12,9 cm	7,9 cm	0,61
stride	pace	pace ⚹	stride	pace	pace ⚹	stride	pace	pace ⚹	stride	pace	pace ⚹	stride	pace	pace ⚹	stride	pace	pace ⚹
125 cm	65 cm	157	113 cm	57 cm	168	119 cm	60 cm	164	153 cm	76 cm	169	133 cm	65 cm	169	170 cm	88 cm	161
WAP	WAP/PL	WAP/IPS	WAP	WAP/PL	WAP/IPS	WAP	WAP/PL	WAP/IPS	WAP	WAP/PL	WAP/IPS	WAP	WAP/PL	WAP/IPS	WAP	WAP/PL	WAP/IPS
13,2 cm	0,94	1,10	6 cm	0,74	0,92	7,2 cm	0,78	1,06	6,8 cm	0,49	0,54	4,6 cm	0,32	0,41	14,1 cm	1,09	1,39

Fig. 5.26: Chevenez—Combe Ronde tracksite, excavation areas 2 and 3, main track level, outline drawings (of the external outline only) of minute and small bipedal trackways, some of which are attributed to morphotype I (MI). Note that only selected, typical parts of the trackways are illustrated, and that the trackways are not drawn to scale.

Interpretation

This trackway is tentatively attributed to morphotype II on the base of its similarity with T43 in the bivariate plots, rather than on the morphology of its best-defined track R3, which does not allow an unambiguous classification.

5.4.7.5 Trackway T12

Description

Similarly to T8, this trackway is dominated by tracks of the preservational morphotype where digits II and IV are fused in a broad heel, resulting in "wide" tracks (Fig. 5.18F). T12 is the only trackway with an inward (negative) rotation for both left and right pes tracks. It is also characterized by a rather high total divarication angle and, together with T30, this is the only trackway of the minute and small bipedal dinosaurs, which has a [W/L]-ratio higher than 0,8 (Fig. 5.26D). In the bivariate plots, this trackway is, together with T30, most similar to the trackways of morphotype II. Despite its low locomotion speed it is quite narrow, as expressed by a [WAP/PL]-ratio smaller than 0,5.

Interpretation

The fact that T12 plots outside of the other minute and small trackways close to the trackways of morphotype II is not expressed in the morphology of the tracks, most of which are poorly-defined. Moreover, the best-defined track R3 exhibits slightly isolated digits and resembles morphotype I. Similarly to T16, T12 suggests low locomotion speed but still a narrow-gauge. However, the tracks of T12 are also similar to those of T8, which is characterized by a rather wide-gauge.

5.4.7.6 Trackway T16 (morphotype I)

Description

Besides T10 and T41, this is another trackway of morphotype I with well-defined tracks. It is one of the trackways of morphotype I with the largest tracks, has a low [W/L]-ratio as observed in T10, and the [WAP/PL]-ratio is even lower than in T10 and T41 (Fig. 5.26E).

Interpretation

T16 may be an older ontogenetic stage of morphotype I than the minute trackways because it is very similar in track morphology. The narrowness of this trackway is not expressed by the low locomotion speed of 9,3 km/h (see also chap. 5.5). This suggests that locomotion speed is not the only factor determining the width or gauge of the minute and small trackways (see also chap. 5.7.5).

5.4.7.7 Trackways T19 and T20

Description

These two trackways are in close proximity one to each other and could only be traced over short distances. They are probably the two trackways with the worst-defined tracks, and most of their tracks exhibit a digit III merged with a round heel (T20, Fig. 5.18A), or digits II and IV merged in a narrow or broad heel (T19).

Interpretation

The fact that T19 is dominated by tracks, with digits II and IV merged in a broad or narrow heel (preservational morphotype) explains that it has the highest mean total divarication angle of all trackways and a high [W/L]-ratio. In trackway T20, on the other hand, digits II and IV are almost not discernible and merged in a round heel, which results in a comparatively low [W/L]-ratio. These two trackways underline the importance of analysing the preservational factors when comparing a suite of tridactyl trackways.

5.4.7.8 Trackway T21 (morphotype I)

Description

Trackway T21 is a dual gauge trackway, because it shows a pronounced change in trackway width after LP4-RP4, from a relatively narrow-gauge with tracks aligned more or less in a straight line to a wide-gauge with tracks aligned in a zig-zag fashion (Fig. 5.26F). This goes in hand with a decrease in stride and pace length and pace angulation. No obvious change in track morphology is detectable, even though there is a trend towards longer tracks in the zig-zag part when compared with the narrow part of the trackway (Table 5.3). The best-defined track (T21-L10) is located at the end of the trackway in the wide-gauge part (Fig. 5.34), but poorly-defined tracks (Fig. 5.18D) can be found along the entire trackway.

Interpretation

Trackway T21 is the only bipedal trackway with a dual gauge. Overall it is characterized by a high [WAP/PL]-ratio (1,09), which is the highest ratio of all bipedal trackways, and also by a high locomotion speed of 16 km/h (Table 5.5).

It is suggested that the increase in trackway width is due to a decrease in locomotion speed. This goes in hand with an increase in pes length, probably due to a less digitigrade stance. However, it has to be considered that the increased pes length also lowers the calculated locomotion speed, even though it is not responsible for the whole difference in speed between the narrow-gauge and the wide-gauge part of the trackway. The wide part, the wide part of the trackway even has a slightly lower mean [WAP/PL]-ratio than the whole trackway because of the longer tracks in that part.

This example shows that care must be taken when comparing mean values of trackway parameters, especially of long trackways with changes in configuration.

5.4.7.9 Trackway T26 (morphotype I)

Description

T26 is the second trackway of morphotype I with a [WAP/PL]-ratio higher than 1. Over its whole length it is characterized by a relatively wide-gauge with tracks aligned in a zig-zag fashion. Moreover, this is one of the few trackways with a pronounced difference between the left (+17°) and the right (+2°) pes rotation (Fig. 5.34).

Interpretation

This trackway has a similar locomotion speed (10 km/h) as the wide part of T21. T26 is too short to say whether the difference between the left and right rotation may reflect an individual walking style or occurs only locally and may be linked for instance to the simple turning of the animal's head to the left. The extension of T26 in the enlargement of excavation area 3 may confirm whether this difference occurs systematically or not.

Trackway number	approximate position within trackway	mean pes length (L)	width of the angulation pattern	[WAP/PL]-ratio	mean stride length (S)	hip height small theropod (hs) = 4,5L	relative stride length (S/hs)	Locomotion speed		
								speed eq. 2 s/h<2,0	speed eq. 5 s/h>2,9	eq. 6=[eq.2+eq.5]/2 2<s/h<2,9
		[m]	[m]	[ ]	[m]	[m]	[ ]	[km/h]	[km/h]	[km/h]
T21	entire TW	0,13	0,14	1,09	1,70	0,58	2,92	12,93	16,03	14,48
T21	R1-L4 narrow part	0,12	0,06	0,46	1,84	0,55	3,35	15,71	18,49	17,10
T21	R4-L10 wide (zig-zag) part	0,15	0,16	1,07	1,64	0,68	2,41	10,08	13,52	11,80

Table 5.3: Chevenez—Combe Ronde tracksite, excavation area 3, main track level, bipedal trackway T21 attributed to morphotype I: Calculation of locomotion speed for the narrow (R1-L4) and wide (R4-L10) part of the trackway. See Chapter 2.7.6 for explanation.

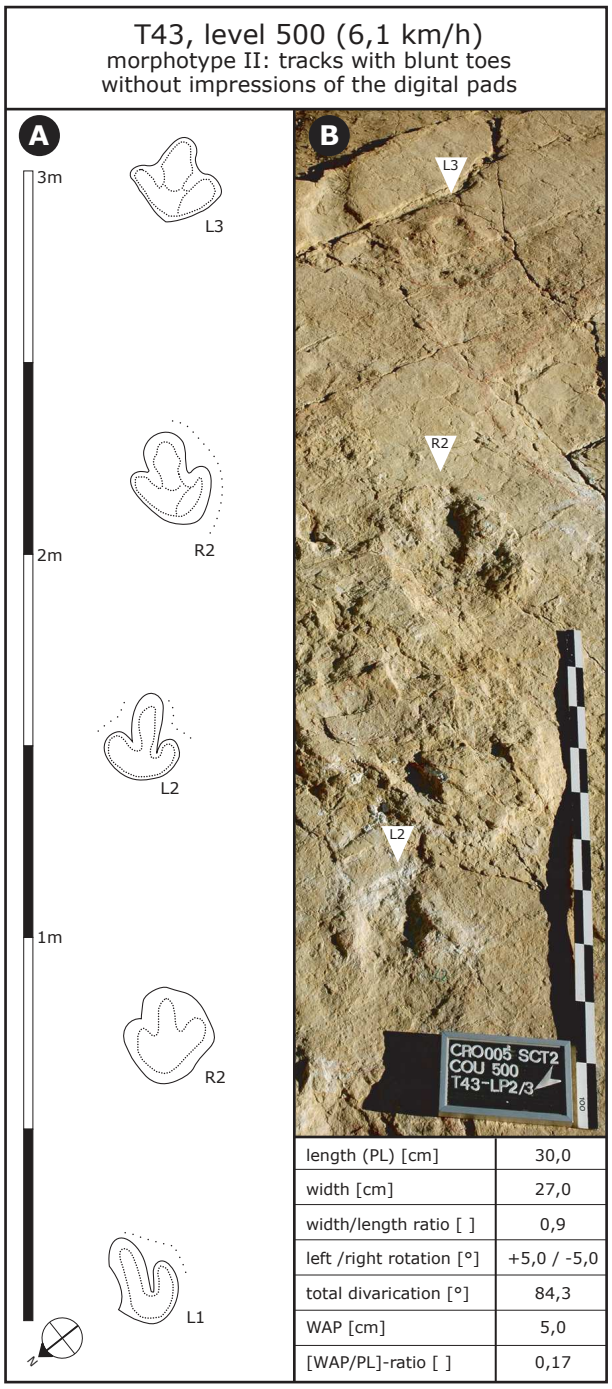
5.4.7.10 Trackway T30

Description

Some tracks of this trackway show evidence for an impression of distal parts of metatarsal(s) (Fig. 5.18 B). Together with T12, this is the second trackway plotting close to those of morphotype II in the bivariate plots, because of a high [W/L]-ratio and a narrow-gauge.

Interpretation

This trackway was considerably extended by the enlargement of excavation area 3 showing that actually every second track of T30 was missing in the studied area. Hence the [WAP/PL]-ratio used here was measured on a double stride and may be somewhat imprecise. This is also the reason why no locomotion speed was calculated for this trackway. Nonetheless, this trackway is particular because it has the widest tracks of the minute and small trackways. A future study of the extension of T30 in the enlargement of excavation area 3 may provide further evidence.



length (PL) [cm]	30,0
width [cm]	27,0
width/length ratio [ ]	0,9
left /right rotation [°]	+5,0 / -5,0
total divarication [°]	84,3
WAP [cm]	5,0
[WAP/PL]-ratio [ ]	0,17

Fig. 5.27: Chevenez—Combe Ronde tracksite, excavation area 2, main track level, bipedal trackway T43. **A:** Outline drawing. **B:** Photo of the sequence L2-R2-L3. Note the narrow gauge of the trackway with left tracks showing a positive rotation, and right tracks showing a negative rotation. Photo in B by B. Migy (SAP); rising sunlight from the right; scale bar is 1 m.

5.4.7.11 Trackway T43 (morphotype II)

Description

T43 is a five step trackway located in the northeastern most part of excavation area 2, crossing the sauropod trackways S10, S11, and S14 (Fig. 5.30). It has a very narrow-gauge (Fig. 5.27), which is also confirmed by the lowest [WAP/PL]-ratio (0,17) of all bipedal trackways. The mean rotation of the tracks is very low, slightly outward (+5°) for the left and slightly inward (-5°) for the right pes tracks. However, it was not obvious to identify left and right tracks, because the trackway is so narrow, and because the tracks are subsymmetric in shape. Further, T43 has the highest difference between the left (96,5 cm) and the right pace (112 cm) of all trackways, giving it an irregular appearance.

Interpretation

Morphotype II is based on the tracks of T43. The very narrow-gauge and irregular configuration (pes rotation) of T43 is further evidence that morphotype II is clearly different from morphotype I, even though such differences in trackway configuration may be related to the ontogenetic evolution of the trackmaker.

The lowest [WAP/PL]-ratio, with tracks with little or no rotation of digit III long axis from the trackway axis suggests a trackmaker with a very narrow posture. This comes along with one of the lowest locomotion speeds (see also chap. 5.5) of all bipedal trackways, which indicates that this particular narrow-gauge is not related to a faster gait.

5.5 Orientation, interactions, and locomotion speed

The Combe Ronde tracksite has an elongate form, orientated N-S (Fig. 5.32), and thus better records trackways oriented in W-E than in N-S directions. This has to be considered when interpreting the orientation data presented hereafter.

Locomotion speed was calculated according to Chapter 2.7.6, using mean trackway parameters (Table 5.4 and Table 5.5). For sauropod trackways, two locomotion speeds were calculated, using a factor of 4 and a factor of 5,9 for the estimation of the hip height. As for both hip heights the relative stride is always smaller than two, equation 2 was used for the speed calculation for all sauropod trackways. The trackways of bipedal dinosaurs are characterized by a wider range of relative stride length and, accordingly, equations 2, 5, or 6 were used. Due to a lack of stride length or poor preservation, the trackways T1, T5, T30, T31, and T35 were excluded from speed calculations.

5.5.1 Sauropod trackways of the main track level

5.5.1.1 Orientation and alignment

Apart from trackways S1 and S2 in excavation area 3, the majority of the sauropod trackways are located in excavation areas 1 (S3-S7) and 2 (S8-S14), areas which are orientated in a WSW-ENE direction (Fig. 5.29, Fig. 5.30, Plate 5.4, Plate 5.5, Plate 5.6). There are two main directions of trackway orientation, heading N-NNE and to the W (Fig. 5.28), related to two groups of sauropods, each with parallel trackways.

Group 1

The first group of parallel trackways heading N-NNE is composed of trackways S3 to S11 with an intertrackway spacing ranging from 1 m to 3 m. Apart from trackways S9 to S11, which are slightly turning, the trackways of group 1 are fairly straight, even though at the western extremity of excavation area 1 (S3-S4) and 2 (S8) they are very short. Group 1 is composed of small sauropods with a small range in mean pes length between 27,7 cm (S7) to 35 cm (S3), and there is no trend for larger tracks being located in a specific position within the group.

Group 2

The second group of parallel trackways is composed of the two trackways with the smallest tracks S12 (mean pes length 19,6 cm) and S13 (22,1 cm) left by tiny sauropods, and trackway S14 with slightly larger tracks (28,7 cm) left by a small sauropod. Trackways S12 and S13 are in very close proximity one to each other, with tracks touching or, in rare cases, overprinting each other. Trackway S14 is straight and located about 3 metres beside trackways S12 and S13, which are both characterized by a slightly irregular course (Fig. 5.30).

Isolated trackways

Trackways S1 and S2, located in excavation area 3 (Plate 5.7, Plate 5.8), are the only isolated sauropod trackways on the main track level, and they are heading to the NW and NE, respectively. With a mean pes length of 37,5 and 39 cm, they are the largest tracks on the main track level. Both trackways are characterized by shallow tracks without displacement rims, and a straight trackway course.

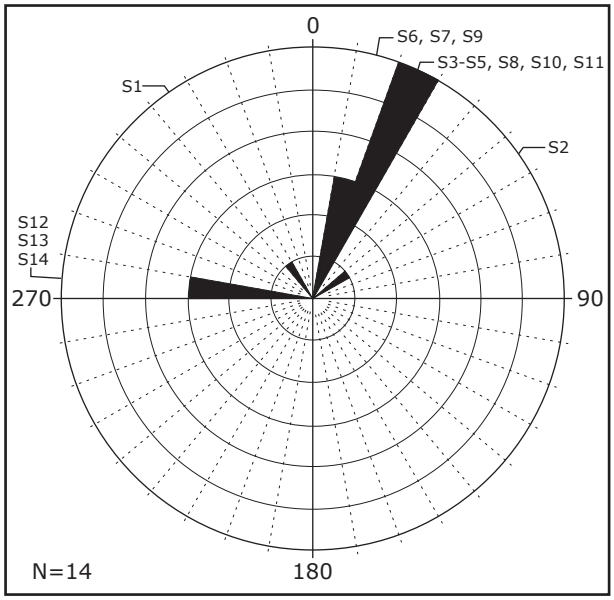


Fig. 5.28: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 (without the enlargement of 2006), main track level: Rose diagram showing the distribution of the directions of the sauropod trackways. The distribution highlights the two groups of parallel trackways, group 1 heading towards N-NNE and group 2 heading towards the W. Compare with Figure 5.50.

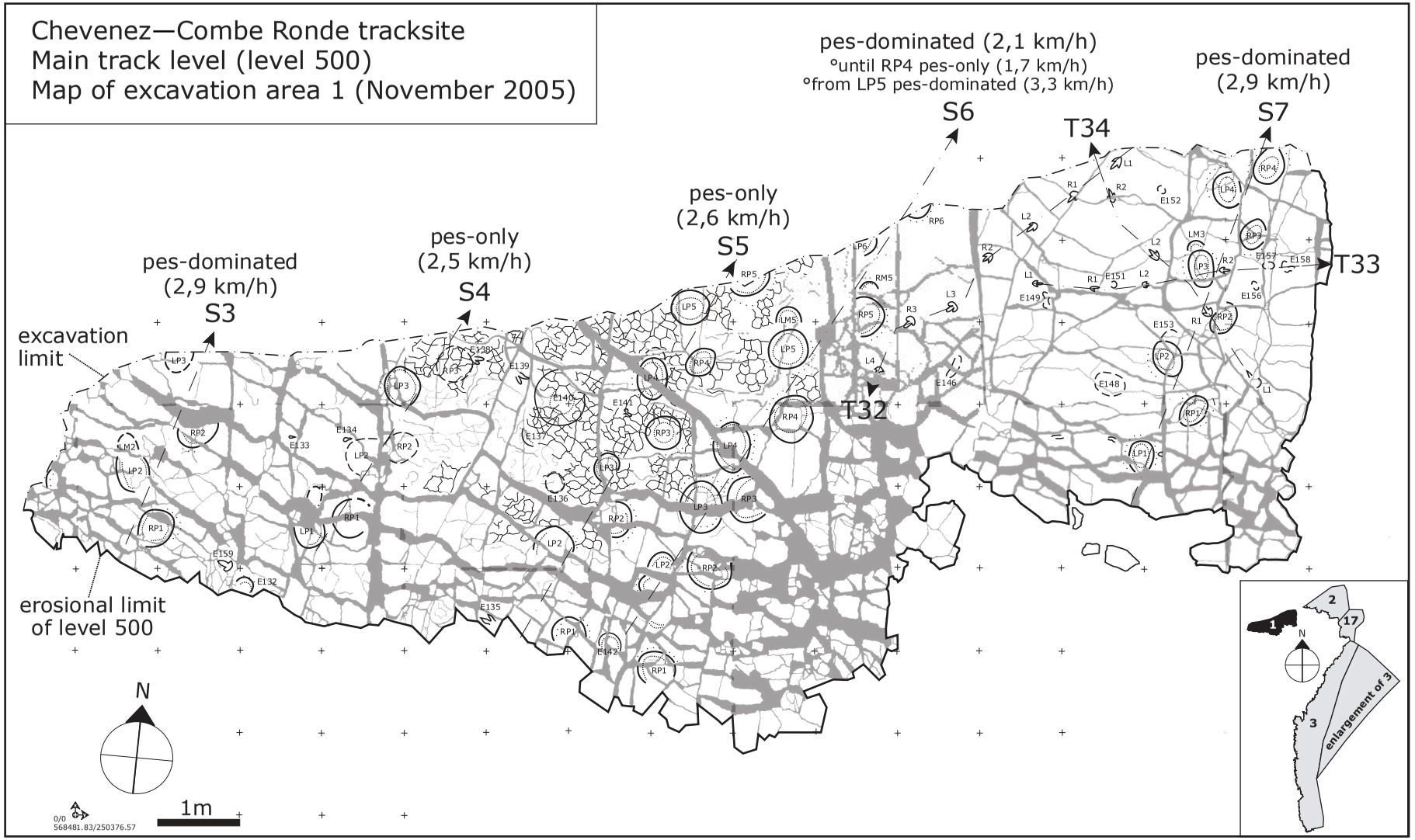
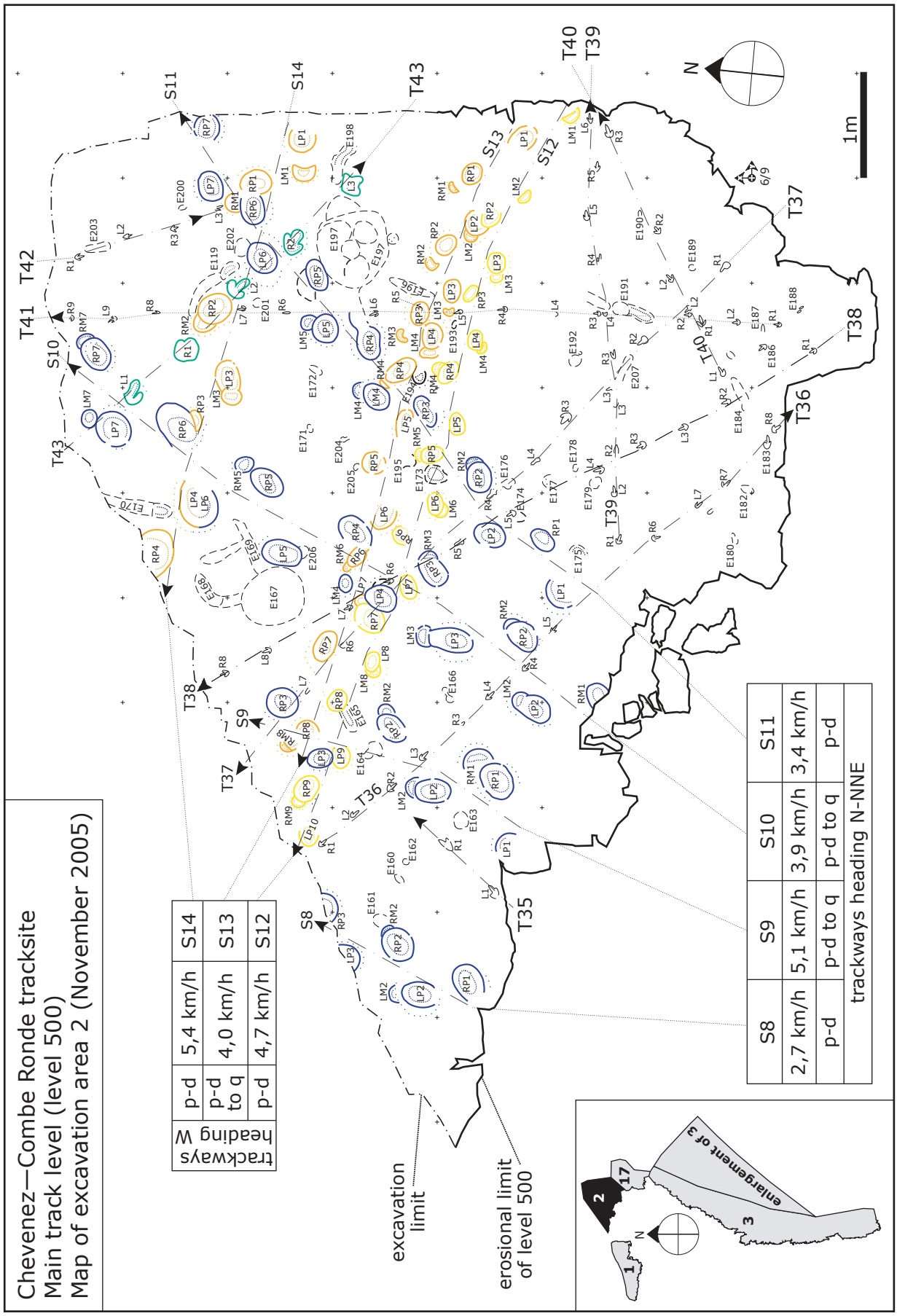


Fig. 5.29: Chevenez—Combe Ronde tracksite, main track level: Map of excavation area 1 with trackway patterns and speed indicated for the parallel sauropod trackways heading N-NNE. Trackway S6 exhibits a change from a slower to a faster gait coupled with reduced overprinting of the manus tracks. Note that in this map the normal faults are shown.

Fig. 5.30 (opposite page): Chevenez—Combe Ronde tracksite, main track level: Map of excavation area 2 with trackway patterns and speed indicated for the sauropod trackways. Note the two groups with parallel trackways and compare with Figure 5.50. Trackways S12 to S14 heading towards the W are faster and have more manus tracks than the other parallel trackways heading N-NNE.


Chevenez—Combe Ronde tracksite
Main track level (level 500)
Map of excavation area 2 (November 2005)
trackways heading W
p-d 5,4 km/h S14
p-d to q 4,0 km/h S13
p-d 4,7 km/h S12
S8 S9 S10 S11
2,7 km/h 5,1 km/h 3,9 km/h 3,4 km/h
p-d p-d to q p-d to q p-d
trackways heading N-NNE
excavation limit
erosional limit of level 500
N
1m
6/9
enlargement of 3
1
2
3
17

5.5.1.2 Trackway interactions and interference

There is no interference between the sauropod trackways of group 1, but within group 2 S12-RP2 clearly overprints S13-LP2 (Fig. 5.29 and Fig. 5.30).

In excavation area 2 the two groups cross each other, and there are numerous interferences between the tracks of both groups. These interferences show that S14 is clearly overprinted by S11 and S10. Somewhat less evident is the interference between S9 and S12, suggesting that S12-LP9 is probably overprinted by S9-LP3, and between S11 and S13 where S11-LP4 is probably overprinted by S13-RP4.

5.5.1.3 Locomotion speed

The values of locomotion speed vary between 2,1 km/h for trackway S6 and 5,4 km/h for S14 (calculated with eq. 2 and ha=4, Table 5.4).

A comparison of the speed values with the two groups of parallel sauropod trackways shows that within group 1 the trackways S3 to S8 are characterized by slightly lower values than the trackways S9 to S11, of which S9 has the highest speed. Group 2 features trackways with higher values than those of group 1, especially when comparing with the trackways S3 to S8. The two isolated trackways S1 and S2 have also rather high speeds.

5.5.2 Sauropod trackways of the overlying levels

The three well-defined trackways of the overlying levels are heading in slightly different directions than those of the main track level.

S1 of level 530 is heading SW, S2 of level 530 E, and S1 of level 540 WSW. There is no interference between the two trackways of level 530, but they are located in close proximity one to each other. After the pes-dominated trackway S6 (2,1 km/h) on the main track level, the pes-only trackway 530-S2 has the lowest locomotion speed. The quadrupedal trackway 530-S1 is slightly faster (3,3 km/h), and the manus-dominated trackway 540-S1 indicates a comparatively high locomotion speed (4,6 km/h).

5.5.3 Trackways of bipedal dinosaurs

5.5.3.1 Orientation and alignment

All trackways are essentially straight, and even the longest trackway T10 shows minor changes in direction. The distribution of the bipedal trackways shows three main directions, heading NE, E, and W, even though some trackways are also heading in other directions (Fig. 5.31). Trackways T10 and T41 (left by the same trackmaker) are the only trackways heading towards the sector between NNW and NNE, and the sector located between S-SSW and WSW is also poorly represented (T32, T5).

Figure 5.32 illustrates the distribution pattern of all trackways of the main track level, showing that the bipedal trackways are quite regularly distributed

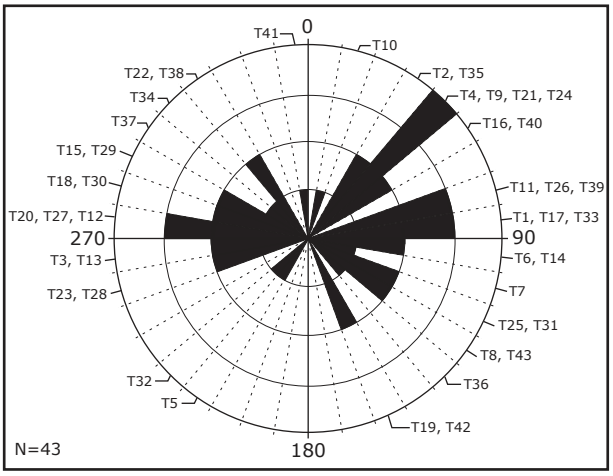
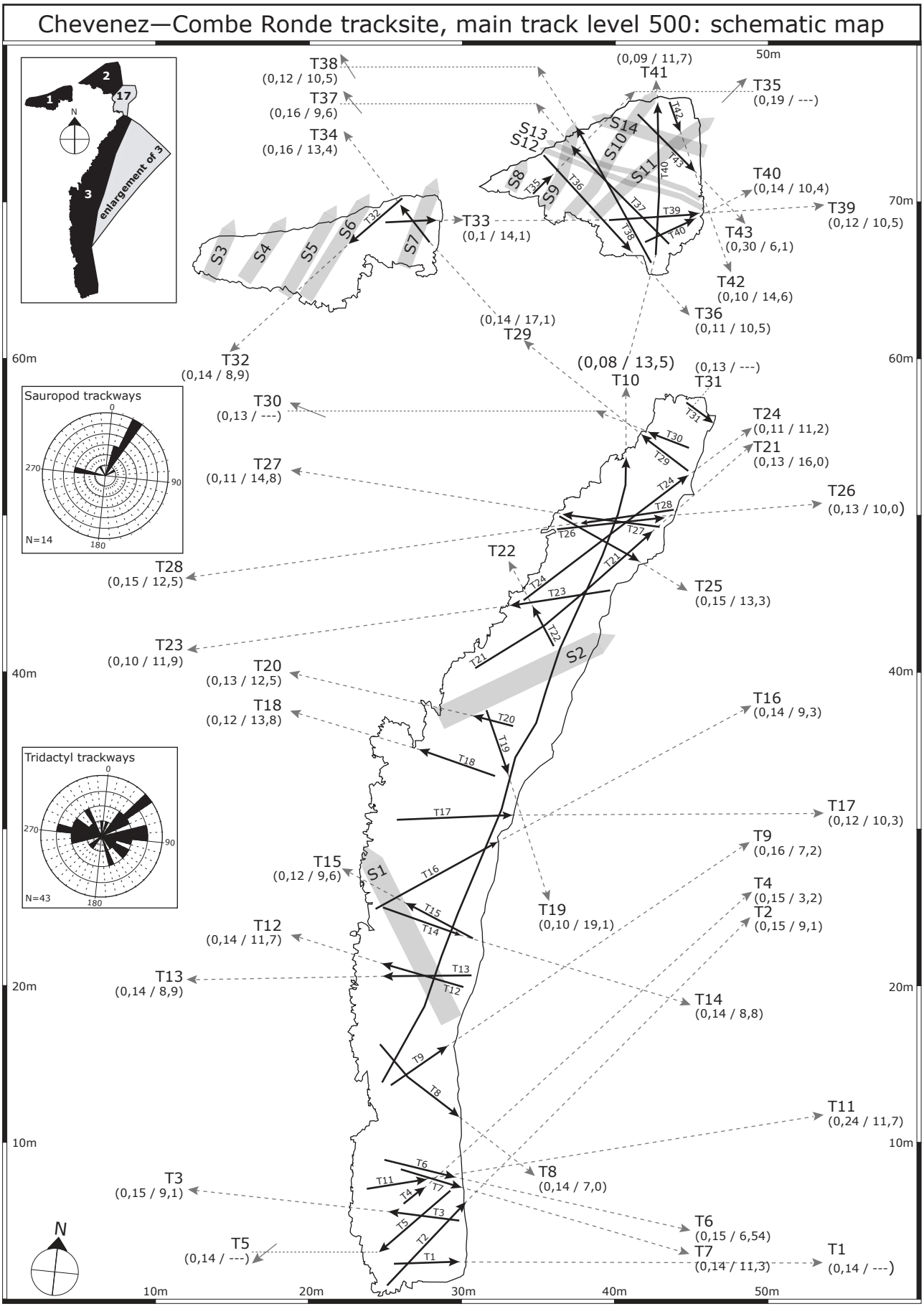


Fig. 5.31: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 (without the enlargement of 2006), main track level: Rose diagram showing the distribution of the directions of the bipedal, tridactyl trackways. The comparison with Figure 5.28 suggests that this distribution is not related with the one of the sauropod trackways.

Fig. 5.32 (opposite page): Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 (without the enlargement of 2006), main track level: Schematic map of the whole tracksite illustrating the position and alignment of the identified trackways of sauropods and bipedal, tridactyl dinosaurs. For the latter the mean pes length in [m] and the locomotion speed in [km/h] are indicated in parentheses. Trackways heading in approximately the same direction are listed in columns. Magnifications of excavation areas 1 and 3 are shown in Figures 5.29 and 5.30. The map of excavation area 3 is not reproduced in this work due to its large size, but it is archived by the PAL A16 (Porrentruy).


Chevenez—Combe Ronde tracksite, main track level 500: schematic map
1
2
17
3
N
enlargement of 3
Sauropod trackways
N=14
Tridactyl trackways
N=43
0
90
180
270
T38 (0,12 / 10,5)
T37 (0,16 / 9,6)
T34 (0,16 / 13,4)
T32 (0,14 / 8,9)
T33 (0,1 / 14,1)
T29 (0,14 / 17,1)
(0,09 / 11,7)
T41
T35 (0,19 / ---)
T40 (0,14 / 10,4)
T39 (0,12 / 10,5)
T43 (0,30 / 6,1)
T42 (0,10 / 14,6)
T36 (0,11 / 10,5)
(0,08 / 13,5)
T10
(0,13 / ---)
T31
T30 (0,13 / ---)
T27 (0,11 / 14,8)
T28 (0,15 / 12,5)
T24 (0,11 / 11,2)
T21 (0,13 / 16,0)
T26 (0,13 / 10,0)
T22
T25 (0,15 / 13,3)
T23 (0,10 / 11,9)
T20 (0,13 / 12,5)
T18 (0,12 / 13,8)
T16 (0,14 / 9,3)
T17 (0,12 / 10,3)
T9 (0,16 / 7,2)
T15 (0,12 / 9,6)
T4 (0,15 / 3,2)
T2 (0,15 / 9,1)
T19 (0,10 / 19,1)
T12 (0,14 / 11,7)
T13 (0,14 / 8,9)
T14 (0,14 / 8,8)
T11 (0,24 / 11,7)
T8 (0,14 / 7,0)
T3 (0,15 / 9,1)
T6 (0,15 / 6,54)
T7 (0,14 / 11,3)
T5 (0,14 / ---)
T1 (0,14 / ---)
S1
S2
S3
S4
S5
S6
S7
S8
S9
S10
S11
S12
S13
S14
10m
20m
30m
40m
50m
60m
70m

over the main track level, in as far that there are no larger areas without trackways. Somewhat higher trackway densities can be observed in the north-northeastern (Fig. 5.34) and southernmost part of excavation area 3, and in excavation area 2.

Together with the mean pes length and the calculated locomotion speed, the alignment of the trackways suggests that T41 in excavation area 2 is the continuation of T10 in excavation area 3, T39 in excavation area 2 of T33 in excavation area 1, and T34 in excavation area 1 of T29 in excavation area 2 (Fig. 5.32). This is very plausible for the first two pairs of trackways and somewhat less for the latter, which are separated by almost 20 m.

Trackways T1, T11, T17, T26, and T39 (continuation of T33) heading NE are approximately parallel and thereof T11, T17, T26, and T39 have a quite regular intertrackway spacing of about 20 m to 25m. Apart from T11, they also have similar mean pes lengths. The closest parallel trackways are T6 and T7 heading E-ESE, located at the southern border of excavation area 3. They are only separated by approximately 30 cm.

The long trackways T21 and T24 heading NE are also parallel and in relative close proximity, with spacing of less than 2 m (Fig. 5.34). All other trackways heading NE (T2, T4, T9, T16, T35, and T40) are separated by more than 4 m, and they show no evidence for a regular alignment. This is also the case for the trackways heading W to W-NW (T3, T12, T13, T15, T18, T20, T27, and T30), even though the four approximately parallel trackways T12, T15, T18, and T20 are located relatively close together, i.e., there are less than 20 m between T12 and T20.

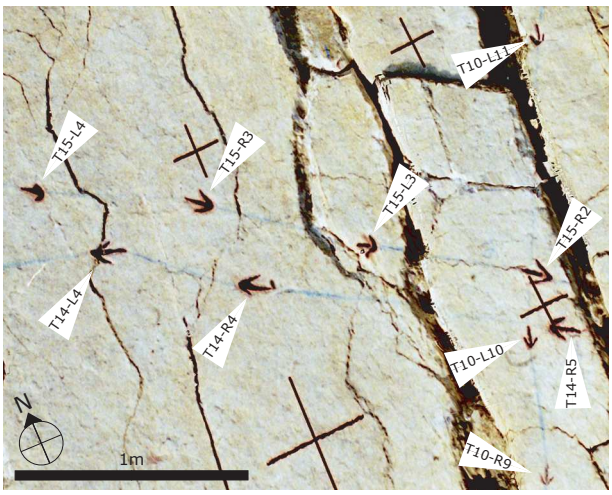


Fig. 5.33: Chevenez—Combe Ronde tracksite, excavation area 3, main track level: Parallel trackways T14 and T15 heading in opposite directions and crossing trackway T10. The tracks (internal track outline) are visualised with water colour; photogrammetry by Terra Data AG (Einsiedeln).

Another particular alignment is shown by the two pairs of approximately parallel trackways heading in opposite directions T14 and T15 (Fig. 5.33), and T26 and T28. They have an intertrackway spacing of less than 0,5 m.

Finally, the two trackways of medium-sized bipedal dinosaur (T11 and T43) are located far away from each other, and they are heading in different directions.

5.5.3.2 Trackway interactions and interference

Crossing trackways are commonly observed, but interferences between tracks of bipedal dinosaurs mainly occur in the northwestern part of excavation area 3, which exhibits the highest density of tridactyl tracks (Fig. 5.34). R34 of T10 is clearly overprinted by T26-R3, and T26-L3 and T28-L4 are interfering in a way suggesting that T26 is superimposed. Besides, T19-R1 and T20-R2 are slightly interfering, but the temporal relationship can not be determined.

5.5.3.3 Locomotion speed

The values of locomotion speed indicated in Table 5.5 were calculated with equations 2, 5, or 6 depending on the relative stride length, and using a factor of 4,5 for mean pes lengths <25 cm, and a factor of 4,9 for mean pes lengths >25 cm.

The calculated values show a relatively large range and vary between 3,2 km/h (T4) and 19,1 km/h (T19), but most bipedal trackways indicate a locomotion speed around the mean value, which is 11,1 km/h (Fig. 5.35 A). Only trackways T19 (19,1 km/h), T29 (17,1 km/h), and T21 (16 km/h) show clearly higher speeds.

Generally, locomotion speed and trackway orientation are poorly correlated (Fig. 5.35B). Parallel trackways in relatively close proximity to each other (<5 m) and a difference in locomotion speed around 1 km/h or less are represented by T23

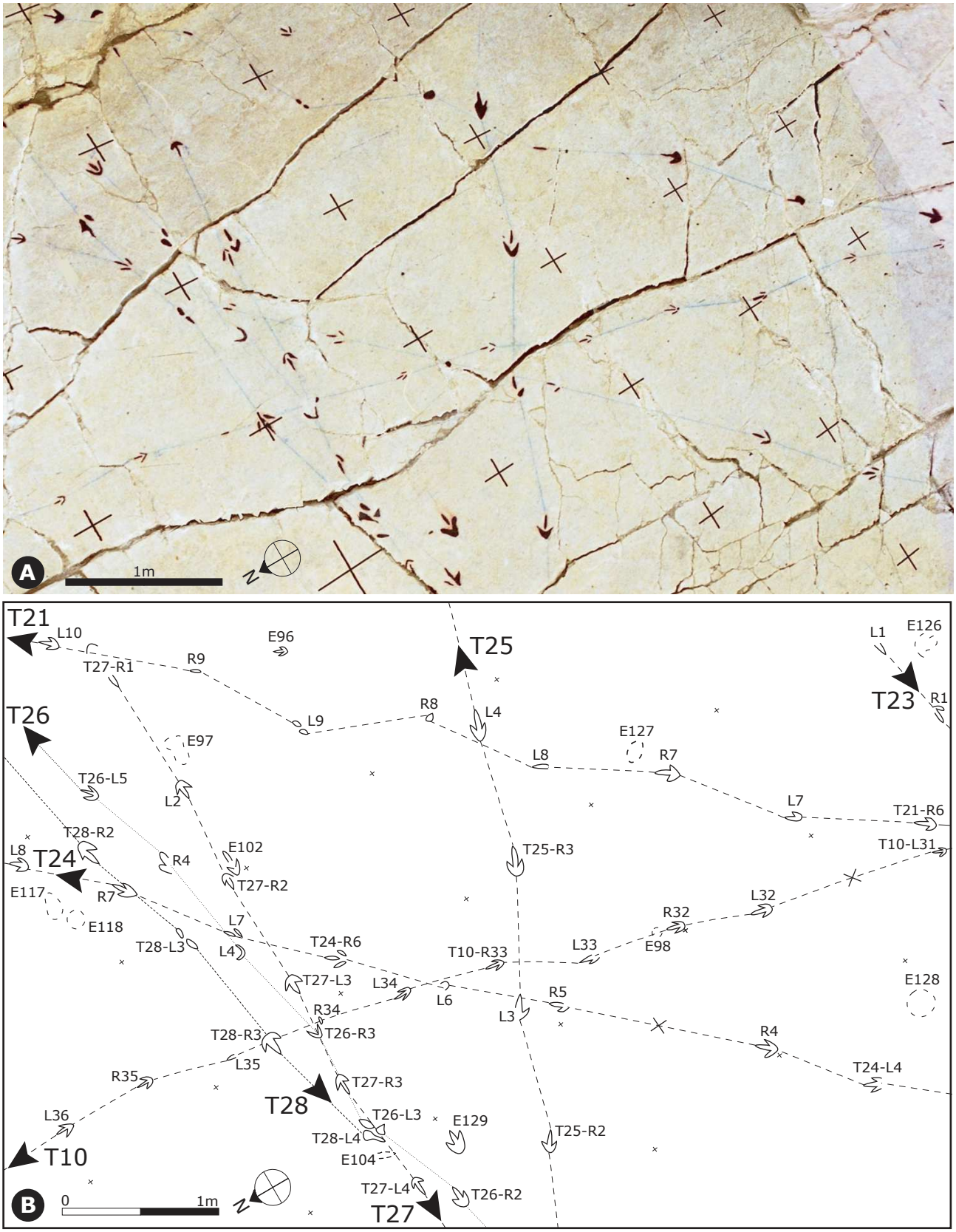


Fig. 5.34: Chevenez—Combe Ronde tracksite, north-northeastern part of excavation area 3, main track level. **A:** Photogrammetry by Terra Data AG (Einsiedeln). **B:** Track and trackway outline drawing of the same area. Note the relatively high density of tridactyl tracks in this area, and the alignment of tracks in a zig-zag fashion in trackways T10, T21, and T26. B is drawn approximately at the same scale as A; 1 m grid in A and B. Tracks (internal track outline) in A are visualised with black water colour.

and T28, T18 and T20, T12 and T15. A difference in speed of less than 5 km/h can be observed amongst the parallel trackways T11, T17, T26, and T39 (=T33), heading northeast. All other trackway groups heading approximately in the same direction show a larger range in the distribution of locomotion speed.

Trackway T21 (16 km/h) indicates a higher speed than the parallel trackway T24 (11,2 km/h). Nevertheless, T21 is characterized by a wider gauge than T24 (Fig. 5.34). The two closest parallel trackways T6 and T7 show a difference in locomotion speed of almost 5 km/h.

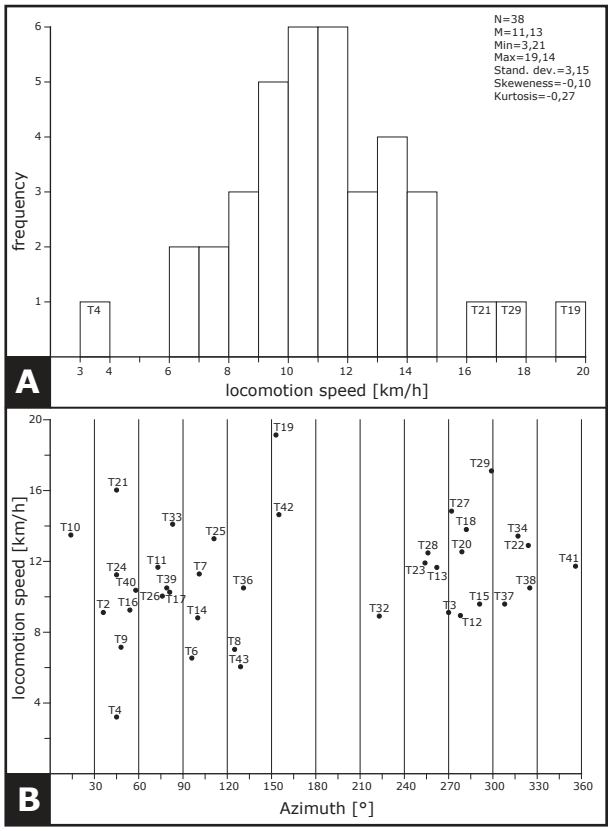


Fig. 5.35: Chevenez—Combe Ronde tracksite, main track level, locomotion speed of the trackways of bipedal, tridactyl dinosaurs. **A:** Histogram showing the distribution of locomotion speed. **B:** Plot of azimuth of trackway orientation against locomotion speed, compare with Figure 5.32.

5.6.4 Trackways of sauropods and bipedal dinosaurs of the main track level

5.6.4.1 Orientation and alignment

The main direction of the sauropod trackways (i.e., N-NNE of group 1) is not represented at all by the bipedal trackways, whereas the direction of orientation of group 2 (i.e., W) is also strongly evident in the bipedal trackways. However, all these latter bipedal trackways are located in excavation area 3 and not in close proximity to the sauropod trackways of group 2 (excavation area 2).

In a general way, none of the bipedal trackways are parallel and in close proximity to any of the sauropod trackways. There are also no eye-catching accumulations of bipedal trackways around the two visible groups of parallel sauropod trackways, or around the two isolated sauropod trackways S1 and S2 in excavation area 3.

5.6.4.2 Trackway interactions and interference

T38-R6 is clearly superimposed on the displacement rim of S10-LP4, and T41-R5 on S13-RP3 (Fig. 5.30). However, T41-R5 was not unambiguously identified and it could likely be another structure. Besides, no interference between sauropod and tridactyl tracks was observed.

However, several sauropod tracks likely overprint tridactyl tracks. In excavation area 2, this is the case for the trackways T35 (overprinted by S9, S12 and/or S13), T37 (L5, R5, L6 overprinted by S10, S12, and/or S13), T38 (R6 and L6 overprinted by S10 and/or S12), T41 (R8 overprinted by S14-RP2 and/or RM2), and T42 (suite overprinted by S14). In excavation area 3, R26 of T10 is overprinted by S2-RP4, and R2 of T14 is possibly overprinted by S1-RP6 or eroded due to a fault in proximity.

Sauropod trackway number		**S1**	**S2**	**S3**	**S4**	**S5**	**S6**	**S7**	**S8**	**S9**	**S10**	**S11**	**S12**	**S13**	**S14**	**530-S1**	**530-S2**	**540-S1**
Level	[ ]	main track level (level 500)														530	530	540
Approximate trackway length	[m]	13	10	2	3	5	7	4	3	5	9	9	11	9	7	6	3	8
Trackway pattern (q=quadrupedal, p-d=pes-dominated; p-o=pes-only; m-d=manus-dominated)	[ ]	q	q	p-d	p-o	p-o	p-d	p-d	p-d	p-d to q	p-d to q	p-d	p-d to q	p-d to q	p-d to q	q	p-o	q m-d
WAP/PL-ratio	[ ]	1,46	1,28	1,53	1,03	1,58	1,57	1,78	1,46	1,94	2,30	1,34	1,31	1,22	1,63	1,13	1,33	1,34
WAP/IPS-ratio	[ ]	1,77	1,57	1,94	1,18	1,80	1,72	2,34	1,81	2,42	2,88	1,70	1,65	1,53	2,00	1,28	1,57	1,55
Pes trackway ratio	[%]	37,0	35,5	39,1	29,2	45,0	34,7	42,6	30,9	32,5	27,3	32,7	33,0	34,7	34,1	45,4	32,4	34,3
TW gauge cf. Romano et al. (2007)		M	M	M	W	M	W	M	W	W	W	W	W	W	W	M	W	W
Mean pes length (L)	[m]	0,38	0,39	0,35	0,30	0,29	0,35	0,28	0,31	0,30	0,30	0,28	0,20	0,22	0,29	0,39	0,48	0,26
Mean pes width	[m]	0,25	0,26	0,22	0,23	0,23	0,29	0,16	0,20	0,19	0,19	0,18	0,12	0,14	0,19	0,30	0,35	0,19
Pes track size index	[m]	0,31	0,32	0,28	0,26	0,26	0,32	0,21	0,25	0,24	0,24	0,22	0,16	0,18	0,23	0,34	0,41	0,22
Mean stride length (S)	[m]	1,55	1,82	1,29	1,06	1,07	1,06	1,10	1,15	1,59	1,37	1,21	1,15	1,13	1,63	1,50	1,42	1,36
Hip height Alexander (ha) = 4L	[m]	1,50	1,56	1,40	1,21	1,18	1,39	1,11	1,25	1,18	1,20	1,13	0,78	0,88	1,15	1,55	1,92	1,03
Relative stride length (S/ha)	[ ]	1,03	1,17	0,92	0,88	0,91	0,76	0,99	0,92	1,35	1,14	1,07	1,47	1,27	1,42	0,97	0,74	1,33
Hip height Thulborn (ht) = 5,9L	[m]	2,21	2,30	2,07	1,78	1,73	2,05	1,63	1,85	1,75	1,77	1,67	1,16	1,30	1,69	2,29	2,83	1,52
Relative stride length (S/ht)	[ ]	0,70	0,79	0,62	0,59	0,62	0,52	0,67	0,62	0,91	0,77	0,73	1,00	0,86	0,96	0,65	0,50	0,90
Locomotion speed (eq. 2, ha)	[km/h]	3,64	4,56	2,91	2,49	2,62	2,12	2,91	2,74	5,03	3,85	3,37	4,74	3,97	5,42	3,32	2,36	4,55
Time represented by trackway	[s]	12,9	7,9	2,5	4,3	6,9	11,9	5,0	3,9	3,6	8,4	9,6	8,4	8,2	4,7	6,5	4,6	6,3
Locomotion speed (eq. 2, ht)	[km/h]	2,34	2,90	1,85	1,58	1,67	1,34	1,85	1,74	3,20	2,44	2,14	3,01	2,52	3,44	2,10	1,50	2,89
Time represented by trackway	[s]	20,0	12,4	3,9	6,8	10,8	18,8	7,8	6,2	5,6	13,3	15,2	13,2	12,9	7,3	10,3	7,2	10,0

Table 5.4 (top): Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 (without the enlargement of 2006): Locomotion speed of the sauropod trackways of all levels, calculated with equation 2 and two assumptions for the calculation of the hip height (ha=4L; ht=5,9L). "TW" = Trackway, "M" = medium-gauge trackways, "W" = wide-gauge trackway.

Trackway number	approximate trackway length	[WAP/PL]-ratio	mean pes length (L)	mean stride length (S)	hip height small theropod (hs) = 4,5L	relative stride length (S/hs)	hip height large theropod (hl) = 4,9L	relative stride length (S/hl)	**Locomotion speed** speed eq. 2 s/h<2,0	speed eq. 5 s/h>2,9	eq. 6=[eq.2+eq.5]/2 2<s/h<2,9	**Time represented by trackway**
	[m]	[ ]	[m]	[m]	[m]	[ ]	[m]	[ ]	[km/h]	[km/h]	[km/h]	[s]
T1	3	0,926	0,14		0,61							
T2	7	0,448	0,15	1,37	0,68	2,01			7,49	10,74	9,11	2,77
T3	4	0,442	0,15	1,37	0,68	2,03			7,49	10,74	9,11	1,58
T4	2	0,207	0,15	0,80	0,65	1,23			3,21	5,59	4,40	2,24
T5	5		0,14		0,62							
T6	5	1,008	0,15	1,25	0,67	1,87			6,54	9,66	8,10	2,75
T7	5	0,699	0,14	1,48	0,61	2,42			9,67	12,91	11,29	1,59
T8	7	0,94	0,14	1,25	0,63	1,99			7,03	10,14	8,58	3,59
T9	4	0,31	0,16	1,36	0,70	1,94			7,15	10,40	8,78	2,01
T10	47	0,735	0,08	1,13	0,37	3,09			11,06	13,49	12,28	12,54
T11	3	0,004	0,24	2,20	1,08	2,04			9,61	13,73	11,67	0,93
T12	5	0,494	0,14	1,53	0,62	2,46			10,03	13,29	11,66	1,54
T13	5	0,814	0,14	1,41	0,62	2,28			8,75	9,12	8,94	2,01
T14	7	0,457	0,14	1,26	0,62	2,01			7,25	10,37	8,81	2,86
T15	5	0,443	0,12	1,25	0,56	2,24			8,06	11,11	9,59	1,88
T16	9	0,322	0,14	1,33	0,64	2,06			7,65	10,84	9,25	3,50
T17	7	0,965	0,12	1,31	0,56	2,35			8,72	11,81	10,26	2,46
T18	5	0,232	0,12	1,55	0,53	2,89			12,32	15,28	13,80	1,30
T19	3	0,544	0,10	1,65	0,44	3,75			17,00	19,14	18,07	0,56
T20	3	0,88	0,13	1,50	0,56	2,66			11,06	14,02	12,54	0,86
T21	17	1,089	0,13	1,70	0,58	2,92			12,93	16,03	14,48	3,82
T22	5	0,547	0,12	1,48	0,53	2,76			11,40	14,40	12,90	1,40
T23	7	0,646	0,10	1,24	0,44	2,82			10,55	13,28	11,91	2,12
T24	15	0,41	0,11	1,41	0,49	2,89			8,08	14,39	11,24	4,81
T25	7	0,697	0,15	1,76	0,67	2,64			11,58	14,97	13,28	1,90
T26	5	1,043	0,13	1,35	0,60	2,23			8,46	11,62	10,04	1,79
T27	6	0,511	0,11	1,48	0,51	2,92			11,93	14,84	13,38	1,46
T28	5	0,621	0,15	1,67	0,66	2,52			10,79	14,17	12,48	1,44
T29	3	0,688	0,14	1,90	0,64	2,97			13,88	17,11	15,50	0,63
T30	3	0,16	0,13		0,56							
T31	2		0,13		0,56							
T32	4	0,395	0,14	1,27	0,62	2,06			7,35	10,48	8,91	1,62
T33	2	0,462	0,10	1,30	0,44	2,95			11,42	14,10	12,76	0,51
T34	3	0,594	0,16	1,86	0,72	2,58			11,67	15,19	13,43	0,80
T35	1		0,19		0,83							
T36	9	0,291	0,11	1,22	0,49	2,49			9,05	11,96	10,50	3,08
T37	8	0,743	0,16	1,46	0,71	2,06			7,92	11,27	9,59	3,00
T38	9	0,375	0,12	1,30	0,54	2,41			8,99	12,02	10,50	3,08
T39	6	0,45	0,12	1,27	0,52	2,45			9,03	12,02	10,52	2,05
T40	4	0,804	0,14	1,44	0,64	2,24			8,74	12,00	10,37	1,39
T41	10	0,784	0,09	1,19	0,42	2,85			10,40	13,06	11,73	3,07
T42	2	0,917	0,10	1,32	0,43	3,06			12,03	14,64	13,34	0,49
T43	4	0,172	0,30	2,07			1,47	1,41	6,05	9,98	8,02	2,38

Table 5.5: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 (without the enlargement of 2006), main track level: Locomotion speed of the bipedal trackways.

5.6 Enigmatic traces of the main track level

Besides dinosaur tracks and numerous structures without a recurrent distinct form, the main track level also revealed a single trace with a scratch mark affinity, and two kinds of recurrent and well-defined enigmatic traces. The latter occur in all three excavation areas and are a common and strikingly distinct feature of the main track level.

5.6.1 Purported scratch mark

5.6.1.1 Description

This trace (named E73) is located about 1 m south of S1-RP1, and about 20 cm S of T20-L3. It has a length of 27 cm, a width of 6 cm, and a depth of 0,5 cm. The trace is a distinct structure with a well-defined and sharp outline. At its one end it exhibits a semicircular depression connected with two elongate grooves with a similar and regular diameter of 1-2 cm, and which are separated by a 1-2 cm wide strip of undeformed sediment. These grooves become increasingly shallow towards the end, one having a round and blurred, the other having a tapered end (Fig. 5.36). This trace is unique at the Combe Ronde tracksite.

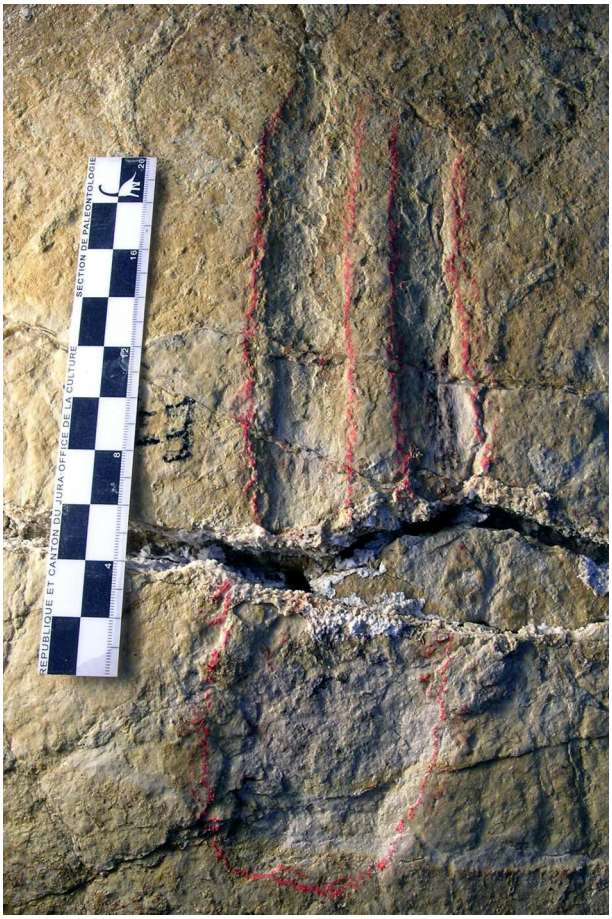


Fig. 5.36: Chevenez—Combe Ronde tracksite, main track level, excavation area 3: Purported scratch mark (E73), characterized by two elongate grooves connected in a semi-circular depression. Scale bar is 20 cm, artificial illumination from upper left.

5.6.1.2 Discussion of potential origin

Trace E73 strongly resembles a scratch mark, most probably left by a vertebrate trackmaker. However, its isolated appearance without any trackway hampers the ichnotaxonomic identification.

The trace is different from scratch or swim marks attributed to theropods (e.g., Milner et al., 2006; Ezquerra et al., 2007), and also differs from tracks and swim marks attributed to crocodiles (e.g., Foster & Lockley, 1997; Romano & Whyte, 2003; Lockley & Meyer, 2004; Mazin & Billon-Bruyat, 2006; Avanzini et al., 2007a; Whyte et al., 2007), or pterosaurs (e.g., Lockley & Wright, 2003). However, it is somewhat similar to tracks produced by turtles walking over incompetent substrate (e.g., Avanzini et al., 2005; Fiorillo, 2005). Late Jurassic turtle tracks and trackways with associated scratch marks have been described from the Late Jurassic of Cerin, France (Bernier et al., 1982; Gaillard et al., 2003), Asturia, Spain (Avanzini et al., 2005), and were observed in Crayssac, France (Billon-Bruyat, pers. comm., 2008).

A turtle origin is plausible since turtles are abundant in the Kimmeridgian of northwestern Switzerland (e.g., Bräm, 1965; Meyer, 1989, 1994a; Billon-Bruyat & Marty, 2004; Marty & Billon-Bruyat, 2004; Billon-Bruyat, 2005b). A few scattered turtle carapace fragments were found at the Combe Ronde tracksite at the top of the laminite interval (layers 542, 550), and a disarticulated turtle carapace was found within the layers 520 to 530 of the same laminite sequence at the nearby Chevenez—Crat tracksite (pers. obs.). Nevertheless, an attribution of this particular trace to a turtle is tentative at best, until more traces and a well-defined trackway are found. Moreover, an attribution to a turtle is somewhat in contradiction with the suggested higher supratidal-flat palaeoenvironment of the main track level (see chap. 4.4.4 and chap. 4.4.6, Fig. 4.3).

5.6.2 Elongate grooves and subcircular depressions

Grooves and depressions can be found over the whole tracksite, but they are most common in excavation area 2. Subcircular depressions are less frequent than grooves.

5.6.2.1 Morphology of elongate grooves

Elongate grooves are always much longer than wide, up to several cm deep, and never surrounded by displacement rims. Most have a length of about 50 cm (e.g., E8, E119, E168-170, E191), but the longest reach up to 1,2 m (e.g., E32, E82). The width is always on the order of 10-15 cm and is constant over the whole length of the grooves. The grooves are either straight, or have an arcuate to sinuous form. Most are characterized by rounded, well-defined ends (Figs. 5.37C & E). Only a few are bifurcated, notably E32, E52, or E169 (Fig. 5.37A).

Some grooves exhibit an internal subdivision into two (e.g., E8, E119, E168, E170) or rarely three (e.g., E191) compartments of equal or different size. The separations between these compartments are generally distinct and well-defined (Fig. 5.37C).

None of the grooves is surrounded by displacement rims, and within all grooves desiccation cracks show the same appearance as on the surrounding surface.

5.6.2.2 Morphology of subcircular depressions

These depressions are subcircular to oval in shape and have a smooth outline.

Subcircular depression E197 in excavation area 2 is with a diameter of 90 cm the largest, and with a depth of 8 cm the deepest depression (Fig. 5.37B). It is further the only depression, which is subdivided into 4 smaller subcircular depressions (Fig. 5.30).

The depressions are never surrounded by displacement rims and always cut by desiccation cracks.

5.6.2.3 Association and interference with other traces and dinosaur tracks

Except for the subcircular depression E167, which is connected with grooves E168 and E169, the depressions are not associated with grooves. Apart from the depression E45, they are always in close proximity to sauropod trackways, but no connections between the depressions and sauropod tracks can be observed.

Many of the grooves are in relative close proximity to either sauropod or bipedal trackways, but in excavation 3 several grooves (e.g., E52, E54, E55) also occur completely isolated in areas without dinosaur tracks.

Some grooves are in an eye-catching way associated with dinosaur trackways. These are notably E32 located in close proximity to sauropod trackway S1, the sinuous groove E83 between RP1 and LP2 of sauropod trackway S2 angled in the direction of the trackway (Figs. 5.37A & E), and E34 located between R1 and L2 of the bipedal trackway T13.

There are only a few interferences with dinosaur trackways. Groove E32 clearly overprints R5 of the bipedal trackway T10 (Fig. 5.37A), groove E191 overprints L4 of trackway T39, and RP8 of trackway S12 probably overprints groove E165 (Fig. 5.37D). However, E165 may also have formed due to slipping or dragging of the right manus track, i.e., RM8 of trackway S12.

5.6.2.4 Discussion of potential origin

Because all depressions and grooves are well-defined, distinct features covered with desiccation cracks, and because some show unambiguous interferences with dinosaur tracks, they are clearly primary features, which formed prior to or during the subaerial exposure of the main track level. An origin due to epikarstification or any other secondary sedimentary (e.g., load marks) or diagenetic processes can clearly be ruled out.

At first glance, some traces are strikingly associated with dinosaur trackways and an origin related to the behaviour of the trackmakers is a spectacular scenario. However, there is no clear and

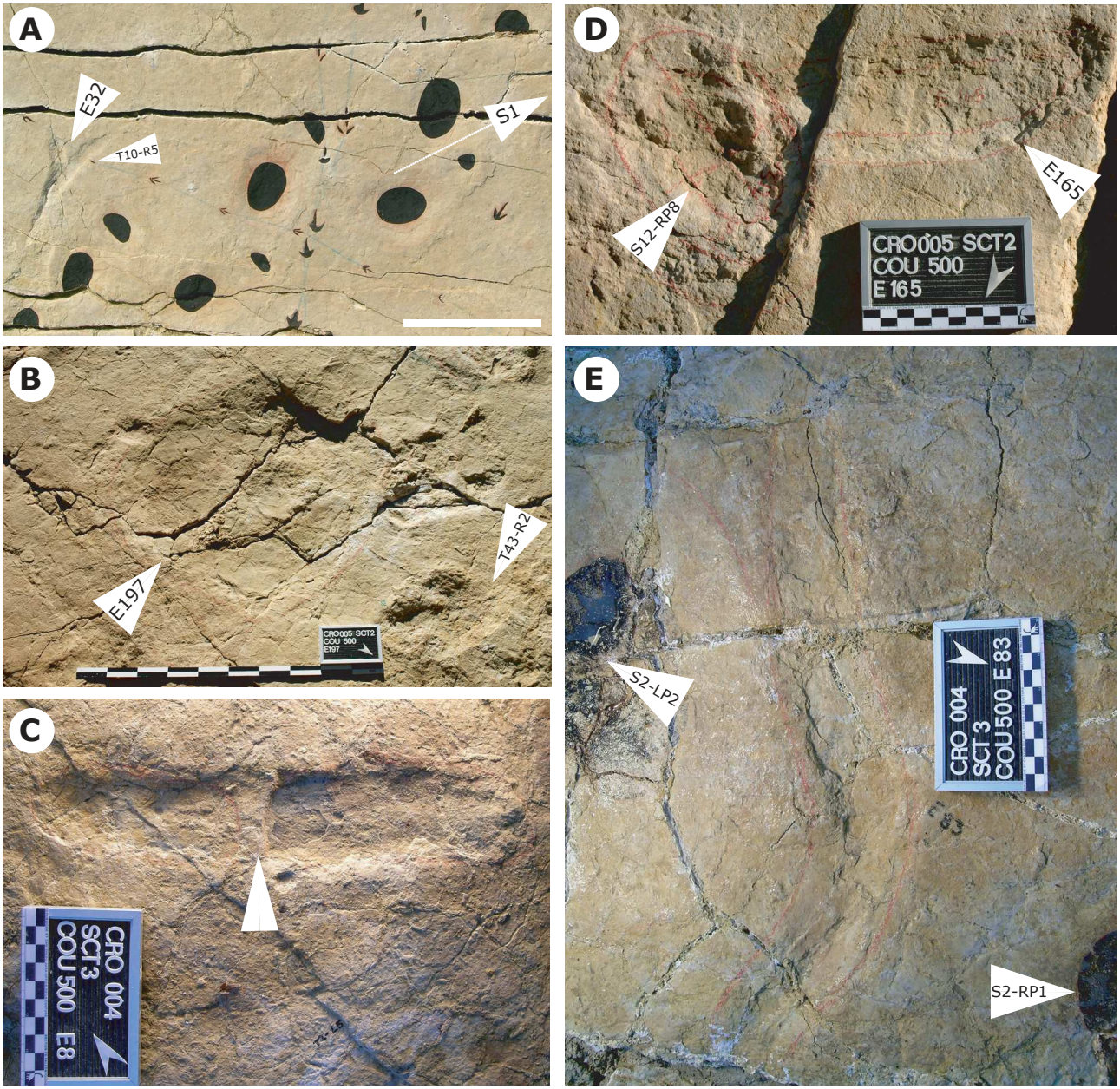


Fig. 5.37: Chevenez—Combe Ronde tracksite, main track level: Elongate grooves and subcircular depressions. **A:** The bifurcated groove E32 is located beside trackway S1. It clearly truncates the right pes R5 of trackway T10. **B:** The subcircular depression E197 subdivided into several smaller subcircular depressions. Note the desiccation pattern within the depression and the medium-sized tridactyl track (T43-R2) on the lower right. **C:** Straight groove E8 with rounded ends, subdivided into two compartments (arrow). **D:** Straight groove E165 at the exterior anterior side of the right pes RP8 of trackway S12, interpreted as a slipping or dragging manus track. **E:** Sinuous groove E83 between S2-RP1 and S2-LP2 and angled in the direction of trackway S2. Scale bar is 1 m in A and B and 20 cm in C-E; daylight in A, B, and D; artificial illumination from upper right in C and from lower left in E; photos B and D by B. Migy (SAP).

systematic association of the depressions and the grooves with the dinosaur trackways observable. The sparse interactions with dinosaur tracks suggest that these traces were, at least partially, formed later. The desiccation cracks within the traces indicate that they were, as the dinosaur tracks, subjected to about the same period of desiccation.

It is assumed that these traces either have a biological or a sedimentary origin, and the following different hypotheses are outlined and their probability evaluated.

Biological origin

A first biological hypothesis could be that these are imprints of wood (trunks), carcasses, or other floatsam. However, the shape of the traces does not support this scenario. Moreover, the formation of desiccation cracks and the truncation of dinosaur tracks can not easily be explained.

Different activities of the dinosaurs or other animals present on the main track level at the time of subaerial exposure or prior to emersion may have resulted in crouching or resting traces, traces of feeding (e.g., for infaunal invertebrates), traces of foraging or scavenging, tail traces, traces of neck or head, or traces related to the construction of nests.

There is no trackway evidence for scavenging or foraging, even though it may not be ruled out that these traces are due to foraging, produced for instance through digging by an animal when the sediment was already so hard that its footprints were not recorded anymore. On modern tidal flats, the formation of "craters" is for instance explained by the feeding behaviour of ducks (Cadée, 1990).

The hypotheses of crouching, resting, and tail traces can be ruled out, because many traces are not associated with dinosaur trackways. Moreover, tail drag marks (e.g., Irby & Albright, 2002; Platt & Hasiotis, 2008), dinosaur crouching and resting traces (e.g., Lull, 1915; Kuban, 1989; Gierliński, 1994, 1996; Avanzini et al., 2001; Lockley et al., 2003; Milàn et al., 2008), and also, resting traces of rays (Martinell et al., 2001) look inherently different.

Also nests of dinosaurs (e.g., Sanz et al., 1995; Lopez-Martínez et al., 2001) or reptiles (e.g., Avanzini et al., 2007b) in tidal-flat environments look different, even though a certain resemblance with sauropod nest structures described by Chiappe et al. (2004) can not be denied. The burying of eggs by turtles may also have resulted in surface traces but detailed studies of morphology of nests of modern marine turtles are scarce (Billes & Fretey, 2001).

Sedimentary origin

On intertidal flats, sedimentary processes related to currents or waves may result in a wide spectrum of sedimentary features including grooves and depressions (e.g., Allen, 1969; Reineck & Singh, 1975). This also includes channels, (ebb) gullies, and creeks (e.g., Eisma, 1998) or ebb-flow channel down-cutting, which is probably related to atypical water movements (e.g., Roehl, 1967). Van der Laan & Wolff (2006) described circular pools in the intertidal seagrass mudflats of the Banc d'Arguin (Mauritania), which they interpret as the result of accretion of non-circular depressions. However, most of these depressions are clearly larger than the ones found at the Combe Ronde tracksite. Tucker & Burchette (1977) described flutes and scour pits on a track-bearing level, which they explained by sheet floods, which in places cut into and removed the track bed where eddies were generated by an obstacle.

If it is assumed that the grooves and depressions were left after the dinosaur tracks (as suggested by the interactions), these scenarios related to water movement are not very likely, because such processes would certainly have affected the dinosaur tracks as well. Moreover, the presence of internal overtracks within the tracks as well as in the grooves and depressions indicates that the main track level was covered up slowly in a supratidal environment (see also chap. 4).

If it is assumed that the grooves and depressions were produced by any of the above cited processes prior to subaerial exposure of the main track level and prior to the formation of the dinosaur tracks, they may still have been filled with water at the time of track formation. This may explain the truncation of some of the tracks, because that part of the track was simply not preserved. Later, the depressions dried out and were subjected to desiccation. However this scenario is not very convincing because of the distinct and recurrent shape of the grooves and depressions.

Microbial mats are responsible for the formation of peculiar and varied surface structures (e.g., Bernier et al., 1991; Gerdes et al., 1993; Schieber et al., 2007a), and algal mat peeling may be another hypothesis for the formation of the grooves and depressions, similar to the formation of ripple patches (e.g., Schieber, 2007). Thereby, complete mats or algal domes may become buoyant, peel off and float away, leaving big scars, which then would be deepened by scouring when the tidal flat was flooded (Monty, 1972). However, such tear-off structures generally have an irregular and not systematically recurrent shape (pers. obs.).

To summarize, controversy remains regarding the possible origin of these peculiar grooves and depressions. None of the above-mentioned biological or sedimentary hypotheses provides a convincing explanation for their formation. In all ichnoassemblages of the Ajoie, these peculiar traces were so far only observed at the Combe Ronde tracksite and only on the main track level.

5.7 Discussion

The aim of this discussion is to compare the studied sauropod tracks and the tridactyl morphotypes with known ichnogenera and to give a short review of possible trackmakers. Afterwards, the variation and correlation of some of the analysed trackway parameters, notably the [WAP/PL]-ratio, will be discussed in greater detail, including the locomotion capabilities of the trackmakers. Concerning the sauropod trackways, the [WAP/PL]-ratio is further compared with the pes trackway ratio (PTR) to establish a relationship between these two ratios and to characterize trackway gauge. Finally, the ichnoassemblage of the main track level and implications for the behaviour and palaeoecology of the trackmakers, ichnofacies, and megatracksites of the Jura carbonate platform will be discussed.

5.7.1 Ichnotaxonomy of sauropod tracks

5.7.1.1 Sauropod trackway gauge

Trackway configuration is traditionally used in the description of dinosaur ichnogenera. This is also the case for sauropod trackways, particularly since Farlow et al. (1989) based the classical description of *Brontopodus birdi* on both track morphology and trackway parameters, and since Farlow (1992) proposed that sauropod trackways could be classified according to trackway width. He introduced the term trackway gauge stressing that sauropod trackways can generally be described as narrow-gauge or wide-gauge. Lockley et al. (1994b) and Meyer et al. (1994) proposed a third category, the medium-gauge, but they also stated that a formal classification of sauropod trackways on gauge alone was premature. Lockley et al. (1994b) further considered heteropody to be a taxonomically important feature, even if heteropody is not considered as a character in the phylogenetic taxonomy of sauropods (e.g., Salgado et al., 1997; Wilson & Sereno, 1998, Wilson & Carrano, 1999), perhaps because it is not a "single" character but instead a relationship between two characters.

When Farlow (1992) introduced the trackway gauge concept, he stressed that trackway configuration including gauge may also be related to substrate properties and locomotion (speed), in a way that the trackmakers of the wide-gauge trackways may have angled their legs inward with respect to the sagittal plane, and if so that trackway gauge would have little systematic value. This was also discussed by Wilson & Carrano (1999), who concluded that "it is unlikely that any single sauropod was able to produce both wide- and narrow-gauge trackways", because they assumed that skeletal morphology is responsible for trackway gauge and that the wide stance was a synapomorphy of the titanosaurids. Meanwhile, the "gauge concept" is commonly used for the classification of sauropod trackways and the identification of their trackmakers (e.g., Lockley et al., 1994b, c, 2002a, b; Moratalla et al., 1994; Lockley & Hunt, 1995; Dalla Vecchia & Tarlao, 2000; Lockley & Meyer, 2000; Day et al., 2002a, 2004; Marty et al., 2003; Moreno & Benton, 2005), and seemed to be confirmed by the work of Wilson & Carrano (1999) and Henderson (2006b).

Nonetheless, Lockley et al. (2002a), based on trackway evidence from the Late Cretaceous of Bolivia, suggested that titanosaurids may have showed changes from a narrow-gauge to a wide-gauge during their ontogenetic growth, and Farlow (pers. comm. 2004 in Wright, 2005) stated that some *Brontopodus* trackway segments of the Paluxy River showed narrow-gauge locomotion along some trackway segments. This led Wright (2005) to recommend that sauropod trackways should be classified primarily on the basis of manus and pes morphology, and only secondarily on trackway gauge. For these reasons, the importance of the "trackway gauge concept" in the classification of sauropod tracks continues to be debated.

Despite this, a quantification of trackway gauge was done only recently by Romano et al. (2007) introducing the pes trackway ratio (PTR). Additionally, in this work the [WAP/PL]-ratio, that is the ratio between the width of the pes angulation pattern and the corresponding pes track length, is introduced to characterize trackway gauge.

Comparison of the [WAP/PL]-ratio with the PTR

To compare the PTR with the [WAP/PL]-ratio, the latter was calculated for some of the trackways, for which Romano et al. (2007) calculated the PTR, and for the schematic trackways figured in Lockley et al. (1994b, Fig. 1; identical with Fig. 4 in Meyer et al., 1994) because it is speculated whether the schematic medium-gauge is an intermediate category or just a difference in scale (Wright, 2005). This was done on magnifications of published outline drawings, and the values are shown in Table 5.6.

In Figure 5.38, the [WAP/PL]-ratio is plotted against the pes trackway ratio. The correlation is very good for the ichnotaxa *Parabrontopodus*, *Breviparopus*, *Brontopodus*, the schematic trackways figured in Lockley et al. (1994b, Fig. 1), cf. *Brontopodus* trackways figured in Santos et al. (1994, Fig. 3), and also the trackways from the Courtedoux—Sur Combe Ronde site. The trackways of the Chevenez—Combe Ronde site show a higher variability (which will be discussed in greater detail in Chapter 5.7.1.7).

The three categories of Lockley et al. (1994b, Fig. 1) are meaningful, even though the "schematic medium-gauge" trackway is closer to the "schematic wide-gauge" than to the "schematic narrow-gauge" trackway, and all three trackways fall into the medium-gauge field defined by Romano et al. (2007). This suggests that trackways previously thought to be narrow-gauge or wide-gauge can be distinguished by means of the PTR and the [WAP/PL]-ratio, even though medium-gauge

Trackway denomination (Reference; Figure)	Locality / Country	Age	Speed [km/h]	PL [cm]	WAP [cm]	[WAP/PL]-ratio	PTR ratio	Trackway gauge
CRO-500-S1, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	3,6	37,5	54,6	1,46	37*	medium
CRO-500-S2, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	4,6	39,0	50,0	1,28	35,5*	medium
CRO-500-S3, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	2,9	35,0	53,5	1,53	39,1*	medium
CRO-500-S4, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	2,5	30,2	31,0	1,03	29,2*	wide
CRO-500-S5, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	2,6	29,4	46,5	1,58	45*	medium
CRO-500-S6, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	2,1	34,7	54,4	1,57	34,7*	wide
CRO-500-S7, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	2,9	27,7	49,3	1,78	42,6*	medium
CRO-500-S8, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	2,7	31,3	45,7	1,46	30,9*	wide
CRO-500-S9, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	5,0	29,6	57,3	1,94	32,5*	wide
CRO-500-S10, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	3,9	30,0	68,9	2,30	27,3*	wide
CRO-500-S11, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	3,4	28,3	37,8	1,34	32,7*	wide
CRO-500-S12, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	4,7	19,6	25,7	1,31	33*	wide
CRO-500-S13, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	4,0	22,1	27,0	1,22	34,7*	wide
CRO-500-S14, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	5,4	28,7	46,7	1,63	34,1*	wide
CRO-530-S1, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	3,3	38,8	43,8	1,13	45,4*	medium
CRO-530-S2, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	2,4	48,0	64,0	1,33	32,4*	wide
CRO-540-S1, this work	Combe Ronde, Switzerland	Early / Late Kimmeridgian	4,6	25,7	34,4	1,34	34,3*	wide
SCR-1000-S3 (Marty et al.,2003; Fig. 10)	Sur Combe Ronde, Switzerland	early Late Kimmeridgian	3,0	43,4	48,5	1,12	44,65*	medium
SCR-1000-S4 (Marty et al.,2003; not fig.)	Sur Combe Ronde, Switzerland	early Late Kimmeridgian	2,4	38,8	45,0	1,16	44,4*	medium
SCR-1000-S10 (Marty et al.,2003; Fig. 5)	Sur Combe Ronde, Switzerland	early Late Kimmeridgian	2,9	46,9	37,1	0,79	51,4*	narrow
Breviparopus taghbaloutensis (Ishigaki, 1989; Fig. 9.5)	Central High Atlas Mountains, Morocco	Middle to Late Jurassic		(2,45*)	(2,25*)	0,92*	51,48**	narrow
Brontopodus birdi (Romano et al., 2007; Fig. 3A)*	Paluxy River Valley, Glen Rose, Texas, U.S.A.	Aptian-Albian		86,5	(2,64*)	1,46*	36,04**	medium
Parabrontopodus mcintoshi (Lockley et al., 1986, Fig. 7B)	Purgatoire Valley Dinosaur tracksite, Colorado, U.S.A.	Late Jurassic	6,8	60	(3,55*)	0,87*	51,9**	narrow
Narrow-gauge trackway 90 (Day et al., 2004; Fig. 7E)	Ardley Quarry Oxfordshire, England	Bathonian		(3,5*)	(3,5*)	1,00*	45,9**	medium
cf. *Brontopodus* (Santos et al., 1994, Fig. 3'a')	Galinha, Fatima, Portugal	Middle Jurassic	3,6	100	(1,96*)	1,51*	37,71**	medium
cf. *Brontopodus* (Santos et al., 1994, Fig. 3'b')	Galinha, Fatima, Portugal	Middle Jurassic	4,7	80	(1,67*)	1,26*	39,74**	medium
Schematic narrow-gauge trackway	(Lockley et al., 1994b; Fig. 1 right)			(1,7*)	(1,325*)	0,78*	49,1*	medium
Schematic medium-gauge trackway	(Lockley et al., 1994b; Fig. 1 middle)			(1,3*)	(1,7*)	1,31*	38,5*	medium
Schematic wide-gauge trackway	(Lockley et al., 1994b; Fig. 1 left)			(1,7*)	(2,65*)	1,56*	35,7*	medium
Assumption 1	Width of the angulation pattern is half of the pes length			1	0,5	0,5	very narrow	
Assumption 2	Width of the angulation pattern equals pes length			1	1	1	narrow	
Assumption 3	Width of the angulation pattern is 1,5 x pes length			1	1,5	1,5	medium to wide	
Assumption 4	Width of the angulation pattern is twice the pes length			1	2	2	very wide	

Table 5.6: Calculation of the [WAP/PL]-ratio and the pes trackway ratio (PTR) for the sauropod trackways from the Chevenez—Combe Ronde tracksite, three selected trackways from the Courtedoux—Sur Combe Ronde site, and selected published trackways including schematic trackways in Lockley et al. (1994b, Fig. 1). Values marked with one asterisk were calculated on magnifications of outline drawings, those marked with two asterisks are PTR taken from Romano et al. (2007, Table 1). Values for pes length (PL) and the width of the pes angulation pattern (WAP) put in parentheses are measures obtained from magnifications of published trackway outline drawings. The PTR of the Chevenez—Combe Ronde site were measured on magnifications of outline drawings (marked with a single asterisk) and the PTR for the three trackways of the Courtedoux—Sur Combe Ronde site were calculated from higher resolution outline drawings than those figured in Marty et al. (2003). This is the reason why the latter slightly differ from the values calculated by Romano et al. (2007; Table 1). Locomotion speed was calculated using ha and equation 2 for the trackways from the Chevenez—Combe Ronde and Courtedoux—Sur Combe Ronde sites, and were taken from the references shown to the left for the other trackways. Compare with Figure 5.38.

trackways are more difficult to characterize. Also, this confirms the essentially narrow-gauge of the trackways from the Courtedoux—Sur Combe Ronde site.

Interpretation of PTR and the [WAP/PL]-ratio

In a general way, the higher the PTR and the lower the [WAP/PL]-ratio are, the narrower the trackway gauge is. The lower the PTR and the higher the [WAP/PL]-ratio are, the wider the trackway gauge is.

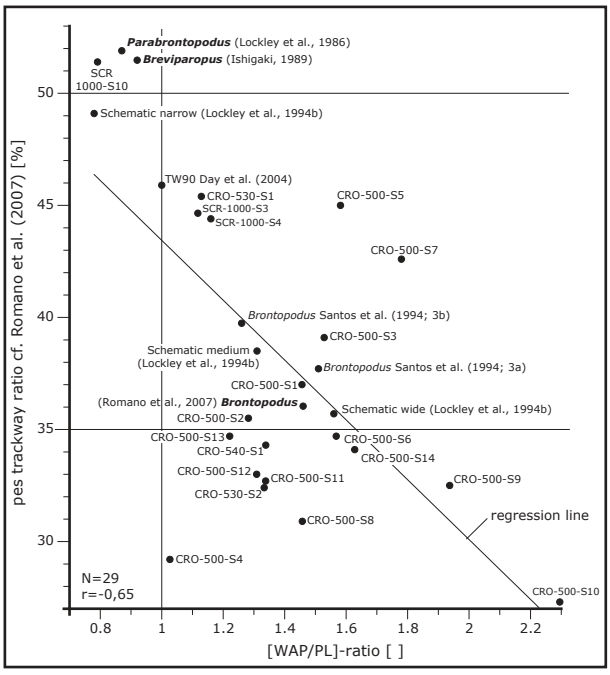


Fig. 5.38: Plot of the [WAP/PL]-ratio against the pes trackway ratio (PTR) of Romano et al. (2007). Provisional boundaries of Romano et al. (2007) between wide-gauge and medium-gauge (PTR=35%), and between medium-gauge and narrow-gauge (PTR=50%) are indicated. A [WAP/PL]-ratio smaller than 1 indicates that pes tracks intersect the trackway midline. Trackways clearly intersecting the trackway midline (i.e., *Parabrontopodus*, *Brontopodus*, and S10 from the main track level of Courtedoux—Sur Combe Ronde) fall into a field defined by a [WAP/PL]-ratio<1 and a PTR>50%. A few trackways of the Chevenez—Combe Ronde site are medium-gauge but most are wide-gauge, and the latter have a wider gauge than *Brontopodus birdi* from the Paluxy River Valley and wide-gauge trackways cf. *Brontopodus* from Portugal. Note the exceptional wide-gauge of the trackway S10 from the main track level of the Chevenez—Combe Ronde site. The trackway CRO-500-S4 plots outside because of doubtful trackway parameters (displaced tracks along a normal fault, Fig. 5.29). For the trackways, which are not from the Chevenez—Combe Ronde and the Courtedoux—Sur Combe Ronde site, the references are put in parentheses. Compare with Table 5.6.

If the [WAP/PL]-ratio equals one (i.e., PL = WAP), the pes tracks are likely to touch the trackway midline, and if the ratio is smaller than one, tracks intersect the trackway midline, which corresponds to the definition of narrow gauge. All three trackways with pes tracks intersecting the trackway midline (i.e., *Breviparopus*, *Parabrontopodus*, and SCR-1000-S10) clearly fall into the field defined by a pes trackway ratio smaller than 50%, and a [WAP/PL]-ratio smaller than one and accordingly these boundaries are meaningful. The schematic narrow-gauge trackway of Lockley et al. (1994b; Fig. 1) falls slightly out of this field, because the majority of the tracks touch but do not intersect the trackway midline.

At the bottom of Table 5.6, several assumptions are shown for the [WAP/PL]-ratio. If the width of the pes angulation pattern (WAP) is smaller than the pes length (i.e., [WAP/PL]-ratio<1), pes tracks will intersect the trackway midline and the trackway is narrow-gauge. If WAP equals PL (i.e., [WAP/PL]-ratio=1), the tracks are likely to touch the trackway midline, and if WAP is larger than PL (i.e., [WAP/PL]-ratio>1), the tracks will not touch the trackway midline anymore being located increasingly farther away from the trackway midline. A trackway with WAP twice as long as PL (i.e., [WAP/ PL]-ratio>2) can be considered as very wide.

This suggests that it is difficult to find a meaningful boundary between wide-gauge and medium-gauge trackways. Assuming that *Brontopodus* as the classical wide-gauge sauropod ichnogenus defined by "pes footprints often well away from the trackway midline" (Farlow et al., 1989), it would be reasonable to include *Brontopodus* in the wide-gauge field by increasing the provisional boundary of the PTR between wide-gauge and medium-gauge from 35% to 40%. A PTR of 40% would correspond to a [WAP/PL]-ratio of about 1,2. Trackways with a PTR between 40% and 50% and a [WAP/PL]-ratio between 1 and 1,2 would then make up the medium-gauge category, which could be considered as a transitional category between narrow-gauge and wide-gauge trackways. This medium-gauge category could characterize trackways neither clearly wide-gauge nor narrow-gauge.

Based on the [WAP/PL]-ratio it would also be meaningful to introduce a further category for very wide trackways, that is trackways with a WAP at least twice as large as PL, resulting in a [WAP/PL]-ratio higher than 2. Judging from Table 1 of Romano et al. (2007) such trackways likely have a PTR smaller than 30%.

Assets and drawbacks of PTR and [WAP/PL]-ratio

Romano et al. (2007) explained in detail, the benefits and disadvantages of the trackway ratio. It is assumed that the trackway ratio and the [WAP/PL]-ratio are subjected to about the same source of error, when measuring them from outline drawings. In particular because it is often not clearly stated whether a given outline drawing marks the interior or exterior track outline (as defined herein), and this can lead to considerable differences in trackway gauge because the exterior trackway outline more readily intersects the trackway midline than the interior track outline, especially in tracks with large displacement rims. Thus, these ratios should whenever possible be measured on the trackways themselves, and always by means of the internal trackway, which is supposed to represent most accurately the margin of the foot of the trackmaker.

Pes outward (or inward) rotation influences the estimation of trackway gauge. If it is assumed that the pes rotation does not depend on the general posture of the trackmaker, a trackway with a more pronounced outward pes rotation (Fig. 5.39C) appears narrower when compared to the same trackway with a less pronounced outward rotation of the pes (Figs. 5.39A & B). This would be expressed by a higher PTR, whilst the [WAP/PL]-ratio is virtually unaffected by the influence of the rotation. Accordingly, a wide-gauge trackway with a very high outward pes rotation will rather be described as medium-gauge using the PTR, while it is still clearly wide-gauge using the [WAP/PL]-ratio (Figs. 5.39A-C), and a medium-gauge trackway with a high outward pes rotation is likely to appear narrow-gauge using the PTR. On the other hand, the [WAP/PL]-ratio is virtually unaffected by the influence of outward (or inward) pes rotation, and may be more adequate for estimating trackway gauge for trackways with a pronounced pes rotation.

A disadvantage of both ratios may be to fix the reference points for measuring. For the [WAP/PL]-ratio this is the intersection of track length and width, and for the PTR the most internal and the most external points of the internal track outline.

It is suggested that systematically measuring the PTR in the field is more difficult and time-consuming than measuring the [WAP/PL]-ratio, especially when dealing with large amounts of data.

Another advantage of the [WAP/PL]-ratio is that, in a regular trackway, the width of the angulation pattern (WAP) can be calculated with Pythagoras' theorem from pace length and stride length (often indicated in published trackway data), if it is assumed that the width of the angulation pattern intersects the stride at a right angle and approximately at the midpoint of the stride.

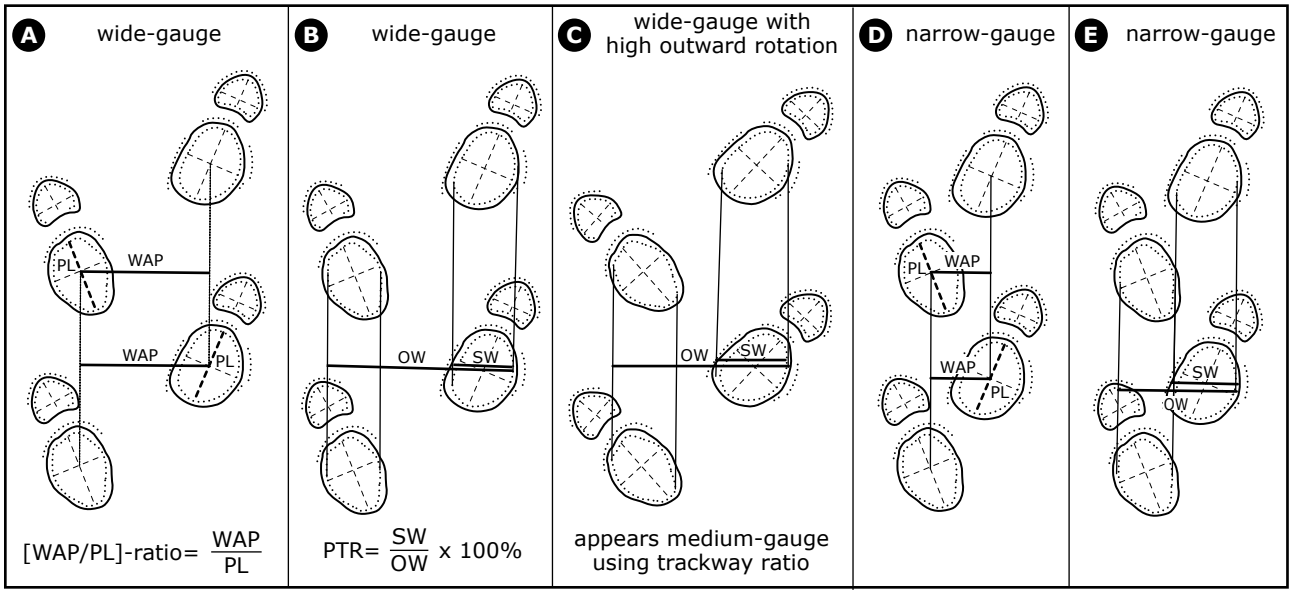


Fig. 5.39: Schematic sauropod trackways illustrating how the [WAP/PL]-ratio and the pes trackway ratio (PTR) of Romano et al. (2007) were measured and calculated. **A-C:** wide-gauge trackways. The trackway in C is the same as in A and B, but it features a higher outward rotation of the pes, which gives the trackway a narrower appearance. This is also expressed by the PTR-ratio, whilst the [WAP/ PL]-ratio is virtually unaffected by the outward (or inward) rotation of the tracks. **D-E:** Narrow-gauge trackways.

5.7.1.2 Review of selected Middle Jurassic to Early Cretaceous sauropod ichnogenera

Sauropod ichnogenera were reviewed by Farlow et al. (1989), Farlow (1992), Lockley et al. (1994b), Meyer et al. (1994), Dalla Vecchia & Tarlao (2000), Avanzini et al. (2003), Dalla Vecchia (2005), and by Wright (2005). Currently, only about a dozen of ichnogenera are attributed to sauropods, and thereof only a few are considered as valid. Hereafter, only selected Middle Jurassic to Early Cretaceous ichnogenera, generally considered to be valid by the majority of the authors cited above, are reviewed and compared with the tracks and trackways of the Combe Ronde site. Further, their trackway gauge is discussed using the pes trackway ratio and the [WAP/PL]-ratio.

Breviparopus *Dutuit & Ouazzou 1980*

This ichnogenus was introduced by Dutuit & Ouazzou (1980) based on trackways from Demnat, central High Atlas, Morocco, which are of Middle Jurassic to Late Kimmeridgian age. They stated, however, that they use this name for description only without any taxonomical value ("*par simple commodité de désignation, et sans que cette appellation ait une quelconque valeur taxonomique*"). Nonetheless, this ichnogenus is considered as valid by all authors cited above. Based on the detailed descriptions provided by Dutuit & Ouazzou (1980), the ichnogenus *Breviparopus* is characterized by:

- A clearly narrow-gauge trackway with pes tracks intersecting the trackway midline ("*l'axe de la piste passe par la partie postérieure des empreintes des pattes postérieures*").
- Manus tracks located further away from the trackway midline than pes tracks ("*l'empreinte du membre antérieur est davantage écartée de l'axe de la marche que celle du membre postérieur*").
- Manus tracks located in front of pes tracks and being (slightly) overprinted by the pes tracks ("*l'empreinte laissée par le membre postérieur suit immédiatement celle du membre antérieur, le bourrelet antérieur de la première et le bourrelet postérieur de la seconde se confondant*").
- Manus tracks with a semi-circular shape without evidence for digit impressions ("*l'empreinte de patte antérieure est sensiblement en demi-cercle (...). Aucun doigt n'est visible*").
- Pes tracks with a slightly oval shape with at least four digit impressions separated by small displacement rims, and evidence for claw marks within the overall displacement rim ("*l'empreinte de patte postérieure s'inscrit dans une figure géométrique intermédiaire entre le triangle à sommet postérieur et petit côté antérieur et l'ovale déformé s'effilant en arrière (...) on remarque aussi la présence d'encoches sur le bourrelet antérieur de l'empreinte postérieure, bourrelet qui témoigne ainsi de l'existence de griffes (...) au moins quatre doigts porteurs à sa patte postérieure. On constate en effet la présence de trois bourrelets interdigitaux*").
- A pronounced heteropody in the order of 1:3,6 ("*La surface d'empreinte postérieure est donc 3,6 fois plus grande que celle de l'empreinte antérieure*").

The pes trackway ratio larger than 50%, and the [WAP/PL]-ratio clearly smaller than 1 indicate that *Breviparopus* is, despite a comparatively pronounced outward pes rotation, characterized by a narrow-gauge trackway.

Brontopodus *Farlow, Pittmann & Hawthorne 1989*

This ichnogenus was defined by Farlow et al. (1989) based on the ichnospecies *B. birdi*, named in honor of the collector R.T. Bird, from the Paluxy River Valley near Glen Rose, Texas (Trinity Group, Aptian-Albian, Early Cretaceous), based on both track morphology and trackway parameters.

Farlow et al. (1989) stated that it is unknown, which features are diagnostic at the genus level and provided the following general diagnosis for *Brontopodus*:

"Sauropod ichnites of small to large size, known pes footprint length ranging 50 to over 100 cm. Manus footprint length and width about the same in well-preserved tracks; manus tracks clawless, somewhat U-shaped, with digit impressions I and V slightly separated from the impression of the conjoined digits II-IV. Pes tracks longer than broad, with large, laterally directed claw marks at digits I-III (diminishing in size from I to III), a small claw, nail, or callosity mark at digit IV, and a small callosity or pad mark at digit V; digit marks IV and V only seen in well-preserved footprints. Manus tracks often (usually?) rotated outward with respect to direction of travel. Manus track medial to a line through pes track long axis, such that manus track centres are somewhat closer to the trackway midline than pes track centres. Trackway broad, with left and right manus and pes footprints often well away from the trackway midline; trackway

width roughly 1-1,5 times pes track length. Outer limits of trackway defined by pes tracks. Manus-pes distance 0,5-1,2 times pes footprint length. Stride length roughly 2-5 times pes track length. Step angle generally 100-120°. Glenoacetabular length c. 3-4 times pes track length. Tail drag marks rare or absent."

This diagnosis is very detailed, because the holotype of *B. birdi* is probably one of the best-preserved sauropod trackways currently known (Lockley et al., 1994b; pers. obs.), and this has to be considered when comparing it with other less well-preserved specimens.

Despite the common assumption that *Brontopodus birdi* is characterized by a very wide-gauge, the pes trackway ratio and the [WAP/PL]-ratio instead characterize *Brontopodus birdi* as rather medium-gauge. This is also the case for other trackways attributed to the ichnogenus *Brontopodus*, for instance those figured in Santos et al. (1994; Fig. 3).

Parabrontopodus *Lockley, Farlow & Meyer 1994*

This ichnogenus was erected by Lockley et al. (1994b) on the basis of the type species *P. mcintoshi* from the Purgatoire Valley Dinosaur tracksite, U.S.A. (Unit B of the Morisson Formation, Late Jurassic). *Parabrontopodus* is considered as valid here, even though Wright (2005) stated that "Lockley et al. (1994b) did not note how *Parabrontopodus* could be differentiated from *Breviparopus*" and that for this reason "*Parabrontopodus* may be a junior synonym of *Breviparopus*".

Lockley et al. (1994b) defined the ichnogenus *Parabrontopodus* as: "Narrow sauropod trackway of medium to large size (footprint length about 50-90 cm), characterized by no space between trackway midline and inside margin of pes tracks. Pes footprint longer than wide with long axis rotated outward. Pes claw impressions, corresponding to digits I, II and III show strong outward rotation. Manus tracks semicircular and small in comparison with pes tracks (i.e., pronounced heteropody)".

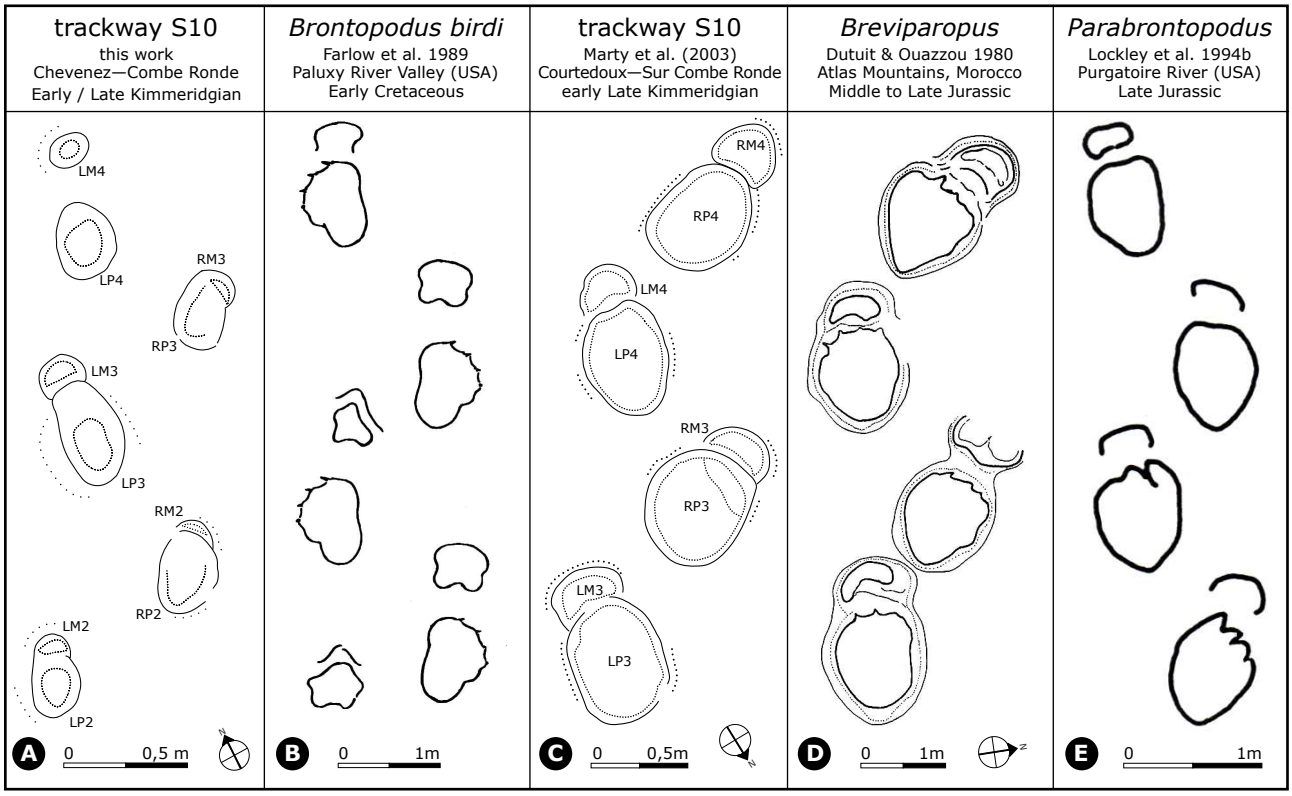


Fig. 5.40: Comparison of trackway S10 from the main track level of the Chevenez—Combe Ronde site and trackway S10 from the main track level of the Courtedoux—Sur Combe Ronde site with other Middle to Late Jurassic and Early Cretaceous sauropod ichnogenera. **A:** Trackway S10 from main track level of the Chevenez—Combe Ronde site. **B:** Redrawn after Farlow et al. (1989; Fig. 42.3, p. 374). **C:** Redrawn after Marty et al. (2003, Fig. 5, p. 212). **D**: Redrawn after Ishigaki (1989; Fig. 9.5, p. 85). **E:** Redrawn after Lockley et al. (1986; Fig. 7b, p. 1170).

This description also applies to the ichnospecies *P. mcintoshi*, and Lockley et al. (1994b) further noted that *P. mcintoshi* has a heteropody of about 1:4 or 1:5 in comparison with *Brontopodus birdi* (1:3).

A PTR larger than 50% and a [WAP/PL]-ratio clearly smaller than 1 confirm that the ichnogenus *Parabrontopodus* is characterized by a narrow-gauge, in about of the same order as *Breviparopus*.

Moreno & Benton (2005) re-described *Iguanodonichnus frenki* Casamiquela & Fasola 1968 from the Tithonian (Late Jurassic) of Chile and attributed it to *Parabrontopodus*, after that Sarjeant et al. (1998) recognized that this ichnogenus was sauropod. It is diagnosed as "Sauropod trackway of medium size (footprint length approximately 50–70 cm), characterized by small space between trackway midline and inside margin of pes tracks. Step angle less than 110°. Pes footprint longer than wide, with long axis rotated outward. Pes claw impression corresponding to digit I is long and narrow and follows a straight line parallel to the footprint axis. Claw impressions in digits II–IV are broad and much less developed than digit I". A third ichnospecies, *Parabrontopodus distercii*, is described from the Early Cretaceous of Soria, Spain (Meijide Fuentes et al., 2001).

5.7.1.3 Diagnosis of the Chevenez—Combe Ronde sauropod tracks and trackways

The similar pes and manus morphology of well-defined sauropod tracks at the Combe Ronde site suggest that all trackways belong to a single morphotype. This is supported by a good correlation between pes length and width, manus length and width (Fig. 5.8), and between the mean indices of pes and manus size (Fig. 5.10B). The latter suggest also a similar heteropody for all trackways. The degree of heteropody, as expressed by the (index of pes size / index of manus size)-ratio, does poorly correlate with the index of pes size (Fig. 5.10C) and can be explained by different degrees of overprinting and differences in manus posture. All this indicates that the sauropod foot shape did not change allometrically during ontogeny. The sauropod trackways of the Chevenez—Combe Ronde site can be diagnosed as:

- Pes tracks are always longer than wide, resulting in a subcircular to oval, elongate shape, and do not show great differences in depth across the track.
- Manus tracks are clearly longer than wide. Due to different degrees in inclination towards the anterior part of the tracks, their shape varies from a semicircular (D-shaped) shape to horseshoe shapes to more subcircular shapes. The subcircular shape exhibits small indentations in the middle (i.e., approximately at the position of the maximum width) of the track at both the interior and exterior side of the track, and this shape is considered as a more or less complete, impression of the manus, i.e., including the impression of the rear. The more semicircular to horseshoe shapes are explained by a more pronounced semi-digitigrade posture of the manus, and are not related to a different manus shape (anatomy). This type of manus track is typically slightly asymmetric and has a larger bulge at the interior than at the exterior side of the track.
- Manus tracks always lack evidence for claw impressions, notably at the position of digit I (the pollex), but some well-defined manus tracks show a crescent-shaped, convex-forward groove in the anterior part of the track (manual phalangeal reduction).
- Manus tracks not deformed by the pes are located typically in front of the pes tracks, with the centre of the manus tracks located on the extension of the pes long axis, and accordingly further away from the trackway midline than the pes tracks.
- Heteropody between pes and manus tracks is pronounced, being between 1:2 when the manus was impressed in a complete way and showing the imprint of the rear, and 1:3, when the manus was impressed in a more digitigrade way.
- Pes and manus tracks are rotated outwards, but the manus generally has a higher outward rotation than the pes.
- Pes and manus tracks are located well away from the trackway midline; pes and manus tracks never touch or intersect the trackway midline.
- Pes tracks are positioned slightly closer to the trackway midline than manus tracks.

5.7.1.4 Differential diagnosis

In the Late Jurassic, the vast majority of quadrupedal trackways are attributed to sauropods, even though quadrupedal trackways could also have been left by ornithischian dinosaurs such as basal ceratopsians, ankylosaurs, or most likely stegosaurs as indicated by the skeletal record (Currie & Padian,

1997; Meyer & Hunt, 1998; Weishampel et al., 2004). Poorly-preserved ornithischian trackways could possibly be misinterpreted as the trackways of smaller sauropods. For instance, trackways of *Deltapodus brodricki* Whyte & Romano 1994 from the Middle Jurassic of England were initially ascribed to sauropods (Whyte & Romano, 1994) but later attributed to a stegosaur (Whyte & Romano, 2001a; Whyte et al., 2007). Other Late Jurassic stegosaur tracks are described from the Morrison Formation (Lockley & Hunt, 1998) and from Poland (Gierliński & Sabath, 2002). Ankylosaur tracks are basically known from the Cretaceous only (review in McCrea et al., 2001), even though an isolated ankylosaur track was recently described from the Morrison Formation (Hups et al., 2008), and an ankylosaur trackway from Dorset (England) may be of Late Jurassic rather than Early Cretaceous age (Wright, 1996; Ensom, 2002).

However, the typical pes and manus morphology and alignment in typical quadrupedal trackways at the Combe Ronde site readily identifies them as sauropod tracks, and excludes ornithischian dinosaurs as probable trackmakers. For this reason, all quadrupedal trackways of the Chevenez—Combe Ronde site are attributed to sauropods. Hereafter, the general description of the sauropod tracks and trackways of the Chevenez—Combe Ronde site is compared with the above cited diagnoses of sauropod ichnogenera, and additionally also with the tracks and trackways from the Courtedoux—Sur Combe Ronde site, described in Marty et al. (2003).

***Chevenez—Combe Ronde trackways vs.* Breviparopus**

The sauropod trackways from the Combe Ronde tracksite are similar to *Breviparopus* because pes tracks are longer than wide, oval in shape, and generally rotated outward; manus tracks are commonly located in front of the pes and partially overprinted; manus tracks are often semicircular in shape and do not show evidence of claw impressions. In addition, manus tracks are located further away from the trackway midline than pes tracks.

The Combe Ronde trackways differ from *Breviparopus* because the trackways are decidedly wider and the pes tracks do never intersect the trackway midline, because the pes tracks show no evidence for impressions of digits and claws, and because the heteropody between pes and manus is smaller.

The preservation of the trackway, which was named by Dutuit & Ouazzou (1980) *Breviparopus taghbaloutensis*, is similar to that of the trackways of the Combe Ronde site: the tracks are not very deep and surrounded by displacement rims. However, these trackways were found in sandstone of a fluviatile setting (Dutuit & Ouazzou, 1980).

***Chevenez—Combe Ronde trackways vs.* Brontopodus**

The Combe Ronde sauropod trackways are similar to *Brontopodus* because the trackways are medium-gauge to wide-gauge (pes tracks well away from the trackway midline), pes tracks are longer than wide, manus tracks are clawless, manus length and width is about the same in well-defined tracks, and well-defined manus tracks show some evidence for digit impressions I and IV slightly separated from the digits II-IV, which are probably conjoined in the anterior groove. Furthermore, manus tracks are usually rotated outward, and there is a similar heteropody between the pes and the manus (1:2 to 1:3).

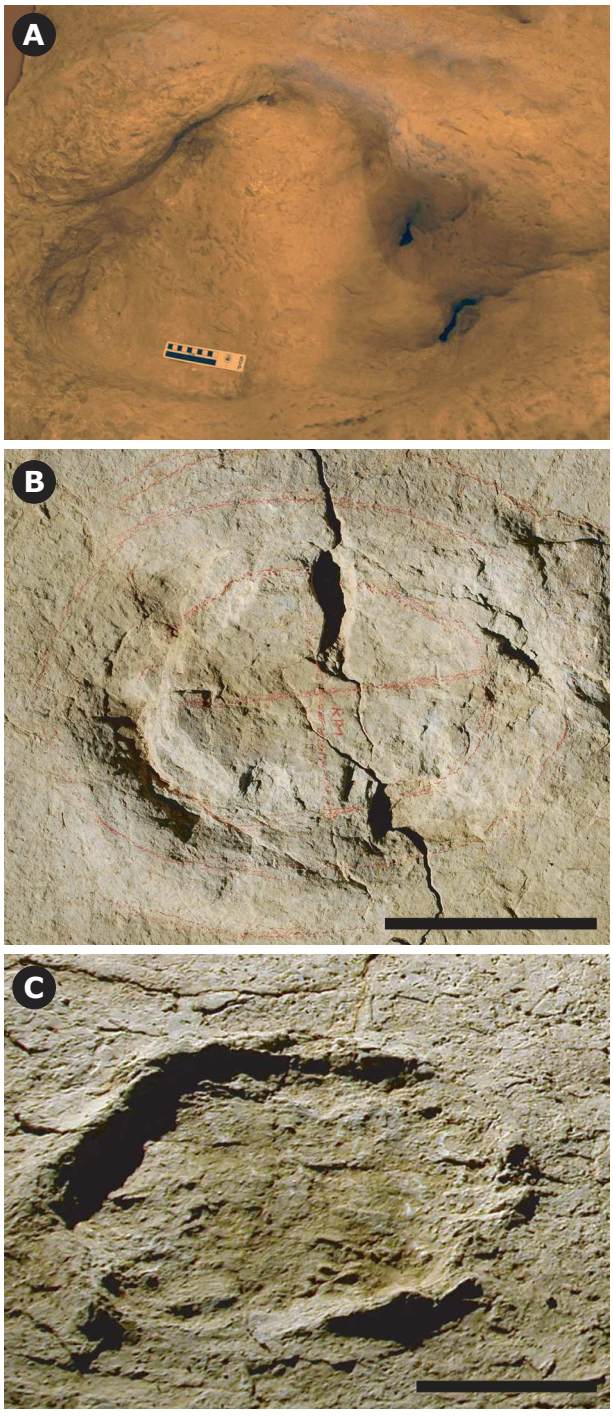
They differ from *Brontopodus* because pes tracks are clawless and show no evidence for digit impressions, because pes tracks are clearly closer to the trackway midline than manus tracks, and because the outer limit of the trackways is generally defined by the manus tracks.

Even though the *Brontopodus* trackways from the Paluxy River Valley (Texas) were left in a nearshore carbonate setting (e.g., Farlow, 1987; Pittman, 1989, 1990, 1992) similar to the trackways from the Combe Ronde site, they still differ regarding the general preservation. The trackways of the Combe Ronde site were left in thin layers of carbonate mud or biolaminites, which resulted in rather shallow tracks, generally surrounded by displacement rims. On the other hand, it is suggested that the holotype of *B. birdi* was left in a water-unsaturated to water-saturated thick layer of carbonate mud with a high plasticity, which resulted in the formation of very deep tracks without displacement rims, facilitating the preservation of anatomical details of the foot including the claws (pers. obs., Fig. 5.41). Thereby, the presence of claw impressions may also have a functional reason (see also chap. 5.7.1.6).

Chevenez—Combe Ronde trackways vs. Parabrontopodus

The sauropod trackways from the Combe Ronde tracksite are similar to *Parabrontopodus* because pes tracks are longer than wide and generally rotated outward, and because manus tracks are often (even though not always) semicircular and generally rotated outward.

They differ from *Parabrontopodus* because they are clearly wider, and pes tracks never intersect the trackway midline. Pes tracks show no evidence for claw impressions, and heteropody between pes and manus is smaller for well-defined, undeformed manus tracks.



The *Parabrontopodus* holotype and paratypes from the Purgatoire Valley Dinosaur tracksite were described from high-energy micritic shoreface limestones with interbedded lacustrine shales, which belong to the Unit B of the Morrison Formation (Lockley et al., 1986; Prince & Lockley, 1989). Judging from illustrations in Lockley et al. (1986, 1994b, 1997), the Purgatoire site exhibits moderately deep and well-defined tracks without pronounced displacement rims, on which the ichnogenus *Parabrontopodus* was defined, and shallower, poorly-defined tracks with displacement rims. The preservation style of the deeper tracks is similar to that of the *Brontopodus* trackways from the Paluxy River Valley. Actually, because they are less well preserved, Bird decided to extract those from the Paluxy River bed instead for display at the American Museum of Natural History (Bird, 1941, 1985). The preservation style of both the deeper and shallower tracks of the Purgatoire site are different from the trackways described here, but the shallower tracks with displacement rims are very similar to the trackways of the Courtedoux—Sur Combe Ronde site (Marty et al., 2003). Such trackways are best explained to have been left in a thin layer of moist to water-saturated mud on top of a consolidated layer (see also chap. 3, Fig. 3.5E).

Fig. 5.41: Comparison of different, typical preservation styles of sauropod tracks reflecting different thickness of the layer susceptible for track recording, and differences in plasticity and yield strength of the substrate. **A:** A well-defined, left pes track with claw impressions from a cast of the holotype of *Brontopodus birdi* Farlow et al. 1989 at display in the Paluxy River State Park (Glen Rose, Texas, U.S.A.). Note the impressions of claws and the well-expressed depth profile within the track. **B:** A typical right pes track (S9-RP1), surrounded by a large displacement rim, from the main track level of the Combe Ronde site. Note that even though the track still carries a part of its fill, there is clearly no evidence for claw marks within the displacement rim. **C:** A typical pes track from the main track level of the Courtedoux—Sur Combe Ronde site. Note the shallowness of the track, small but accentuated displacement rims and absence of impressions of digits and claws. Direction of progression in A and B is from left to right, in C from right to left; scale bar is 10 cm in A, 20 cm in B and C; in A artificial illumination from the right; in B rising sunlight from the left, photo by B. Migy (SAP); in C artificial illumination from upper left, photo taken at night by B. Meyer-Cesta (PAL A16).

Chevenez—Combe Ronde vs. Courtedoux—Sur Combe Ronde

Marty et al. (2003) provided a general diagnosis for the trackways of the main track level at the Courtedoux—Sur Combe Ronde site, mainly based on the best-defined trackway S10 (Fig. 5.42). Their diagnosis is detailed here as:

- Large oval pes track longer than wide.
- Semicircular convex-forward manus track wider than long.
- Pes and manus without evidence of claw impressions.
- All trackways are characterized by a narrow-gauge with little or no space between the inside of the pes tracks, or pes tracks intersecting the trackway midline.
- Pronounced heteropody on the order of 1:4.
- Pes and manus rotated outward. Outward manus rotation is generally higher than for the pes, and the centres of the manus tracks are placed farther away from the trackway midline than the centres of the pes tracks.

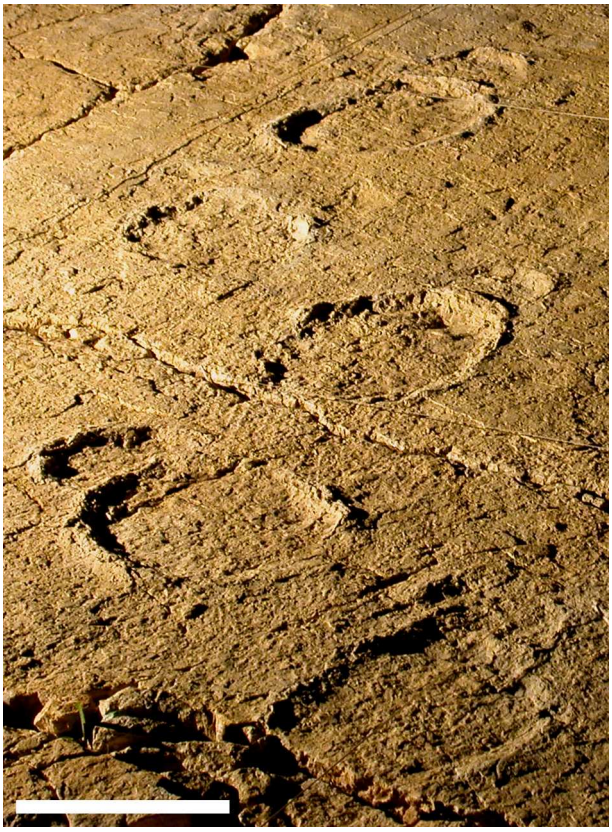


Fig. 5.42: Courtedoux—Sur Combe Ronde tracksite, main track level, narrow-gauge trackway S10. Pes tracks clearly intersect trackway midline. Scale bar is approximately 40 cm. Photo by B. Meyer-Cesta (PAL A16), taken at night with artificial illumination from the left.

Based on the narrow-gauge, strong heteropody and the outwardly rotated manus, Marty et al. (2003) attributed these trackways to the ichnogenus *Parabrontopodus*, without providing further differential diagnosis with the other ichnogenera reviewed herein, notably the other narrow-gauge ichnogenus *Breviparopus*. The pes trackway ratio and the [WAP/PL]-ratio confirm that the Courtedoux—Sur Combe Ronde trackways are generally narrow, but only trackway S10 is clearly narrow-gauge, trackways S3 and S4 fall into the medium-gauge field (Fig. 5.38).

The sauropod trackways from the Chevenez—Combe Ronde tracksite are similar to those of the Courtedoux—Sur Combe Ronde site because the pes tracks are longer than wide, oval in shape, and generally rotated outward. Manus tracks are wider than long, often (even though not always) semicircular convex forward, and rotated outwards. Manus tracks generally show a higher outward rotation than the pes tracks, neither pes nor manus show evidence for claw impressions, and the centres of the manus tracks are placed farther away from the trackway midline than the centres of the pes tracks.

They differ from the Courtedoux—Sur Combe Ronde trackways because pes tracks never intersect the trackway midline, manus length and width is about the same in well-defined tracks, well-defined manus tracks show some evidence for digit impressions I and V slightly separated from digit impressions II-III, and because the heteropody between pes and manus is clearly smaller for well-defined, undeformed manus tracks.

The majority of the Chevenez—Combe Ronde trackways are wider than those of the Courtedoux—Sur Combe Ronde site, and none of the trackways are narrow gauge. However, some trackways of the Courtedoux—Sur Combe Ronde site (i.e., S3 and S4 of the main track level) have a pes trackway ratio smaller than 50%, and a [WAP/PL]-ratio higher than 1, and these two trackways have a similar gauge to the trackway of the Chevenez—Combe Ronde site with the highest pes trackway ratio and the lowest [WAP/PL]-ratio, which is trackway S1 of level 530 (Fig. 5.38). However, this trackway has the shallowest and most poorly-defined tracks of all trackways and is not considered to be representative of the Chevenez—Combe Ronde samples.

The preservation style of the trackways from the main track level at the Courtedoux—Sur Combe Ronde site differs slightly from those of the Chevenez—Combe Ronde site. Even though the Courtedoux—Sur Combe Ronde tracks are commonly surrounded by small displacement rims, they are rather shallow and were most probably left in a thin layer of moist to water-unsaturated mud on top of a consolidated layer (Fig. 5.41C). The trackways of the Chevenez—Combe Ronde site, on the other hand, were either left in a rather thick layer of moist to water-unsaturated mud or microbial mat and are rather deep and surrounded by large displacement rims, or they were left in almost dry sediment and are very shallow without displacement rims.

5.7.1.5 Ichnotaxonomical attribution

The comparisons of the Chevenez—Combe Ronde trackways with the different sauropod ichnogenera and the trackways from the Courtedoux—Sur Combe Ronde site suggest that track morphology is affected by the sediment properties at the time of track formation. By comparison of the very deep *Brontopodus* tracks from Texas with the less deep tracks from the Chevenez—Combe Ronde site and the shallow tracks from the Courtedoux—Sur Combe Ronde site (Fig. 5.41), it is evident that the sediment consistency had an influence on track morphology, and maybe also on the kinematics of the trackmaker and hence trackway configuration (track rotation, trackway gauge).

It is concluded that the trackways of the Chevenez—Combe Ronde site share the characteristics of several of the above described sauropod trackways. The general morphology of the pes and manus tracks is similar to the narrow-gauge ichnogenera *Breviparopus* and *Parabrontopodus* and also to the trackways of the Courtedoux—Sur Combe Ronde site, but the trackways from the Chevenez—Combe Ronde site differ regarding trackway gauge and heteropody. For the latter reasons the trackways of the Chevenez—Combe Ronde site are most similar to the ichnogenus *Brontopodus*, despite their different preservation style. They are tentatively assigned to the ichnogenus *Brontopodus*, but better-defined tracks with the impressions of the digits and/or claws are required for confirmation.

5.7.1.6 Trackmaker identification

Generally, it is not possible to identify the trackmaker species from any given track, unless the animal is preserved at the end of its fossil trackway, similarly to *Mesolimulus* at the end of its trackway named *Kouphichnium* (e.g., Goldring & Seilacher, 1971), or unless tracks and trackmakers are found in close stratigraphic proximity one to each other (e.g., Diedrich, 2002c; Hunt, 2002; Voigt et al., 2007). If this is not the case, the trackmaker may generally at best be identified at the family level, as suggested by Rainforth (2005) on a study of the well-preserved vertebrate tracks of the Newark Supergroup (Early Jurassic).

When trying to identify possible trackmakers, it has further to be considered that many dinosaurs may be known from tracks only, because their skeletal remains were not found (as yet), and vice versa. Moreover, it is also difficult to relate body fossils to tracks, because the soft tissues (“pads”) around the bones are generally not preserved (Farlow & Chapman, 1997; Lockley, 1998a). The identification of trackmakers is further complicated by vertebrate ichnotaxonomy, which lacks a standardized theoretical basis, and which suffers from inclusion of extrinsic factors such as the substrate properties or the behaviour of the trackmaker (e.g., Bertling et al., 2006; Bertling, 2007). Here, the purpose is to provide a short review of skeletal material found on, or in proximity to, the Jura carbonate platform and to propose some possible trackmakers for the sauropod trackways identified at the Chevenez—Combe Ronde tracksite.

Based on trackway gauge

Lockley et al. (1994e) stated that narrow- and wide-gauge sauropod trackways are consistently associated with particular stratigraphic units, i.e., narrow-gauge trackways are more common in the Jurassic than in the Cretaceous, and wide-gauge trackways in the Cretaceous than the Jurassic. Lockley & Meyer (2000, p. 169) suggested that the change to predominantly wide-gauge trackways may have occurred somewhere between the Kimmeridgian and the Tithonian. Or as Wilson & Carrano (1999) pointed out “wide-gauge trackways were the products of wide-gauge sauropods, rather than narrow-gauge sauropods of different sizes or engaged in different behaviours”. Lockley (1999, 2001) and Wilson & Carrano (1999) suggested that

more derived sauropods like the titanosaurs were the trackmakers of wide-gauge trackways, also because titanosauriform trackmakers are not known from the skeletal record before the Late Jurassic (e.g., Upchurch, 1995; Upchurch et al., 2004).

Subsequently, wide-gauge trackways were generally attributed to more derived sauropods (e.g., Day et al., 2002a, 2004; Lockley et al., 2002a, 2002b; Henderson, 2002, 2006b), whilst narrow-gauge trackways were attributed to more "basal" sauropods, basal macronarians, or diplodocoidea *sensu* Wilson & Sereno (1998) (e.g., Day et al., 2002a, 2004; Marty et al., 2003; Le Loeuff et al., 2006). Accordingly, the wide-gauge trackways of the Chevenez—Combe Ronde tracksite could have been left by the more derived and robust "brachiosaurid" or "titanosaurid" dinosaurs. These are characterized by forelimbs longer than the hindlimbs, a shorter tail, and a larger head when compared to more "basal" sauropods, basal macronarians, or Diplodocoidea *sensu* Wilson & Sereno (1998). The latter are characterized by a laterally compressed body and/or feet planted near the sagittal plane, by large hindlimbs longer than forelimbs, a long tail, and a short neck (e.g., Wilson & Sereno, 1998; Lockley, 1999, 2001). Because the Diplodocoidea were identified as possible trackmakers of the narrow-gauge trackways at the slightly younger Courtedoux—Sur Combe Ronde site (Marty et al., 2003), the identification of sauropod trackmakers based on trackway gauge would indicate the presence of both more derived and more "basal" sauropods in very close temporal relationship on the Jura carbonate platform.

Marty et al. (2003) suggested that the occurrence of narrow-gauge trackways attributed to the ichnogenus *Parabrontopodus* in the early Late Kimmeridgian of the Courtedoux—Sur Combe Ronde site was an important pinpoint, because it is the first record of *Parabrontopodus* trackways on the Jura carbonate platform, and one of the youngest well-dated occurrences of *Parabrontopodus*. However, on the Jura carbonate platform narrow-gauge sauropod trackways, attributed to the ichnogenus *Parabrontopodus,* have meanwhile also been reported from the Tithonian at Coisia, France (Le Loeuff, 2005, 2006), and the Middle Berriasian at Gex/Echenevez, France (Charollais et al., 2008). Other new occurrences of narrow-gauge sauropod trackways come from the Late Tithonian of the Adriatic carbonate platform of Croatia (Mezga et al., 2007) and from the Tithonian of Chile (Moreno & Benton, 2005). Finally, "relatively narrow-gauge medium-gauge" trackways have also been described from the Early Cretaceous of the Adriatic-Dinaric carbonate platform and were named *Titanosaurimanus nana* (Dalla Vecchia & Tarlao, 2002).

Regarding the Jura carbonate platform, there is no evidence that tracksites with wide-gauge trackways are younger than those with narrow-gauge trackways. The wide-gauge trackways of the Chevenez—Combe Ronde site are even older than the narrow-gauge trackways of the Courtedoux—Sur Combe Ronde site. Furthermore, a recent enlargement of the Courtedoux—Sur Combe Ronde site revealed a very wide-gauge trackway on the same level as narrow-gauge trackways (pers. obs.). This would indicate that both groups of dinosaurs were present in the same environment, at the same time. Similar evidence led Day et al. (2002a) to suggest that sauropods "may have formed multispecies herds as part of defence against predation and/or as a by-product of shared migration routes". However, this is nothing more than speculation, because even at large sites such as the Ardley quarry described by Day et al. (2002, 2004) the trackway evidence is insufficient to confirm such a scenario. Day et al. (2002a) further assumed that the wide-gauge trackways of the Ardley quarry are direct evidence that titanosaurs had diverged from other sauropods by the Bathonian, and this is supported by the occurrence of wide-gauge trackways in the Middle Jurassic of Portugal (Santos et al., 1994, 2004). This is contrary to what would be expected by the skeletal record, which places the divergence between brachiosaurs and titanosaurs in the Late Jurassic (Upchurch, 1995).

Consequently, the general assumption that wide-gauge trackways were more frequent in the Cretaceous and narrow-gauge trackways in the Jurassic should be questioned. This was recently done by Wright (2005) by plotting tracksites by stage, and by Romano et al. (2007) based on the calculation of pes trackway ratios for sauropod trackways ranging in age from Early Jurassic to Late Cretaceous. The latter suggested a more complex temporal distribution of sauropod trackways with respect to trackway gauge than previously suggested. This may be related to a different temporal distribution of the trackmakers than shown by the skeletal record (e.g., Day et al., 2002a). However, if it is assumed that narrow-gauge and wide-gauge trackways are not related to sauropods with anatomical differences in posture, it could simply be the result of locomotion style and/or ontogeny (e.g., Lockley et al., 2002a; Wright, 2005). Other reasons like sexual dimorphism can also not be excluded.

Based on synapomorphies

Sauropod pes and manus are characterized by a number of synapomorphies such as presence and number of claws that could be recognized in tracks and used for their classification (Salgado et al., 1997; Wilson & Sereno, 1998; Wilson & Carrano, 1999; Carrano & Wilson, 2001; Bonnan, 2003, 2005; Wilson, 2005). Lockley et al. (1994b) stated that "recent discoveries also indicate that sauropod pes tracks reveal different digit impression patterns", and that "well-preserved sauropod tracks that lack well-defined pes claw impressions reflect feet with small claws or claws that are more completely enclosed in flesh than those that leave pronounced claw impressions". Dalla Vecchia & Tarlao (2000) grouped sauropod ichnogenera into three groups based on manual print morphology and on the configuration of digit I. However, the correlation of pes and manus synapomorphies with track morphology is insufficiently understood in order to facilitate their consistent application in the classification of sauropod tracks.

The sauropod trackways at the Combe Ronde site neither exhibit claw impressions on pes nor manus tracks. Because in brachiosaurid or titanosaurid sauropods the ungual claw on digit I is strongly reduced or absent (Bonnan, 2003; Wright, 2005), the lack of a claw mark on digit I of the manus prints of the Combe Ronde site could thus be further evidence for a brachiosaurid or titanosaurid trackmaker. This is also suggested by the best-defined, semicircular manus tracks (those of trackways S1 of level 540). These are similar to the manus tracks of *Brontopodus birdi* and suggest that digits II, III, and IV were bound together in a pad, which formed the deep anterior crescent-shaped groove of the tracks. Digits I and V were probably slightly offset distally from the three central digits and formed the two lateral bulges of the tracks. Digit I, the pollex, left a more pronounced imprint than digit IV, but there is no evidence for an impression of a stout ungual or a claw mark on digit I.

However, the presence or absence of claws may be a preservational artefact (Wright, 2005), and could also be related to the behaviour of the trackmaker, which may have used the claws in different ways (e.g., Upchurch, 1994), and maybe also depending on substrate consistency. Pittman & Gillette (1989), based on observations of trackways from the Early Cretaceous of Arkansas, suggested that "the claws were "wrapped" around the lateral margin of the foot, and on softer substrates the claws were often extended forward, probably to provide better traction", and Gallup (1989) suggested that the trackmaker of the deep Paluxy River *Brontopodus* trackways may have been choosing carefully where to put its next step and in doing that the claws may have improved the animals' footing providing a "snowshoe" effect. Furthermore, Lockley et al. (2002a) noted that the lack of claw impressions might suggest that any claws may have been enclosed by flesh (fleshy pad) or held in such a way that their sharp distal ends did not leave any impressions. Such a functional scenario implies that shallow tracks left on a rather stable surface would not show claw impressions, whilst tracks left in unstable, and slippery sediment would show claw impressions (Fig. 5.41).

In favour of a functional scenario or preservational artefact may be the fact that the narrow-gauge trackways of the Courtedoux—Sur Combe Ronde site do not exhibit any evidence of claws on the pes and they also do not show a claw mark on digit I of the manus, as would be expected for "diplodocids" (e.g., Bonnan, 2005; Wright, 2005). Interestingly, new excavations at the Courtedoux—Sur Combe Ronde site and in coeval layers at the Courtedoux—Tchâfouè tracksite revealed several trackways with well-defined digit and claw impressions on the pes tracks, but so far not the manus tracks. The ongoing analysis of these trackways will show whether a certain number of pes claw marks is systematically associated with wide-gauge or narrow-gauge trackways, and whether their presence is a preservational artefact or related to a functional reason.

Wright (2005) suggested that crescent-shaped manus impressions could have been left by neosauropods (diplodocids), which would fit well with the narrow-gauge trackways of the Sur Combe Ronde site. However, at the Chevenez—Combe Ronde site, both crescent-shaped and semicircular-shaped manus impressions were found. This seems to be related to differences in the general posture of the manus, which may have varied from semi-digitigrade to more plantigrade depending on the behaviour of the trackmaker, resulting in differences in the shape of the manus tracks.

Based on the sauropod skeletal record of the Jura carbonate platform

The fossil skeletal record of sauropods on the Jura carbonate platform is scarce. At least, *Cetiosauriscus greppini* Von Huene 1927 is likely to be one of the trackmakers because it has been described from almost

coeval strata of the Early Kimmeridgian of Moutier (Switzerland), in relative close proximity to the Combe Ronde site (Greppin, 1870; Von Huene, 1922, 1927; Meyer & Thüring, 2003a). However, *C. greppini* is considered a *nomen dubium* (Glut, 1994; Schwarz et al., 2007a) and is currently under re-description by Schwarz et al., including phylogenetic analyses.

Sauropod bones are also known from the Oxfordian of Damparis, France (Lapparent, 1943). These were attributed to *Bothriospondylus madagascariensis* (Buffetaut, 1988), re-examined by Moine (1999), and assigned to *Brachiosaurus* by Wilson (2002, 2005), indicating that "brachiosaurid" sauropods were present as well on the Jura carbonate platform during the Late Jurassic.

5.7.1.7 Locomotion capabilities

Sauropodomorph dinosaurs came from bipedal ancestors but reverted to quadrupedalism (e.g., Carrano, 2005; Curry-Rogers & Wilson, 2005; Tidwell & Carpenter, 2005; Wilson, 2005). Their terrestrial locomotion capabilities were not recognized for a long time (Coombs, 1975) but are today evident from the morphology of the sauropod limbs, axial bones (e.g., Bakker, 1971; Coombs, 1975; Wilson, 2005), and pneumaticity of the neck (Wedel, 2003; Schwarz et al., 2007b). In addition, trackways also suggest that sauropods had a fully erect stance. Surprisingly, greater controversy is now again surrounding their swimming than their terrestrial capabilities because of manus-only trackways, which are further discussed below.

At the Chevenez—Combe Ronde site, pes tracks are generally characterized by a rather flat track bottom without pronounced changes in depth. This indicates that the trackmakers put the hindfeet in a plantigrade way and that the weight was equally distributed over the pes, as was also suggested from the study of the cross-sections in Chapter 4. However, sauropod tracks are often characterized by a conspicuous topography (Lockley, et al., 1986; Farlow et al., 1989; Fig. 5.41A), and the flat topography of the bottom of the Combe Ronde tracks may be related to particular sediment properties, which did not permit to record a differential weight distribution of the foot.

A semi-digitigrade to digitigrade posture is suggested for the manus because of the inclination of the track bottom towards the anterior part and a crescent-shaped groove in the anterior part of the track, which is surrounded by a displacement rim.

Differences in trackway configuration

Even though sauropod dinosaurs were probably restricted to walking gaits (e.g., Bakker, 1986; Alexander, 1985, 1989; Thulborn, 1989; Christiansen, 1997a) the movements of four limbs can be combined in many different ways (Hutchinson, 2005, 2006). This is expressed at the Combe Ronde site by many different sauropod trackway configurations and patterns observed.

On the main track level, different configurations of quadrupedal trackways can be observed between parallel trackways with similar locomotion speed and tracks of very similar morphology, size, and track preservation (Fig. 5.12). The most pronounced differences concern the relative position of pes and manus tracks and the different degrees of their outward rotation. The variation in heteropody depends on differences in the posture of the manus. There is no evidence that these different trackway configurations are related to trackway gauge. The wide-gauge trackways from the Chevenez—Combe Ronde site show similar differences in the relative position of pes and manus tracks and their outward rotation as the narrow-gauge trackways from the Courtedoux—Sur Combe Ronde site.

On the main track level of the Combe Ronde site, the trackways of the two tiny animals exhibit the most irregular configuration (i.e., extreme outward rotation, exterior position of the manus). This could suggest that trackway configuration is related to ontogeny because smaller animals were moving in a different way than larger animals. However, in the present case these irregular trackways are rather related to a particular behaviour (see also chap. 5.7.6.5). The common very exterior position of the manus tracks coupled with an extreme outward rotation indicates higher latero-medial mobility of sauropod forelimbs than previously suggested (e.g., Christiansen, 1997a, b).

It is suggested that differences in the relative position of pes and manus and the different degrees of their outward rotation are generally related to the behaviour of the trackmakers, for example standing still and accelerating (irregular progression), turning of the neck to the left or the right, or presence of another animal nearby. The latter reason could explain the different configurations between the parallel trackways of sauropod group 1 (S3-S11) and group 2 (S12-S14), suggested to cross each other in excavation area 2 (see also chap. 5.7.6.5). Finally, they may also be related to substrate properties and locomotion speed, or they

may be an expression of an individual walking style since not every animal of a species moves in precisely the same way.

The wide range of different trackway configurations observed at the Chevenez—Combe Ronde tracksite appears to be inherent to the locomotion capabilities of their sauropod trackmakers.

Differences in trackway gauge

Even though all trackways of the Combe Ronde site are medium-gauge to wide-gauge, they are subjected to a considerable variation in trackway gauge (Fig. 5.38).

The width of the pes angulation pattern (WAP) and the [WAP/PL]-ratio are both poorly correlated with track size (Figs. 5.43C & D), and the variability in trackway gauge also poorly correlates with relative stride length and locomotion speed, for both the trackways from the Combe Ronde site and the three trackways from the Sur Combe Ronde site (Figs. 5.43E & F). This indicates that these differences are neither related to ontogeny nor to locomotion speed. The variability in trackway gauge may thus be related to individual walking style and/or behaviour, which can be related to substrate properties or other extrinsic factors.

Farlow (1992) suggested that sauropods may have created different trackway gauges when walking across substrates of different consistency. At the Chevenez—Combe Ronde site the trackway S1 of level 530 with the shallowest tracks of all trackways is the narrowest trackway, similar to the narrow-gauge trackways of the Courtedoux—Sur Combe Ronde site and the trackway of Day et al. (2004) (Fig. 5.38). The pes-only trackway S2 of the same level 530 is the trackway with the deepest tracks (underprints) of the Chevenez—Combe Ronde site, and this trackway is amongst the wider trackways. A similar trend can be observed on the main track level, where the two shallow trackways (i.e., S1 and S2) are amongst the rarer medium-gauge trackways, whilst the trackways with the deeper tracks tend to have a wider gauge (Fig. 5.38). This suggests that pronounced differences in substrate resulted in differences in trackway gauge, but that this did not affect the general wide-gauge or narrow-gauge appearance of the trackways of a given trackmaker. Thus, it can not be excluded that the exceptional very wide-gauge of trackway S10 from the main track level of the Chevenez—Combe Ronde site is an expression of a wider posture related to another trackmaker species, or even to sexual dimorphism. The latter has recently been suggested for *Camarasaurus*, based on long bone histology (Klein & Sander, 2008).

Differences in trackway patterns

Pes-only or pes-dominated (e.g., Meyer, 1990; Santos et al., 1992; Fischer, 1998), and manus-only or manus-dominated trackways are commonly described from sauropod tracksites. Even though occasional bipedalism has been suggested for titanosaurs (for reviews see Wilson & Carrano, 1999; Upchurch et al., 2004), the apparent "bipedalism" of sauropods as expressed by pes-only trackways can easily be explained by overprinting of the relatively small manus track by the subsequent considerably larger pes track. This is not possible in the case of manus-only trackways, which are the reason for the debate surrounding the swimming capabilities of sauropods.

In trackways of quadrupedal tetrapods the degree of overprinting generally depends on locomotion speed and, in the case of overstepping, a pes track may even be located in front of its corresponding manus track (e.g., Peabody, 1959; Haubold, 1971). Regular quadrupedal sauropod trackways with a normal configuration and undeformed manus tracks are thus likely to form at lower speeds and pes-only trackways, or trackways in which the pes overprints the manus, at higher speed. This can also be observed with elephants, which tend to overprint the manus at higher speeds, even though they can also lift the manus and put the pes at virtually the same position whilst almost standing still (pers. obs.).

Figure 5.50 shows the distribution of relative (pes) stride length, mean pes length, locomotion speed, orientation, and pattern of the trackways of the main track level. There is a tendency towards quadrupedal or at least pes-dominated trackways at higher locomotion speeds, whilst pes-only trackways seem to be associated with lower locomotion speeds. This is further supported by trackway S6, showing a transition from a pes-only to a quadrupedal pattern, coupled with a pronounced increase in locomotion speed. This is in contradiction with the above made assumption that overprinting occurs at higher locomotion speeds.

However, differences in trackway pattern may also be related to the substrate consistency and a special behaviour related to it (Marty et al., 2006b). Animals

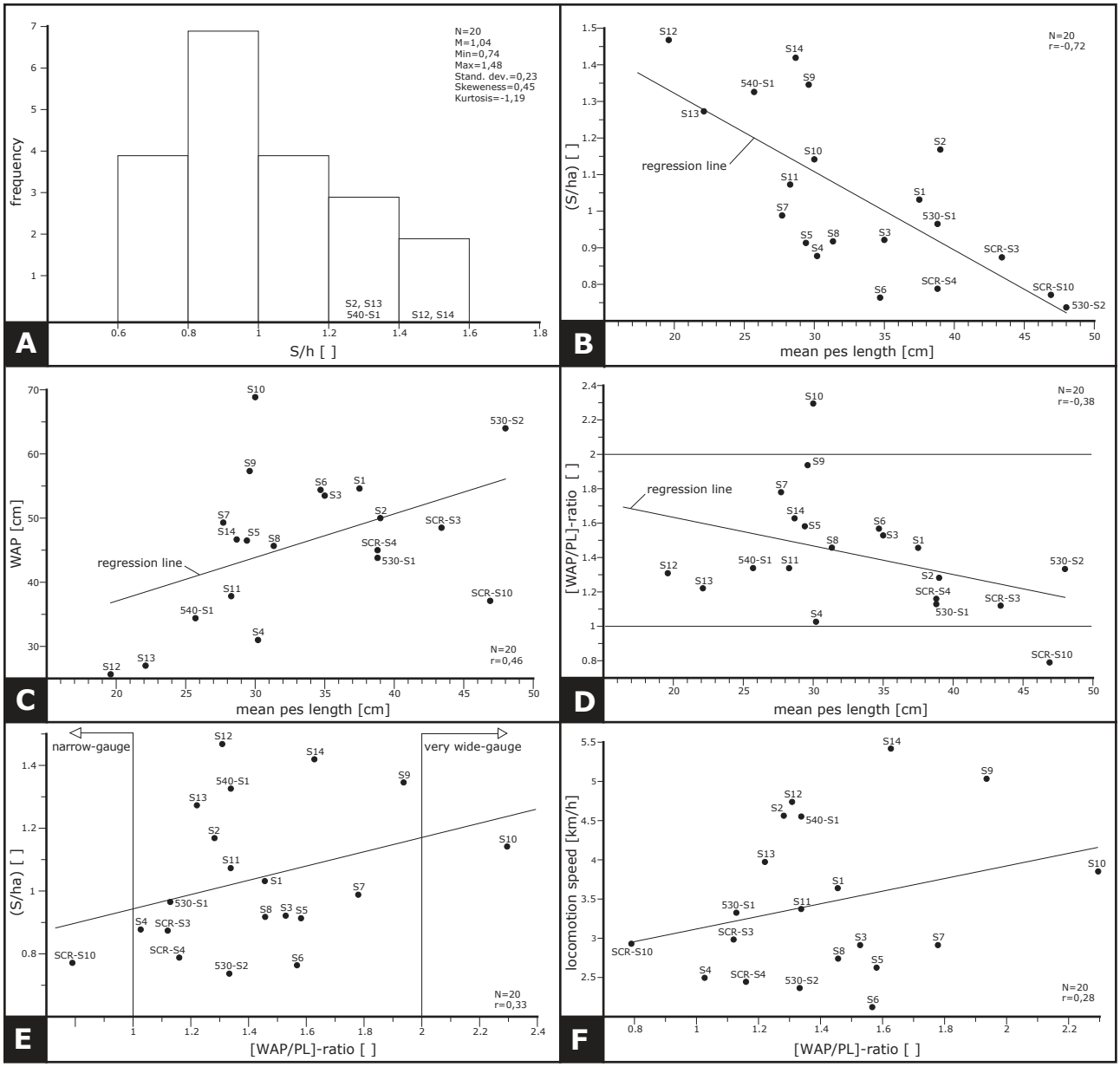


Fig. 5.43: Sauropod trackways of the Chevenez—Combe Ronde tracksite and three selected trackways (i.e., SCR-S3, SCR-S4, and SCR-S10) of the main track level of the Courtedoux—Sur Combe Ronde site (Marty et al., 2003). **A:** Histogram showing the distribution of relative stride length (S/h). **B:** Plot of the mean pes length against the mean relative stride length (using ha of Table 5.4). **C:** Plot of mean pes length against mean width of the pes angulation pattern (WAP). Trackway width (WAP) correlates poorly with mean pes length. **D:** Plot of mean pes length against [WAP/PL]-ratio. Note the poor correlation indicating that within the Combe Ronde trackways gauge not depends on the ontogenetic stage. **E:** Plot of [WAP/PL]-ratio against relative stride length. **F:** Plot of [WAP/PL]-ratio against locomotion speed (calculated after Table 5.4 using ha and eq. 2). Note the poor correlation indicating that within the trackways of the Combe Ronde site trackway gauge does not depend on locomotion speed.

do not behave the same way when moving over stable or unstable surfaces. Humans for example prefer to put their feet in tracks previously left whilst moving over an unstable substrate (e.g., deep snow, mud), and quadrupedal animals may behave in a similar way. This could explain overprinting of the manus at low locomotion speeds. At the Chevenez—Combe Ronde site, the substrate possibly had an influence on trackway patterns observed on levels 515, 520, 530, and 540:

- On the levels 515 and 520, no clear manus tracks were identified and all trackways were pes-only, even though their identification is tentative and they were not subjected to systematic descriptions (Annex 5.1).
- The pes-only trackway on level 530, characterized by the deepest tracks and a low locomotion speed, may indicate that the trackmaker put the pes precisely at the position of the manus because he was walking in unstable sediment with a higher water-content when compared with the other palaeosurfaces.

The manus-dominated trackway S1 of level 540 is striking because it has a normal trackway configuration with manus tracks clearly deeper than pes tracks. For 540-S1, an undertrack origin (e.g., Lockley & Rice, 1990; Vila et al., 2005) can be excluded because it consists of true tracks. Even though in sauropods the centre of mass was positioned rather posteriorly (e.g., Alexander, 1989; Wilson & Sereno, 1998; Henderson, 2004) or even in the trunk (Schwarz et al., 2006; Schwarz et al., 2007b), different locations of the centre of mass as shown by Henderson (2004) for macronarians and diplodocids, may have resulted in differences between the pressure exerted per square centimetre on the pes and manus tracks.

Manus-dominated (and manus-only) trackways are also commonly encountered amongst trackways attributed to pterosaurs (e.g., Lockley et al., 1995; Bennett, 1997; Unwin, 1997, Mazin et al., 1997). Mazin et al. (2003) showed that because of the much smaller surface of the manus tracks, the pressure per square centimetre on the manus track would have been around 8 times higher than the one on the pes (assuming forelimbs and hindlimbs had supported the same mass). They suggested that depending on the substrate properties deeper manus tracks may readily form, whilst pes tracks are not necessarily impressed if the sediment is too hard, or "healed" in non-competent sediment after foot withdrawal. Lockley et al. (1995) also noted that slight erosion would remove shallow pes tracks but not deeper manus tracks.

Similarly, trackway 540-S1 may have been left by a trackmaker exerting more pressure on the manus than the pes (e.g., Lockley & Rice, 1990). This may have been enhanced by a more digitigrade manus posture due to particular substrate properties and/or a special behaviour of the trackmaker related to it (Marty et al., 2006b), rather than a different trackmaker species with a more anteriorly positioned centre of mass.

Finally, manus-only, manus-dominated, and pes-only, trackways are interpreted to have been left by swimming sauropods assuming that the trackmakers were touching the ground with their forelimbs or hindlimbs only, and this will be discussed hereafter.

Swimming capabilities of sauropods

Bird (1944) and later Ishigaki (1989) interpreted manus-only and manus-dominated sauropod trackways as evidence for a swimming sauropod touching the ground only with his forelimbs. Since then, manus-dominated, manus-only, and more recently even pes-only sauropod trackways are a focus of debate concerning the swimming capacities of sauropods.

Most manus-only trackways reported from the Paluxy River by Bird (1944, 1985) and from Morocco by Ishigaki (1989) exhibit a regular trackway configuration and relatively well-defined manus tracks without unequivocal evidence of an underwater origin (e.g., flow-back and/or collapse structures, scratch marks). This is atypical for tracks of swimming or floating animals (e.g., Coombs, 1980; McAllister, 1989; Currie, 1995; Whyte & Romano, 2001b; Swanson & Carlson, 2002; Lockley & Wright, 2003; Milner & Lockley, 2006; Ezquerra et al., 2007), and it is unlikely that a single trackmaker would produce a regular trackway configuration when swimming (Vila et al., 2005). Moreover, a very particular sedimentation regime is required to preserve a track formed under several metres of water, and it

is difficult to prove that during track impression the palaeosurface was situated below the water surface (Brand & Tang, 1991; Lockley et al., 1992b), and to estimate palaeo water depth even if ripple marks are present (e.g., Tanner, 1971; Diem, 1985).

Lockley & Rice (1990) provided a detailed discussion on the swimming vs. non-swimming scenarios, and they showed that these trackways can be explained as underprints or undertracks related to manus tracks exerting more pressure per square centimetre than the pes and hence sinking deeper into the sediment, which may have been enhanced by a particular gait of the trackmaker. In this scenario the manus tracks stand up better to erosion and differential erosion may lead to the formation of manus-only trackways with relatively well-defined manus tracks but without evidence for pes tracks (Lockley & Rice, 1991; Vila et al., 2005). Subsequently, most occurrences of manus-only trackways (e.g., Lockley et al., 1992c; Lockley & Santos, 1993; Lockley et al., 1994f; Santos et al., 1994; Fischer, 1998; Vila et al., 2005) were explained following Lockley & Rice (1990).

Nonetheless, Lee & Huh (2002, 2006) interpreted a very particular trackway from the Late Cretaceous (Uhangri Formation, South Korea) as a manus-only trackway left by a swimming sauropod trackmaker. This was questioned by Thulborn (2004), who provided two other "delamination" scenarios for these unusual tracks with internal ridges, explaining them as extramorphological features related to particular substrate properties. Recently, Hwang et al. (2008) re-examined the Uhangri tracks, and they concluded that they are undertracks left by a tridactyl, most probably ornithopod trackmaker walking on a layer of overlying tuffaceous sand. They suggested that the internal ridges are molds of radial cracks on the underside of the tuffaceous sand bed.

Based on computer models that employ the basic physics of buoyancy and equilibrium, Henderson (2004) investigated how the bodies of sauropods would have reacted when immersed in water. Because his models showed that immersed sauropods are in a situation of unstable equilibrium and would probably roll onto their sides, he suggested that this reinforces the idea that sauropods were primarily terrestrial animals. However, Henderson's models did not exclude the possibility that sauropods could successfully walk in water as deep as their chest height and showed that *Brachiosaurus* and *Camarasaurus* when starting to float were likely to produce manus-only trackways, whilst diplodocids were unlikely to do so but may have produced pes-only trackways. Wilson & Fisher (2003) also suggested that sauropods in general, submerged in shoulder-deep water, would experience a forward shift in their centre of mass by virtue of their body shapes, and that this would be most pronounced in *Brachiosaurus*, the sauropod with the most forwardly positioned centre of mass.

This led Li et al. (2006) to conclude that a pes-only to pes-dominated and later quadrupedal trackway from the Early Cretaceous (Gansu Province, China) was made by a sauropod first floating and then walking out of the water. For such a trackway a roaring behaviour, which has been postulated for sauropod dinosaurs (see Upchurch et al., 2004 for references), could also be suggested. However, pes-only trackways are more readily explained by occasional overprinting of the manus by the pes and lateral differences in substrate consistency than by swimming or roaring behaviour.

It is believed that it has not yet been demonstrated conclusively from trackways that sauropods were able to walk or even to swim when partially submerged, and it is suggested that without detailed sedimentological analyses of the tracks and the encasing sediment, speculative interpretations about the behaviour of the trackmaker should be avoided.

At the Chevenez—Combe Ronde site an origin due to swimming sauropods can be excluded for both pes-only and manus-dominated trackways because they are all located on levels interpreted as supratidal palaeosurfaces (see also chap. 4), and in this tidal-flat palaeoenvironment the water was never deep enough.

5.7.2 Ichnotaxonomy of tridactyl tracks attributed to morphotype I

5.7.2.1 Diagnosis

Morphotype I can be diagnosed as:

- Mesaxonic slightly asymmetric, tridactyl track, clearly longer than wide with isolated digits.
- Digit III is always the longest and digit IV is longer than digit II, which is shorter posteriorly.
- Claw impressions on all three digits.
- Phalangeal pad formula 2-3-3.
- Low total divarication angle, and divarication angles of the same order between digits II and III, and III and IV, respectively.
- Narrow-gauge trackway with a small outward rotation of tracks.

5.7.2.2 Comparison with similar Middle Jurassic to Early Cretaceous ichnogenera

In Late Jurassic and Early Cretaceous carbonate platform settings, smaller tridactyl tracks are not very common (e.g., Meyer & Pittman, 1994; Lockley, 1998b; Lockley & Meyer, 2000) and often poorly preserved (e.g., Dalla Vecchia, 1998a; Conti et al., 2005). Hence, they have not yet been in the focus of taxonomic descriptions.

Carmelopodus Lockley et al. 1998 and *Irenichnites* Sternberg 1932 are the only similar ichnogenera to morphotype I (Fig. 5.45), even though they are not so close in stratigraphic (Middle Jurassic and Early Cretaceous respectively) and palaeogeographic proximity to the Late Jurassic deposits of NW Switzerland. Both ichnogenera are based on specimens from fluviatile settings and preservational factors, which may differ between fluviatile and carbonate settings, can influence some of the typical track features.

Carmelopodus is characterized by the same phalangeal pad formula 2-3-3, and tracks with slender digits with claw impressions and a very similar general outline as morphotype I.

Based on observations made on the holotype (NMC8552) and a slab of a trackway attributed to *I. gracilis* (NMC8558), both stored at the Natural History Museum of Canada (Ottawa), a 2-3-3 phalangeal pad formula may also be suggested for *Irenichnites gracilis*, but this is tentative because the holotype does not clearly show the impressions of the phalangeal pads. However, *Irenichnites* clearly differs from morphotype I because of a pronounced median symmetry of the tracks, a similar and relative high divarication angles between digits II and III and digits III and IV (Fig. 5.44), and because of a commonly round and isolated impression of the heel.

It is interesting to note that *Skartopus australis* Thulborn & Wade 1984 from the Middle Cretaceous of Australia (Lark Quarry tracksite) is also characterized by a lack of the fourth proximal pad on digit IV. However, because of the large stratigraphical and palaeogeographical difference, this ichnogenus is not discussed here.

Morphotype I differs in a general way from the smaller tridactyl tracks described from the periadriatic region of the Early Cretaceous (Dalla Vecchia & Venturini, 1995; Dalla Vecchia, 1998a; Dalla Vecchia & Tarlao, 2000; Dalla Vecchia et al., 2002; Nicosia et al., 2007; Petti et al., 2008), from more recently discovered (even though larger than 20 cm) Middle and Late Jurassic tridactyl tracks from southern Italy (Conti et al., 2005), and from small tridactyl tracks from the Late Jurassic of Crayssac (Mazin et al., 2000; Billon-Bruyat, pers. comm., 2008). Generally, all these tracks seem to be characterized by less slender, fleshier tracks with the "normal grallatorid" 2-3-4 phalangeal pad formula rather than with a reduced formula for

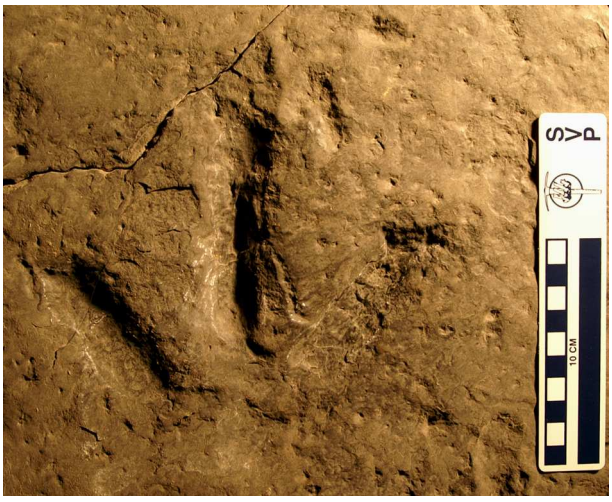


Fig. 5.44: Left pes 2 of the holotype slab (NMC8552) of *Irenichnites gracilis* Sternberg 1932, stored at the Natural History Museum of Canada (Ottawa). Track outlined with white chalk, artificial illumination from the upper right, scale bar is 10 cm.

digit IV. Moreover, Conti et al. (2005) also described a morphotype (their type 2 based on three specimens) which shares the same functional character with *Carmelopodus*, i.e., the lack of the fourth proximal pad on digit IV. This track is characterized by rather broad digits and thus clearly different from the tracks of the Combe Ronde site.

5.7.2.3 Ichnotaxonomical attribution

Owing to the particular phalangeal pad formula 2-3-3 and the isolated, slender, and slightly tapered digits with claw impressions, morphotype I can be assigned to the ichnogenus *Carmelopodus* Lockley et al. 1998.

Morphotype I differs from *C. untermannorum*, which is characterized by a widely divergent digit II and an interdigital angle between II-III, which is consistently higher than the one between III-IV, resulting in a relatively high (width/length)-ratio for that ichnospecies (Lockley et al., 1998a). This is clearly not the case in morphotype I, which further exhibits less tapered digits than *C. untermannorum*.

Lockley et al. (1998a) attributed a specimen from the Middle Jurassic of England, which was illustrated by Delair & Sarjeant (1985, Fig. 5), to the ichnogenus *Carmelopodus* (Fig. 5.45C). This specimen also lacks a widely divergent digit II and thus is similar to morphotype I of the Combe Ronde site.

However, at the present time there is not enough evidence to name a new ichnospecies. However, the attribution of morphotype I to the ichnogenus *Carmelopodus* has implications for palichnostratigraphy since *Carmelopodus* is considered to be one of the typical Middle Jurassic ichnogenera (Lucas, 2007). This is also supported by recent finds of *Carmelopodus*-type tracks from the Late Jurassic of Morocco (Meyer and Belvedere, pers. comm., 2008).

5.7.3 Ichnotaxonomy of tridactyl tracks attributed to morphotype II (T43)

5.7.3.1 Diagnosis

Morphotype II can be diagnosed as:

- Subsymmetric tridactyl tracks almost as wide as long (high divarication angle).
- Blunt toes without evidence for digital pad and claw impressions.
- Digit III with a slightly angular, trapezoidal shape with the maximum width located in the anterior part of the digit.
- Digit III separated from digits II and IV, and digits II and IV merged in the heel without evidence for a postero-medial indentation.
- Digit III longer than digits II and IV, which are of similar length.
- Very narrow-gauge trackway with an irregular configuration (inward rotation of some tracks).

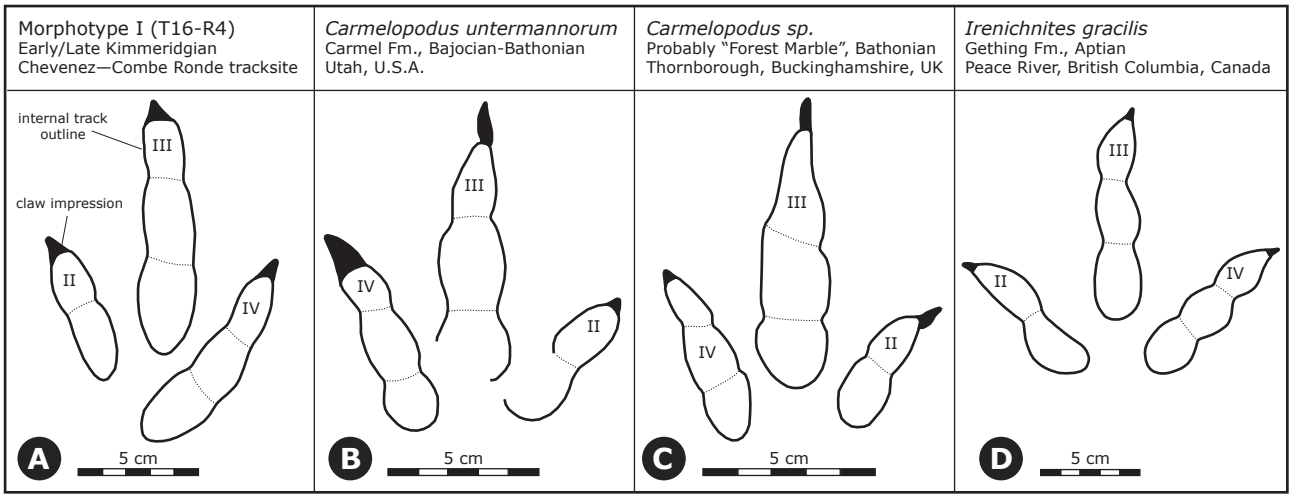


Fig. 5.45: Comparison of morphotype I (T16-R4) with other similar Middle Jurassic and Early Cretaceous tridactyl ichnotaxa discussed in this work. **A:** Typical track (T16-R4) of the Combe Ronde site. **B:** Outline drawing after Lockley et al. (1998a; Fig. 9, right track, p.264). **C:** Outline drawing after Lockley et al. (1998a; Fig. 9, left track, p. 264) and after Delair & Sarjeant (1985; Fig. 5, p. 140). **D:** Originally described by Sternberg (1932), schematic outline drawing after Holotype (NMC8552) stored at the Natural History Museum (Ottawa, Canada) and illustrated in Figure 5.44.

It is suggested that morphotype II (T43) is not part of the ontogenetic suite of morphotype I, and that the lack of digital pads on the tracks of T43 is not due to particular substrate conditions or to the kinematics of its trackmaker. The particular trapezoidal form of digit III could indicate a separation of digit III into two distinct pads, but more and better preserved specimens are required for confirmation. Digits that are not clearly separated coupled with the general absence of well-defined phalangeal pads may be evidence for a well-padded, fleshy foot.

5.7.3.2 Comparison with similar Late Jurassic to Early Cretaceous ichnogenera

In Late Jurassic low latitude environments, tridactyl tracks with a pes length longer than approximately 20 cm are generally attributed to ichnogenera of theropod affinity. Common and widespread ichnogenera are *Megalosauripus* (Lockley et al., 1996, 1998c) and *Therangospodus* (Lockley et al., 1998b), less frequent are *Bueckeburgichnus* (Kuhn, 1958), *Euthynichnium* (Nopsca, 1923), *Hispanosauripus* (Mensink & Mertmann, 1984), and *Megalosauropus* (Colbert & Merrilees, 1967; Kaever & Lapparent, 1974). However, at the moment there is no consensus about the validity of several of these ichnogenera, in particular *Megalosauripus*, *Megalosauropus*, and *Bueckeburgichnus* (e.g., Lockley et al., 1996, 1998c; Lockley, 2000; Thulborn, 2001). Hereafter, the latter three ichnogenera are used *sensu* Lockley et al. (1998c).

Large Late Jurassic tridactyl tracks from Utah, U.S.A. (Lockley et al., 1998d), Poland (Gierliński et al., 2001; Gierliński & Sabath, 2002), Spain (e.g., García-Ramos et al., 2002) and Portugal (Mateus & Milàn, 2005) have been attributed to ornithischian or ornithopod trackmakers, and the occurrence of such ichnogenera within the Late Jurassic is also suggested by the skeletal record (e.g., Galton, 1980; Mateus & Antunes, 2001). In the Late Jurassic, the only ornithopod ichnogenus so far described is *Dinehichnus* from Utah (U.S.A.), and from Portugal (Lockley et al., 1998d). In the Early Cretaceous, common ornithopod ichnogenera are *Amblydactylus* (Sternberg, 1932), *Camptosaurichnus* (Casamiquela & Fasola, 1968), *Caririchnium* (Leonardi, 1984), *Iguanodonichnus* (Casamiquela & Fasola, 1968), and *Iguanodontipus* (Sarjeant et al., 1998). As for the theropod tracks, the validity of some of these ichnogenera and their attribution to ornithopod or more particularly "iguanodontid" dinosaurs is debated (e.g., Sarjeant et al., 1998). Morphotype II (trackway T43) shares similarities with some of the Late Jurassic theropod and Late Jurassic to Early Cretaceous ornithopod ichnogenera (Fig. 5.46).

Morphotype II clearly differs from *Megalosauripus sensu* Lockley et al. (1998c), which is characterized by more slender, "long heeled" tracks with isolated digits often with claw impressions and well-defined discrete impressions of the digital pads (e.g., Lockley et al., 1996, 1998c). *Megalosauripus* trackways are often irregular, narrow to wide, and with alternating short

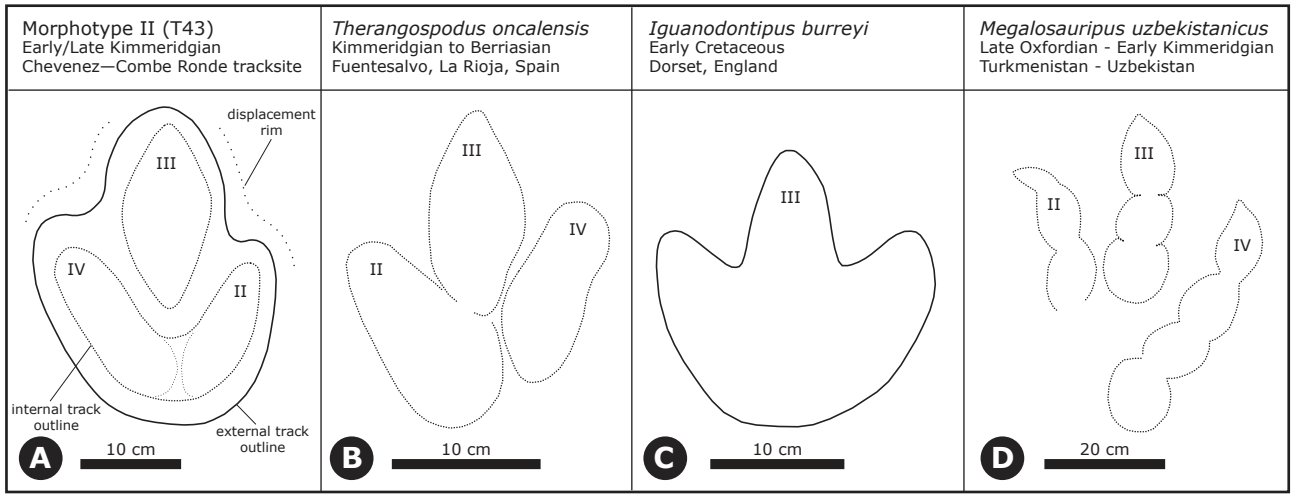


Fig. 5.46: Comparison of morphotype II with selected Late Jurassic and Early Cretaceous ichnotaxa featuring large tridactyl tracks. **A:** Schematic outline drawing highlighting the typical features of morphotype II of the Combe Ronde tracksite (based on T43). **B:** Outline drawing after photo in Lockley et al. (1998b; Fig. 7, p. 346); scale bar after measurements given in their Table 1 (p. 341), which also identifies this track (R2) as a right pes track. **C:** Outline drawing after Sarjeant et al. (1998; Fig. 12D, p. 194), scale bar after measurements given in their Table 1 (p. 193) **D:** Outline drawing after Lockley et al. (1998c; Fig. 8, lower right, p. 325); identification of digits after trackway shown in their Figure 12D.

and long steps, and they may have inward rotated tracks (e.g., Meyer & Lockley, 1997; Lockley et al., 1998c), as observed in T43 for the right pes.

Morphotype II differs from *Bueckeburgichnus* and *Euthynichnium* which are both asymmetric, elongate with tapered digits and occasional claw impressions, and they are tetradactyl because of the impression of the hallux (Lockley, 2000). It also differs from *Hispanosauropus* from the Kimmeridgian of Spain, which is more elongate and has slender digits with evidence for claw impressions (Mensink & Mertmann, 1984). The latter is doubtful because the holotype may be lost to erosion (Lockley et al., 2007b).

Morphotype II is quite similar to the ichnogenus *Therangospodus*, which is characterized by oval, digital pads, not separated into discrete phalangeal pads and a narrow trackway with little or no rotation of digit III long axis from the trackway axis (Lockley et al., 1998b). However, the tracks of morphotype II differ from *Therangospodus* because they lack a clear postero-medial indentation on the heel, because of their particular trapezoidal form of digit III, and because of their rather subsymmetrical than asymmetrical form. The tracks of T43 further differ from the two so far described *Therangospodus* ichnospecies, because *T. pandemicus* is characterized by more elongate and asymmetric tracks with faint indentations at the margins of pads, which sometimes reveal the location of the phalangeal pads, and because *T. oncalensis* has a V-shaped, slightly tapered digit III and a postero-lateral indentation at the heel (Lockley et al., 1998b). In the Berriasian of the Cameros Basin (Soria, Spain) parallel trackways were attributed to *T. oncalensis* and interpreted as evidence for gregarious behaviour amongst medium-sized theropods (Barco et al., 2006). Judging from figures 2 and 4 in Barco et al. (2006), these tracks are quite similar to morphotype II, but they also show a striking similarity with ornithopod tracks. Moreover, these trackways show evidence of manus tracks (C.A. Meyer, 2007, pers. comm.).

Morphotype II shares some of the typical general characteristics of ornithopod ichnogenera such as *Iguanodontipus*: symmetric tracks almost as wide as long, the absence of a postero-medial indentation on the heel, oval digits without evidence for impressions of discrete phalangeal pads and claws, and a high total divarication angle. Furthermore, narrow trackways with obvious inward rotation of digit III are typically described from ornithopod ichnogenera (e.g., Moratalla et al., 1988, 1992; Lockley et al., 1998d; Sarjeant et al., 1998; Meyer & Thüring, 2003b). Morphotype II differs from ornithopod ichnogenera because of the particular trapezoidal form of digit III, and because digit III is slightly longer than digits II and IV. There is no evidence of possible handprints, which are often described from ornithopod trackways (e.g., Moratalla et al., 1992; Pérez-Lorente et al., 1997; Wright, 1999; Lockley & Wright, 2001; Meyer & Thüring, 2003b). However, this may also be related to the fact that the area of T43 is strongly dinoturbated by several other sauropod trackways. Morphotype II also differs from *Dinehichnus*, which is characterized by quadripartite, symmetric, tridactyl tracks with a distinctive circular heel pad impression (Lockley et al., 1998d), unless that the circular heel pad impression is not discernible in T43 owing to peculiar substrate conditions or because of modification after track formation (e.g., by overgrowth of a microbial mat).

Finally, morphotype II is quite similar to trackway T18 of the main track level of the Courtedoux—Sur Combe Ronde site, whose best-preserved tracks are also characterized by a trapezoidal but slightly rounder digit III (Marty et al., 2003), and to recently discovered tracks at the Tchâfouè site, (Marty et al., 2006a, 2007c), which all await further description.

5.7.3.3 Ichnotaxonomical attribution

For the time being, morphotype II can not be unambiguously attributed to any of the above cited tridactyl ichnogenera. It is most similar to the ichnogenus *Therangospodus*, but on the other hand also shares many characteristic features of ichnogenera attributed to ornithopod dinosaurs. However, continued analyses and comparison of other specimens from the Ajoie ichnoassemblages are likely to better define this morphotype.

5.7.4 Identification of possible bipedal trackmakers

Minute to medium-sized tridactyl tracks were either left by theropod or ornithischian dinosaurs, or by birds (the latter are not included in this discussion). Generally, the tracks of theropod (saurischian) and ornithischian dinosaurs are difficult to distinguish from each other (e.g., Thulborn, 1990; Meyer & Pittman, 1994; Farlow & Chapman, 1997; Lockley, 1997b), even when using osteometric and statistical approaches (e.g., Moratalla et al., 1988; Demathieu, 1990; Weems, 1992; Farlow & Lockley, 1993; Olsen, 1995; Olsen et al., 1998).

Furthermore, theropod tracks are morphologically conservative (Lockley, 1998b). Thulborn (2001) believes that few theropod ichnogenera are sufficiently diagnosed to be distinguished, and that the classification and nomenclature of theropod tracks remain in disarray because most are in serious need of revision.

5.7.4.1 Tracks of morphotype I (Carmelopodus)

Carmelopodus has been attributed to a theropod trackmaker, without further precision (Lockley et al., 1998a; Lockley & Meyer, 2000). This attribution is also suggested by the tracks of morphotype I of the Combe Ronde site, because they have slender and narrow, slightly tapered digits with claw impressions, and trackways that are essentially narrow with tracks showing no or little, generally outward, rotation. Nonetheless, it has to be considered that many of the smaller bipedal ornithischians also had relatively long, narrow toes, probably leaving slender tracks longer than wide as well (e.g., Farlow & Chapman, 1997).

The tracks of morphotype I are clearly longer than wide, which is also expressed by a low [W/L]-ratio. The [W-L]-ratio also falls, for the majority of the minute and small tracks, in the range of tracks of theropod affinity as suggested by Thulborn (1990), which is not the case for the total divarication angle, falling clearly in the range of small ornithopods (Thulborn, 1990) (Fig. 5.47). However, the ranges proposed by Thulborn (1990) are based on small samples of tracks, and the total divarication angle also strongly depends on the preservation of the tracks and the kinematics of the trackmaker (see also chap. 5.4.2). Consequently, the ranges of Thulborn (1990) may not be that meaningful for the distinction between theropods and ornithischians.

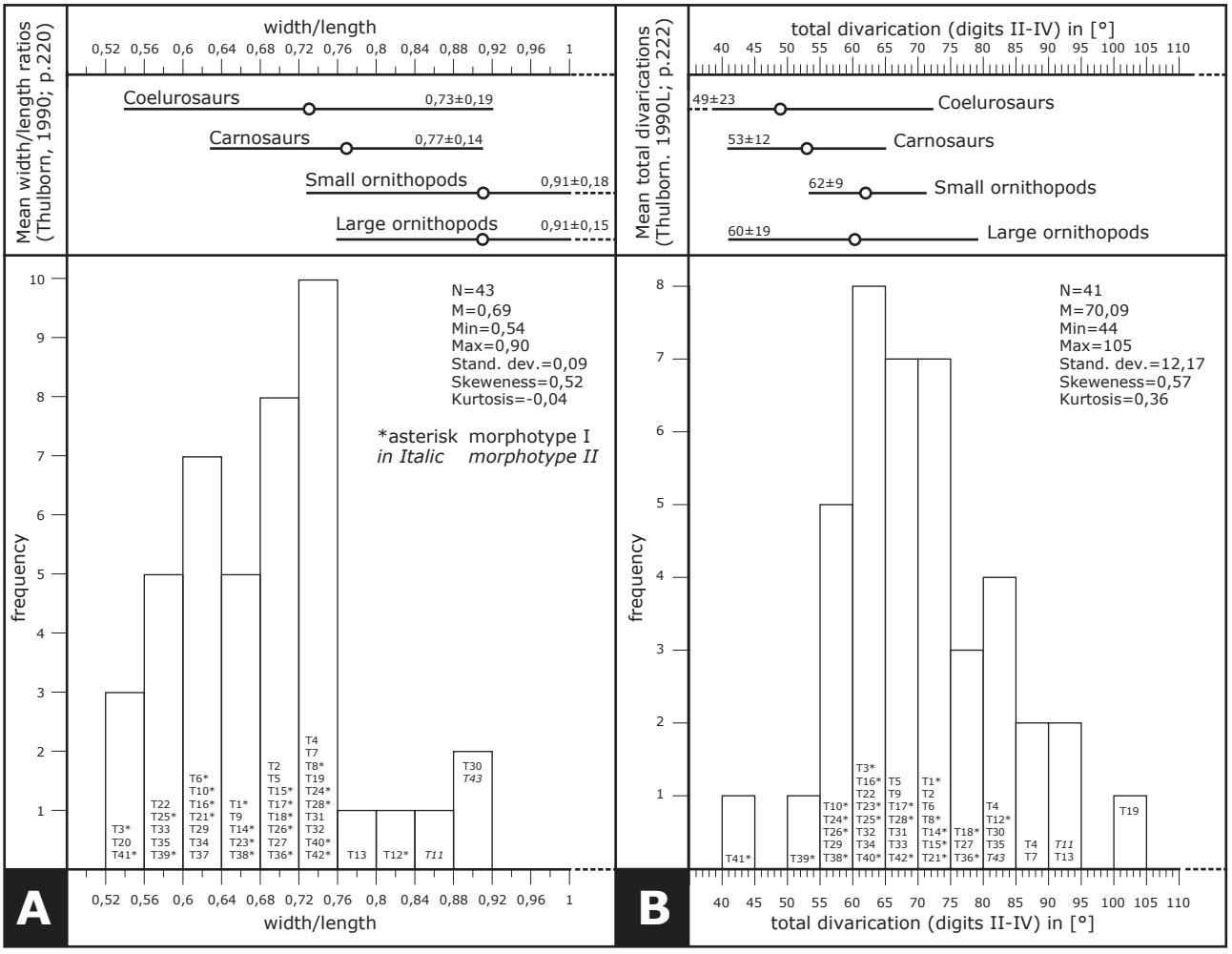


Fig. 5.47: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3, main track level. **A:** Distribution of the (width/length)-ratio. Suggested ranges of selected dinosaur groups after Thulborn (1990; p. 220). **B:** Distribution of the mean total divarication angle (angle between digits II and IV). Suggested ranges of selected dinosaur groups after Thulborn (1990; p. 222). Note that Thulborn's ranges of the selected dinosaur groups are based on published values and that Thulborn's large ornithopods include iguanodonts and hadrosaurs.

Even if it can not be said whether the tracks of morphotype I were left by young or adult animals, it is interesting to note that several well-known small, functionally tridactyl avian and non-avian theropod trackmakers have been described from the Late Jurassic of central Europe. These include *Archaeopteryx* (e.g., Hecht et al., 1985; Mayr et al., 2005), and the theropods *Compsognathus* (e.g., Bidar et al., 1972; Ostrom, 1978; Peyer, 2006) and *Juravenator* (Göhlich & Chiappe 2006).

Archaeopteryx can not be considered as a probable trackmaker due to its small size and the same holds true regarding the size of the pes of the Bavarian *Compsognathus* specimen and *Juravenator* both from the Solnhofen area (Germany), which would have left tracks even smaller than the smallest ones discovered at the Chevenez—Combe Ronde site. The *Compsognathus* specimen from Canjuers (*Département du Var*, France), on the other hand, is "some 50% larger than the original (Solnhofen) specimen" (Norman, 1990), and the length of digit III can be estimated at about 6-8 cm judging from figure 11 in Peyer (2006, p. 893). A similar sized dinosaur is likely the trackmaker of the minute tracks, notably those of trackways T10 and T41, revealed at the Chevenez—Combe Ronde site. Further evidence may be provided by a more detailed comparison of their skeletal pes morphology with the tracks (cf. Farlow & Lockley, 1993).

5.7.4.2 Tracks of morphotype II (T43)

Because morphotype II can at the moment not be clearly attributed to any tridactyl ichnogenera, it is difficult to make any precise assumption about its trackmaker.

Morphotype II is most similar to *Therangospodus*, and this ichnogenus was attributed to "large and robust" theropods (Lockley et al., 1998b). A theropod rather than ornithopod affinity of the tracks of morphotype II is suggested by the well-developed and rather narrow digit III, which is separated from digits II and IV and slightly longer, as well as the probably separated digits II and IV.

Assuming a "large and robust" theropod as the trackmaker, this could be an *Allosaurus*, "carnosaur *sensu lato*", or a "megalosaur" or "megalosaurid" dinosaur (e.g., Lockley, 1998b, 2000; Lockley et al., 1998b). However, megalosaurs are poorly understood, both in their anatomy and their phylogenetic affinities (Molnar et al., 1990; Holtz, 1998; Benson et al., 2008). Thulborn (2001) stated that "there exists no definite conception of megalosaurs or of their tracks". Further, an identification of a probable large theropod trackmaker is not helped by the rarity of their skeletal remains in Late Jurassic deposits of the Jura carbonate platform. In NW Switzerland, such findings are restricted to an isolated tooth probably of *Ceratosaurus* affinity from the Oxfordian of Röschenz (Meyer & Thüring, 2003a), two isolated teeth from the Solothurn Turtle limestone of "small" theropods, one of which is similar to dromaeosaurid teeth (Meyer & Thüring, 2003a), and a tooth from Moutier figured in Greppin (1870), which can be attributed to the genus Ceratosaurus (Meyer and Schwarz, pers. comm., 2008). In France, several isolated vertebrae from the Late Jurassic of Plaimbois-du-Miroir, Doubs (Pharisat, 1993), are attributed to a very large theropod of uncertain affinity (Allain & Suberbiola, 2003).

Nevertheless, an ornithopod trackmaker such as an "iguanodontid" or "camptosaurid" dinosaur can for the moment not be excluded because morphotype II also exhibits a number of features, which are typical of ornithopod trackmakers. These are: digits with rounded terminations and without evidence for claw marks; comparatively wide tracks, digit III not much projecting anteriorly beyond digits II and digit IV, digit IV not longer posteriorly than digit II, low values for the relative stride (e.g., Thulborn & Wade, 1984; Thulborn, 1990; Moratalla et al., 1992; Farlow & Chapman, 1997; Sarjeant et al., 1998; Dalla Vecchia et al., 2002). Furthermore the tracks are characterized by high interdigital angles, which fall clearly beyond the range of large ornithopods (Thulborn, 1990). The same holds true for the (width/length)-ratio (Figs. 5.47A & B). Skeletal remains of ornithischian dinosaurs on the Jura carbonate platform are restricted to a broken left femur attributed to a (quadrupedal) stegosaur from Oberbuchsiten, Switzerland (Meyer & Hunt, 1998).

5.7.5 Locomotion capabilities of the bipedal dinosaurs

Obligate or habitual bipedality is one of the outstanding characteristics of theropods and tridactyl dinosaurs in general (e.g., Farlow et al., 2000; Wilson, 2005). Bipeds move their legs in different ways, resulting in distinct gaits such as walking, trotting,

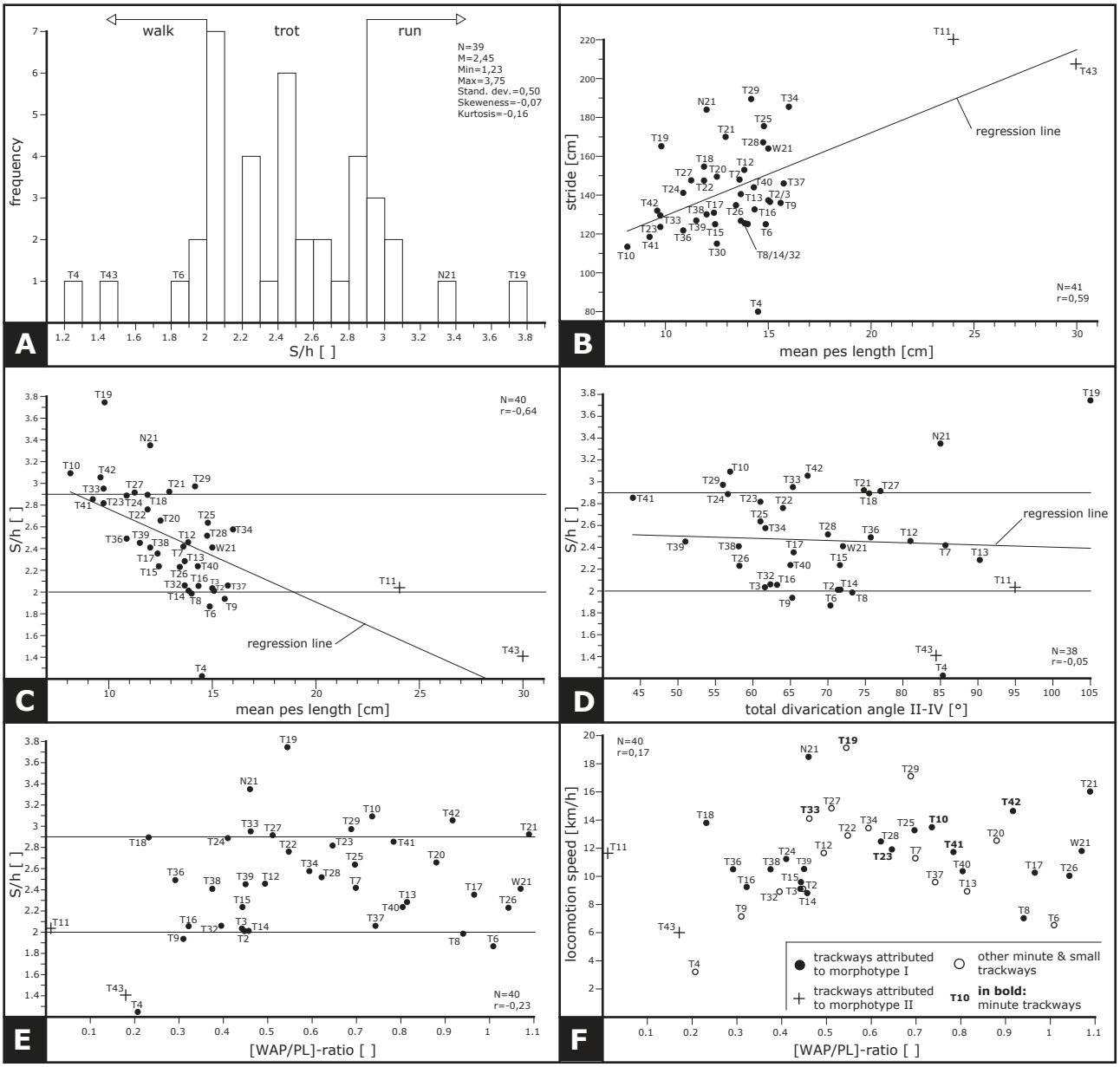


Fig. 5.48: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3, main track level, bipedal trackways. **A:** Histogram showing the distribution of the relative stride length (S/h). **B:** Plot of the mean pes length against the mean stride length. **C:** Plot of the mean pes length against the relative stride length. **D:** Plot of the mean total divarication angle (angle between digits II and IV) and the relative stride length (S/h). **E:** Plot of the [WAP/PL]-ratio against the relative stride length. **F:** Plot of the [WAP/PL]-ratio against locomotion speed (calculated after Table 5.5), regression line is not indicated. In all plots, morphotype II is indicated by crosses. Additionally, trackways attributed to morphotype I and the other minute and small trackways are distinguished in F. Note that not all trackways are plotted in each diagram because the given measurements could not always be obtained for all 43 bipedal trackways. According to Table 5.3, the narrow (N21) and wide (W21) part of trackway T21, as well as the "overall trackway" (T21) are separately plotted. Boundaries between walking, trotting, and running gaits following Thulborn (1990) are indicated in A and C-E. For the calculation of the relative stride length (S/h) and locomotion speed see Table 5.3 and Table 5.5.

running, and hopping, even though trackways with alternating tracks generally indicate a "striding" gait (Alexander, 1989; Hutchinson & Gatesy, 2001; Hutchinson et al., 2005).

Thulborn (1984) suggested that the trotting ("slow running") gait was a transitional gait of high energetic cost that bipedal dinosaurs generally avoided, but Farlow et al. (2000) showed that there is no evidence for this. At the Combe Ronde tracksite, the relative stride length (S/h) distribution of the bipedal trackways of the main track level (Fig. 5.48A) shows that the majority of the trackways indicates a trotting gait. Only a few trackways indicate walking or running gaits. This suggests that some minute and small bipedal dinosaurs preferred a trotting gait. However, more data is needed because a given set of data from a single horizon may be biased by a particular behaviour of the trackmakers at that given moment or in that given environment, and does not necessarily reflect the typical gait of the trackmakers.

Bigger trackmakers are characterized by longer strides and shorter relative stride lengths than smaller ones (e.g., Thulborn, 1990). This holds true for the bipedal trackways of the Combe Ronde site, even though the minute and small trackways show quite a wide range, due to differences in locomotion speed (Figs. 5.48B & C). The total divarication angle is poorly correlated with the relative stride length (Figs. 5.48B & C). This suggests that it is not very helpful for the characterization of the tridactyl morphotypes of the Combe Ronde site (see also Fig. 5.47).

In a bipedal "dual-gauge" trackway of a large theropod from the Middle Jurassic of England, the faster gait is associated with a higher pace angulation and narrower trackway and the slower gait with a lower pace angulation and wider trackway. It was suggested that the trackmaker used different hindlimb postures for walking and running (e.g., Day et al., 2002b; Mossman et al., 2003).

This is also evident at the Combe Ronde site in trackway T21, where a decrease in locomotion speed is associated with a transition to a wider gauge. However, the general analysis of the trackway configuration, notably trackway gauge (expressed by the [WAP/PL]-ratio) and of the relative stride (S/h) and locomotion speed show that neither all "slow trackways" are characterized by a wider gauge, nor that narrow trackways are always characterized by a higher locomotion speed. This is confirmed by the plot of the [WAP/PL]-ratio against (S/h), which shows that (S/h)-ratios indicating walking (S/h<2) or trotting (2<S/h<2,9) are associated with low (<0,5) or high (>0,7) [WAP/PL]-ratios. There is a conspicuous gap for (S/h)-ratios smaller than about 2,5 for [WAP/PL]-ratios between 0,5 and 0,7 (Fig. 5.48E). The same conspicuous distribution can be seen in the plot of the [WAP/PL]-ratio against locomotion speed, where the gap is even more pronounced (Fig. 5.48F). In both plots, trackways with a running gait (S/h>2,9) are associated neither with narrower nor wider trackways. Instead, the fastest trackways are located approximately at top of the gap or around the gap for the lower (S/h)-ratios.

The present evidence indicates that the trackmakers could switch between different hindlimb postures (expressed by a narrower and a wider gauge) at lower speeds, and that they preferred an intermediate posture or gauge at higher speeds. The poor correlation between trackway gauge and the (S/h)-ratio (Fig. 5.48E) may also indicate that the walk-run transition was not sharp but gradual. Many recent ground-dwelling birds are characterized by a smooth walk-run transition without including an aerial phase (e.g., Gatesy & Biewener, 1991; Hancock et al., 2007).

5.7.6 Dinosaur palaeoecology

Tracks are considered to be representative of ancient animal communities and hence useful for palaeoecological census studies (e.g., Lockley, 1997b, 1998a), because it is possible to gain much size-frequency data from large track assemblages, because these data represent living individuals and populations (biocoenoses) (Lockley, 1994), and because track assemblages are generally little affected by time averaging (Cohen et al., 1993). Size-frequency data of track assemblages have also been used to infer age groups (e.g., Matsukawa et al., 1999), and to make conclusions on the population structure and the age of dinosaurs represented at a given locality (e.g., Lockley, 1994; Avanzini & Lockley, 2002; Breithaupt et al., 2002). The analysis of the alignment and orientation of trackways provides insight into the behaviour of trackmakers (e.g., Bird, 1944; Lockley et al., 1983; Lockley, 1986; Lockley, 1991b; Barnes & Lockley, 1994; Lockley et al., 1994g; Lockley & Hunt, 1995; Lockley & Matsukawa, 1999; Lockley & Meyer, 2000; Matsukawa & Matsui, 2001).

Nonetheless, for palaeoecological analysis based on trackways, some restrictions have to be considered. What the track record makes up in abundance, it lacks in resolution (Lockley, 1997b).Tracks are often poorly preserved, and the precise trackmaker species is generally unknown. Even when dealing with a sample of true tracks with a very similar preservation located on a single palaeosurface, it is generally not possible to evaluate the precise temporal relationships between tracks, i.e., whether the trackmakers were present at the same moment, hour or day. Moreover, Cohen et al. (1993) suggested from observations of modern vertebrate tracks in recent environments that tracksites smaller than 1000 m^2 are unlikely to register the majority of species inhabiting a given area, that the shoreline exerts a strong influence on the distribution of animal activity, and that extrapolation of track data to a regional or broader temporal scale requires multiple coeval tracksites. Even on relative large tracksites, the time represented by the trackways is very short, and the track assemblage represents nothing more than a snapshot of a given community at a given location and a given moment. This can also be expressed by the time that a given trackmaker needs to make a given trackway as calculated from locomotion speed (Table 5.4 and Table 5.5). In a similar way, Lockley (1995) calculated the minimal time for the Davenport Ranch herd to cross the area of the tracksite.

At the Chevenez—Combe Ronde site, the longest presence of a sauropod dinosaur is about 20 seconds and is represented by trackway S2 (Table 5.4); for the bipedal dinosaurs it is about 15 seconds represented by the trackways T10 and T41 (Table 5.5). This highlights the low probability that the trackways at the Combe Ronde site document any special, individual behaviour such as running or foraging, or a behaviour due to an interaction between individuals of the same (e.g., mating habits) or different species (e.g., predation, instincts to escape), despite the relatively large size of the site. The purpose here is to disclose what can be inferred from the ichnoassemblage of the main track level of the Combe Ronde site, and to point out the prospects for future, more detailed palaeoecological census studies, based on larger data sets now available from the Ajoie ichnoassemblages.

5.7.6.1 Ontogeny and population structure of the sauropods

From the alignment of the trackways on the main track level (see also chap. 5.5), variable track size, and from trackway pattern and configuration it is suggested that every sauropod trackway of group 1 and group 2 represents a single animal, whilst it can not be excluded that the two isolated, larger trackways (S1 and S2) were left by a single trackmaker, who made a 90° turn just outside the tracksite.

The peculiarity of the sauropod tracks of the Combe Ronde site is clearly the dominance of trackways of tiny and small sauropods and the lack of larger animals. This is also revealed by the size-frequency distributions of the mean pes and manus size from the trackways of the main track level (Fig. 5.7), which show that the sauropod assemblage is characterized by 10 small animals with a mean pes length between 26 cm and 32 cm and two small sauropods with a pes length between 37 cm and 39 cm, accompanied by two trackways (S12 and S13) of tiny animals with a pes length of 19,6 and 22,1 cm respectively. When estimating the size of the trackmakers from these trackways, it becomes clear that these animals were really small. The gleno-acetabular distance of the two smallest trackways S12 and S13 is 56,5 cm and 66,8 cm and varies between 80 cm and 137 cm for the other trackways. The estimated hip heights (using a factor of 4) are 78 cm and 88 cm for the two tiny animals, and they vary between 111 cm and 156 cm for the other small animals. From a comparison with Late Jurassic sauropods with small gleno-acetabular distances (e.g., Sanders et al., 2006; Schwarz et al., 2007c), the

total length of the trackmakers may have been in the order of several metres, maybe 2 m to 4 m for the two smallest and up to about 6 m to 10 m for the larger animals, but it is difficult to estimate, since the precise trackmaker species is not known. However, the two tiny trackways were left by very small animals (that were not bigger than large domestic dogs).

Generally, large sauropod tracks are more frequent than smaller ones (e.g., Lockley & Hunt, 1995; Lockley & Meyer, 2000), even though this may be in part related to taphonomic bias or rapid early growth rates of these animals (Lockley, 1994). Nevertheless, tracks of small sauropods are known from a number of sites. Most reported occurrences of small sauropod tracks with a pes length smaller than 25 cm come from fluvial and lacustrine environments and include specimens from the Early Jurassic of Poland (e.g., Gierliński, 1997, 2002; Gierliński & Sawicki, 1998; Gierliński & Pienkowski, 1999), the Middle Jurassic of Mexico (Ferrusquia-Villafranca et al., 1996; Rodríguez-de la Rosa, 2004), the Oxfordian of Poland (Gierliński, 2002; Gierliński & Niedzwiedzki, 2002), the Early Cretaceous of the Potomac Group, Maryland, U.S.A. (Stanford et al., 2007), the Cretaceous Jindong Formation, South Korea (e.g., Lim et al., 1989, 1994; Lockley, 1994; Lee et al., 2000; Hwang et al., 2002, 2004; Huh et al., 2003; Lockley et al., 2006; Lim et al., 2008), and the Cretaceous of Chabu, China (Lockley et al., 2002b). The smallest tracks attributed to sauropods currently known are a pes track from the Jindong Formation with a length of 9 cm (Lee et al., 2000; Lockley et al., 2006), and a manus track with a length of 3,2 cm and a width of 4,4 cm from the Potomac Group (Stanford et al., 2007).

Small sauropod tracks are clearly scarcer in carbonate platform environments, but they are known from the Kimmeridgian of Langenberg, northern Germany (N. Knötschke, pers. comm., 2004) and are commonly found in the Cretaceous of the Adriatic-Dinaric carbonate platform (review in Dalla Vecchia, 2005). This led Dalla Vecchia et al. (2001) and Dalla Vecchia (2005) to speculate that the Late Albian and Late Cenomanian sauropod ichnocoenoses, both dominated by tracks of small sauropods with very few specimens longer than 25 cm, may be an expression of dwarfism because of isolation and reduction of the emergent area on the platform. The concept of dwarf sauropods dates back to Nopcsa (1914), in particular *Magyarosaurus dacus* Nopcsa 1915 (Jianu & Weishampel, 1999). More recently, Sander et al. (2006), based on bone histology of the Late Jurassic sauropod *Europasaurus* from the Kimmeridgian of Langenberg (northern Germany), also suggested that this was an island dwarf species, evolved through a decrease in growth rate from its larger ancestor. This implies that dwarfed sauropods found a suitable habitat in insular, coastal marine environments. Interestingly, *Europasaurus* is approximately of the same age (Kimmeridgian) as the Combe Ronde tracksite and also found in shallow marine deposits, characterized by an invertebrate (e.g., Kastner, 1988; Delecat et al., 2001) and vertebrate fauna (e.g., Karl et al., 2006) very similar to the Kimmeridgian of the Ajoie region.

Marty et al. (2003) stated that the trackways from the main track level of the nearby, slightly younger Courtedoux—Sur Combe Ronde tracksite are amongst the smallest sauropod trackways known from the Late Jurassic, and Marty & Cavin (2003) noted an even smaller trackway from an overlying level (level 1030) of the same site. However, at the Chevenez—Combe Ronde site trackways with a pes length of nearly 40 cm were found on the main track level, a trackway with a pes length of almost 50 cm occurred on level 530, and an even larger trackway with a pes length of nearly 60 cm was found in the same levels at the close-by tracksite Courtedoux—Béchat Bovais.

Moreover, tracks of huge sauropods, with a pes length of more than 1 m are also commonly encountered in the Ajoie ichnoassemblages, even though so far only in the slightly younger intermediate and upper track-bearing levels (e.g., Marty et al., 2006a, 2007a, 2007c). This makes the Ajoie ichnoassemblages together with other large samples such as the one from the Jindong Formation, one of the ichnocoenoses with the largest range of sauropod track size classes. This evidence strongly suggests that the small sauropod tracks of the Chevenez—Combe Ronde site do not represent an isolated, dwarfed population, but that they were indeed left by young individuals.

Because dinosaur track size is a reflection of dinosaur body size and age (Lockley, 1994), sauropod tracks smaller than 20 to 25 cm are often referred as belonging to "baby" sauropods or "post-hatchling" individuals in their first year of growth (e.g., Lim et al., 1994; Lockley, 1994). Sauropod tracks with a pes length of about 30 to 35 cm are attributed to juvenile animals not more than one or two years old (e.g., Lockley & Santos; 1993; Lockley, 1994). Even if it can not be excluded that the feet of the sauropods may have been over-proportionally big

for younger animals, as can be observed for instance in living elephants (e.g., Western et al., 1983; Lee & Moss, 1995), it is suggested that the two smallest trackways (S12 and S13) can be attributed to "baby" sauropods probably younger than a year old. The other trackways of group 1 and group 2 and the two isolated trackways S1 and S2 may belong to not much larger juvenile to sub-adult animals.

The assumption that the sauropod track ichnoassemblage of the Combe Ronde site does not represent an isolated, dwarfed population opens other vistas. Based on trackway evidence, it has been debated whether coastal marine settings were one of the sauropod habitats, or whether sauropods were rather chance visitors, migrating over tidal flats in the search of new territories (e.g., Lockley et al., 1992a; Meyer & Pittman, 1994; Meyer et al., 2006). The presence of young individuals in their first years of growth may suggest that they were living the early stage of their lives in this area, implying the presence of nearby nesting grounds. Dinosaur eggs and nests attributed to sauropods (mostly Cretaceous titanosaurs, however) are commonly found in fluvial and lacustrine environments (e.g., Carpenter et al., 1994; Chiappe et al., 1998; Carpenter, 1999; Chiappe et al., 2004; Grellet-Tinner et al., 2006), but there is some evidence that some dinosaurs may have preferred nesting sites close to the sea shore or on tidal flats (e.g, Sanz et al., 1995; Lopez-Martínez et al., 2000). Accordingly, it can not be excluded that sauropods, and also other bipedal dinosaurs, nested on the Jura carbonate platform. Chiappe & Dingus (2001) even supposed site fidelity for sauropods, which means that they returned to their nesting sites. However, based on the trackway evidence currently at hand this is difficult to prove or disprove.

Nonetheless, the sauropod assemblage of the Chevenez—Combe Ronde site suggests that the Jura carbonate platform with its tidal-flat environments were one of the sauropod habitats, rather than sauropods were chance visitors only, migrating coincidentally (in the sense of nomadic migration) over the Jura platform from the London-Brabant Massif to the Massif Central or vice versa (see also chap. 5.7.9).

The ichnoassemblage of the main track level further suggests that different age groups of sauropods lived in the same area. However, this evidence does not exclude the possibility that sauropods including young animals were migrating over the year, as do extant terrestrial megaherbivores (e.g., Owen-Smith, 1988; Olff et al., 2002) and preferred different environments and feeding habitats depending on the seasonality, maybe also to avoid temperature and moisture extremes (e.g., Moore & Ross, 1994; Lockley & Hunt, 1995). Finally, Chiappe & Dingus (2001) suggested extreme precociousness for sauropods from the rarity of hatchlings or juveniles in the nesting grounds containing sauropod eggs, and this could also imply that they were capable of migrating over considerable distances at a very young age.

5.7.6.2 Ontogeny and population structure of the bipedal dinosaurs

When analysing size-frequency data from trackways, the simplest assumption is to infer that one trackway represents one animal (Lockley, 1994). This is certainly true for the two medium-sized bipedal trackways of morphotype II because of their difference in size. However, the tridactyl track assemblage is dominated by minute and small trackways, and because these are very similar in size, it can not be excluded that the same animals crossed the site twice or several times. Even though, the differences in size suggest at least several different trackmakers.

The size-frequency distribution (Fig. 5.21) shows that only three trackways have a pes length longer than 16 cm, and two of these trackways are attributed to morphotype II. The trackways with a mean pes length between 8 and 16 cm are clearly most common. This includes all trackways attributed to morphotype I (Table 5.2). The small gap visible between the minute and the small trackways may suggest that the arbitrarily-defined boundary (10 cm) between minute and small tridactyl tracks is meaningful, possibly indicating two age classes.

Hip heights have been calculated using a factor of 4,5 for all trackways except the largest one T43 where a factor of 4,9 was used (Table 5.5). Even though the calculation of hip height is somewhat arbitrary for the reasons stated in Chapter 2.7.6, they provide an idea of the size of the trackmakers. This calculation results in a hip height of 37 cm for the smallest trackway T10, indicating that this trackmaker was quite small, only slightly larger than a turkey. For the other minute and small bipedal trackways, hip heights between 44 cm and 83 cm result. The hip heights estimated for the majority of the bipedal trackways are around 60 cm, which is similar to an emu, and these animals were clearly larger than the one who left the smallest

trackway T10. A hip height higher than 1 m only results for the two trackways T11 (1,1 m) and T43 (1,5 m) of morphotype II, indicating that these were clearly larger animals, about the size of an ostrich. Since the mean track length of T43 is precisely 30,0 cm, its trackmaker could also be considered as a large bipedal dinosaur and. If that was a theropod, it could likely have threatened the tiny sauropods and/or the smaller bipedal dinosaurs.

The presence of minute and small tridactyl tracks suggests *in situ* populations of small tridactyl dinosaurs on the Jura carbonate platform, which may have been well adapted to the tidal-flat palaeoenvironment.

5.7.6.3 Dinosaur community structure

The main track level of the Combe Ronde site exhibits a diverse ichnoassemblage, which consists of medium-gauge to wide-gauge trackways of tiny and small sauropods, of trackways of minute and small bipedal dinosaurs, and of trackways of medium-sized bipedal dinosaurs.

A recurrent presence of sauropods is further indicated by several track-bearing levels within the laminite sequence. Tridactyl tracks are absent within the overlying levels of the Combe Ronde site, but they were found at the Courtedoux—Béchat

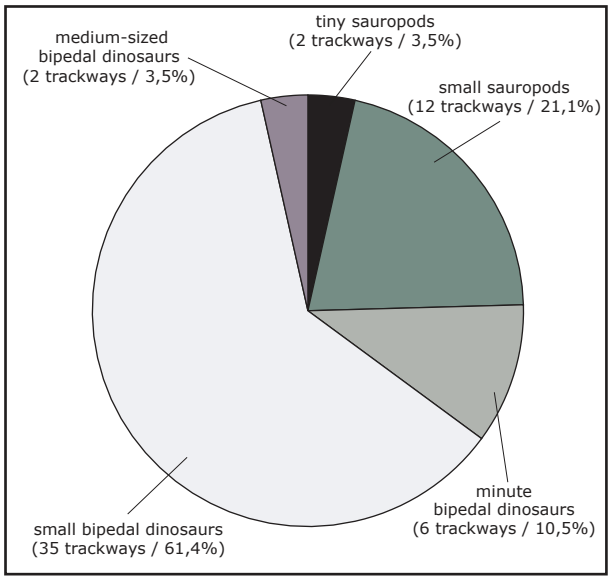


Fig. 5.49: Chevenez—Combe Ronde tracksite, main track level: Relative frequency of all trackways identified. 21 out of 41 minute and small bipedal trackways are attributed to morphotype I (*Carmelopodus*); both trackways of medium-sized bipedal dinosaurs are attributed to morphotype II.

Bovais tracksite on overlying levels of the same lower laminite sequence (pers. obs.). Regarding the presence or absence of sauropod or tridactyl tracks on the palaeosurfaces of the Chevenez—Combe Ronde site only, sauropods are dominant because they are present on all track-bearing levels, while tridactyl tracks are only present on the main track level. This is not evident from the total number of tracks and trackways excavated, because tridactyl trackways (43) are more abundant than sauropod trackways (17 clearly identified trackways), while tridactyl tracks (approximately 550 pes tracks) are less abundant than sauropod tracks (approximately 600 pes and manus tracks).

The ichnoassemblage of the main track level is dominated by trackways of minute and small bipedal dinosaurs, followed by those of tiny and small sauropods, whilst those of medium-sized bipedal dinosaurs are rare (Fig. 5.49). The scarcity of larger tridactyl tracks could support the hypothesis that they were left by theropods rather than ornithopods, because large carnivores are at the end of the food chain.

The ichnoassemblage of the main track level testifies to a tidal-flat environment of the Jura carbonate platform with the coeval presence of these different groups of dinosaurs and indicates dinosaur diversity higher than previously suggested. Together with the recurrent presence of sauropod tracks within the overlying laminites this also suggests *in situ* dinosaur populations on the Jura carbonate platform. However, the ichnoassemblages of the Combe Ronde site are only "snapshots" of the local dinosaur populations and not representative for the dinosaur community structure of the Jura carbonate platform.

5.7.6.4 Shoreline trend and implications for the palaeoenvironment

In modern environments, the shoreline significantly controls the distribution of animal activity. Transects perpendicular to the shoreline detect trackways running parallel to the shoreline but generally miss those running perpendicular to the shoreline (Cohen et al., 1993). It has to be considered that the orientation pattern may be somewhat biased because of the elongate shape of the Combe Ronde site, notably of excavation area 3.

The general orientation of all trackways, which does not exhibit a clear bimodal alignment for either the sauropod or the bipedal dinosaurs, indicates that

the orientation pattern is not significantly shoreline controlled. This suggests that the palaeoenvironment was a wide supratidal flat with no proximal shoreline. This helps to confirm the palaeoenvironmental interpretation made in Chapter 4.4.4, and shows that the orientation of trackways can be useful for the reconstruction of the palaeoenvironment.

The trackway orientation of the main track level of the Chevenez—Combe Ronde site clearly differs from that of the slightly younger Courtedoux—Sur Combe Ronde site. Here a shoreline trend can more readily be inferred, because of the presence of a bimodal pattern of sauropod trackway orientation (Marty et al., 2003).

5.7.6.5 Behavioural pattern of the sauropods

The main track level is characterized by two conspicuous groups of parallel trackways, named group 1 (composed of trackways S3 to S11) and group 2 (composed of trackways S12 to S14), which show a perpendicular orientation and which are crossing each other in excavation area 2, resulting in a higher dinoturbation index (Fig. 5.30 and Fig. 5.32). Parallel trackways either result from a gregarious behaviour ("herding") and/or a physically-controlled pathway such as a shoreline corridor (e.g., Ostrom, 1972; Lockley, 1986; Lockley, 1991b).

It is suggested that both groups of parallel sauropod trackways at the Combe Ronde site have a biological explanation, i.e., gregarious behaviour. First, all tracks show a very similar preservation, suggesting that they were left during the same and short time period. Second, in each group the tracks are of different size (even though the differences are small), and the differences in trackway pattern and configuration (Fig. 5.50) are evidence that none of the trackways was made by an animal crossing the site twice. Third, there is no distribution in the orientation of the two sauropod groups that would indicate a shoreline (physically controlled pathway). Fourth, the intertrackway spacing is regular and in the order

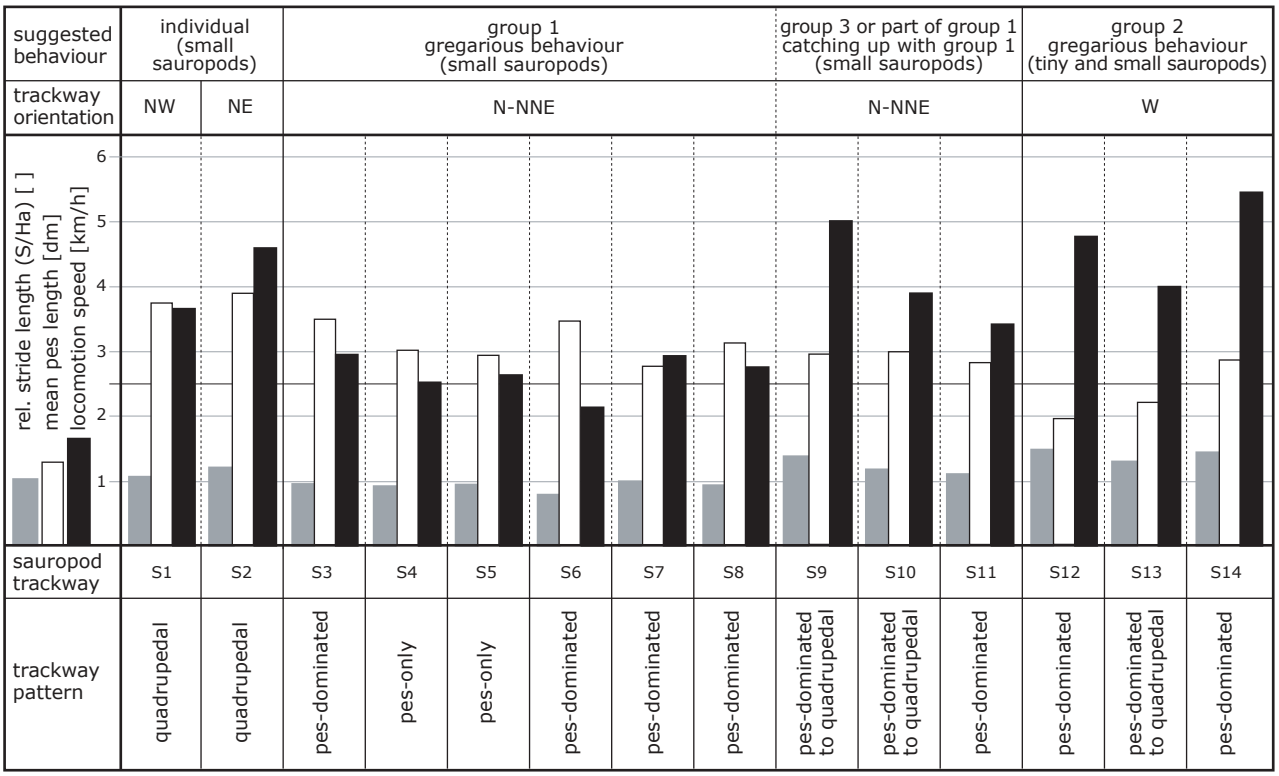


Fig. 5.50: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 (without the enlargement of 2006), main track level: Distribution of relative stride length, mean pes track length (here indicated in dm), and locomotion speed (here indicated is the speed calculation using ha=4L shown in Table 5.4). The two groups with parallel trackways correlate fairly well with the distribution of relative stride length, mean pes length, and locomotion speed. The distribution of locomotion speed suggests that within group 1 heading N-NNE three individuals either composed a group 3 or they were catching up with or heading in front of the other animals of group 1. Note that the trackway numbering between S3 and S11 also represents the distribution of these trackways from WNW to ESE (see also Fig. 5.29 and Fig. 5.30).

of 1-3 m (Figs. 5.29 & 5.30). Finally, further evidence comes from the analysis of locomotion speed, which is very similar for all individuals of group 2. Within group 1, the six westernmost trackways imply a similar speed, whilst the three easternmost trackways are slightly faster, which could indicate that these animals were catching up with the rest of the group. Group 1 is further characterized by a very regular intertrackway spacing, which is typical for animals moving together (Lockley, 1989).

The relative temporal relationship between group 1 and group 2 is suggested from track interference. The sauropod making trackway S14 would have been one of the first to cross the site, followed by S11, S13, S12, and S9. In this scenario, the sauropods of both groups were present more or less at the same time, crossing the area in two different directions. The animals of both groups walked in a "staggered fashion" (with respect to the direction of progression) rather than one beside another, in order to avoid collision with each other. This could also be the reason for some of the observed unusual trackway patterns and configurations, which could result from special behaviour of the animals such as slowing down or accelerating in order to avoid other animals. Another peculiarity is that, within group 2, the two trackways of tiny sauropods are so close that their trackmakers could not have been walking one beside each other. This is confirmed by several tracks of S12, which clearly overprint tracks of S13. Also S12 is faster than S13, and S13 exhibits evidence for a standing still or slowing down phase, either because it waited for S12 or because it had to let pass by an animal of group 1.

Besides the two groups of parallel trackways, there are also two isolated sauropod trackways (S1 and S2), perpendicular one to each other. They were left later than the two groups of parallel trackways (group 1 and group 2), because they are characterized by clearly shallower tracks without displacement rims. They are of similar size, in close proximity one to each other (Fig. 5.32), and also share some similarities in trackway configuration, notably the striking internal position of the right manus (Fig. 5.12). It can therefore not be excluded that they were left by the same trackmaker. The animal may either have turned 90° towards the East just outside excavation area 3, or it may have turned farther away and crossed the site twice. However, this interpretation is tentative at best, because trackway S1 is slower than S2 and characterized by a more pronounced outward position of the left manus, even though these differences could be related to an acceleration of the animal after it had turned to the East.

The time period between the formation of the deep parallel and shallow isolated sauropod trackways is difficult to estimate, as in a supratidal environment the duration of the desiccation of the sediment depends on climate and tidal regime. Nevertheless, personal observations in similar recent environments (see also chap. 3, and the discussion in chap. 4) suggest that this time window was relatively short, on the order of several days rather than weeks or months. However, the two very distinct different preservational morphotypes indicate that sauropods were (during the period facilitating track recording) present at least on two occasions. If the tracks had been left on several occasions during a longer period, whilst the substrate was drying up, this would have resulted in more distinct preservational morphotypes (see also chap. 3).

Wright (2005) noted that no tracksites have ever shown evidence of complex social behaviour such as a strategic herd structure, and suggested that large herds may have trampled the ground so extensively that no discrete trackways are preserved. Even though it is evident that the two groups of parallel trackways on the main track level are an expression of sauropods moving together, a large strategic herd composed of hundreds of animals can of course not be inferred, and the two isolated trackways suggest that some animals were moving on their own. Nevertheless, intense dinoturbation is probably much more frequent than supposed by Wright (2005), but because tracks can often not clearly be identified and because it is even more difficult to identify discernible trackways such heavily dinoturbated sites are not the preferred haunt of ichnologists. At the Combe Ronde site, the high dinoturbation without discernible trackways on palaeosurfaces 515 and 520 may be an expression of a larger group or herd of sauropods and/or a recurrent presence of sauropods. This has also been inferred from other heavily dinoturbated sites such as the Moutier tracksite (NW Switzerland), also known as the "dinosaur disco" (e.g., Meyer, 1997; Lockley & Meyer, 2000), or from the Morrison Formation (dinovulsion of Jones & Gustason, 2006).

5.7.6.6 Behavioural pattern of the bipedal dinosaurs

The two trackways attributed to morphotype II are isolated and far away from each other (Fig. 5.32). Their rarity suggests that medium-sized bipedal dinosaurs were either not common or that they were not frequent visitors at the Combe Ronde site. Their isolated occurrence could be further evidence for theropod trackmakers, because ornithopod trackways are often (e.g., Casanovas et al., 1993; Cotton et al., 1998; Matsukawa & Matsui, 2001; Zhang et al., 2006), though not always (e.g., Currie, 1995; Meyer & Thüring, 2003b), found in parallel alignment.

The general orientation pattern of the minute and small bipedal trackways shows multiple orientations, suggesting that the orientation pattern of the bipedal dinosaurs was not significantly shoreline controlled.

Amongst the minute and small bipedal trackways there are several groups of approximately parallel trackways (Fig. 5.32). However, almost all these groups show high intertrackway spacings, differences in mean pes length, and/or locomotion speed. Only the four parallel trackways T1, T17, T26, and T39 (suite of T33) heading approximately east show a similar speed and mean pes length, but they have very high intertrackway spacings on the order of 20 m to 25 m. Besides, there are two groups of two parallel trackways both heading W-WNW (T12 & T15 and T18 & T20), with similar pes length, locomotion speed, and a relatively small intertrackway spacing in the order of 5 m. These parallel trackways were either left by animals of similar size moving together, different animals of similar size moving at different times but for a certain reason in the same direction, or a single trackmaker frequently crossing the area. Gregarious behaviour amongst small (i.e., <25 cm) bipedal dinosaurs has been suggested from similar trackway alignments (e.g., Lockley & Matsukawa, 1999), but for the reasons stated above, gregarious behaviour for the minute and small bipedal dinosaurs can hardly be inferred from the trackway evidence of the main track level at the Combe Ronde site.

The long, linear and mostly regular trackways, the scarcity of very slow animals, and the absence of resting and crouching traces all indicate a directional, rather fast movement of the minute and small bipedal dinosaurs across the site and do not suggest behaviour such as milling or foraging. This is particularly well expressed by trackway T10 and its continuation T41, almost 60 m long, without significant changes in direction. The presence of several preservational morphotypes, incomplete trackways, and isolated tracks suggests that the minute and small trackways were not left on a single occasion, but rather on a frequent basis over the time window susceptible for track recording. This time window was probably on the order of a few days because a supratidal flat dries up fast after wetting (see also chap. 4). This implies a frequent, maybe even daily, presence of the minute and small bipedal dinosaurs. The supratidal flat was probably not their favourite hunting ground and they possibly crossed the flat rapidly to get from a resting ground to a feeding or drinking ground and vice versa. The absence of a bimodal distribution, which could be expected in such a "crossing scenario" can be explained by the very flat and unstructured palaeoenvironment and by the high activity of the trackmakers. Evidence for this scenario is also the regular distribution of the minute and small bipedal trackways over the site. Finally, several trackways may have been left by the same animals, and the number of trackways may overestimate the number of minute and small bipedal dinosaurs present.

5.7.6.7 Possible trackmaker interactions

There is no trackway evidence such as a bipedal trackway following a sauropod trackway, which could suggest that there was an interaction between the sauropods and the bipedal dinosaurs. Regarding the general orientation of the trackways, the direction (N-NNE) of sauropod group 1 is completely absent for the bipedal trackways, but there is a peak in the NE orientation of the bipedal trackways. Moreover, apart from T40, they are not in close proximity to the sauropods. The orientation of sauropod group 2 is closer to that of the bipedal trackways, but they are not in close proximity. Furthermore, areas with higher densities of bipedal trackways are never in immediate proximity to any sauropod trackway. All this suggests that the orientation of the bipedal trackmakers is not controlled by the presence of the sauropods and vice versa.

The medium-sized, bipedal trackways do not interfere with the sauropod tracks, but their similar preservation (i.e., deep tracks surrounded with displacement rims) suggests that they were left in close temporal relationship. Trackway T43 is very close to the sauropod trackways in excavation area 2 and crosses S10 and S11, but it is perpendicular to

the trackways of group 1 and almost in the opposite direction to those of group 2. T11 is far away from T43 and from all sauropod trackways. Furthermore, the medium-sized bipedal trackways are not associated in a recognizable way with the minute and small bipedal trackways, and there is also no interference between them. This suggests that both medium-sized, bipedal dinosaurs were moving on their own, and that there was no interaction between the medium-sized, bipedal dinosaurs and the tiny and small sauropods. There was also no interaction between the medium-sized, bipedal dinosaurs and the minute and small bipedal dinosaurs, thus excluding a "stampede scenario" (cf. Thulborn & Wade, 1979, 1984).

The temporal relationship between the sauropods of group 1 and 2 and the minute and small bipedal dinosaurs is difficult to reconstruct because of the sparse track interference. The sauropods tend to overprint the bipedal trackways, and only T38 clearly overprints a sauropod track and was hence left later. This suggests that the minute and small bipedal dinosaurs were present before and also after the passage of the sauropods, and not to exclude a presence during the passage of the sauropods.

Finally, the shallow tracks of sauropod trackways S1 and S2 were most probably left later than the bipedal trackways, when the surface was almost dry and not susceptible for track recording of small animals anymore. This does not exclude that they were still present but left their tracks only in areas that were still slightly humid.

5.7.7 Comparison of the Combe Ronde ichnoassemblages with other ichnoassemblages of NW Switzerland

Even though many tracksites are meanwhile known in the Jura Mountains, the track diversity is low and restricted to tracks of sauropods and large bipedal dinosaurs, chiefly attributed to theropods (large carnosaurs). This may be related to the fact that most of these tracksites were either subjected to erosion over years, that others are small sites or are not well accessible, and finally that illumination is most of the time far from ideal. This makes it difficult to find tracks of smaller animals. Consequently, the ichnoassemblages of the Combe Ronde site are important because they were all excavated, include small tracks, and offer better preservation conditions.

5.7.7.1 Comparison with the Ajoie ichnoassemblages

Besides the ichnoassemblages of the Chevenez—Combe Ronde tracksite described herein, many more ichnoassemblages have meanwhile been revealed by ongoing excavations of the PAL A16 at several localities and within three stratigraphic intervals (review of the tracksites in Marty et al., 2007a). Even though these ichnoassemblages await detailed description, they can already be characterized in a very general way, and here they are referred to as the Ajoie ichnoassemblages.

At the Courtedoux—Sur Combe Ronde site, this includes ichnoassemblages of (1) trackways of small to medium-sized sauropods and medium-sized bipedal dinosaurs on the main track level (Marty et al., 2003), and of (2) a trackway of a tiny sauropod with tracks of medium-sized sauropods on level 1030 (Marty & Cavin, 2003).

At the Courtedoux—Tchâfouè site, this includes ichnoassemblages of (1) tiny to medium-sized sauropods and small, medium-sized, and large bipedal dinosaurs on the main track level; (2) tiny to small sauropods and a large bipedal dinosaur on level 1015; (3) small sauropods and medium-sized to large bipedal dinosaurs on level 1030; (4) small sauropods and tiny to small bipedal dinosaurs on level 1055; (5) tiny to large sauropods and small to medium-sized bipedal dinosaurs on level 1060; (6) small to large bipedal dinosaurs on level 1065; and (7) small to medium-sized bipedal dinosaurs on level 1069 (Marty et al., 2007c). Some of the minute and small tridactyl tracks exhibit a grallatorid phalangeal pad formula, some can possibly be attributed to *Carmelopodus*, and some of the medium-sized and large to *Megalosauripus* (Marty et al., 2007c). Others are similar to the medium-sized tridactyl tracks of morphotype II of the Chevenez—Combe Ronde tracksite.

The Ajoie ichnoassemblages further exhibit diverse trackway orientation patterns and trackways with changes in gauge and gait for both sauropods and bipedal dinosaurs (Marty et al., 2006a, 2007c). The majority of these ichnoassemblages reveal tracks of small and gracile bipedal dinosaurs, including particularly well-defined tracks, revealing more anatomical details of the feet of their trackmakers than those from the Chevenez—Combe Ronde site (e.g.,

Marty et al., 2006a, 2007a, c). Because these small tridactyl tracks are clearly more frequent than the tracks of sauropods and other large bipedal dinosaurs, they can be considered as the typical element of these ichnoassemblages. Marty et al. (2006a, 2007c) suggested that, even if only partially reflecting the former terrestrial vertebrate ecosystem of the Jura platform, the wealth and diversity of these ichnoassemblages indicate a recurrent presence of different groups of predominantly saurischian dinosaurs. The absence of tracks that can clearly be attributed to ornithischian dinosaurs may indicate that they were not (frequently) present in the tidal-flat palaeoenvironments of the Jura carbonate platform, even though it can not be ruled out that some of the tridactyl tracks of the Ajoie ichnoassemblages were left by ornithischian dinosaurs. Finally, the lack of tracks of other animals such as pterosaurs, turtles, and crocodilians is surprising, since those animals were present as indicated by the skeletal record of coeval strata of nearby localities (e.g., Marty & Hug, 2004; Billon-Bruyat & Marty, 2004; Billon-Bruyat, 2005a, b), and of the Late Jurassic of NW Switzerland in general (e.g., Bräm, 1965; Meyer, 1994a; Meyer & Hunt, 1999).

When compared with the other ichnoassemblages of the Ajoie, the ichnoassemblage of the main track level at the Combe Ronde site can be considered as "typical" because of the dominance of small tridactyl tracks. However, the dominance of sauropod tracks and the absence of bipedal trackways within the overlying levels are exceptional. This may be related to a slight change in the palaeoenvironment, which was avoided by the bipedal dinosaurs, or where particular substrate conditions prevented the preservation of smaller tracks.

5.7.7.2 Comparison with other ichnoassemblages of the Jura Mountains

Apart from the tracksites and ichnoassemblages of the Ajoie, all other tracksites of the Jura Mountains are characterized by tracks of mostly medium-sized to large sauropods and medium-sized to large tridactyl tracks (*Megalosauripus* or *Therangospodus*), which are chiefly attributed to large theropods (see also chap. 2.1; Table 2.1).

Small, tridactyl tracks were previously unknown from the Jura carbonate platform. They are generally rare in low latitude carbonate settings (e.g., Pittman, 1992; Lockley & Hunt, 1995; Lockley & Meyer, 2000; Farlow et al., 2006), even though tridactyl tracks smaller than 20 cm are known from several Cretaceous localities within the Adriatic-Dinaric platform (e.g., Dalla Vecchia et al., 1994, 2001, 2002; Dalla Vecchia & Tarlao, 2000).

Accordingly, the ichnoassemblage of the main track level of the Combe Ronde site is the first assemblage described from the Jura Mountains, which not only exhibits small tridactyl tracks, but is even dominated by them. Moreover, the sauropod tracks are decidedly smaller than those described from the other tracksites of the Jura Mountains.

5.7.8 Implications for tetrapod ichnofacies

The repeated association of sauropod and large theropod tracks in marine shoreline carbonates and evaporites was defined as the *Brontopodus* ichnofacies (Lockley et al., 1994a). Sauropod-dominated and sauropod-common track assemblages (including *Parabrontopodus* and related types) were subsequently attributed to the *Brontopodus* ichnofacies (e.g., Meyer & Hauser, 1994; Meyer & Pittman, 1994; Lockley & Meyer, 2000), and accordingly Marty et al. (2003) assigned the ichnoassemblage of the main track level of the Courtedoux—Sur Combe Ronde site to the *Brontopodus* ichnofacies.

Recently, Hunt & Lucas (2006, 2007) argued that all tetrapod ichnofacies defined prior to 2005 (notably also the *Brontopodus* ichnofacies of Lockley et al., 1994a) should be considered as ichnocoenoses, as "they represent the traces of specific communities that lack the stratigraphic and geographic range that would warrant their consideration as archetypal ichnofacies". They defined vertebrate ichnofacies as "recurrent ichnocoenoses that represent a significant portion of Phanerozoic time" and they defined five archetypal tetrapod ichnofacies for nonmarine environments: *Chelichnus, Grallator, Brontopodus, Batrachichnus* and the *Characichichnos* ichnofacies. Thereby, their *Brontopodus* ichnofacies is defined as "majority of tracks are terrestrial, quadrupedal herbivores with small quantities (generally >10%) of terrestrial carnivore tracks; medium-high diversity (4-8 ichnogenera)", and it comprises four ichnocoenoses, i.e., the *Ceratopsipes*, *Carichnium*, *Chelonichnium*, and the *Brontopodus* ichnocoenosis (Hunt & Lucas, 2007). In other words, what was defined by Lockley et al. (1994a) as an ichnofacies is considered as an ichnocoenosis by Hunt & Lucas

(2007) and they summarize several ichnocoenoses in an ichnofacies. Thus, the vertebrate ichnofacies terminology is finding itself under reconsideration. These two paradigms have been referred to by Lockley (2007) as the "old paradigm" (*sensu* Lockley et al., 1994a) and the "new paradigm" (*sensu* Hunt & Lucas, 2007.

Because the Ajoie ichnoassemblages are dominated by the tracks of small and gracile tridactyl dinosaurs (probably carnivores), followed by tracks of sauropods, and tracks of medium-sized to large bipedal dinosaurs including tracks of large theropods, they are clearly different from other ichnofacies and ichnocoenoses so far described, notably the *Brontopodus* ichnofacies of Lockley et al., 1994a) and the *Brontopodus* ichnocoenosis of Hunt & Lucas (2007). It could thus be argued that the Ajoie ichnoassemblages are a different expression of the *Brontopodus* ichnofacies of the "old paradigm", or that they constitute a new ichnocoenosis of the *Brontopodus* ichnofacies of the "new paradigm".

Accordingly, the dominance of gracile and small bipedal dinosaurs within the Ajoie ichnoassemblages may be related to a particular palaeoenvironment, which was frequently entered by these small animals. This could for example indicate the presence of a protected environment nearby, where these small animals found a suitable habitat. Such an environment could be an area covered with vegetation or eolian dune deposits. For the Middle to Late Jurassic Curtis Formation (eastern Utah, U.S.A.), Lockley et al. (2007c) suggested a small theropod ichnofacies to be associated with eolianites and a *Megalosauripus-Therangospodus* ichnofacies with a transgressive surface. There is currently no sedimentological evidence for eolianites in the Kimmeridgian of the Jura carbonate platform. However, vegetated areas may have existed because wood remains are frequently found in the Marnes à *virgula* (e.g., Billon-Bruyat et al., 2006, 2007).

However, the dominance of the small bipedal dinosaurs within the Ajoie ichnoassemblages may also be related to a different community structure or simply to a palaeoenvironment with very favourable preservational conditions for small tracks. Finally, the small tridactyl tracks may also be dominant, because all ichnoassemblages were excavated and freshly exposed so that small tracks were readily found. Maybe the *Brontopodus* ichnofacies of the "old paradigm" respectively the *Brontopodus* ichnocoenosis of the "new paradigm" are dominated by larger tracks (in occurrence of sauropods and large, robust theropods), because at many tracksites smaller tracks were already eroded away prior to the investigation of the tracksites. Nonetheless, to a certain degree, weathering (e.g., of amalgamated track fills) can also reveal small tracks, which may not be visible on a freshly excavated surface. Thus, advanced weathering may explain the lack of small tracks at some tracksites, but weathering alone can not explain the general lack of small tracks in the *Brontopodus* ichnofacies.

It is suggested that the Ajoie ichnoassemblages are dominated by small tridactyl tracks because the represented tidal-flat palaeoenvironments were frequently entered by the trackmakers and offered favourable preservational conditions for small tracks. The general lack of other small tracks such as of turtles, of pterosaurs, or of crocodiles may indicate that these animals were not or less frequently present in those palaeoenvironments or at least not during the periods favourable for track formation and preservation.

The composition of a tetrapod ichnofacies or ichnocoenosis certainly depends on many factors. The palaeoenvironment and the prevailing preservational conditions within are important factors, but the behaviour of the animals is important as well. The frequent presence of a trackmaker species in a given palaeoenvironment during the period susceptible for track formation and preservation depends on its behaviour, which in turn may be related to a number of complex factors. This led Lockley (2007) to suggest that vertebrate ichnofacies are inherently differentiated and more readily differentiated than invertebrate ichnofacies, because vertebrates are complex organisms with varieties of behaviour.

Also, if a vertebrate ichnofacies *sensu* the "old paradigm" or ichnocoenosis *sensu* the "new paradigm" is not defined on the basis of a large and well-defined track sample, it is unlikely to reflect the former tetrapod biocoenosis of a given palaeoenvironment or area, which may lead to a poor understanding of the distribution and the palaeoecology of the trackmakers.

5.7.9 Dinosaur tracks and palaeogeography of the Jura carbonate platform

The importance of dinosaur track-bearing palaeosurfaces in delineating sequence stratigraphic boundaries has long been recognized (e.g., Lockley & Fleming, 1990; Lockley, 1992; Hasiotis et al., 2002; Santisteban, 2005; Meyer et al., 2006; Phillips et al., 2007). In shallow-marine carbonate platform settings, dinosaur tracks have become important for palaeogeographical reconstruction, because they are often the only unequivocal evidence for emersive conditions and the presence of larger landmasses (e.g., Meyer, 1993; Dalla Vecchia et al., 2001; Bosellini, 2002; Dalla Vecchia, 2003; Meyer & Thüring, 2003b; Conti et al., 2005; Dalla Vecchia, 2005; Nicosia et al., 2007). In such settings, the preservation of dinosaur track-bearing palaeosurfaces is generally associated with transgressive deposits (see also chap. 4).

If it can be shown that several tracksites of a given area are of coeval age, they constitute a megatracksite, defined as "a regionally extensive single surface, or very thin package of beds, that is track-bearing or track-rich over a large area, on the order of hundreds to thousands of square kilometres" (Lockley, 1991b, 1997a, b). Owing to this definition, the megatracksite concept enables very detailed palaeogeographical reconstructions on a larger scale, and very detailed palaeoenvironmental reconstructions on a smaller scale. Moreover, if ichnogenera and possible trackmakers can be identified, the megatracksite concept may even allow palaeobiogeographical reconstructions or conclusions about migratory behaviour.

Obviously, the major difficulty of applying the megatracksite concept is to establish the temporal relationship between different track-bearing surfaces at different localities. Consequently, the megatracksite concept was so far mostly applied in a more general way, i.e., to tracksites not exactly of coeval age but located in the same stage, formation, or member (e.g., Lockley & Fleming, 1990; Lockley & Hunt, 1995; Moratalla & Sanz, 1997; Kvale et al., 2001; Diedrich, 2004).

This is not different regarding the Swiss Jura Mountains, where the known tracksites are currently attributed to the "megatracksite in the Lower Reuchenette Formation" and the "megatracksite in the Upper Reuchenette Formation" (Meyer & Thüring, 2003a; Meyer et al., 2006), which were previously also named "Middle Kimmeridgian megatracksite" and "Late Kimmeridgian megatracksite" (Meyer, 2000), respectively (Fig. 5.51). Marty et al. (2003) suggested that some of these terms are questionable since the Kimmeridgian is formally only divided into the Early (Lower) and Late (Upper) Kimmeridgian, and since the Reuchenette Formation is formally not divided (e.g., Thalmann, 1966; Gygi, 2000a, b). Furthermore, a boundary between a

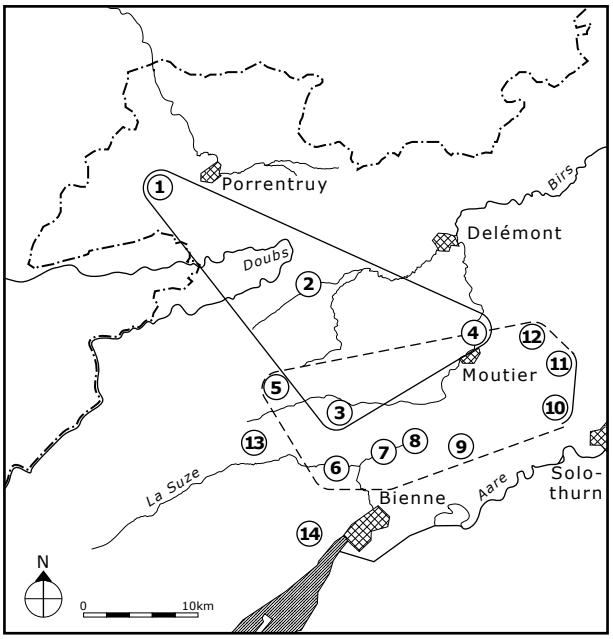


Fig. 5.51: Schematic map of the central Swiss Jura Mountains showing the approximate position of the two megatracksites. The continuous line encompasses the tracksites and track-bearing levels currently attributed to the "megatracksite in the Lower Reuchenette Formation" ("Middle Kimmeridgian megatracksite"): (1) Ajoie ichnoassemblages encompassing the tracksites of the excavations along the Transjurane highway and adjacent localities, (2) Glovelier I & II, (3) Reconvilier, and (4) Moutier I-IV.
The dashed line encompasses the tracksites and track-bearing levels currently attributed to the "megatracksite in the Upper Reuchenette Formation" ("Late Kimmeridgian megatracksite"): (5) Montbautier, (6) La Heutte I-IV, (7) Bürenberg, (8) La Plagne, (9) Grenchenberg I & II, (10) Lommiswil, (11) Gänsbrunnen, and (12) Corcelles I & II. The tracksites (13) Pierre Pertuis I-IV and (14) Twannberg are attributed to the Tithonian Twannberg Formation. After Meyer (2000) and Meyer & Thüring (2003a), modified from Marty et al. (2003). Note that not all tracksites listed in Table 2.1 are shown in this figure.

Lower and Upper Reuchenette Formation is not officially defined. Besides the Kimmeridgian tracksites, the tracksites located in the Tithonian Twannbach Formation are likely to define another megatracksite (e.g., Meyer, 2000; Meyer & Thüring, 2003a), which correlates with the occurrence of dinosaur tracks in the Tithonian near Neuchâtel (unpublished data of Marty et al.) and possibly in Coisia, France (Le Loeuff et al., 2006).

Marty et al. (2003) attributed the early Late Kimmeridgian Courtedoux—Sur Combe Ronde site to the "megatracksite in the Lower Reuchenette Formation", because it is stratigraphically closer to the other tracksites of that megatracksite than to those attributed to the "megatracksite in the Upper Reuchenette Formation". Accordingly, the Chevenez—Combe Ronde site could also be attributed to the "megatracksite in the Lower Reuchenette Formation", since it is even older than the Courtedoux—Sur Combe Ronde tracksite.

However, as stated in Chapter 2.5, dinosaur tracks are now known in the Ajoie, on the Transjurane highway and in the Chevenez – Courtedoux area, at three distinct stratigraphical time intervals, and within each interval on several superimposed levels (Fig. 2.5). These three intervals are very well dated by ammonites (Fig. 2.5), which is not the case for the other tracksites of the Jura Mountains. Nonetheless, since most tracksites of the "megatracksite in the Lower Reuchenette Formation" are located below the Marnes du Banné, these sites are generally older, and since those of the "megatracksite in the Upper Reuchenette Formation" are all located above the Marnes à *virgula sensu lato*, they are clearly younger than the three track-bearing intervals composing the Ajoie ichnoassemblages.

Regarding the tracksites of the Ajoie ichnoassemblages, very precise correlations are possible between several of the excavated levels, notably the main track levels, which are located at the base of each of the three track-bearing laminite intervals. Coupled with sedimentological analyses of the surfaces and of tracks (as carried out in chap. 4), this will allow making very detailed palaeoenvironmental reconstructions of the tidal-flat palaeoenvironment and its evolution, and help to better understand the palaeoecology of the dinosaurs in those environments. This was recently demonstrated on multiple reptile track-bearing horizons of Early to Middle Triassic carbonate tidal flat deposits from northern Germany (Diedrich, 2007).

Regarding the tracksites of NW Switzerland, at least five dinosaur track-bearing, emersive intervals exist in the Kimmeridgian and the Tithonian defining five distinct megatracksites. Many more track-bearing intervals are likely to exist, since evidence for emersion is known from other time intervals (e.g., Colombié, 2002; Jank et al., 2005; 2006a, b).

Meyer et al. (2006) suggested that the five track-bearing intervals of the Jura Mountains are not large continuous surfaces and that the occurrence of tracksites is controlled by ancient basement structures (see Wetzel et al., 2003, Allenbach & Wetzel, 2006), because all tracksites are located on Permian horst structures. They postulated that these horst structures, which are aligned in ESE-NNW direction between the northeastern corner of the Massif Central and the southwestern corner of the London-Brabant Massif (Fig. 2.4), were emergent during sea-level lowstands and used as recurrent migration routes by dinosaurs. However, even if the Jura carbonate platform may have regularly served as a "faunal exchange corridor" (in the sense of long-distance, nomadic migration) between these two massifs, this does not exclude that *in situ* dinosaur populations were present or that larger dinosaurs (e.g., sauropods, large theropods) seasonally migrated into these tidal-flat environments of the Jura carbonate platform from the adjacent massifs, at least during periods of sea-level lowstands.

Future work should focus on the establishment of a more detailed stratigraphical correlation between the tracksites and ichnoassemblages of the Ajoie and the other tracksites of NW Switzerland and the Jura Mountains. The stratigraphical framework for such correlations is provided by recent advance in lithostratigraphical, sequence-stratigraphical, and cyclostratigraphical studies carried out in the Late Jurassic of NW Switzerland (for references see chap. 2.5 and review by Strasser, 2007). If the dinosaur track-bearing intervals are integrated into this stratigraphical framework, they will contribute towards a better understanding of the evolution of the terrestrial palaeoecosystem and palaeoenvironment, of the extent of the megatracksites, of the palaeogeography of the Jura carbonate platform, and of dinosaur palaeobiogeography and possible dinosaur migration behaviour and migration routes.

5.8 Conclusions

This chapter investigated the ichnoassemblage of the main track level of the Combe Ronde site (excavation areas 1, 2, and 3), composed of 14 trackways of tiny and small sauropods, 41 trackways of minute and small bipedal dinosaurs, and 2 trackways of medium-sized bipedal dinosaurs, as well as three sauropod trackways from overlying levels.

The systematic analysis of the track and trackway data provided insight into the locomotion capabilities of the trackmakers and their behaviour and palaeoecology on the Jura carbonate platform.

Sauropod tracks and trackways

Because the importance of the "trackway gauge concept" in the classification of sauropod trackways is debated, particular emphasis was put on the characterization of sauropod trackway gauge by calculating the pes trackway ratio (PTR) of Romano et al. (2007) and the herein defined [WAP/PL]-ratio. Both ratios are meaningful to characterize trackway gauge, and they are important for the analysis and comparison of sauropod trackways, ichnotaxonomy and trackmaker identification, and the interpretation of locomotion capabilities.

The comparison of these ratios of the sauropod trackways from the Chevenez—Combe Ronde tracksite with trackways of the Courtedoux—Sur Combe Ronde site and selected sauropod ichnogenera established a relationship between the PTR and the [WAP/PL]-ratio.

Sauropod trackways with a [WAP/PL]-ratio smaller than 1 and a PTR larger than 50% can be considered as narrow-gauge, those with a [WAP/PL]-ratio between 1 and 1,2 corresponding to a PTR of about 40-50% as transitional or medium-gauge between narrow-gauge and wide-gauge, those with a [WAP/PL]-ratio between 1,2 and 2 corresponding to a PTR of about 30-40% as wide-gauge, and those with a [WAP/PL]-ratio higher than 2 corresponding to a PTR of less than about 30% as very wide-gauge trackways. It is suggested to increase the provisional PTR boundary of Romano et al. (2007) between the wide-gauge and medium-gauge category from 35% to 40% to include the ichnogenus *Brontopodus* in the wide-gauge field.

The sauropod trackways from the Chevenez—Combe Ronde site are attributed tentatively to the ichnogenus *Brontopodus*, because of their medium-gauge to wide-gauge and a small heteropody, but they also share some of the characteristics of narrow-gauge ichnogenera such as *Breviparopus* and *Parabrontopodus*, and of the trackways from the Courtedoux—Sur Combe Ronde site.

Based on trackway gauge, the trackways from the Chevenez—Combe Ronde site can be attributed to derived and robust "brachiosaurid" or "titanosaurid" dinosaurs, contrary to the narrow-gauge trackways of the Courtedoux—Sur Combe Ronde site attributed to basal macronarians or "diplodocid" sauropods. This indicates the very close temporal and regional presence of both groups of sauropods on the Jura carbonate platform.

At the Chevenez—Combe Ronde tracksite, many different trackway patterns and configurations, amongst them parallel trackways with tracks of similar size and preservation, indicate a wide range of locomotion capabilities for their sauropod trackmakers. The analysis of the mean trackway parameters suggests that trackway patterns (the degree of manus overprinting by the pes) and different trackway configurations including trackway gauge are not only related to locomotion speed, and there is no evidence of a relation to ontogeny. It is suggested, that differences in trackway pattern and configuration are an expression of "individual walking style" and/or the behaviour of the trackmakers, which may be related to the presence of other animals nearby and also to the substrate properties. These circumstances are referred to "behavioural trackway variation" and "trackway variations related to differences in substrate", respectively (cf. Wilson, 2005).

As narrower trackways tend to have shallower tracks, the observed variation in trackway gauge may be related to differences in substrate properties, but this does not change the general medium-gauge to wide-gauge appearance of the Chevenez—Combe Ronde trackways. The trackway S10 from the main track level of the Combe Ronde site is the only trackway with a remarkable very wide-gauge. This can hardly be explained by substrate and behaviour contributes only, and may be an expression of a wider posture possibly related to another trackmaker species or sexual dimorphism.

Manus-dominated trackways are explained by trackmakers exerting more pressure on the manus than the pes. This may have been enhanced by a more digitigrade manus posture due to particular substrate

properties and/or a special behaviour of the trackmaker related to it, rather than a different trackmaker species with a more anteriorly positioned centre of mass. Subjected to weathering such trackways may rapidly degrade into manus-only trackways.

At the Chevenez—Combe Ronde site, an origin of pes-only and manus-dominated trackways due to swimming sauropods can be excluded because within the supratidal flat palaeoenvironment the water was never deep enough. This confirms that they are related to the terrestrial locomotion capabilities and behaviour of their trackmakers.

Tridactyl tracks and trackways

Most of the minute and small tridactyl tracks are attributed to preservational morphotypes. A few tracks are considered as anatomical morphotypes, described as morphotype I, which is assigned to the ichnogenus *Carmelopodus* based on a 2-3-3 phalangeal pad formula and isolated, slender and slightly tapered digits with claw impressions. This extends the appearance of this ichnogenus from the Middle Jurassic to the Late Jurassic. The ichnogenus *Carmelopodus* is affiliated with theropods and a possible trackmaker could be a small theropod dinosaur similar in size as the Late Jurassic *Compsognathus* or *Juravenator*.

The medium-sized trackway T43 defines morphotype II, characterized by oval and blunt digits, a digit III with an elongated trapezoidal shape, a high total divarication angle, and a very narrow-gauge and irregular trackway. This morphotype shares some of the typical features of the ichnogenus *Therangospodus* (attributed to large and robust theropods) but also some of ornithopod ichnogenera.

Carmelopodus and *Therangospodus* are commonly attributed to theropods but tridactyl tracks of (saurischian) theropods and ornithischian dinosaurs are generally difficult to distinguish from each other. Ornithischian trackmakers can not be excluded neither for the tracks of morphotype I nor for those of morphotype II.

The [WAP/PL]-ratio of the minute and small bipedal trackways suggests that their trackmakers may have switched between different hindlimb postures at lower speeds (expressed by narrower and wider gauges), and that they may have preferred an intermediate posture or gauge at higher speeds. The poor correlation between trackway gauge and relative stride length could indicate that the walk-run transition was gradually rather than sharp.

Dinosaur palaeoecology, ichnofacies, and palaeo(bio)geography

At Chevenez—Combe Ronde site, the recurrent presence of sauropod tracks on several superimposed palaeosurfaces, the presence of tiny sauropod tracks attributed to "post-hatchling" individuals in their first year of growth, and of minute, small, and medium-sized tridactyl tracks suggest that dinosaurs formed *in situ* populations on the Jura carbonate platform. However, the ichnoassemblage of the main track level is just a snapshot of these dinosaur populations and is not representative for the relative frequencies of the different dinosaur groups (community structure)and their size classes present on the Jura carbonate platform.

On the main track level, the two groups of parallel sauropod trackways clearly indicate gregarious behaviour amongst tiny and small sauropods. The pattern of overprinting between tracks of the two groups and the differences in trackway patterns and configurations in excavation area 2 suggest that the two groups may have met each other. They may have wandered over the supratidal flats to get from one of their drinking or feeding grounds to another, and they may have been present at least seasonally.

The minute and small bipedal dinosaurs were frequent visitors on the supratidal flats and left their trackways on several occasions during the period susceptible for track recording. Their linear and mostly regular trackways indicate that they rapidly crossed the supratidal flats to get to one of their favourite hunting grounds, which may for example have been tidal ponds where fish got captured during low tides. Accordingly, the number of trackways may overestimate the number of minute and small bipedal dinosaurs present in that environment at any given time period.

The trackway orientation pattern of the main track level does not indicate the presence of a nearby shoreline, and it provides no evidence of interactions between the different groups of dinosaurs.

The ichnoassemblage of the main track level from the Chevenez—Combe Ronde site is the first ichnoassemblage from the Jura Mountains, which exhibits minute (< 10 cm) tridactyl tracks. It is one of several ichnoassemblages of the Ajoie, which are characterized by the dominance of minute and small tridactyl tracks, followed by tracks of tiny to large sauropods, and tracks of medium-sized to large bipedal dinosaurs including large theropods. Since the majority of these tracks is of saurischian affinity it is suggested that the former tetrapod biocoenosis was dominated by saurischian dinosaurs.

Because of the abundance of small tridactyl tracks, the ichnoassemblage of the main track level of the Combe Ronde site, is clearly different from other dinosaur-dominated ichnoassemblages of carbonate settings. Thus, it can not be attributed to the *Brontopodus* ichnofacies of Lockley et al. (1994a) or the *Brontopodus* ichnocoenosis of Hunt & Lucas (2007).

In the case of those ichnoassemblages commonly attributed to the *Brontopodus* ichnofacies or ichnocoenosis, the lack or rareness of small tridactyl tracks may indicate the absence of small trackmakers in those palaeoenvironments or unsuitable conditions for the formation and preservation of small tracks. However recent weathering of small tracks can also not be excluded as a reason for the lack of small tridactyl tracks at least at some heavily weathered tracksites.

The Ajoie ichnoassemblages in general are dominated by small tridactyl tracks, indicating that small tridactyl trackmakers were frequently present during time periods susceptible for track formation and preservation in environments favourable for the preservation of small tracks. Consequently, the lack of other small tracks such as of turtles, of pterosaurs, or of crocodiles suggests that these animals were not or less frequently present in those mostly supratidal palaeoenvironments.

The frequent presence of large sauropod tracks within the Ajoie ichnoassemblages excludes dwarfed insular animals as the trackmakers of the tiny and small trackways of the Combe Ronde tracksite. Also, this suggests that during periods of sea-level lowstand, the Jura carbonate platform was an emergent area connected with the larger landmasses of the London-Brabant Massif in the northeast and the Massif Central in the southwest. Even if during sea-level lowstands, dinosaurs may have used these emergent areas as long-distance migration routes between the massifs, *in situ* dinosaur populations were present on the Jura carbonate platform as well. The larger dinosaurs (e.g., the sauropods) may also have seasonally migrated into these tidal-flat environments from the adjacent massifs.

5.9 Outlook and perspectives

The detailed analysis of a large trackway sample from the Chevenez—Combe Ronde site offers a snapshot of dinosaur life on the tidal-flats of the Jura carbonate platform in the Late Jurassic, but many issues regarding ichnotaxonomy, identification of possible trackmakers, locomotion capabilities, and dinosaur palaeoecology are still poorly understood. Some of these are likely to be answered by systematic analyses of the larger data base of the Ajoie ichnoassemblages and their comparison with the other tracksites of the Jura Mountains or other similar dinosaur ichnoassemblages and ichnocoenoses. This may reveal the typical behaviour of the trackmakers in tidal-flat palaeoenvironments.

Recently excavated ichnoassemblages of the Ajoie comprise well-defined sauropod and tridactyl tracks with impressions of the digits and/or claws and may facilitate a better classification of the sauropod trackways.

Well-defined tridactyl tracks (anatomical morphotypes) could be measured including more specific parameters (e.g., Weems et al., 1992; Olsen et. al., 1998) and more specific statistical analyses could be carried out (e.g., Moratalla et al., 1988; Demathieu, 1990; Gand & Demathieu, 2005; Gand et al., 2005), than done in this work.

In this study, only mean trackway parameters were analysed. A better insight into the locomotion capabilities can be provided by analyses of the variation in track and trackway parameters along the course of trackways (e.g., Mossman et al., 2003), such as the long bipedal trackway T10 and its continuation T41 from the main track level. The minute tracks of this trackway could be compared

with the pes of small Late Jurassic tridactyl dinosaurs (e.g., *Compsognathus*, *Juravenator*) and combined with evolutionary robotics models (e.g., Sellers et al., 2005; Sellers & Manning, 2007).

In quadrupedal trackways, besides the [WAP/PL]-ratio, the ratio between the width of the angulation pattern of the manus and the corresponding manus track width, that is the [WAM/MW]-ratio, characterizes the trackway gauge of the manus tracks. The ratio between the [WAP/PL]-ratio and the [WAM/MW]-ratio, that is the [WAP/PL]-ratio/[WAM/MW]-ratio), characterizes the relative position of pes and manus tracks with respect to the trackway midline. The latter two ratios were not as yet systematically analysed. Moreover, in both the [WAP/PL]-ratio and the [WAM/MW]-ratio the indices of pes (IPS) and manus (IMS) track size, respectively, could also be used instead of the pes length (PL) and the manus width (MW). It still has to be analysed whether these ratios would prove more meaningful for the characterization of trackway gauge.

Sauropod ichnotaxa continue to be debated because the gauge concept has been questioned. Ongoing analyses of patterns and configurations (including trackway gauge) of sauropod trackways will contribute towards a better understanding of the general locomotion capabilities of sauropod dinosaurs. Such research could be stimulated by comparisons with recent large quadrupedal animals such as elephants (e.g., Hutchinson et al., 2003) and their trackways.

This will help to differentiate the influence of behaviour, locomotion speed, and substrate on track morphology (e.g., presence or absence of claw impressions), trackway patterns (degree of overprinting of the manus by the pes), differences in depth and heteropody between pes and manus tracks, and trackway configuration (e.g., trackway gauge, relative position of pes and manus tracks). Synapomorphies and typical trackway configurations can then better be recognized and integrated in diagnoses of sauropod ichnotaxa.

* * *

6 - General conclusions and outlook

Fossil vertebrate tracks are at the interface of sedimentological, palaeontological, and biomechanical research, because they resulted from the complex interaction of a foot with the substrate in a given environment. Their study is a complex matter, and they can only be fully understood if they are analysed using an interdisciplinary approach.

Vertebrate tracks should first be seen as deformed and lithified sediment or as macrosedimentary structures, which offer a great potential for sedimentological and palaeoenvironmental interpretations. Notably the tracks of large vertebrates such as sauropod dinosaurs exert a heavy impact on the substrate of a given environment and at a given time. This impact leads to the formation of specific structures on the sediment surface, notably the true track and overall track, but also within the sediment underneath and around the track, for instance in the form of undertracks in laminated sediment or in the form of underprints and deep tracks in unlaminated, deep, and water-saturated sediment.

The true track corresponds to the sediment surface that was in direct contact with the foot and the overall track encompasses the true track and all structures such as displacement rims, ejecta, or other extramorphological features associated with the true track. When a foot is put in a perfect way onto an ideal substrate, true tracks may exceptionally reveal details of the foot anatomy, and only such tracks should be used for ichnotaxonomy and the identification of the trackmaker. Nonetheless, poorly-defined tracks should also be integrated into ichnological studies, because they are related to the behaviour of the trackmaker, to particular substrate conditions and the environment, or to taphonomic processes acting after track formation. They may be used to interpret the behaviour of the trackmaker and of the substrate properties (notably water content) at the time of track formation.

Taphonomic processes acting on a track after its formation depend on sedimentary processes affecting the depositional environment. This is demonstrated on recent tidal flats, where most exposed and consolidated vertebrate tracks are affected by taphonomic processes. The ubiquitous microbial mats play an important role because they consolidate or lithify shortly after track formation and preserve a track, or because renewed and/or repeated growth of the microbial mat may modify a true track leading to the formation of modified true tracks, internal overtracks, and overtracks. Amongst consolidated footprints of recent tidal flats poorly-defined true tracks, modified true tracks, and overtracks were most frequently observed whilst unmodified, and clearly identifiable true tracks were only rarely found.

These processes observed on recent tidal flats can be inferred from fossil tracks. This is facilitated by systematic level-by-level excavations of track-bearing intervals as well as by the analysis of the overlying and underlying layer in the case of a single track-bearing level. The absence of overtracks on top of deep tracks surrounded by large displacement rims may indicate covering up by storm sedimentation, which may also be indicated by trapping of coarse sediment within the tracks. Poorly-defined tracks are cut into serial-sections to study the underlying sediment. This provides insight into the substrate properties at the time of track formation. A stack of undertracks indicates biolaminated sediment, whilst the absence of any undertracks may point to a thick and non-laminated sediment layer. The truncation of track structures by an undeformed layer can be explained by consolidation of that layer prior to the formation of the track, which is important for reconstructing the consolidation history of the sediment. Finally, track morphology and associated track features that resulted from taphonomic processes can be linked to the exposure index, making tracks useful in palaeoenvironmental reconstructions.

Once the palaeoenvironment and the processes acting during the formation and preservation of tracks are understood, tracks can be used in ichnological studies. Anatomical morphotypes reflecting the foot morphology, and which are little affected by the kinematics of the trackmaker and substrate properties, can be identified and used in ichnotaxonomy. Based on ichnodiversity, the composition of the ancient terrestrial vertebrate palaeoecosystem in a given environment or area can be interpreted, even if the precise trackmaker species remains unidentified.

Trackways reflect the locomotion capabilities of the trackmakers and their behaviour, which may partially be related or influenced by the environment and the substrate in which the tracks were left. Systematic trackway analyses disclose the "behavioural variation" and the "variations related to differences in substrate" of the trackways of a given ichnotaxon, and trackways representative of typical trackmaker behaviour can be recognized. The configuration, including trackway gauge, of such typical trackways can then be used in the diagnosis of an ichnotaxon, and this in turn may help to attribute trackways with poorly-defined tracks to a given ichnotaxon. Moreover, the systematic analysis of trackways is a valuable contribution to the understanding of the general locomotion capabilities of the trackmaker, even though it will remain difficult to provide exact speed calculations based on trackways. Finally, the alignment of trackways is an expression of the behaviour of the trackmakers in a given environment, and the relative frequency of trackways can be used to make conclusions about the community structure of the trackmakers in a given area. Size-frequency data of trackways attributed to a single ichnotaxon may be representative of the population structure of the corresponding trackmaker.

The Chevenez—Combe Ronde tracksite

The systematic and detailed level-by-level excavation and analysis of a large trackway sample from the Chevenez—Combe Ronde site offer a snapshot of dinosaur life on the Jura carbonate platform in the Late Jurassic, and provide insight into the (tidal-flat) palaeoenvironment and the sedimentary processes acting within.

The sedimentological and taphonomical analysis of sauropod tracks and track cross-sections discloses the sediment properties at the time of track formation and consolidation history prior to track formation, and reveals the processes that modified the tracks during subaerial exposure and that integrated them into the sedimentary record.

Track morphology, associated track features, and sedimentary structures identify the palaeoenvironment as a supratidal flat or marsh located relatively far away from a coastline and characterized by an exposure index higher than 60%-90% for most of the time. This implies that vertebrate tracks are commonly preserved also in environments with a high exposure index.

If these supratidal flats were not susceptible for track recording during most of the time, because they consolidated rapidly after wetting, sauropod tracks may only exceptionally have been registered and incorporated into the sedimentary record. Accordingly, the presence of six palaeosurfaces with sauropod tracks within an elementary sequence (20 kyr) suggests that sauropods were regular rather than chance visitors. However, if the supratidal flats were susceptible for track recording during longer periods, an occasional presence of sauropods is rather suggested, as is also indicated by the absence of completely dinoturbated levels.

The level-by-level documentation of the superposed surfaces enables to identify true tracks and to distinguish them from undertracks and overtracks, which was often not possible from a purely morphological point of view. At the Combe Ronde site, true tracks are most common, and many of these are modified true tracks due to the presence of internal overtracks.

Cross-sections of sauropod tracks provide insight into the sediment consolidation history and walking dynamics of dinosaurs and confirm that sauropods put their hindfeet in a pronounced plantigrade way on the ground.

At the Combe Ronde site, the most diverse ichnoassemblage is the main track level. It is characterized by the dominance of trackways with minute and small tridactyl tracks, followed by trackways of tiny and small sauropods attributed to post-hatchling individuals in their first year of growth, and of medium-sized bipedal dinosaurs. This suggests that these dinosaurs formed *in situ* populations on the Jura carbonate platform during periods of emersion.

The alignment of trackways on the main track level shows no evidence of a nearby shoreline and

of interactions between the different groups of dinosaurs. It indicates gregarious behaviour amongst tiny and small sauropods and suggests that minute and small bipedal dinosaurs were frequent visitors on the supratidal flats.

The sauropod trackways are all medium-gauge to wide-gauge and are tentatively assigned to the ichnogenus *Brontopodus* attributed to derived and robust "brachiosaurid" or "titanosaurid" dinosaurs.

Based on their 2-3-3 phalangeal pad formula, some of the minute and small tridactyl tracks can be assigned to the ichnogenus *Carmelopodus*, extending it from the Middle Jurassic into the Late Jurassic. The minute and small tridactyl tracks were likely left by a small theropod dinosaur similar in size as *Compsognathus* or *Juravenator*. The medium-sized trackway T43 defines morphotype II, characterized by a digit III with an elongated trapezoidal shape and a very narrow-gauge irregular trackway. This morphotype shares some of the typical features of the ichnogenus *Therangospodus* (attributed to large and robust theropods), but also some of ornithopod ichnogenera.

The analyses of trackway parameters including trackway gauge provide insight into the locomotion capabilities of both bipedal and sauropod dinosaurs. The variability of the trackways reflects the general locomotion capabilities of the trackmakers and is an expression of individual walking style and behaviour, which may be related to substrate properties. The gauge of sauropod trackways can be quantified with the pes trackway ratio and the here introduced [WAP/PL]-ratio (width of the pes angulation pattern / pes length).

The mean parameters of the sauropod trackways analysed suggest that trackway patterns (the degree of manus overprinting by the pes) and different trackway configurations (including trackway gauge) are not only related to locomotion speed, and they provide no evidence of a relation with ontogeny. Trackway gauge is possibly dependent on substrate properties and a special behaviour of the trackmaker related to it, but this does not change the overall medium-gauge to wide-gauge appearance of a given trackway.

The manus-dominated and pes-only sauropod trackways of the Combe Ronde site are explained by trackmakers exerting more pressure on the manus than the pes, and by overprinting of the manus by the pes, respectively.

The Ajoie ichnoassemblages

The ichnoassemblage of the main track level from the Chevenez—Combe Ronde site is the first from the Jura Mountains with minute and small tridactyl tracks and furthermore exhibits tracks of tiny sauropods. Because it is only a snapshot of dinosaur life and only one of several ichnoassemblages of the Ajoie, it is not representative of the relative frequencies of the different dinosaur groups (community structure) and their size classes (population structure) present on the Jura carbonate platform during the Late Jurassic.

The Ajoie ichnoassemblages are characterized by the dominance of minute and small tridactyl tracks, followed by tracks of tiny to large sauropods, and tracks of medium-sized to large bipedal dinosaurs including large theropods. Sauropod trackways include narrow-gauge and wide-gauge trackways indicating the presence of "basal" and derived sauropods.

The frequent presence of large sauropod tracks within the Ajoie ichnoassemblages excludes the presence of dwarfed, insular animals as the trackmakers of the tiny and small trackways of the Chevenez—Combe Ronde tracksite.

During periods of sea-level lowstand, the Jura carbonate platform was an emergent area connected with the larger landmasses of the London-Brabant Massif in the northeast and the Massif Central in the southwest. Even if during sea-level lowstands, dinosaurs may have used these emergent areas as long-distance migration routes between the massifs (in the sense of nomadic migration), *in situ* dinosaur populations were present on the Jura carbonate platform as well. The larger dinosaurs (e.g., sauropods, large theropods) may furthermore have seasonally migrated into these tidal-flat environments from the adjacent massifs.

Because the Ajoie ichnoassemblages are dominated by small tridactyl tracks, they differ from other Jurassic tetrapod ichnofacies in carbonate settings, notably from the *Brontopodus* ichnofacies. In the case of those ichnoassemblages commonly attributed to the *Brontopodus* ichnofacies, the lack or rareness of small tridactyl tracks may indicate the absence of small trackmakers in those palaeoenvironments or unsuitable conditions for the formation and preservation of small tracks.

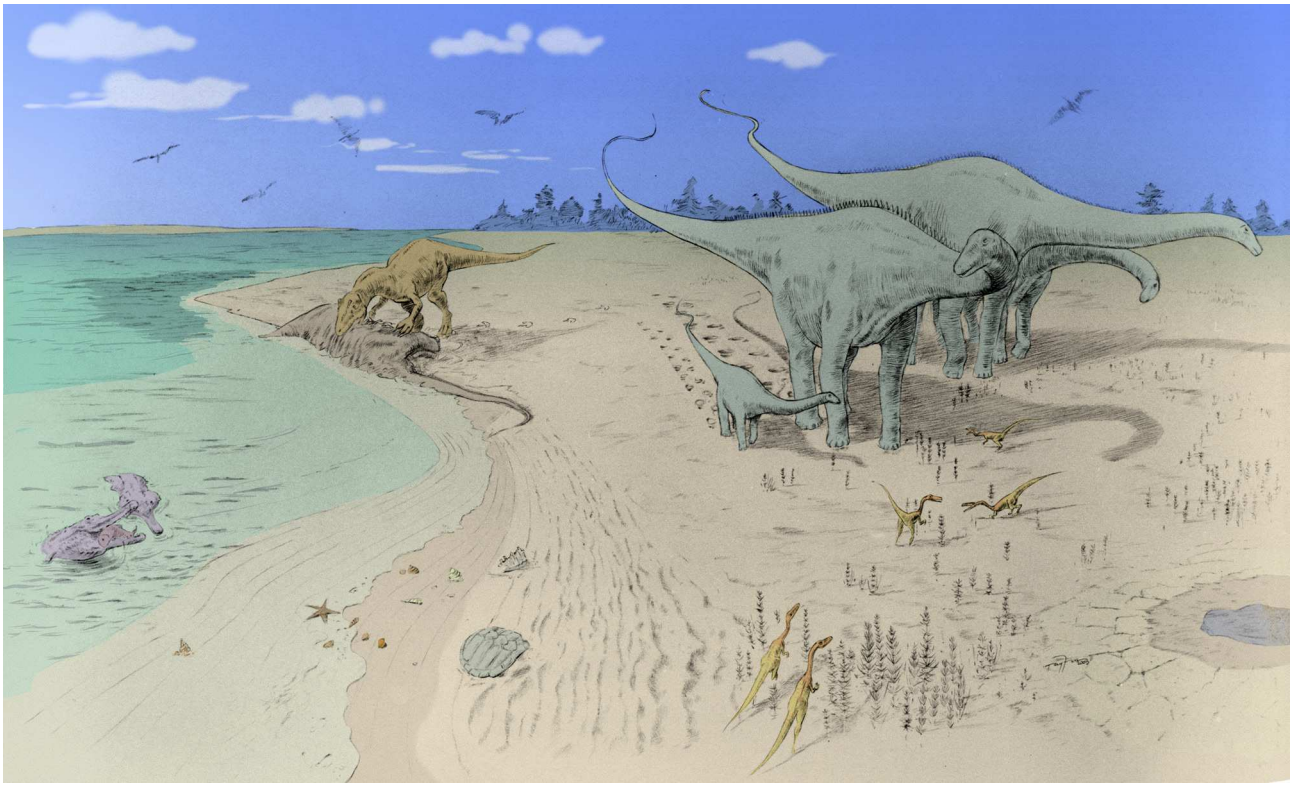


Fig. 6.1: Life reconstruction of a Late Jurassic tidal-flat palaeoenvironment on the Jura carbonate platform, based on ichnological evidence of the Ajoie ichnoassemblages and body fossils of the excavations of the PAL A16. Note that the Combe Ronde tracksite is not suggested to be located in close proximity to any coastline, as shown in this reconstruction. Drawing by Tayfun Yilmaz (PAL A16), courtesy of the PAL A16, ©OCC–SAP (*Office de la culture, Section d'archéologie et paléontologie*).

Outlook

By the end of 2006, the dinosaur track excavations in the Ajoie, along the Transjurane highway and in the Chevenez–Courtedoux area, resulted in the uncovering of dozens of ichnoassemblages composed of over 4200 tracks and 280 trackways. Here, these ichnoassemblages are referred to as the Ajoie ichnoassemblages.

This study highlights the benefits of systematic sedimentological and ichnological analyses of large track and trackway samples, which disclose variations related to behaviour and to differences in substrate. This allows recognizing anatomical morphotypes and trackway configurations representative of typical trackmaker behaviour. The latter can then also be used in ichnotaxonomical classification. Similar approaches should be in the focus of future work and performed on the remaining Ajoie ichnoassemblages. This will provide further insight into the Late Jurassic terrestrial palaeoecosystem of the Jura carbonate platform, and opens new vistas in research on dinosaur palaeoecology.

Future work should also focus on the establishment of a more detailed stratigraphical correlation between the tracksites and ichnoassemblages of the Ajoie and the other tracksites of NW Switzerland and the Jura Mountains. If the dinosaur track-bearing intervals are integrated into a well-defined stratigraphical framework, they will contribute towards a better understanding of the extent of the megatracksites and palaeogeography, and of dinosaur migration behaviour and migration routes on the Jura carbonate platform.

Finally, well-preserved anatomical morphotypes of the Ajoie ichnoassemblages should be accurately compared (e.g., landmark analysis) with similar tracks from other Late Jurassic localities worldwide. This will contribute to a better understanding of Late Jurassic dinosaur ichnotaxonomy, and this may be important for Late Jurassic dinosaur palaeobiogeography.

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Plate 2.1 – Systematic level-by-level excavation and documentation (2003-2005)

A: Chevenez—Combe Ronde tracksite, excavation area 3: Opening of the excavation area 3 in August 2003 with a shovel excavator. View towards the south.

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C: Chevenez—Combe Ronde tracksite, excavation area 3: Excavation of the main track level in the middle part of excavation area 3 in September 2004.

D: Chevenez—Combe Ronde tracksite, excavation area 3: Documentation of level 520 in the middle part of excavation area 3 in September 2004.

E: Chevenez—Combe Ronde tracksite, excavation area 3: Documentation of the main track level by laserscanning and photogrammetry, carried out by Terra Data AG (Einsiedeln) in September 2004. The *Cyrax* laserscanner is attached to the working platform of the *Manitou* crane. View towards the north-northeast.

F: Chevenez—Combe Ronde tracksite, excavation area 2: Documentation of the main track level by laserscanning, carried out by Terra Data (Einsiedeln) in November 2005. Tracks are coloured, view towards the southwest.

G: Chevenez—Combe Ronde tracksite, excavation area 3: Fabrication of silicon casts of the trackways of the main track level at the southern end of excavation area 3. View towards the south.

H: Chevenez—Combe Ronde tracksite, excavation area 3: Fabrication of silicon casts of the trackways of the main track level in the middle part of excavation area 3. In the foreground the sauropod trackway S1, heading towards the reader, is visible. Tracks are coloured, view towards the south.


A


B


C


D


E


F


G


H

Plate 2.2 – Overview of the excavation areas 1, 2, and 3

A: Chevenez—Combe Ronde tracksite, excavation areas 2 and 3 in June 2004, view towards the south-southwest.

B: Chevenez—Combe Ronde tracksite, excavation area 3 in September 2004, view towards the south-southwest.

C: Chevenez—Combe Ronde tracksite, excavation areas 1, 2, and 3 in September 2004. Picture is taken from top of the *Manitou* crane, which was used for the laserscanning. Note the sauropod trackway S2 at the bottom of the picture. Tracks are coloured, view towards the north.

D: Chevenez—Combe Ronde tracksite, excavation areas 1 and 2, in September 2004. Picture is taken from top of the *Manitou* crane. Note the normal fault between excavation areas 1 and 2, which uplifts area 2 by about two metres. View towards the north.

E: Chevenez—Combe Ronde tracksite, excavation area 3 in September 2004. The *Manitou* crane was used for laserscanning and photogrammetry. View towards the south-southwest.

F: Chevenez—Combe Ronde tracksite, excavation areas 2 and 3 in October 2004 during the open days for the public. View towards the south-southwest.

G: Chevenez—Combe Ronde tracksite, excavation area 1 in October 2004 during the open days for the public. Trackways are coloured, view towards the south.

H: Chevenez—Combe Ronde tracksite, excavation area 17 in February 2007. The tracks of sauropod trackway S17 are coloured, view towards the north. Note that the data of this excavation area are not included in the present work. Photo by Y. Marti (PAL A16).


A
Area 3
Area 2
B
C
Area 1
Area 2
Area 3
D
Area 1
Area 2
E
F
Area 2
G
H

Plate 2.3 – Emergency excavation and bridge extension (2006-2007)

This plate illustrates the excavation of the main track level on the enlargement of excavation area 3, and the successive construction of the additional highway bridge crossing the tracksite. Note that the data of the enlargement of excavation area 3 are not included in this study. All photos by Y. Marti (PAL A16).

A: Chevenez—Combe Ronde tracksite, main track level: Enlargement of excavation area 3 in June 2006 with the help of heavy shovel excavators. View towards the south-southwest.

B: Chevenez—Combe Ronde tracksite, main track level: Uncovering of the last 10 m of the enlargement of excavation area 3 in June 2006. Note the Combe Ronde viaduct in the background. View towards the southwest.

C & D: Chevenez—Combe Ronde tracksite, main track level: Aerial views of the enlargement of excavation area 3 in June 2006. Note the position of the pillars, of which silicon casts were produced prior to destruction (arrow).

E: Chevenez—Combe Ronde tracksite, enlargement of excavation area 3: Documentation of the main track level in June 2006. Note sauropod trackway S2 heading towards the reader, and shovel excavator digging a hole for a pillar in the background. Tracks are coloured, view towards the southwest.

F: Chevenez—Combe Ronde tracksite, enlargement of excavation area 3, June 2006: Excavated fundament of one of the pillars within the main track level. Scale bar in the upper right corner of the hole measures 50 cm.

G: Chevenez—Combe Ronde tracksite, enlargement of excavation area 3, August 2006: The main track level has been covered up with sand and gravel, and the construction of the additional bridge started.

H: Chevenez—Combe Ronde tracksite, enlargement of excavation area 3, February 2007: The construction of the additional bridge is finished, and the main track level still covered with sand and gravel.

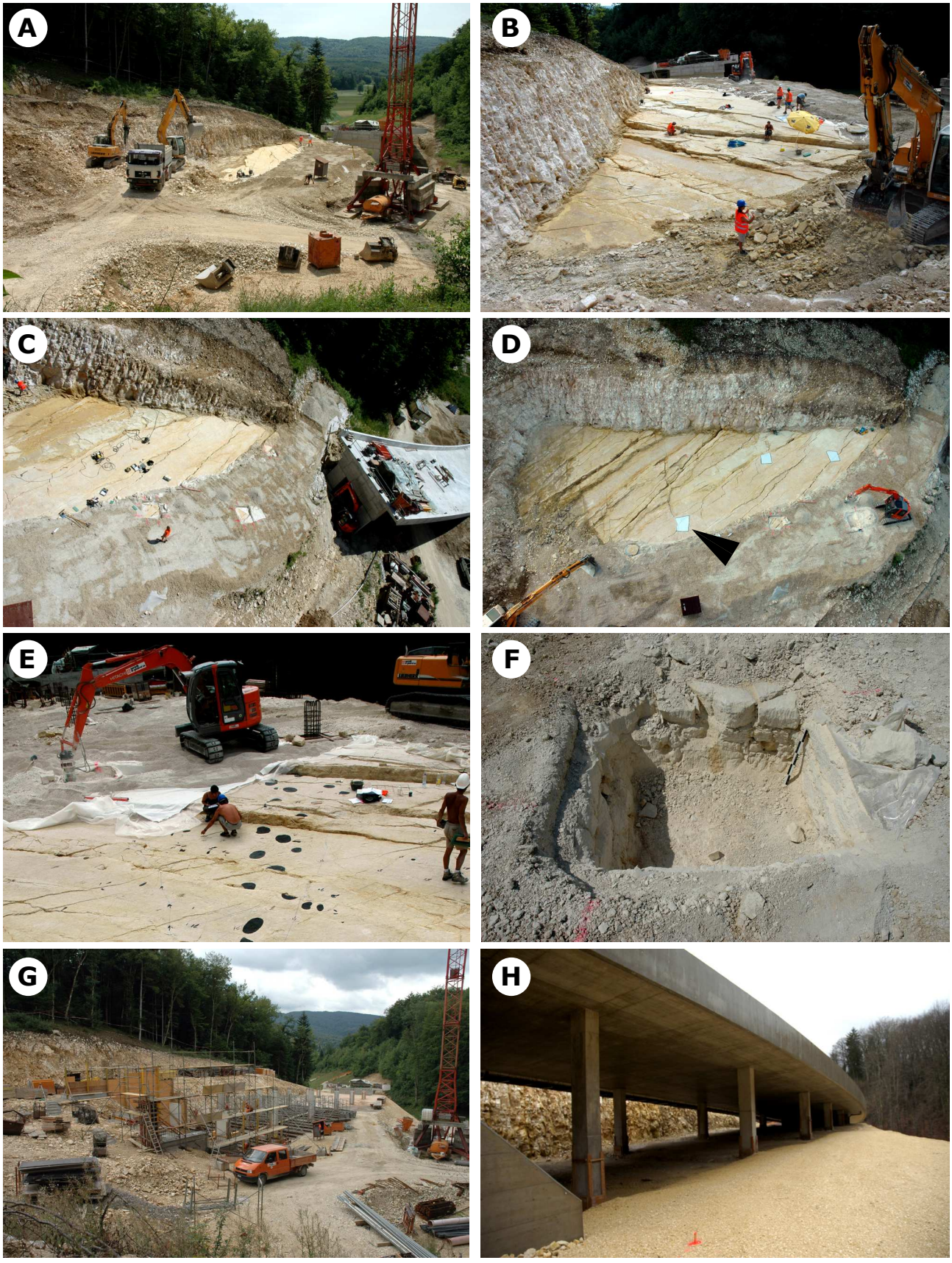
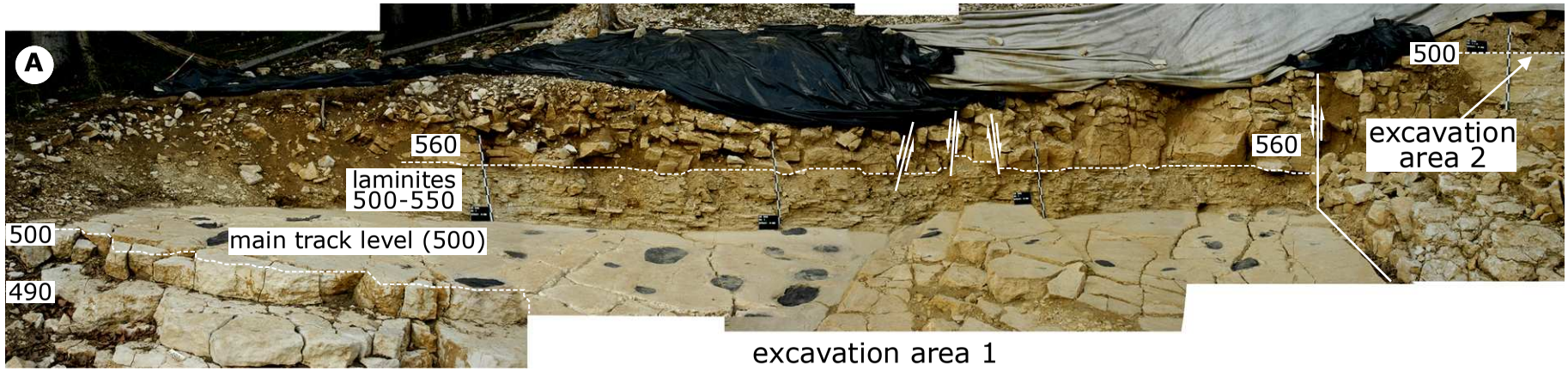

A
B
C
D
E
F
G
H

Plate 4.1 – Excavation limits of area 1 and 2

A & B: Chevenez—Combe Ronde tracksite: Photomontage showing the excavation limit (October 2005) of excavation areas 1 (**A**) and 2 (**B**). Photos and photomontage by Y. Marti (PAL A16). Note the thinly-bedded limestone (layers 480, 490) below the main track level (level 500), the sharp upper limit of the laminites, and the massively-bedded limestone (layers 560, 570) on top of the laminites. Within the laminites, 3 units (501-530; 530-540; 540-550) may be distinguished; the borders between these three units are approximate. The normal fault at the right of excavation area 1 uplifts the main track level of excavation area 2 about two metres. All scale bars are 1 m.


A
500
560
laminites
500-550
560
excavation
area 2
500
main track level (500)
490
excavation area 1

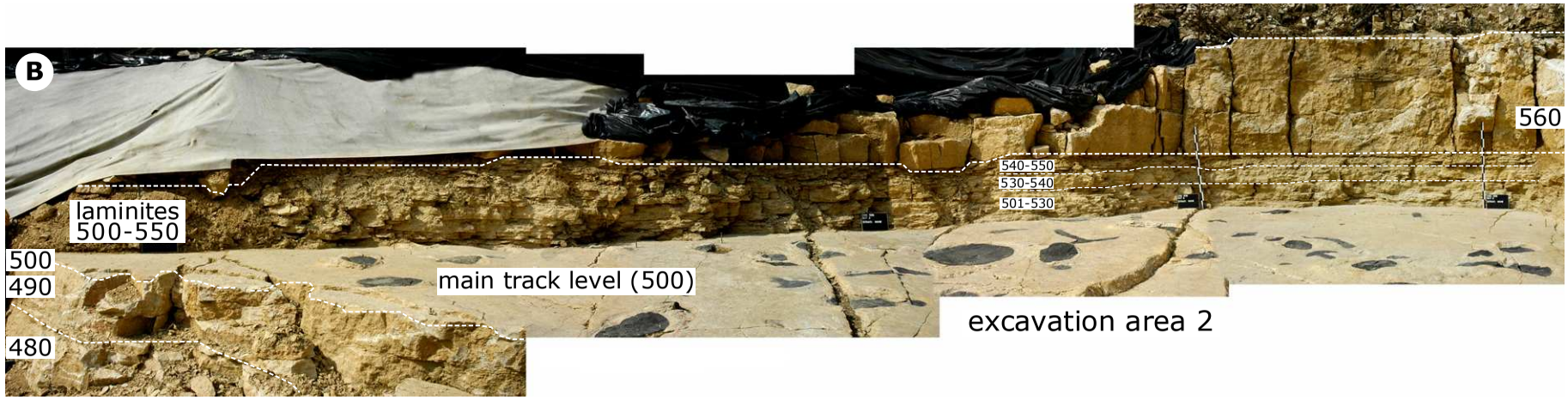

B
560
540-550
530-540
501-530
laminites
500-550
500
490
main track level (500)
480
excavation area 2

Plate 4.2 – Non-skeletal grains and sedimentary structures

A: Chevenez—Combe Ronde tracksite, layer 525 (track fill), thin-section CRO004-186n: Framboidal pyrite, characterized by diffuse boundaries.

B: Chevenez—Combe Ronde tracksite, layer 505, thin-section CRO004-81a: Coated, angular, micritic (clotted) intraclast in an ostracod wackestone. Note the high content of small-grained, poorly-defined dolomite rhombs, and that ostracods are exclusively preserved as single valves.

C: Chevenez—Combe Ronde tracksite, layer 525, thin-section CRO004-186m: Coated, angular, micritic intraclasts forming a microbreccia. Note that the matrix is essentially made up of dolomite.

D: Chevenez—Combe Ronde tracksite, layer 545, thin-section CRO004-92: Irregular laminoid fenestrae, parallel to bedding, associated with irregular lamination, which is marked by a network of dense (clotted) micrite. Note spar-filled cavity in the middle of the picture.

E: Chevenez—Combe Ronde tracksite, layer 545, thin-section CRO004-92: Euhedral to subhedral (diffuse boundaries) dolomite rhombs. Note cloudy centres and dark micrite lining dolomite crystals.

F: Chevenez—Combe Ronde tracksite, layer 531, thin-section CRO004-3a: Circumgranular cracking (curved planes) around blackened, dense nodules of different size. Note also the laterally more or less continuous irregular laminoid fenestrae, underlining cryptmicrobial lamination.

G: Chevenez—Combe Ronde tracksite, layer 516, thin-section CRO004-186k: Circumgranular cracking and formation of nodules (glaebules), which look darker than the surrounding matrix.

H: Chevenez—Combe Ronde tracksite, layer 516 thin-section CRO004-186k: Circumgranular cracking and formation of nodules (glaebules). The nodule is darker than the surrounding matrix and partially coated and dolomitized.

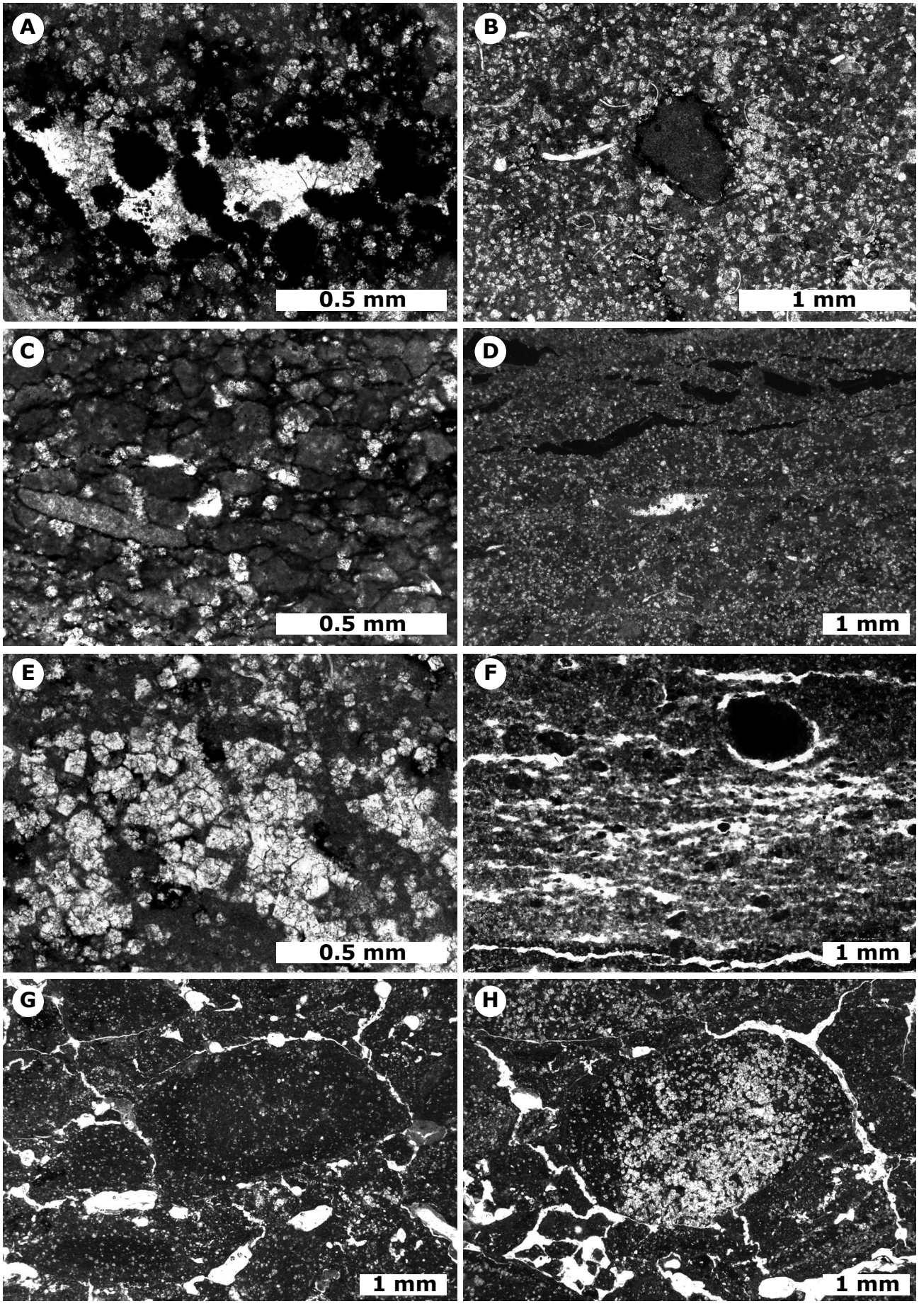

A
0.5 mm
B
1 mm
C
0.5 mm
D
1 mm
E
0.5 mm
F
1 mm
G
1 mm
H
1 mm

Plate 4.3 – Skeletal grains

A: Chevenez—Combe Ronde tracksite, layer 515, thin-section CRO004-186c: Thick-shelled complete ostracods filled with sparry calcite.

B: Chevenez—Combe Ronde tracksite, layer 520, thin-section CRO004-186o: Single valve of a thin-shelled ostracod (O), echinoid spine in cross-section (E), and a shell fragment of a pinnid bivalve (Bi).

C: Chevenez—Combe Ronde tracksite, layer 505, thin-section CRO004-189: Single valve of a thin-shelled ostracod (O), unidentified foraminifer (F), and fragment of a bivalve shell (Bi).

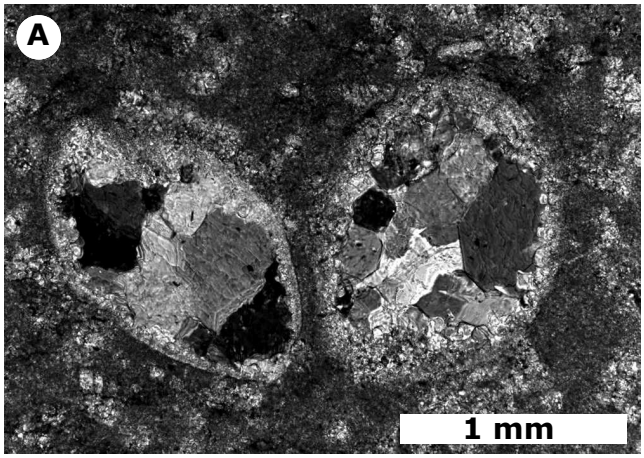
D: Chevenez—Combe Ronde tracksite, layer 530, thin-section CRO004-117a: Lateral section of a miliolid foraminifer, probably *Quinqueloculina* sp.

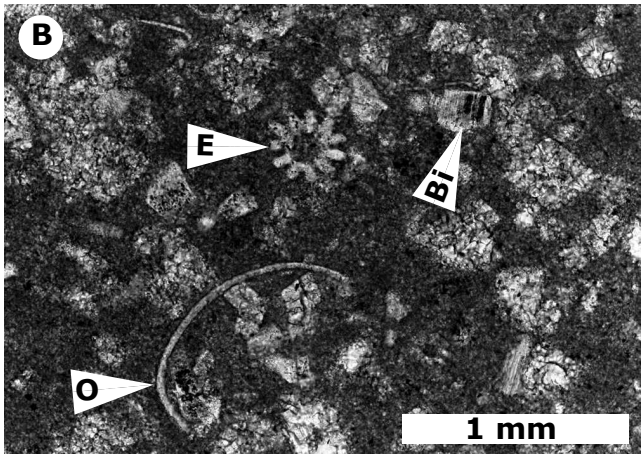
E: Chevenez—Combe Ronde tracksite, layer 525, thin-section CRO004-186j: Equatorial section of *Lenticulina* sp.

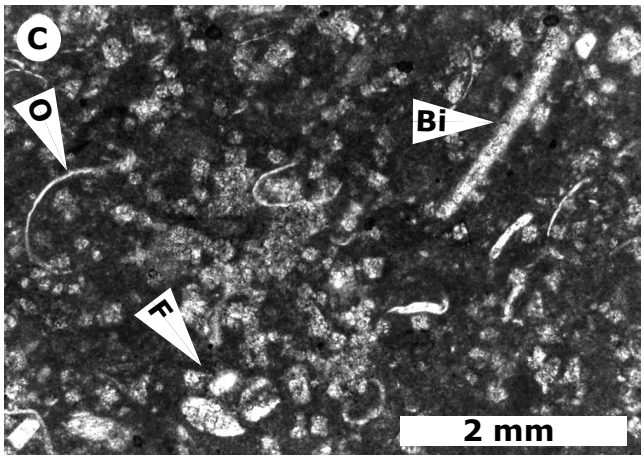
F: Chevenez—Combe Ronde, layer 505, thin-section CRO004-82a: Transversal section of *Alveosepta* sp. or a small cyclamminid foraminifer.

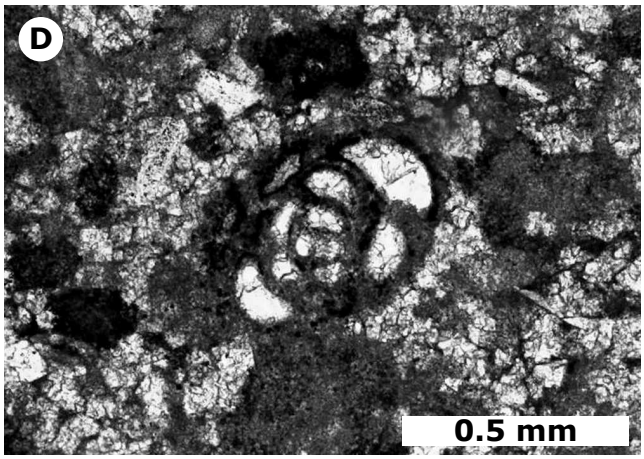
G: Chevenez—Combe Ronde tracksite, layer 510, thin-section CRO004-186b: *Everticyclammina* sp. (E), and single valve of a thin-shelled ostracod (O).

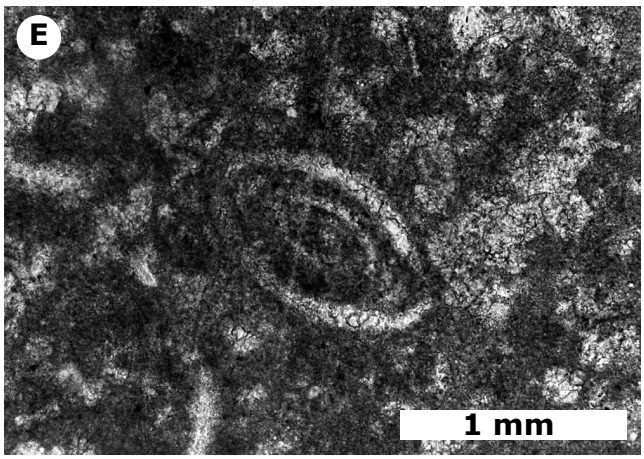
H: Chevenez—Combe Ronde tracksite, layer 505, thin-section CRO004-186l: transversal section of a dasycladacean algae, similar to *Acicularia* sp.

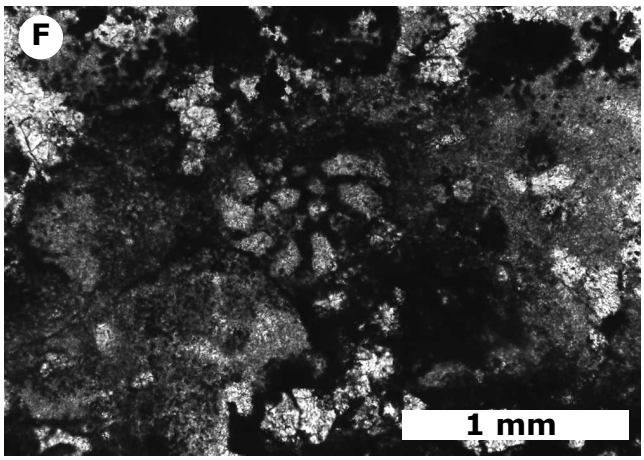

A
1 mm

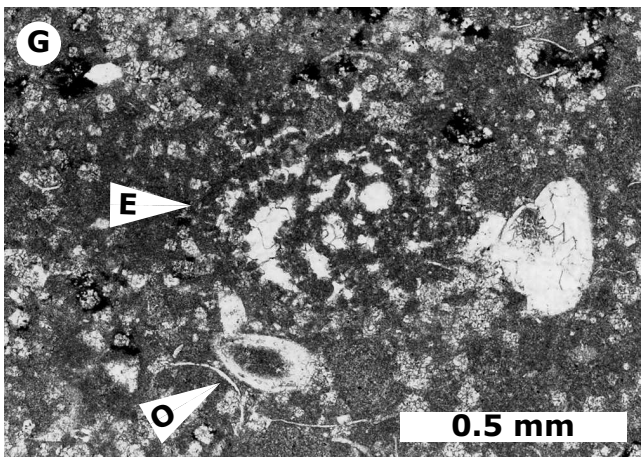

B
E
Bi
O
1 mm


C
O
Bi
F
2 mm


D
0.5 mm


E
1 mm


F
1 mm


G
E
O
0.5 mm

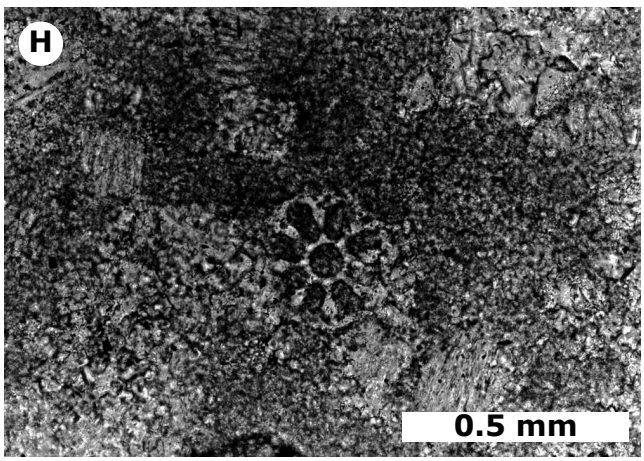

H
0.5 mm

Plate 4.4 – Invertebrate burrows

A: Chevenez—Combe Ronde tracksite, layer 531, thin-section CRO004-4: Section of a slightly curved, vertical burrow with a completely blackened fill. The blackening diminishes towards the exterior of the burrow.

B: Detail of A: Close-up of the burrow fill, characterized by angular mudclasts and a blackened miliolid foraminifer (F).

C: Chevenez—Combe Ronde tracksite, layer 530, thin-section CRO004-117a: Burrow with intense dolomitization and blackened miliolid foraminifers (F). This burrow contains comparatively few peloids but more coated, angular intraclasts.

D: Chevenez—Combe Ronde tracksite, layer 545, thin-section CRO004-132a: Horizontal burrow in cross-section, with a relatively coarse and more or less blackened grains. Note the completely dolomitized burrow matrix and surrounding of the burrow ("burrow dolomite" of Rameil, 2006).

E: Chevenez—Combe Ronde tracksite, layer 535, thin-section CRO004-101d: Large, oblique burrow with a coarse fill of round to elliptical peloids and mudclasts. There is more dolomite in the burrow fill than in the surrounding sediment, but a dolomite halo is lacking.

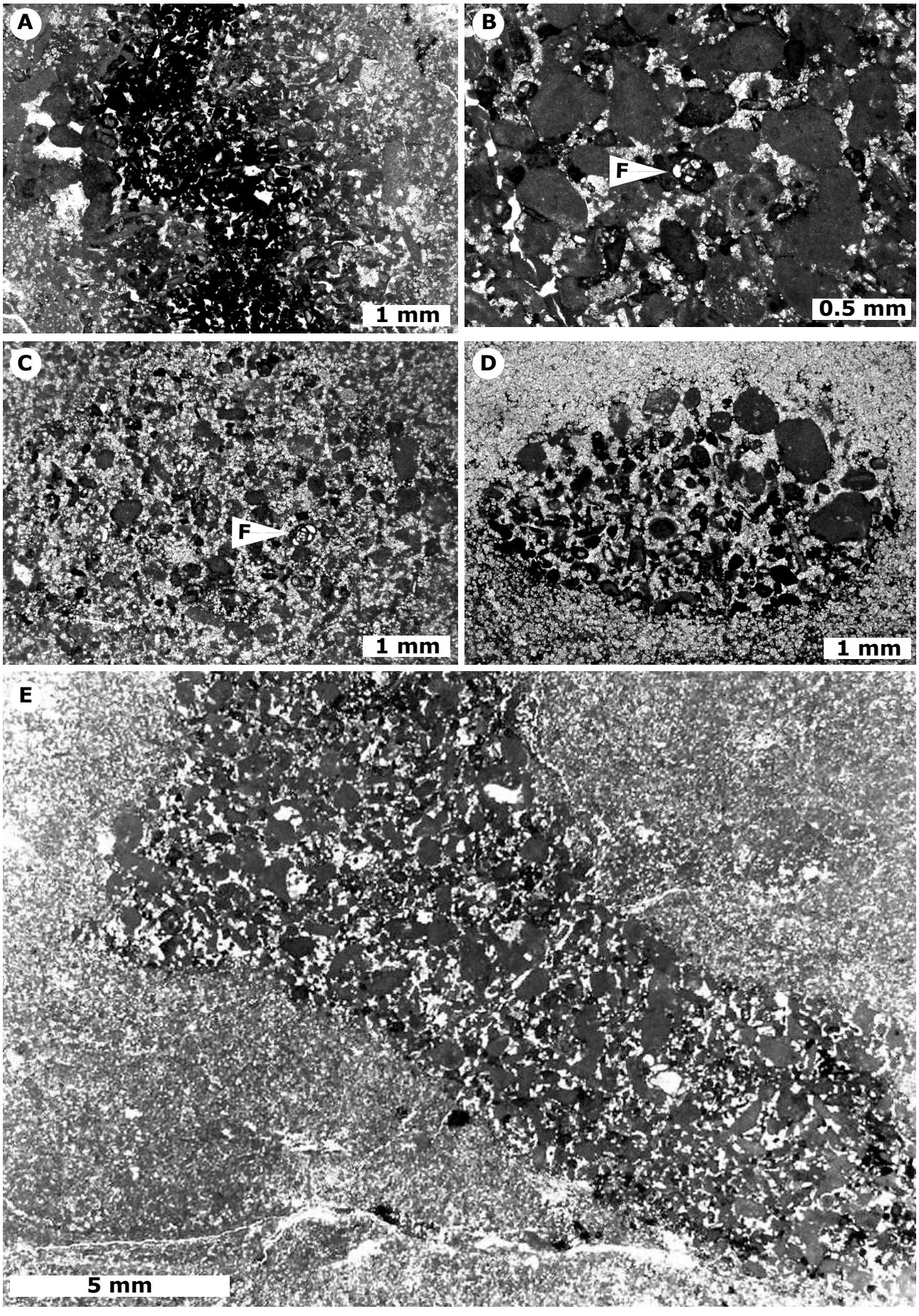

A
1 mm
B
F
0.5 mm
C
F
1 mm
D
1 mm
E
5 mm

Plate 4.5 – Recovery of sauropod tracks and fabrication of serial-sections

A: Chevenez—Combe Ronde tracksite, level 520: After the excavation and documentation selected tracks were cut into blocs or slabs with a stone saw.

B: Chevenez—Combe Ronde tracksite, level 530: Several excavated blocs of a pes-only trackway of a sauropod. S2-RP2 (CRO004-52) was used for the serial-sections shown in Figure 4.10, and the track fill of the slab of S2-LP2 was used for the serial-section illustrated in Figure 4.11.

C: Chevenez—Combe Ronde tracksite, level 520: This is the bloc with the sauropod pes track T16 of level 520, which was used for the serial-sections shown in Fig. 4.9 and in Plate 4.6 and Plate 4.7. The rectangle indicates the approximate dimensions of the slab finally extracted for the serial-sections.

D: Chevenez—Combe Ronde tracksite, level 520: After the cutting, a layer of silicon was put around the bloc.

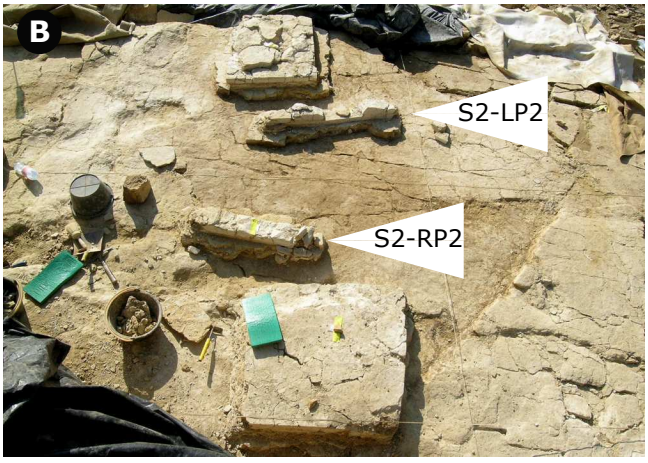
E: Chevenez—Combe Ronde tracksite, level 520: Plastering of the bloc.

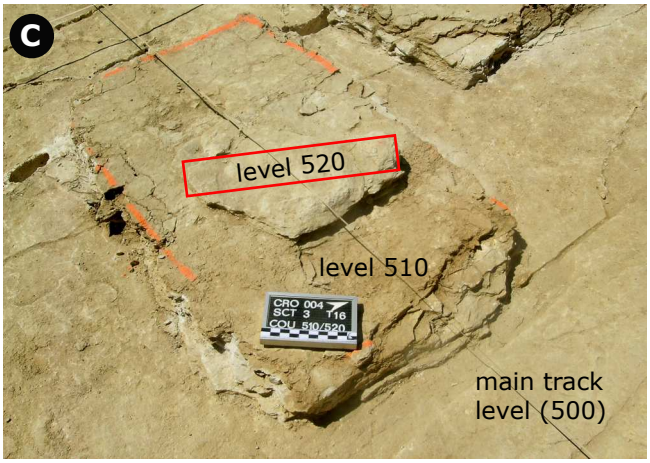
F: Chevenez—Combe Ronde tracksite, level 520: Recovery of the bloc. Larger blocs were recovered with the aid of a shovel excavator.

G: Cutting of a bloc with a sauropod pes track of layer 530 with an industrial stone saw.

H: Chevenez—Combe Ronde tracksite, level 530, CRO004-51: Sauropod pes track (S2-RP1) of layer 530 cut into serial-sections. Scale bar in the lower left is 20 cm.


A


B
S2-LP2
S2-RP2


C
level 520
level 510
main track
level (500)


D


E


F


G

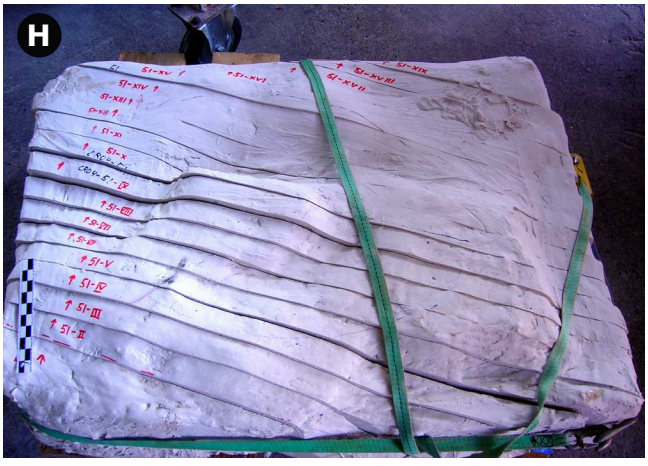

H

Plate 4.6 – Cross-section of the sauropod pes track T16 of level 520 (front of slab)

Chevenez—Combe Ronde tracksite, excavation area 3: Sauropod pes track T16 of level 520, cut vertically, approximately along the longitudinal axis of the pes. This is the slab (sample CRO004-185), which is shown in Plate 4.5C. All photos except D by B. Migy (SAP).

A: General view of the slab: The track is clearly marked by the fractured and compacted zone in the middle of the slab.

B: Detail of A: Note the large displacement rim, attributed to layer 520, and the homogeneous track fill (layer 525). Faint undertracks are discernible on levels 515 and 510. Level 505 is unaffected by the track formation, either due to earlier consolidation or due to insufficient track penetration depth. Track penetration depth amounts to about 6-9 cm.

C: Detail of B: Layer 515 is compacted and heavily fractured. Note the uplifted block of layer 515 in the middle part of the picture, between the two thrust faults. Layer 510 is less fractured but significantly compacted, especially at the rear of the track. This probably indicates that the sauropod put more weight on the posterior part of the foot than on the anterior part. The marly layers 511 and 516 are conspicuously thicker than laterally, locally forming mosaic breccia (mb). This is probably also enhanced by sub-recent karstification; sk points to a *Skolithos*-type burrow at the base of the track fill. The true track *sensu stricto* (the track bottom) was at least partially impressed on top of layer 516 or 515 and the track can thus be considered as an underprint.

D: Scan of a thin-section from the opposite, second slab, which was used to make the thin-sections: Note the well-developed mosaic breccia within the mottled marly layers 511 and 516.

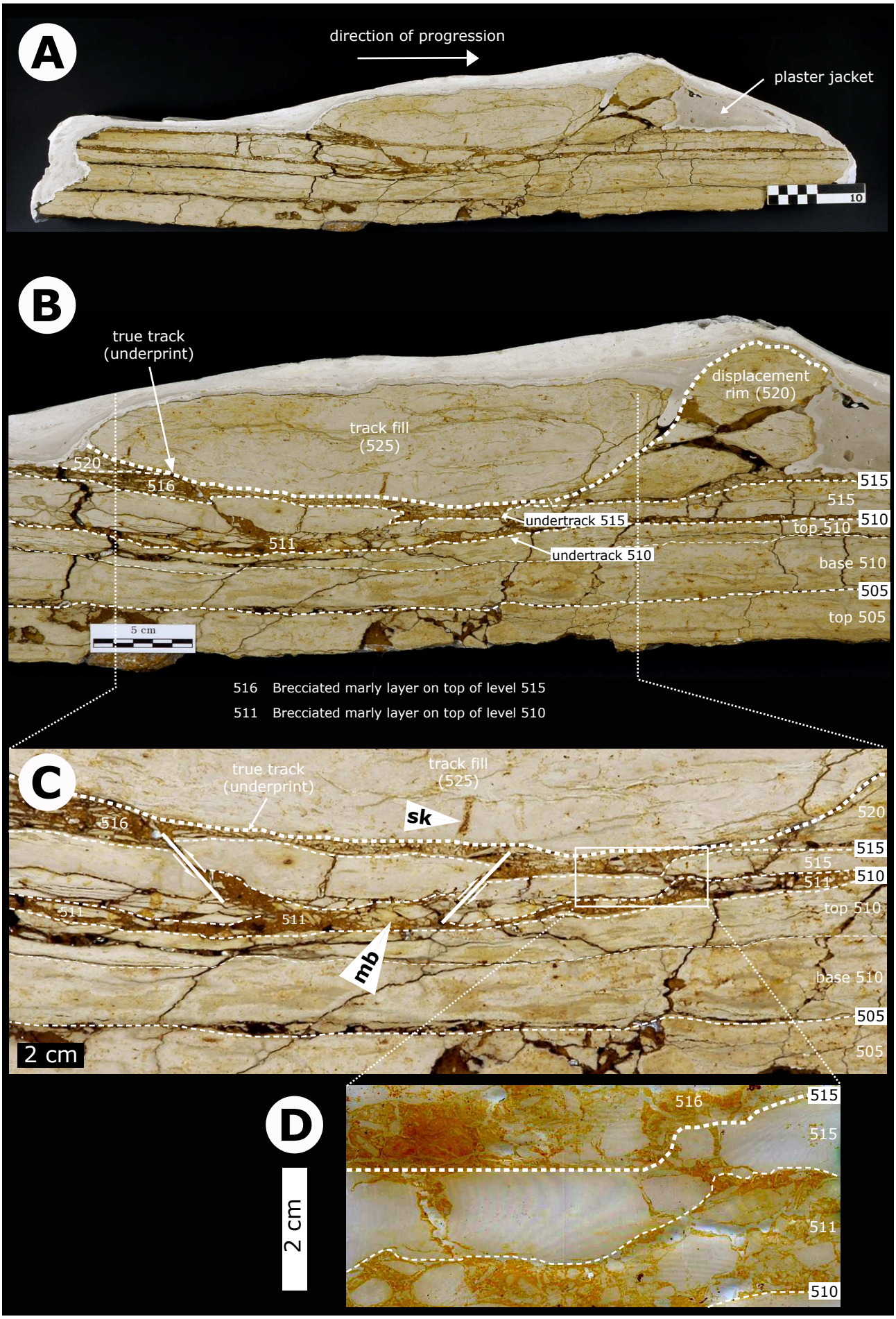

A
direction of progression
plaster jacket
10
B
true track
(underprint)
displacement
rim (520)
track fill
(525)
520
516
515
515
undertrack 515
510
top 510
511
undertrack 510
base 510
505
top 505
5 cm
516 Brecciated marly layer on top of level 515
511 Brecciated marly layer on top of level 510
C
true track
(underprint)
track fill
(525)
sk
516
520
515
515
510
511
511
511
top 510
mb
base 510
505
505
2 cm
D
2 cm
516
515
515
511
510

Plate 4.7 – Cross-section of the sauropod pes track T16 of level 520 (back of slab)

Chevenez—Combe Ronde tracksite, excavation area 3: Sauropod pes track T16 of level 520, cut vertically, approximately along the longitudinal axis of the pes. This is the reverse side of the slab (sample CRO004-185) shown in Plate 4.5C, and consequently, the direction of progression is opposite. All photos by B. Migy (SAP).

A: Note absence of the displacement rim and the heavily fractured zone on the rear of the track. Scale bar is 10 cm.

B & C: Detail of A: Note the completely fractured and disintegrated zone on the rear of the track. Layers 515 and 510 are affected by track formation and layer 515 is completely brecciated. Some of the clasts float in the matrix and are rotated (rc) forming matrix-supported breccia (msb), other still fit together forming mosaic breccia (mb). The initial fracturing due to track formation is enhanced by sub-recent karstification leading to a mottled appearance.

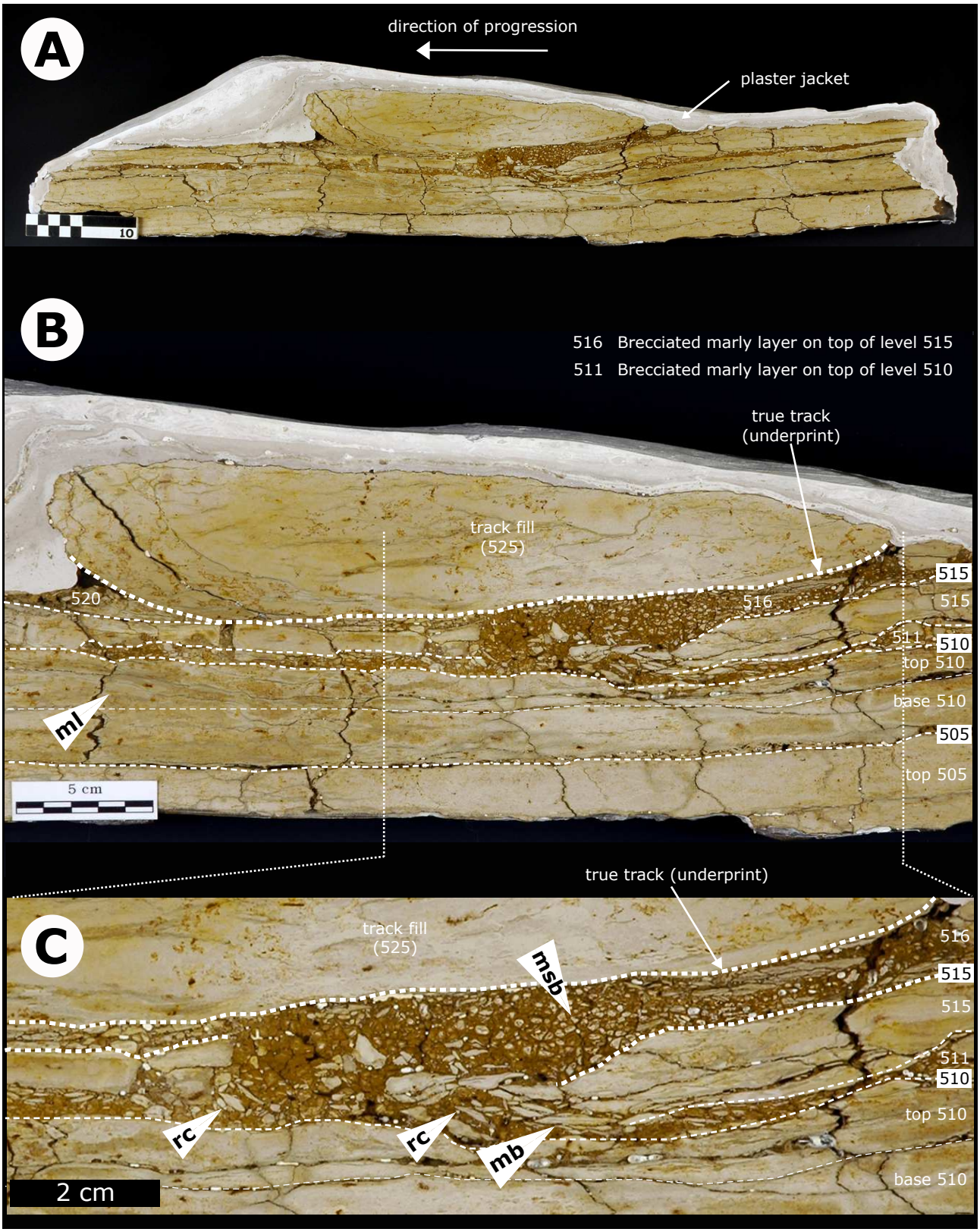
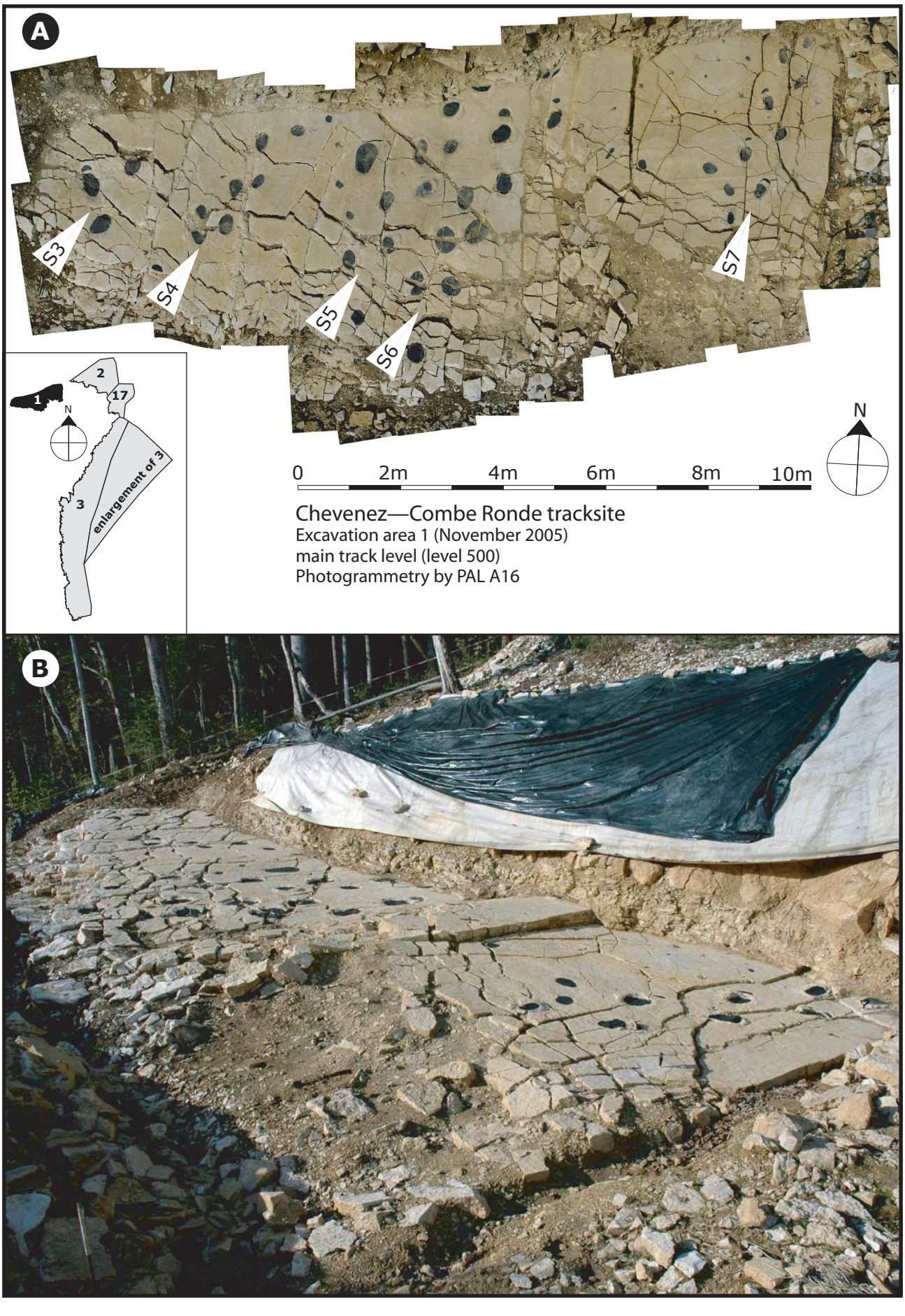

A
direction of progression
plaster jacket
10
B
516 Brecciated marly layer on top of level 515
511 Brecciated marly layer on top of level 510
true track
(underprint)
track fill
(525)
520
516
515
515
511
510
top 510
base 510
505
top 505
ml
5 cm
true track (underprint)
C
track fill
(525)
msb
516
515
515
511
510
top 510
base 510
rc
rc
mb
2 cm

Plate 5.1 – Photogrammetry and overview of the main track level in excavation area 1

A: Chevenez—Combe Ronde tracksite, excavation area 1: Photogrammetry of the main track level: Note the parallel sauropod trackways, and that several tracks and trackways are displaced by normal faults. Tracks are artificially coloured, photos and photogrammetry by Y. Marti (PAL A16). Inset shows the general position of excavation area 1 within the Combe Ronde tracksite.

B: Chevenez—Combe Ronde tracksite, excavation area 1: General view of the main track level in October 2005, photo by Y. Marti (PAL A16).



Chevenez—Combe Ronde tracksite
Excavation area 1 (November 2005)
main track level (level 500)
Photogrammetry by PAL A16

Plate 5.2 – Photogrammetry of the main track level in excavation area 2

Chevenez—Combe Ronde tracksite, excavation area 2: Photogrammetry of the main track level: Note the two groups of parallel sauropod trackways, group 1 (S8 to S11) and group 2 (S12 to S14), and the trackway of a medium-sized bipedal dinosaur in the upper right. Tracks are artificially coloured, photos and photogrammetry by Y. Marti (PAL A16). Inset shows the general position of excavation area 2 within the Combe Ronde tracksite.

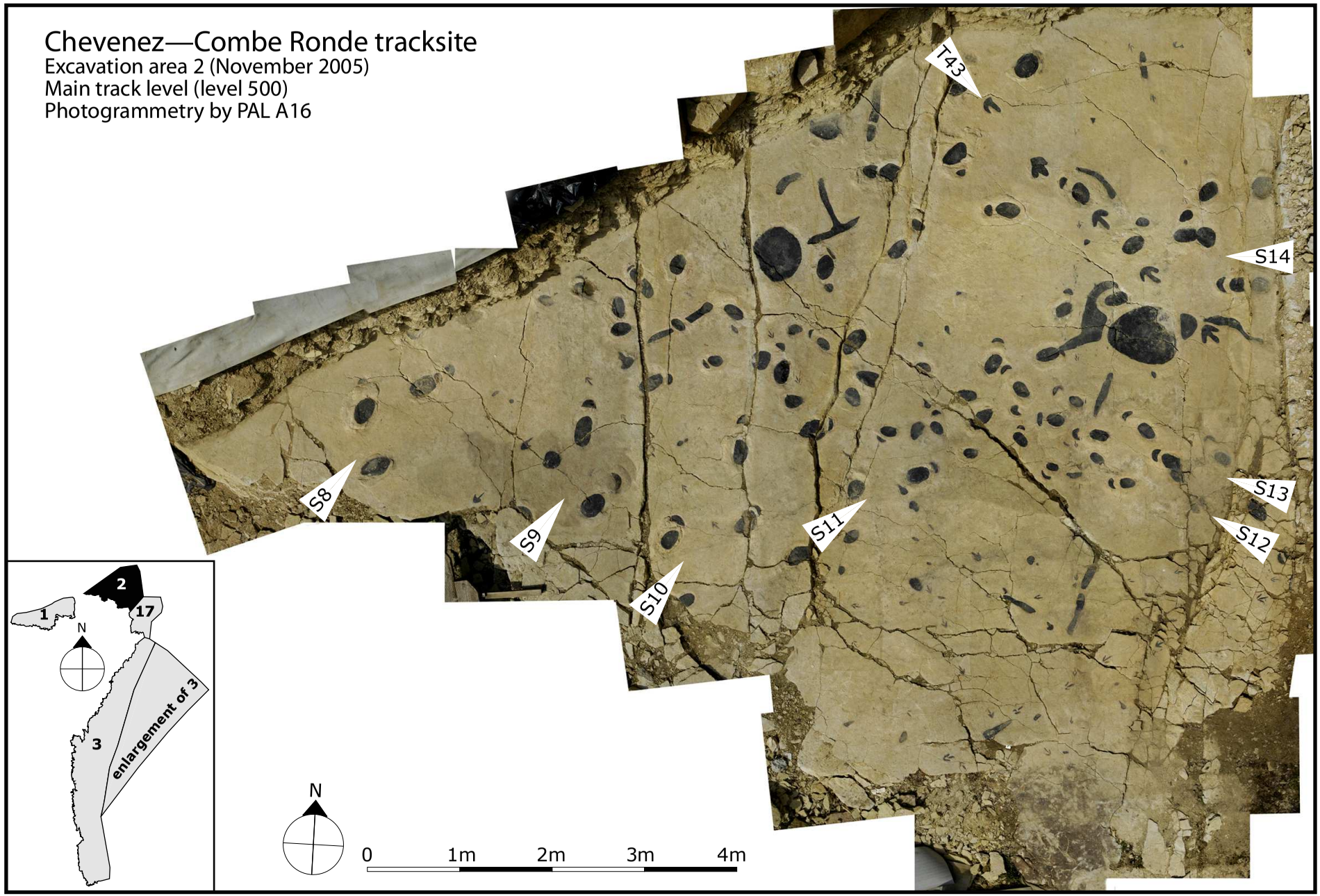

Chevenez—Combe Ronde tracksite
Excavation area 2 (November 2005)
Main track level (level 500)
Photogrammetry by PAL A16
T43
S14
S13
S12
S11
S10
S9
S8
2
1
17
N
3
enlargement of 3
N
0
1m
2m
3m
4m

Plate 5.3 – Overview of the main track level in excavation area 2

A: Chevenez—Combe Ronde tracksite, excavation area 2, main track level: Note the well-marked sauropod tracks, surrounded by large displacement rims, and desiccation cracks covering the whole surface. View towards the southwest, rising sunlight from the upper side, author for scale, photo by B. Migy (SAP), October 2005.

B: Chevenez—Combe Ronde tracksite, excavation area 2, main track level: View from approximately the same angle as in A, but the tracks have been artificially coloured in black prior to the laserscanning. View towards the southwest, rising sunlight from the upper side, photo by Y. Marti (PAL A16), November 2005.


A
T43-R1
S11-LP7


B
T43-R1
S11-LP7

Plate 5.4 – Photogrammetry of the main track level in excavation area 3 (south)

A: Chevenez—Combe Ronde tracksite, southern part of excavation area 3: Photogrammetry of the main track level: Note sauropod trackway S1 with the pronounced outward position of the left manus, and several trackways of minute and small, bipedal, tridactyl dinosaurs, tracks are coloured. Inset shows the general position within excavation area 3 and within the Combe Ronde tracksite. Tracks have been artificially coloured in black prior to the laserscanning.

B: Chevenez—Combe Ronde tracksite, main track level: Bird's eye view of the southern part of excavation area 3 in September 2004. Note the pronounced SE-NW oriented normal faults, and the gradual disintegration of the main track level towards the western, exterior part of the site. View towards the south. Tracks have been artificially coloured in black prior to the laserscanning.

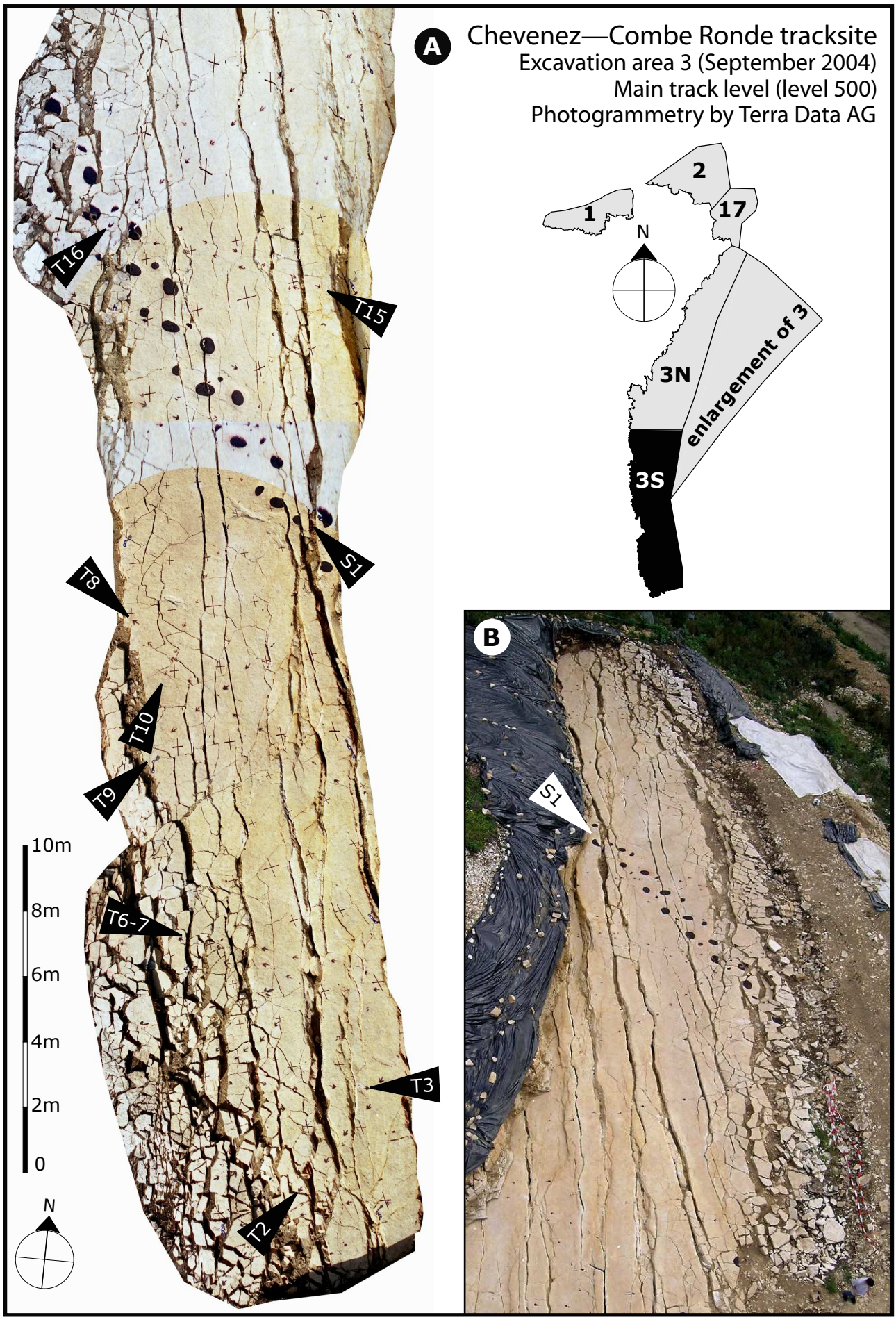

A
Chevenez—Combe Ronde tracksite
Excavation area 3 (September 2004)
Main track level (level 500)
Photogrammetry by Terra Data AG
2
1
17
N
3N
enlargement of 3
3S
T16
T15
S1
T8
T10
T9
T6-7
T3
T2
10m
8m
6m
4m
2m
0
N
B
S1

Plate 5.5 – Photogrammetry of the main track level in excavation area 3 (Nord)

A: Chevenez—Combe Ronde tracksite, northern part of excavation area 3: Photogrammetry of the main track level: Note the sauropod trackway S2, and several trackways of minute and small bipedal, tridactyl dinosaurs, tracks are coloured. Inset shows the general position within excavation area 3 and within the Combe Ronde tracksite. Tracks have been artificially coloured in black prior to the laserscanning.

B: Chevenez—Combe Ronde tracksite, main track level: Bird's eye view of the northern part of excavation area 3 in September 2004. Note the pronounced SE-NW oriented normal faults, and the gradual disintegration of the main track level towards the western, exterior part of the site. Dark strip is the shadow of the crane, view towards the north. Tracks have been artificially coloured in black prior to the laserscanning.

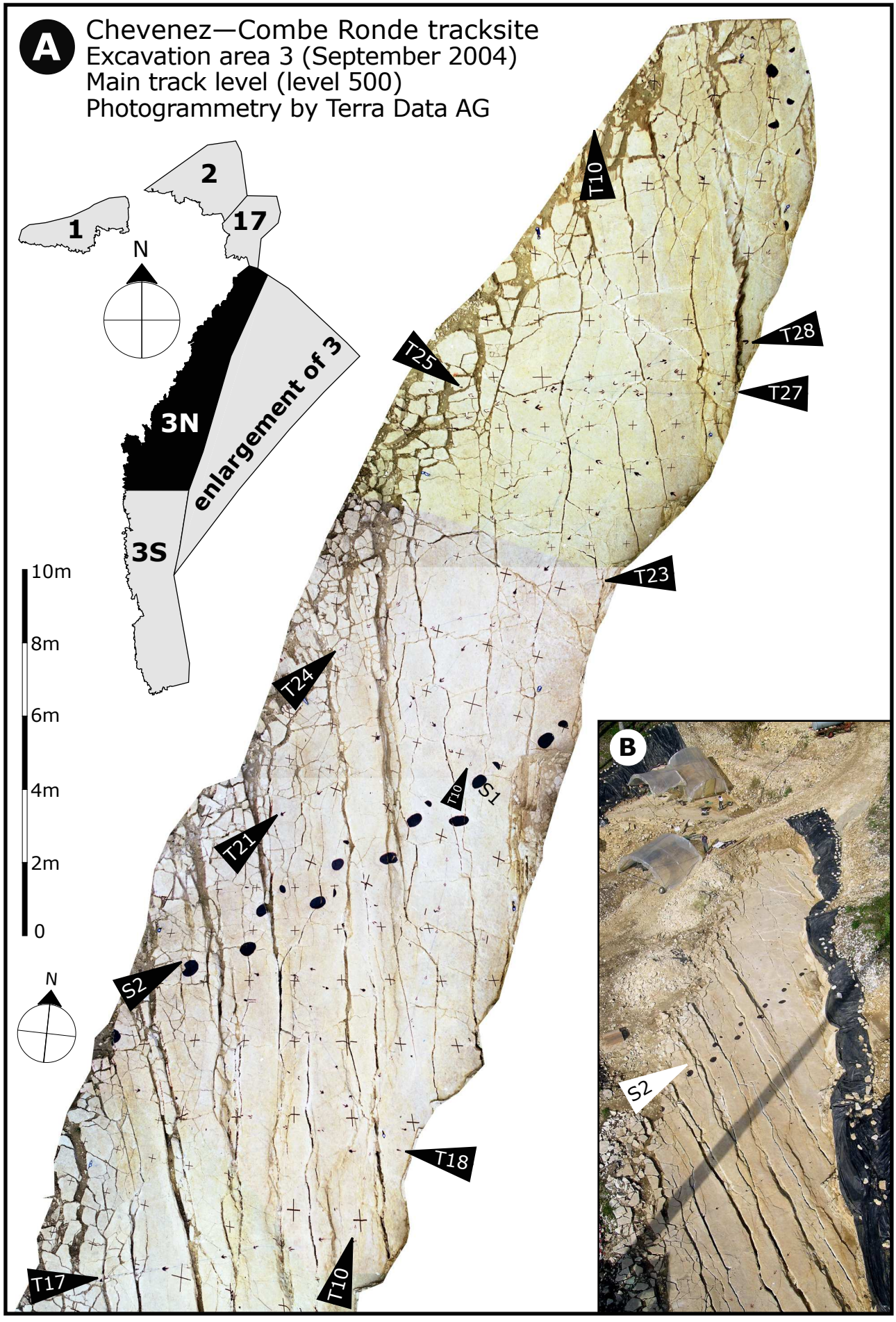
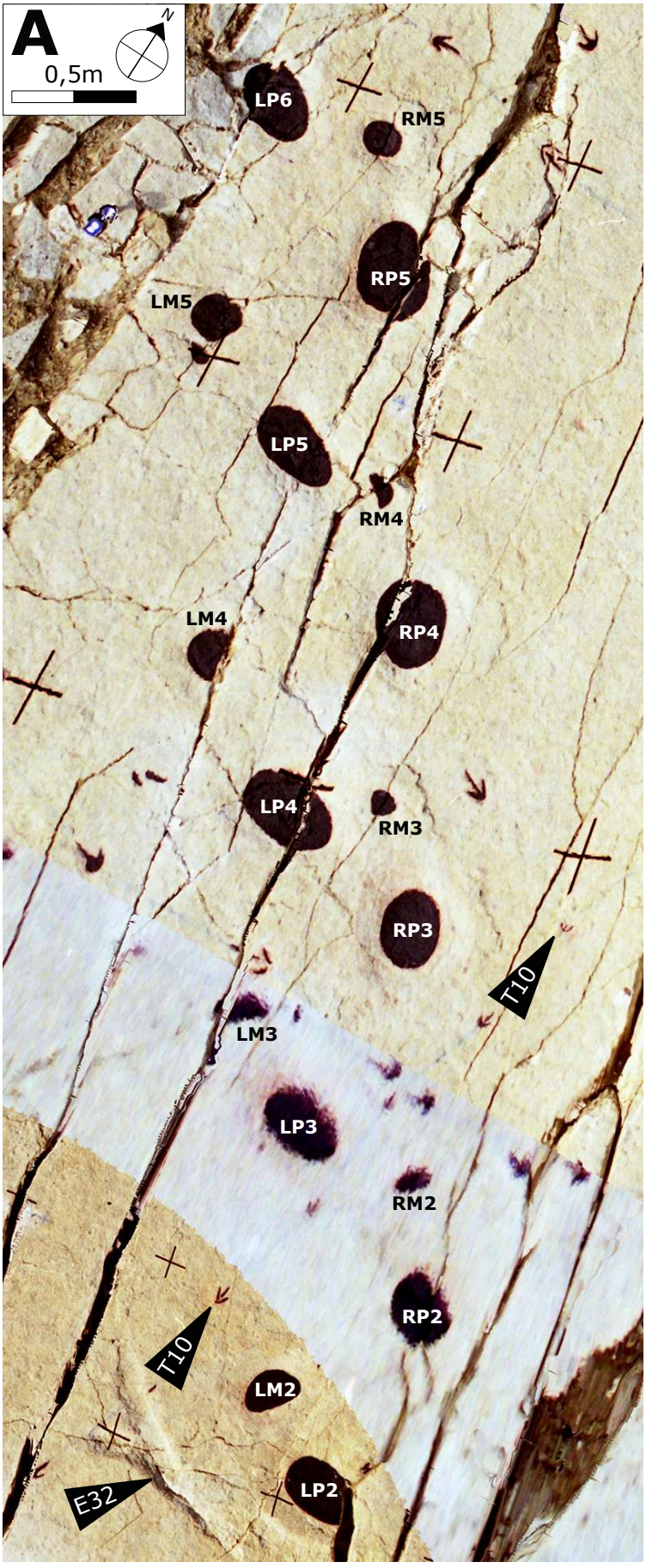
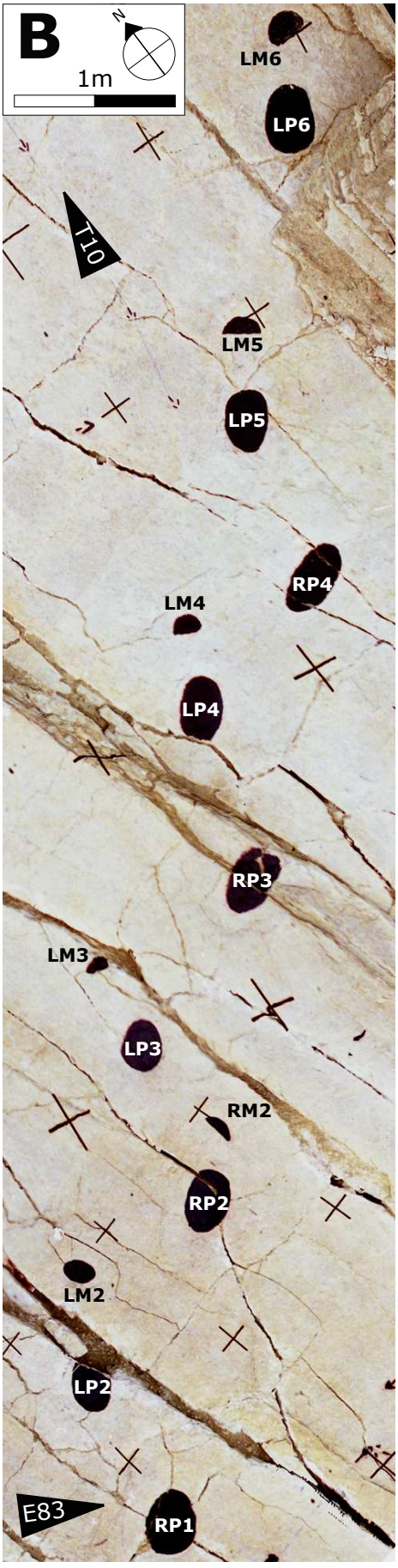

A
Chevenez—Combe Ronde tracksite
Excavation area 3 (September 2004)
Main track level (level 500)
Photogrammetry by Terra Data AG
1
2
17
N
3N
3S
enlargement of 3
10m
8m
6m
4m
2m
0
N
T10
T25
T28
T27
T23
T24
T10
S1
T21
S2
T18
T17
T10
B
S2

Plate 5.6 – Photogrammetry of sauropod trackways S1 and S2 (main track level)

A: Chevenez—Combe Ronde tracksite, southern part of excavation area 3, sauropod trackway S1: Photogrammetry by Terra Data AG (September 2004), tracks are artificially coloured. A close-up of the beginning of the trackway and the enigmatic trace (bifurcated prolate groove, E32) is shown in Figure 5.37A. Note that S1 is crossed by the trackway T10 of a minute bipedal dinosaur.

B: Chevenez—Combe Ronde tracksite, middle part of excavation area 3, sauropod trackway S1: Photogrammetry by Terra Data AG (September 2004), tracks are artificially coloured. A close-up of the enigmatic trace E83 (prolate groove) is shown in Figure 5.37E. Note that S2 is crossed by the same trackway T10 of a minute bipedal dinosaur as S1.


A
0,5m
N
LP6
RM5
RP5
LM5
LP5
RM4
LM4
RP4
LP4
RM3
RP3
T10
LM3
LP3
RM2
RP2
T10
LM2
E32
LP2


B
1m
N
LM6
LP6
T10
LM5
LP5
RP4
LM4
LP4
RP3
LM3
LP3
RM2
RP2
LM2
LP2
E83
RP1

Annex

Annex 4.1 – Relative frequency of selected microfacies elements

Annex 5.1 – Invalid trackways not analysed

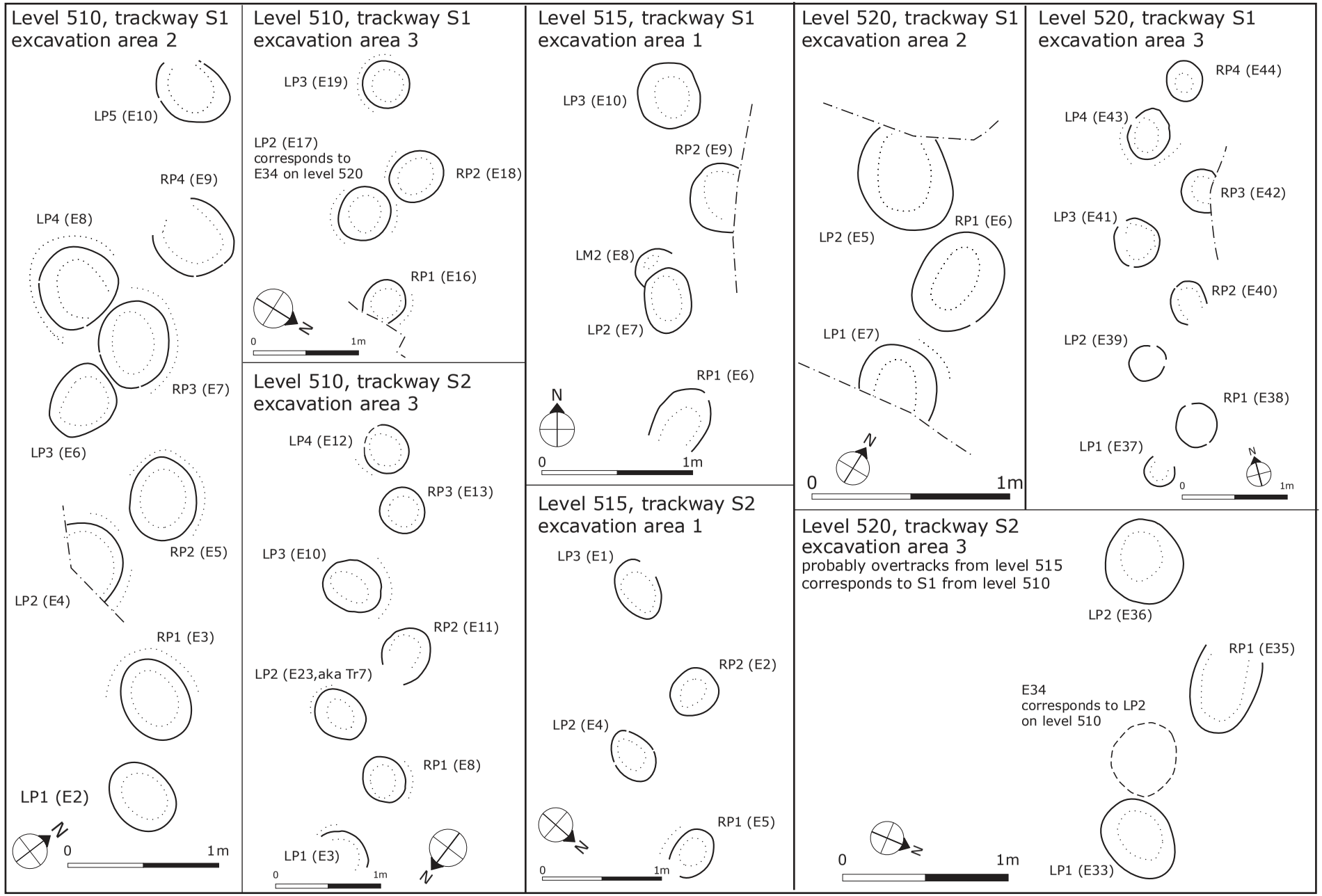
Annex 4.1 – Relative frequency of selected microfacies elements

Relative frequency of selected microfacies elements in the thin-sections analysed.

Relative abundance of selected microfacies elements					Non-skeletal grains										Skeletal grains										
Layer	**Number of thin section**	**Microfacies (Dunham)**	**Microfacies (Folk)**	**Characteristic features**	Dolomite	Quartz	Microbial lamination	Planar lamination	Wavy lamination	Peloids	Intraclasts	Bioturbations	Circumgranular cracks	Brecciation	Fenestrae	Ostracods	Articulated ostracods	Disarticulated Ostr.	Thin-shelled ostracods	Thick-shelled ostracods	Foraminifers	Miliolid foraminifers	Mollusc fragments	Oyster fragments	Echinoderm fragment	Dasycladacean algae	Organic matter
560 Base	CRO4-63a, 63b, 63c 15-30 cm above base	Packstone	Biopelmicrite	Marine but clearly less bioclastica and burrows than at the base of layer 560	1	1	0	0	0	3	0	2	0	0	0	1	1	1	0	0	2	1	2	1	2	0	0
560 Base	CRO4-178a, 178b, 178c, 178d, 178e	Packstone	Biopelmicrite	Bioturbations, filled with a grainstone consisting of (blackened) peloids, foraminifers, and other marine bioclasts	4	1	0	0	0	4	3	4	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0
560 Base	CRO4-178a, 178b, 178c, 178d, 178e	Packstone to grainstone	Biopelmicrite	Matrix contains less dolomite than the laminites but abundant marine bioclasts, in particular gastropods	1	1	0	0	0	4	0	4	0	0	0	1	1	1	0	0	3	1	3	1	3	0	0
550	no thin section	(green) marls	-	Very pronounced lamination, disturbed by abundant burrows, which are connected with layer 560	-	-	4	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
546 Top	CRO4-85b	Mudstone	Biomicrite, Biopelmicrite in burrows	Abundant bioturbations, lamination, matrix without marine bioclasts	4	1	1	1	0	2	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2
546 Base	CRO4-85b	Wackestone	Biomicrite, Biopelmicrite in burrows	Ostracod shelllbeds and marine bioclasts, no lamination	4	1	0	0	0	0	0	3	0	0	0	2	1	2	0	1	1	0	2	0	1	0	0
545 Top	CRO4-92, 132a, 132b	Mudstone	Biomicrite	Matrix without marine bioclasts but with lamination, burrows with (blackened) foraminifers	4	1	1	1	1	2	3	2	0	0	0	0	0	0	0	0	1	0	0	0	0	1	3
545 Base	CRO4-92, 132a, 132b	Wacke- to Packstone	Biomicrite	Ostracod shellbeds, (blackened) foraminifers only in burrows, no lamination	4	2	0	0	0	0	1	2	0	0	0	2	0	2	0	0	0	0	3	1	2	0	1
544	CRO4-119	Mudstone	Biomicrite, Biopelmicrite in burrows	Mudstone without marine bioclasts, burrows with completely blackened fill	3	1	0	0	0	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
543	CRO4-84, 87	Mudstone	Biomicrite	Pronounced lamination, underlined by organic matter, few marine bioclasts	4	1	2	2	0	2	3	0	0	0	0	1	0	1	0	0	0	0	1	0	1	2	3
542	CRO4-86	Wackestone	Biomicrite	Few marine bioclasts & ostracods, no foraminifers	4	1	0	0	0	0	2	0	0	0	0	1	0	1	0	0	0	0	1	1	1	0	2
540	CRO4-109, 111, 112	Wackestone	Biomicrite, Biopelmicrite in burrows	Matrix with many foraminifers, slightly less ostracods than in 535 and no ostracod shellbeds	4	1	1	1	1	1	2	1	0	0	0	2	1	2	1	0	2	1	2	0	1	0	2
538	CRO4-6, 97a, 97b, 97c	Wackestone	Biomicrite, Biopelmicrite in burrows	Alternation between shellbeds with ostracods & foraminifers and lamination, burrows	4	1	0	0	0	2	2	1	0	0	0	3	1	3	0	0	1	1	1	0	1	0	2
535	CRO4-101a, 101b, 101c, 101d, 108	Wackestone	Biomicrite, Biopelmicrite in burrows	Pronounced alternation between shellbeds with ostracods & foraminifers and lamination, burrows	4	1	1	1	0	2	3	1	0	0	0	3	1	3	1	1	2	1	1	0	2	1	1
532	CRO4-106	Mudstone	Biomicrite, Biopelmicrite in burrows	Burrows with (blackened) peloids and foraminifers, lamination	4	1	1	1	1	2	3	1	1	2	0	1	0	1	0	0	1	0	0	0	0	0	0
531	CRO4-3a, 3b, 4, 5a, 5b	Wackestone	Biomicrite, Biopelmicrite in burrows	Burrows with (blackened) peloids and foraminifers, lamination underlined with organic matter	4	1	2	2	0	1	2	1	1	0	0	2	1	2	1	1	1	0	1	0	1	1	2
530	CRO4-53a, 53b, 117, 117a, 149a ,149b	Wackestone	Biomicrite, Biopelmicrite in burrows	Ostracods are common, many marine bioclasts and foraminifers	4	2	0	0	0	2	2	1	0	0	0	2	1	2	1	1	1	1	2	1	2	1	2
528	No thin section	marl	-	Brecciation	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-
525	CRO4-54, 59, 114, 114a, 115a, 115b, 190a, 190b	Mud- to Wackestone	Biomicrite	Few ostracods and bioclasts, lamination, dense	4	2	1	1	0	1	2	1	0	0	0	1	1	1	0	0	1	1	2	0	1	0	0
521	CRO4-186a, 186f, 186i, 186k, 186m	marl	-	Brecciation and circumgranular cracks dominant, organic matter common	1	1	0	0	0	0	4	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	3
520	CRO4-31, 62a, 62b, 62c, 62d, 121a, 121b, 121c, 142	Mud- to Wackestone	Biomicrite, Biopelmicrite in burrows	Few ostracods and bioclasts, burrows, lamination	4	2	1	1	0	2	2	2	0	0	0	2	0	2	0	0	1	1	1	1	1	1	2
516	CRO4-186a, 186c, 186e, 186i, 186k, 186m	marl	-	Brecciation and circumgranular cracks dominant, organic matter common	1	1	0	0	0	0	4	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	3
515	CRO4-69a, 69b, 69c	Ostracod-Wackestone	Biomicrite	Ostracods and bioclats common, lamination	4	2	1	1	0	0	2	1	0	0	0	3	0	3	0	0	1	1	1	0	1	1	2
511	CRO4-186a, 186e, 186m, 186p	marl	-	Brecciation and circumgranular cracks dominant, organic matter common	1	1	0	0	0	0	4	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	3
510	CRO4-23, 65, 68a, 68b, 107, 107a	Ostracod-Wackestone	Biomicrite	Ostracods common, marine bioclasts, lamination, dense	4	2	1	1	1	1	2	1	0	0	0	3	1	3	1	1	1	0	1	0	1	1	2
508	CRO4-98	Ostracod-Wackestone	Biomicrite	Ostracods common, marine bioclasts, lamination, dense	4	1	0	0	0	0	0	0	0	0	0	3	1	3	1	1	0	0	1	0	1	0	0
505	CRO4-81a, 81b, 82a, 99a, 99b, 99c, 124a, 124b, 183, 187a, 187b, 189	Ostracod-Wackestone	Biomicrite	Ostracods dominant, marine bioclasts, lamination common	4	2	2	1	1	1	3	2	0	0	0	4	2	4	1	1	1	0	1	1	1	1	3
501	CRO4-123, 179, 181, 191	Ostracod-Wackestone	Biomicrite	Ostracods common, lamination	4	2	1	1	0	0	3	0	0	0	0	3	2	3	1	1	1	1	0	0	0	0	3
500	CRO4-180, 182a, 182b, 182c	Ostracod-Wackestone	Biomicrite	Ostracods dominant, marine bioclasts, no lamination	4	1	0	0	0	1	3	0	0	0	0	4	2	4	1	1	1	0	1	0	1	0	3

Annex 5.1 – Invalid trackways not analysed

Sequences of sauropod tracks labelled as trackways during the excavation of the levels 510, 515, and 520. The subsequent analysis of these trackways suggested that they can not be considered unequivocally as valid. Consequently, they were not subjected to further trackway analyses in this work. Note that these three levels were characterized by the highest dinoturbation index of all excavated levels, and that on all levels tracks undertracks or overtracks of one of the other levels occurred, as was shown in Chapter 4. This is also the reason why trackways were difficult to identify. Compare also with Figure 4.16 and with Figure 4.17.


Level 510, trackway S1
excavation area 2
LP5 (E10)
RP4 (E9)
LP4 (E8)
RP3 (E7)
LP3 (E6)
RP2 (E5)
LP2 (E4)
RP1 (E3)
LP1 (E2)
N
0
1m
Level 510, trackway S1
excavation area 3
LP3 (E19)
LP2 (E17)
corresponds to
E34 on level 520
RP2 (E18)
RP1 (E16)
N
0
1m
Level 510, trackway S2
excavation area 3
LP4 (E12)
RP3 (E13)
LP3 (E10)
RP2 (E11)
LP2 (E23,aka Tr7)
RP1 (E8)
LP1 (E3)
0
1m
N
Level 515, trackway S1
excavation area 1
LP3 (E10)
RP2 (E9)
LM2 (E8)
LP2 (E7)
RP1 (E6)
N
0
1m
Level 515, trackway S2
excavation area 1
LP3 (E1)
RP2 (E2)
LP2 (E4)
RP1 (E5)
N
0
1m
Level 520, trackway S1
excavation area 2
LP2 (E5)
RP1 (E6)
LP1 (E7)
N
0
1m
Level 520, trackway S1
excavation area 3
RP4 (E44)
LP4 (E43)
RP3 (E42)
LP3 (E41)
RP2 (E40)
LP2 (E39)
RP1 (E38)
LP1 (E37)
N
0
1m
Level 520, trackway S2
excavation area 3
probably overtracks from level 515
corresponds to S1 from level 510
LP2 (E36)
RP1 (E35)
E34
corresponds to LP2
on level 510
LP1 (E33)
N
0
1m

Curriculum Vitae

Daniel Marty (martydaniel@hotmail.com)

Born: 05. August 1973 in Basel (Switzerland)
Nationality: Swiss

Educational and professional background

1989-1992:	General qualification for university entrance (*Gymnasium Münchenstein*, Switzerland), *Matura A*
1993-1994	Studies in earth sciences, University of Basel (Switzerland)
1994-1997	Working for United Bank of Switzerland (Basel, Switzerland) and Pro Center Tommy Friedl (Egypt)
1997-2001	Continuation of studies in earth sciences, University of Basel and ETH Zürich (Switzerland)
07-08/1999	Internship at the Sinai Manganese Company (Sinai, Egypt)
02/2000-10/2001	Palaeontology A16 (40%): palaeontologist and vice project leader
2001	Master (MSc) in earth sciences and geophysics. Master thesis in sedimentology and palaeontology (palaeoecology) supervised by PD Dr. C.A. Meyer, Prof. A. Wetzel, and Prof. L. Hottinger
10/2001-01/2002	Palaeontology A16 (80%): research palaeontologist
01/2002-03/2006	Palaeontology A16 (100%): research palaeontologist responsible for excavations of dinosaur tracks, and the coordination of scientific research in Mesozoic strata along the future course of the Transjurane highway
04/2004-04/2008	PhD Thesis, University of Fribourg (Switzerland)
04/2006-04/2008	Palaeontology A16 (75%): same field of responsibility as above National Research Foundation (25%): PhD thesis, co-supervision of Bachelor and Master students
From 04/2008	Palaeontology A16 (100%): same field of responsibility as above
10/2008	PhD in earth sciences (geology), University of Fribourg, supervised by Prof. A Strasser: this work

Research interests

Vertebrate and invertebrate ichnology, palaeontology and palaeoecology; regional geology of the Jura Mountains (litho- and biostratigraphy); sedimentology of ancient and recent carbonate and carbonate-siliciclastic sedimentary systems (carbonate platforms, palustrine carbonates); palaeontological excavation

Publications

1. Marty, D., Cavin, L., Hug, W.A., Meyer, C.A., Lockley, M.G. & Iberg, A. 2003: Preliminary report on the Courtedoux dinosaur tracksite from the Kimmeridgian of Switzerland. Ichnos, 10, 209-219.
2. Marty, D., Cavin, L., Hug, W.A., Jordan, P., Lockley, M.G. & Meyer, C.A. 2004: The protection, conservation and sustainable use of the Courtedoux dinosaur tracksite, Canton Jura, Switzerland. Revue de Paléobiologie, Volume spécial, 9, 39-49.
3. Marty, D., Meyer, C.A. & Billon-Bruyat, J.-P. 2006: Sauropod trackway patterns expression of special behaviour related to substrate consistency? An example from the Late Jurassic of northwestern Switzerland. Hantkeniana, 5, 38-41.

4. Marty, D. & Meyer, C.A. 2006: Insight into depositional conditions of carbonate-dominated palustrine sedimentation around the K/T-boundary (*Faciès Rognacien*, northeastern Pyrenean foreland, southwestern France). Geological Society of America, Special Paper, 416, 169-187.
5. Marty, D., Strasser, A. & Meyer, C.A. (in press): Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. Ichnos.

Congress abstracts

1. Marty, D. & Cavin, L. 2003: A "baby"-sauropod trackway from the Late Jurassic Courtedoux Dinosaur Tracksite Excavations, Canton Jura, Northern Switzerland. Abstract, 1st Meeting of the European Association of Vertebrate Palaeontologists, Basel, 15.-19. July, Basel, p. 29.
2. Marty, D., 2004: Dinosaur track excavations along the "Transjurane" highway (Late Kimmeridgian, northwestern Switzerland): Latest results. Abstract, 32nd International Geological Congres, Scientific sessions: abstracts (part 1), p. 599.
3. Marty D. & Billon-Bruyat J.-P. 2004: A new reptilian fauna from the Late Jurassic of Western Europe (Kimmeridgian, Switzerland). Journal of Vertebrate Paleontology, 24 (supplement to no. 3), p. 90A.
4. Marty, D. & Hug, W.A. 2004: Protection of dinosaur tracksites along the future "Transjurane" highway (Canton Jura, Northwestern Switzerland) in a Jura Geopark. Abstract, 32nd International Geological Congres, Scientific sessions: abstracts (part 1), p. 581.
5. Marty, D. 2005: Sedimentology and taphonomy of dinosaur track-bearing Plattenkalke (Kimmeridgian, Canton Jura, Switzerland). 4th International Symposium on Lithographic Limestone and Plattenkalk, 12th-18th September 2005, Eichstätt, Zitteliana, B26, p. 20.
6. Marty, D., Paratte, G., Meyer, C.A., Billon-Bruyat, J.-P., Ayer, J. 2006: New multiple ichnocoenoses of Switzerland: evidence for enduring dinosaur communities on the northern Tethys platform. Sixty-sixth annual meeting Society of Vertebrate Paleontology, Ottawa October 18-21, Journal of Vertebrate Paleontology, 26 (supplement to no. 3), p. 96A.
7. Marty, D., Strasser, A. & Meyer, C.A. 2007: Formation and preservation of human footprints in present-day microbial mats of tidal-flat environments (Bahamas, Belize, Egypt, Tunisia): implications for the study of fossil footprints. 5th Annual Meeting of the European Association of Vertebrate Palaeontologists, 15.-20.05.2007, Carcassone, France, Abstract Volume, p. 45-46.
8. Marty, D. 2007: Comparative taphonomy of human footprints left in microbial mats of tidal flats and dinosaur footprints of Late Jurassic biolaminites; a key for the interpretation of fossil vertebrate tracks. 5th Swiss Geoscience Meeting, 16.-17.11.2007, Geneva, 2 pp. (*Award for best paper and presentation of the Commission of the Swiss Palaeontological Memoirs*)

Lectures, teaching, popular activities

1999-2000	Assistance (25%) for PD Dr. C. A. Meyer, University of Basel
2002-2008	Related to the dinosaur track excavations of the Palaeontology A16: open days, popular excursions, scientific excursions, popular and scientific lectures, museographical activities, films, interviews, field trip & congress organisation
2004-2008	Co-supervision of bachelor and master students in collaboration with the Universities of Basel, Fribourg, Geneva, Neuchâtel (all Switzerland), and Würzburg (Germany)

Postgraduate field trips and courses

05/2004	(Actuo-) sedimentological/palaeontological field trip to Eleuthera Island (Bahamas), CUSO course leaded by P. Kindler, E. Davaud, G. Gorin, & A. Strasser
05/2005	(Actuo-) sedimentological/palaeontological field trip of the University of Geneva to Tunisia (Pleistocene, Holocene and Mesozoic carbonate environments)
10/2006	(Actuo-) sedimentological/palaeontological field trip to the Sinai, Egypt (Coral Reef Ecosystems: Past and Present – a case study in the Red Sea), CUSO course
02/2007	(Actuo-) sedimentological/palaeontological field trip to Belize
09/2007	(Actuo-) sedimentological/palaeontological field trip to Colombia (Evolution d'un archipel océanique des Caraïbes, San Andrés et Providencia), CUSO course

Professional memberships

AAPG, Association Dinosauria, European Association of Vertebrate Palaeontologists, Freunde des Naturhistorischen Museums Basel, IAS, SEPM, SVP, Swiss Association of Petroleum Geologists, Swiss Palaeontological Society, PalAss

Already published:

Vol. 1 **HILLGÄRTNER, Heiko** (1999) The evolution of the French Jura platform during the Late Berriasian to Early Valanginian: controlling factors and timing (203 pp.).

Vol. 2 **DUPRAZ, Christophe** (1999) Paléontologie, paléoécologie et évolution des faciès récifaux de l'Oxfordien Moyen-Supérieur (Jura suisse et français) (247 pp.).

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Vol. 5 **PICOT, Laurent** (2002) Le Paléogène des synclinaux du Jura et de la bordure sud-rhénane: paléontologie (Ostracodes), paléoécologie, biostratigraphie et paléogéographie (240 pp.).

Vol. 6 **DAPPLES, Florence** (2002) Instabilités de terrain dans les Préalpes fribourgeoises (Suisse) au cours du Tardiglaciaire et de l'Holocène: influence des changements climatiques, des fluctuations de la végétation et de l'activité humaine (158 pp.).

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