

Remarks on the identification of the Albian/Cenomanian boundary and taxonomic clarification of the planktonic foraminifera index species *globotruncanoides*, *brotzeni* and *tehamaensis*

MARIA ROSE PETRIZZO*†, MICHÈLE CARON‡ & ISABELLA PREMOLI SILVA*

*Dipartimento di Scienze della Terra ‘A. Desio’, Università degli Studi di Milano,
via Mangiagalli 34, I-20133 Milano, Italy

‡Département de Géosciences, Géologie et Paléontologie, Université de Fribourg, Chemin du Musée, 1700 Fribourg,
Switzerland

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Abstract – The planktonic foraminifera assemblage across the Global Boundary Stratotype Section and Point (GSSP) for the base of the Cenomanian Stage defined at Mont Risou (Haute-Alpes in France) is here restudied to clarify the identification and stratigraphic distribution of *Thalmaninella globotruncanoides* (= *Rotalipora globotruncanoides* Sigal, 1948) and *Pseudothalmanninella tehamaensis* (= *Rotalipora tehamaensis* Marianos & Zingula, 1966) whose appearance levels are primary and secondary criteria for placing the Albian/Cenomanian boundary. Since the ratification of the GSSP in 2002, the identification of the foraminifera index species across the Albian/Cenomanian boundary has been reported to be sometimes difficult either because of their rarity or uncertainty in the taxonomic identifications. We discuss the taxonomic status of *Thalmaninella brotzeni* Sigal 1948, a species regarded for a long time to be a junior synonym of *Th. globotruncanoides*, through images of Sigal’s type materials deposited at the Musée National d’Histoire Naturelle (Paris), and elucidate the taxonomically important characters that enable unequivocal identification of *Th. brotzeni*, *Th. globotruncanoides* and *Ps. tehamaensis*. Planktonic foraminifera marker species from Mont Risou are compared with well-preserved specimens from Blake Nose Plateau (ODP 171B, North Western Atlantic Ocean) to verify the reliability and stratigraphic distribution of these marker taxa outside the Mediterranean Tethyan area.

Keywords: Cenomanian Stage, Global Boundary Stratotype Section and Point, planktonic foraminifera, Mont Risou (Haute-Alpes, France), Blake Nose Plateau (ODP 171B, NW Atlantic Ocean), taxonomy, biostratigraphy.

1. Introduction

The Global Boundary Stratotype Section and Point (GSSP) for the base of the Cenomanian Stage of the Upper Cretaceous was defined on the southern side of Mont Risou, east of Rosans, Haute-Alpes in France (Fig. 1). According to the definition of the stratotype (Kennedy *et al.* 2004), the base of the Cenomanian Stage is a level at 36 m below the top of the Marnes Bleues and coincides with the appearance level of the planktonic foraminifera *Thalmaninella globotruncanoides* (= *Rotalipora globotruncanoides* Sigal, 1948).

The stratigraphic interval from the middle Albian to the upper Cenomanian records the evolution and diversification of the polyphyletic *Rotalipora* group (Wonders, 1978; Robaszynski *et al.* 1994, 2008; Kennedy *et al.* 2004; Gonzalez-Donoso, Linares & Robaszynski, 2007; Gale *et al.* 2011). The distinctive rotaliporid assemblage that occurs at the base of the Cenomanian is composed of trochospiral,

single-keeled species with supplementary apertures on the umbilical side that have been assigned to two different genera: (1) *Pseudothalmanninella* (*ticinensis*, *tehamaensis*), and (2) *Thalmaninella* (*appenninica*, *balernaensis*, *gandolfii*, *brotzeni*, *globotruncanoides*) (see Wonders, 1978, 1980 and discussion in Gonzalez-Donoso, Linares & Robaszynski, 2007 and Lipson-Benitah, 2008). The genera assignment is based on the identification of distinctive lineages that originated in late Albian time, as follows: (1) *Ticinella praeticinensis* – *Pseudothalmanninella subticinensis* – *Pseudothalmanninella ticinensis* – *Pseudothalmanninella tehamaensis* lineage; (2) *Ticinella raynaudi* group: *Thalmaninella praebalernaensis* – *Thalmaninella balernaensis* – *Thalmaninella appenninica* – *Thalmaninella brotzeni* – *Thalmaninella globotruncanoides* lineage.

The genus *Thalmaninella* is used to identify spiroconvex and umbiliconvex forms that seem, however, to belong to different lineages. For this reason Lipson-Benitah (2008) introduced the genus *Parathalmanninella* to accommodate the species (*praebalernaensis*, *balernaensis* and *appenninica*) that evolved from

†Author for correspondence: mrose.petrizzo@unimi.it

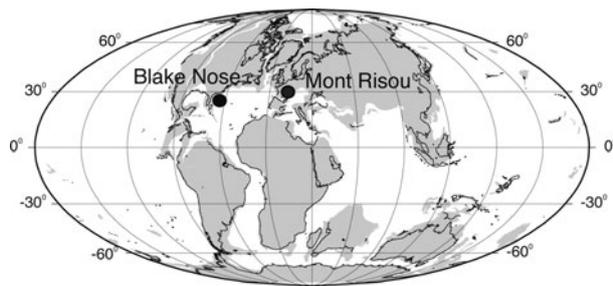


Figure 1. Palaeogeographic reconstruction for the late Albian (101.0 Ma) according to Hay *et al.* (1999) showing the position of the GSSP for the base of the Cenomanian at Mont Risou (Hautes-Alpes, France) and the Blake Nose Plateau (NW Atlantic Ocean).

the *Ticinella raynaudi* group. The species *brotzeni* and *globotruncanoides* were regarded by Lipson-Benitah (2008) as belonging to a new phyletic lineage descendent from *Pseudothalmanninella tehamaensis* and, thus, were included in the emended genus *Thalmanninella*. To date we adopt the taxonomy of Wonders (1978) and Gonzalez-Donoso, Linares & Robaszynski (2007) because *Pseudothalmanninella tehamaensis* can hardly be regarded as ancestral to *Th. brotzeni* and *Th. globotruncanoides* according to the data presented in this paper. However, as we suspect that the genus *Thalmanninella* may be polyphyletic, further investigations are in progress to identify the ancestral species of *brotzeni* and *globotruncanoides* and, hence, to clarify their phylogeny and taxonomic position.

Pseudothalmanninella tehamaensis has been rarely documented to occur in latest Albian to early Cenomanian assemblages (Marianos & Zingula, 1966). *Thalmanninella globotruncanoides* has been reported to be very rare at the beginning of its stratigraphic range (Bellier & Moullade, 2002; Petrizzo & Huber, 2006a; Robaszynski *et al.* 2008), its first occurrence being difficult to detect due to the presence in the same assemblage of either transitional specimens close to *Th. globotruncanoides* (e.g. *Rotalipora* aff. *globotruncanoides*, see Bellier & Moullade, 2002) or specimens closely resembling *Th. brotzeni* or other intermediate forms belonging to the *Thalmanninella* lineage (Robaszynski *et al.* 2008).

The species *brotzeni*, included in the genus *Rotalipora* by Sigal (1958) and Robaszynski & Caron (1979), was regarded as the marker species of the homonymous zone extending from near the Albian/Cenomanian boundary through the lower Cenomanian (Sigal, 1977; Robaszynski & Caron, 1995; Premoli Silva & Sliter, 1995). Wonders (1978, 1980) considered the species *brotzeni* to be a junior synonym of *Th. greenhornensis*, and, in agreement with van Hinte (1976), he equated the top of the Albian Stage with the extinction level of *Planomalina buxtorfi*. Gonzalez-Donoso & Linares in Robaszynski *et al.* (1994) re-interpreted *R. brotzeni* as a junior synonym of the species *globotruncanoides* and replaced the lower Cenomanian *Rotalipora brotzeni*

Zone with the *Rotalipora globotruncanoides* Zone (Robaszynski & Caron, 1995; Gale *et al.* 1996). Recently, Gonzalez-Donoso, Linares & Robaszynski (2007) and Robaszynski *et al.* (2008) reiterated that the two species are synonyms and included the species *globotruncanoides* in the genus *Thalmanninella*.

Therefore, owing to the difficulty in reliably distinguishing between the two species described by Sigal (1948), *Thalmanninella brotzeni* and *Rotalipora globotruncanoides*, reconsideration of the species concepts adopted by the scientists was needed. To verify the taxonomic status of Sigal's species, Caron & Premoli Silva (2007) examined the type specimens deposited at the Musée National d'Histoire Naturelle (MNHN) in Paris. According to Caron & Premoli Silva's (2007, p. 529) re-description and observation of the holotypes of *Thalmanninella brotzeni* and *Rotalipora globotruncanoides*, the two species 'are not conspecific and must be considered two discrete taxa. From a stratigraphic point of view *Th. brotzeni* first occurs slightly earlier than *Th. globotruncanoides*'.

Consequently, in this study we aim to clarify the taxonomy of the index species *Th. globotruncanoides*, *Th. brotzeni* as well as *Ps. tehamaensis* and to document their stratigraphic distribution across the Albian/Cenomanian boundary in the stratotype section at Mont Risou (Kennedy *et al.* 2004). In addition, the assemblages at Mont Risou are compared with the equivalent and well-preserved planktonic foraminifera associations recorded at Blake Nose Plateau (Ocean Drilling Program, ODP Leg 171B, North Western Atlantic Ocean; Petrizzo & Huber, 2006a) in order to elucidate the reliability and the stratigraphic distribution of the marker taxa outside the Mediterranean Tethys (Fig. 1). Sigal's type specimens are discussed and for the first time illustrated through stereoscopic images taken by Annachiara Bartolini, curator at the Musée National d'Histoire Naturelle in Paris.

This study is part of a long-term project of the Mesozoic Planktonic Foraminifera Working Group focusing on the taxonomy and phylogeny of Jurassic–Cretaceous planktonic foraminifera by studying and re-illustrating primary type specimens and by documenting stratigraphic changes in wall microstructure and shell morphology. The working group has published results in the peer-reviewed literature (e.g. Petrizzo & Huber, 2006a,b; Ando & Huber, 2007; Caron & Premoli Silva, 2007; Gonzalez-Donoso, Linares & Robaszynski, 2007; Georgescu & Abramovich, 2008; Lipson-Benitah, 2008; Spezzaferri & Caron, 2008; Georgescu & Huber, 2009; Georgescu, Saupe & Huber, 2009; Premoli Silva *et al.* 2009; Falzoni & Petrizzo, 2011; Huber & Leckie, 2011; Petrizzo, Falzoni & Premoli Silva, 2011; Petrizzo *et al.* 2012, 2013; Ando, Huber & Premoli Silva, 2013; Falzoni *et al.* 2014; Huber & Petrizzo, 2014; Haynes, Huber & MacLeod, in press, among others) and has built an online taxonomic database posted on the CHRONOS website (<http://www.chronos.org>).

2. Considerations on the primary and secondary types of *Thalmanninella brotzeni* and *Thalmanninella globotruncanoides*

The stereoscopic images of the primary and secondary types of *Th. brotzeni* and *Th. globotruncanoides* show that the specimens are recrystallized and infilled; however, they retain the most important taxonomic characters. The collection includes the holotype (Fig. 2a–c) and one paratype (Fig. 2d–g) of *Th. brotzeni*, and the holotype (Fig. 2h–j) and three paratypes (Fig. 2k–u) of *Th. globotruncanoides*. Sigal (1948) erected each species based on holotypes from Sidi Aissa in Algeria, whereas the paratype(s) are from Morocco. It is worth mentioning that the designation of primary types from different localities was common in earlier foraminiferal classification and, in agreement with Ando & Huber (2007), this practice is no longer acceptable because it leaves the status of the paratypes questionable, especially if not supported by an accurate record of their stratigraphic ranges.

Caron & Premoli Silva (2007), after examination of the type materials of *Th. globotruncanoides* and *Th. brotzeni* deposited at the MNHN in Paris, considered the two species to be separate taxa based on the differences in growth rate, chamber morphology and position of the supplementary apertures. Because of the museum's curatorial policy at that time, Sigal's type materials could not be photographed and Caron & Premoli Silva (2007) re-described and redrew the holotypes of both *Th. brotzeni* and *Th. globotruncanoides* (p. 527, fig. 2), and illustrated by scanning electron microscope (SEM) only topotype material (p. 258, plate 1, figs 1, 2). According to Caron & Premoli Silva (2007), *Th. globotruncanoides* differs from *Th. brotzeni* by being larger in size, in having an almost plano-convex profile instead of symmetrically biconvex, more petaloid chambers on the spiral side and a faster growth rate, a shorter inner spire with the spiral suture lying in a marked depression, a larger and shallower umbilicus, a higher arched primary aperture and supplementary apertures migrating along the sutures out of the umbilical area in the last chambers of the last whorl.

These observations are slightly different from those by Ando & Huber (2007, p. 173), who examined the topotypes (metatypes) of *Th. globotruncanoides* and *Th. brotzeni* deposited in the Cushman Collection at the Smithsonian NMNH. In their opinion *Th. globotruncanoides* 'diagnostically exhibits fish-hook ornamentation on the umbilical chamber surfaces in the later part of the last whorl, where it is illustrated by a combination of keeled periphery, raised umbilical suture, peri-umbilical ridge, and adumbilical (= toward umbilicus) ridge parallel to the posterior chamber margin'. Ando & Huber's (2007) species concept fits with the diagnosis given by Robaszynski *et al.* (2008, p. 127) that stated '*globotruncanoides* has curved and raised sutures between all chambers'. Moreover, Ando & Huber (2007) did not exclude the possibility that *Th. brotzeni*

may be a pre-adult given the size difference with *Th. globotruncanoides* (Caron & Premoli Silva, 2007, p. 525).

Our re-examination of Sigal's holotypes of *Th. globotruncanoides* and *Th. brotzeni*, based on the new stereoscopic images, confirms the emended description by Caron & Premoli Silva (2007) and demonstrates that both *Th. globotruncanoides* and *Th. brotzeni* possess on the umbilical side slightly raised sutures on the first chambers of the last whorl becoming smoother and depressed in the last two chambers (Fig. 2a–c, h–j). Therefore, beside the morphological differences mentioned by Caron & Premoli Silva (2007), the most important distinguishing feature for a consistent species assignment is the position of the supplementary apertures, which are completely umbilical in *Th. brotzeni*, whereas in *Th. globotruncanoides* the supplementary apertures progressively migrate out of the umbilical area and become sutural on the last chamber.

The paratypes of *Th. brotzeni* and *Th. globotruncanoides* (Fig. 2d–g, k–m, n–p, r–u) were collected by Sigal (1948) from an unclearly specified middle Cenomanian level in Morocco. The paratype of *brotzeni* (Fig. 2d–g) was illustrated by Sigal (1948, plate II, fig. 7) only in umbilical view (here reproduced in Fig. 2g). In our opinion, this specimen cannot be attributed to *brotzeni* as it possesses nine chambers in the last whorl, which are banana-shaped and separated by fully depressed, strongly backwards-curved sutures in umbilical view. It possesses umbilical supplementary apertures, a short inner spire that is depressed with respect to the outer whorl, chambers on the spiral side from subpetaloid in the first three (possibly four) separated by slightly keeled sutures, to radially elongate and separated by keeled sutures, and an acute peripheral margin, keeled and asymmetrically biconvex with the spiral side close to flat and the umbilical side convex. Based on these features, this specimen looks to be transitional to *Thalmanninella greenhornensis* and does not belong either to *brotzeni* or *globotruncanoides*, as already suggested by Ando & Huber (2007, p. 172). A second specimen identified as a paratype of *brotzeni* and illustrated only in spiral and umbilical views by Sigal (1948, plate II, fig. 6a, b) is not present on the microslide deposited in the repository.

Based on our observations of the paratypes of *globotruncanoides*, we consider paratype 4 (Fig. 2k–m) illustrated by Sigal (1948, plate II, fig. 4a, b) to be similar to the holotype. On the contrary, *globotruncanoides* paratype 3 (Fig. 2n–q) illustrated by Sigal (1948, plate II, fig. 3a, b, here reproduced in Fig. 2q) does not look like a typical *globotruncanoides*. In edge view and on the umbilical side, the first chambers of the last whorl are narrower and more elongate and separated by more depressed and very curved sutures. These features suggest paratype 3 is a primitive form transitional to *Th. greenhornensis* (Morrow, 1934). Paratype 5 (Fig. 2r–u) illustrated by Sigal (1948, plate II, fig. 5), shows a symmetrically biconvex profile, an

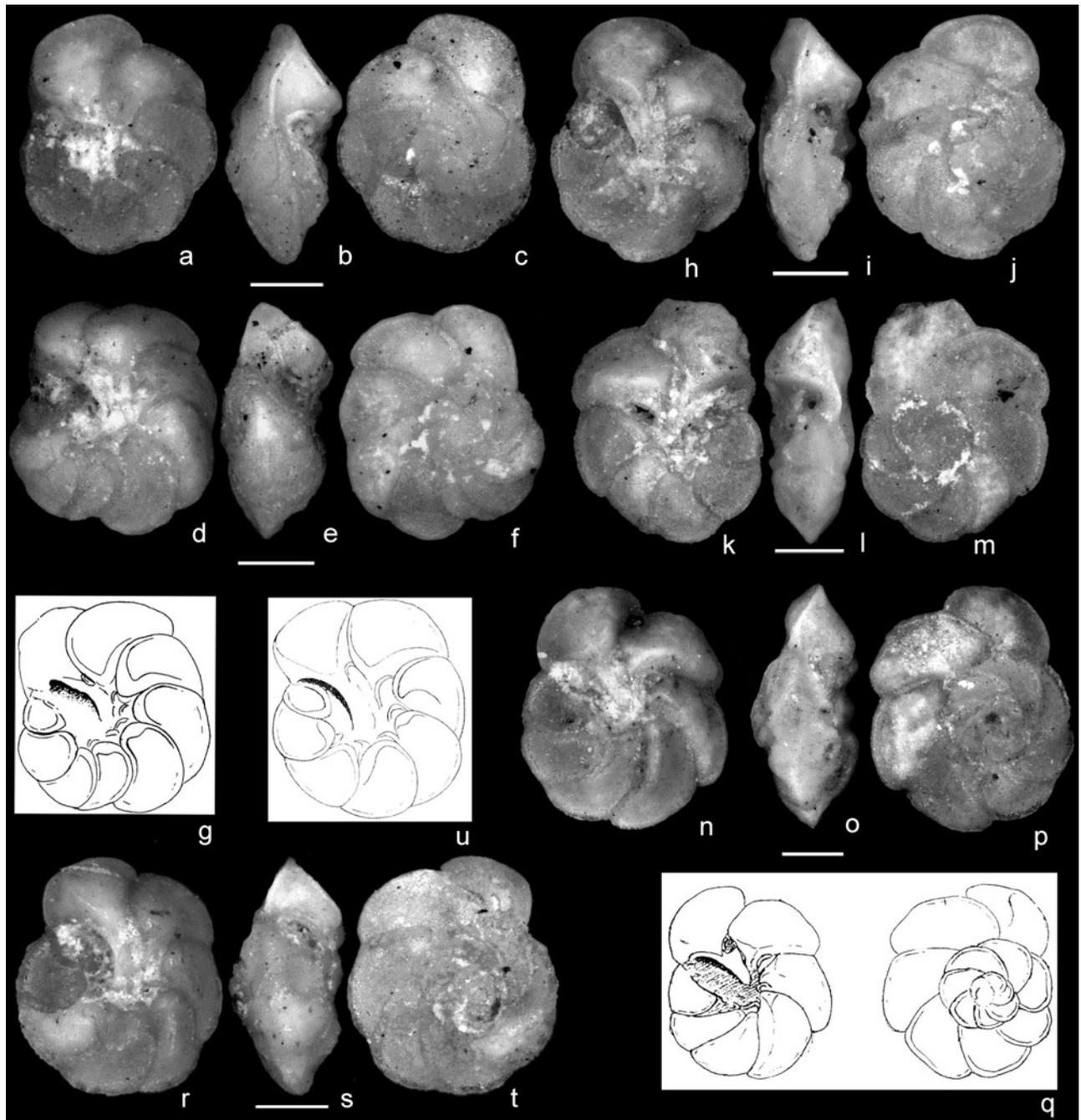


Figure 2. Sigal's type specimens deposited at the Musée National d'Histoire Naturelle in Paris. (a–c) *Thalmanninella brotzeni*, holotype F6 0843, Sigal, 1948, pl. I, fig. 5a–c, refigured in Sigal, 1952, fig. 25, from the type-level of Sidi Aissa, Algeria, middle Cenomanian, in (a) umbilical, (b) edge and (c) spiral view. (d–g) *Thalmanninella brotzeni*, paratype F6 0843, Sigal, 1948, pl. II, fig. 7 (original drawing reproduced in (g)), from the middle Cenomanian of Morocco, in (d) umbilical, (e) edge and (f) spiral view. The specimen is here interpreted as a transitional form to *Th. greenhornensis* (see text). (h–j) *Thalmanninella globotruncanoides*, holotype F6 0840, Sigal, 1948, pl. I, fig. 4a–c, refigured in Sigal, 1952, fig. 24, from the type-level of Sidi Aissa, Algeria, middle Cenomanian, in (h) umbilical, (i) edge and (j) spiral view. (k–m) *Thalmanninella globotruncanoides*, paratype 4, Sigal, 1948, pl. II, fig. 4a, b, from the middle Cenomanian of Morocco, in (k) umbilical, (l) edge and (m) spiral view. (n–q) *Thalmanninella globotruncanoides* paratype 3, Sigal, 1948, pl. II, fig. 3a, b (original drawings reproduced in (q)), from the middle Cenomanian of Morocco, in (n) umbilical, (o) edge and (p) spiral view. The specimen is here interpreted as a primitive form transitional to *Th. greenhornensis* (see text). (r–u) *Thalmanninella globotruncanoides*, paratype 5, Sigal, 1948, pl. II, fig. 5 (original drawing reproduced in (u)), from the middle Cenomanian of Morocco, in (r) umbilical, (s) edge and (t) spiral view. The specimen is possibly as an intermediate form between *globotruncanoides* and *greenhornensis* (see text). Scale bars = 100 μm

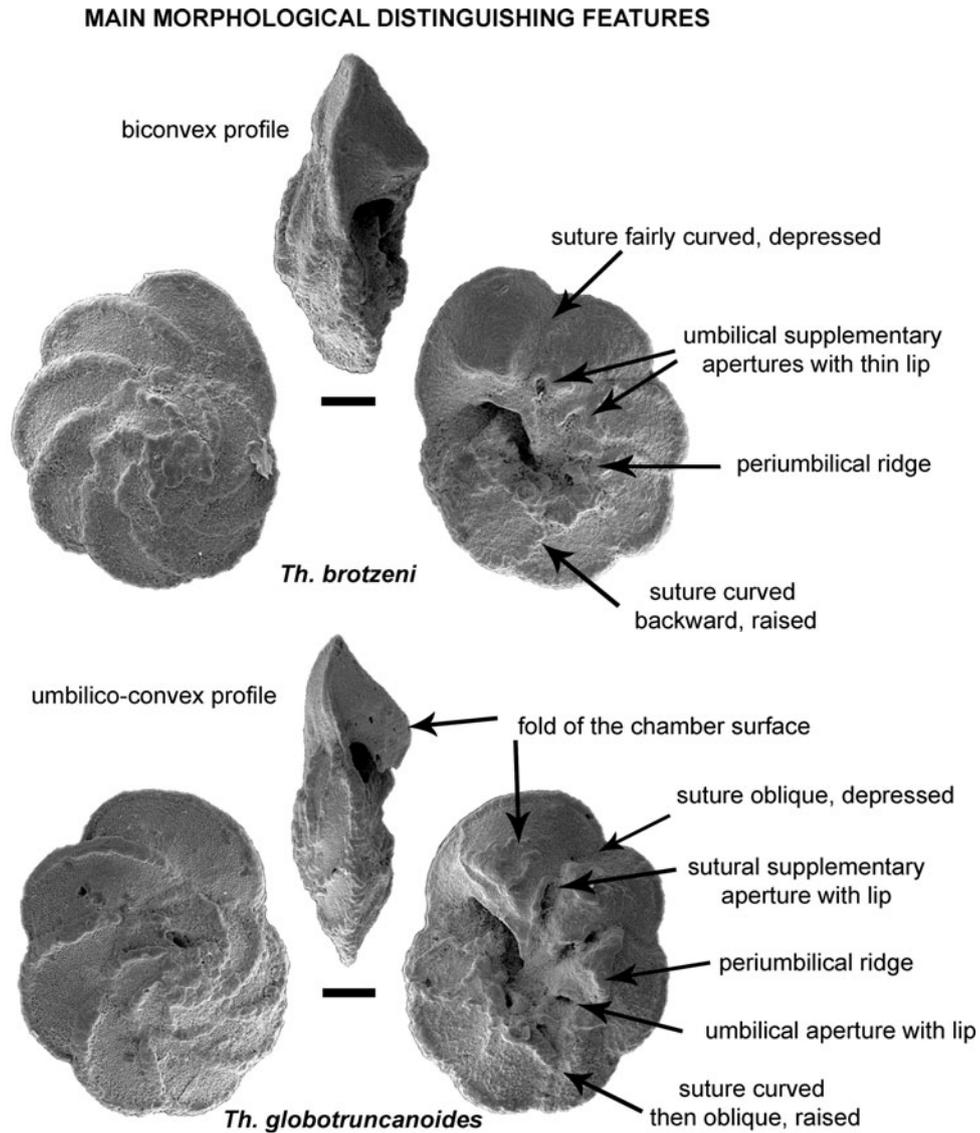


Figure 3. Distinguishing morphological features of *Th. brotzeni* and *Th. globotruncanoides*. Specimens are from sample 1050C-26R-3, 15–17 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean. See text for further explanation. Scale bar = 100 μm

inner spire flush with the test and supplementary apertures only within the umbilicus (Fig. 2u). The shape of the first chambers in umbilical view as well as the growth rate and the petaloid shape of the last chambers in spiral view recall the features of *globotruncanoides*. It may represent an intermediate form between *globotruncanoides* and *greenhornensis*; however, this assumption is pending in the absence of a precise documentation of the stratigraphic distribution of the paratypes.

Emended descriptions of *Th. brotzeni* and *Th. globotruncanoides* are provided to stabilize the species concepts. In addition, the main distinguishing morphological features of the two species are summarized in Figure 3.

Genus *Thalmaninella* Sigal, 1948, emended Gonzalez-Donoso, Linares & Robaszynski, 2007
Type species. *Thalmaninella brotzeni* Sigal, 1948

Thalmaninella brotzeni Sigal, 1948, emended Figure 2a–c (holotype MNHN F6 0843, Sidi Aissa, Algeria); Figure 4g–i (Mont Risou, France); Figure 4s–u (ODP 1050, Blake Nose Plateau, NW Atlantic Ocean).

1948 *Thalmaninella brotzeni* Sigal, pl. I, fig. 5a–c, refigured in Sigal, 1952, fig. 25 (Sidi Aissa, Algeria).

2007 *Thalmaninella brotzeni* Sigal; Ando & Huber, pl. A1, fig. 2a–c (metatype USNM P3930, Sidi Aissa, Algeria).

2007 *Thalmaninella brotzeni* Sigal; Caron & Premoli Silva, pl. 1, fig. 1 (topotype, Sidi Aissa, Algeria).

Emended description. Test coiled in a low to moderate trochospire, almost equally biconvex; equatorial outline subcircular to ovoid, initially compact passing to very slightly lobate; in edge view peripheral

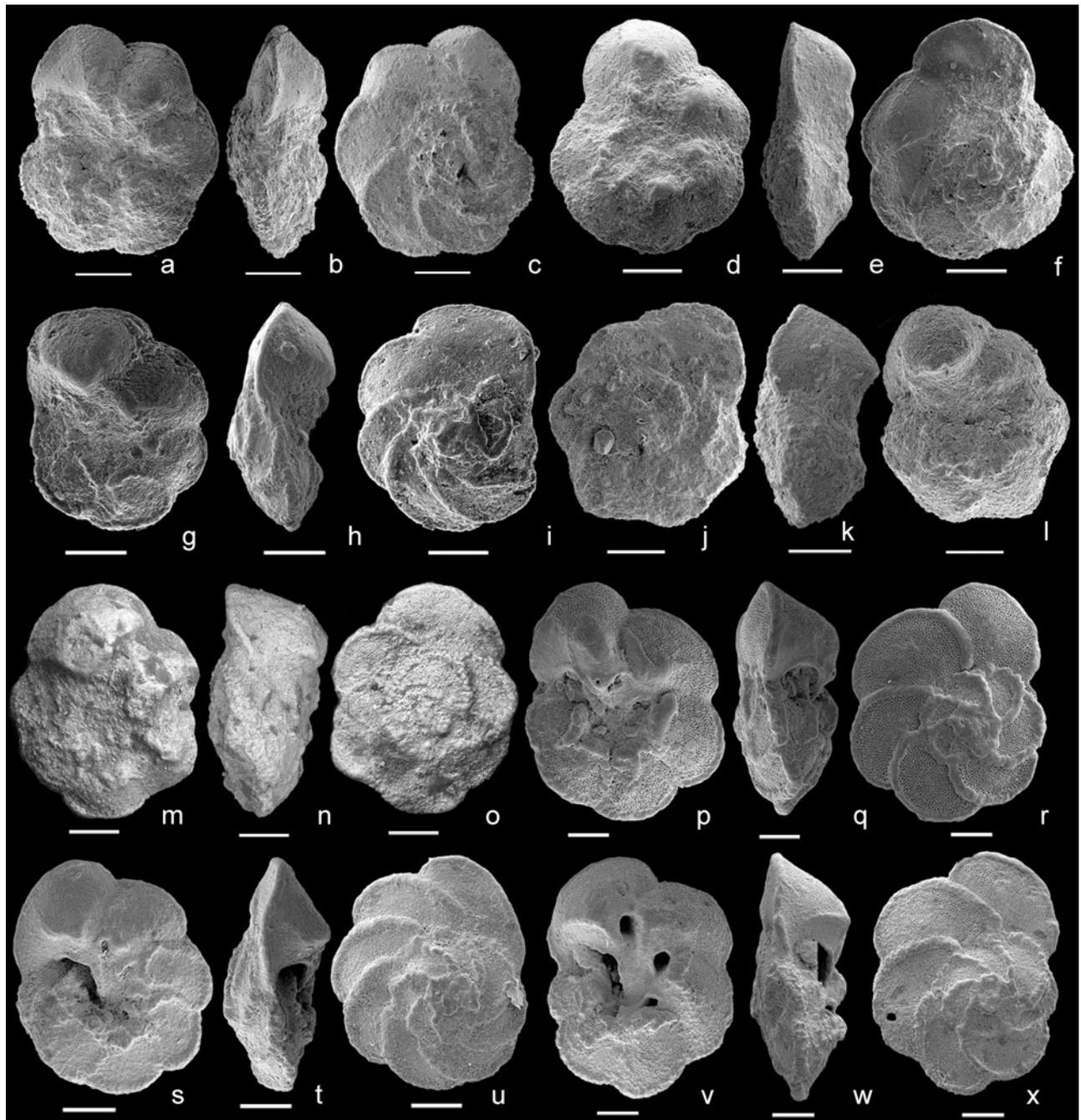


Figure 4. (a–c) *Thalmanninella globotruncanoides*, sample –36 m, Mont Risou, Hautes-Alpes, France, in (a) umbilical, (b) edge and (c) spiral view. (d–f) *Thalmanninella globotruncanoides*, sample –30 m, Mont Risou, Hautes-Alpes, France, in (d) umbilical, (e) edge and (f) spiral view. (g–i) *Thalmanninella brotzeni*, sample –27 m, Mont Risou, Hautes-Alpes, France, in (g) umbilical, (h) edge and (i) spiral view. (j–l) *Thalmanninella gandolfii*, sample –48 m, Mont Risou, Hautes-Alpes, France, in (j) umbilical, (k) edge and (l) spiral view. (m–o) *Thalmanninella gandolfii*, holotype NHM Basel C 25557, level 55, Breggia section, Ticino, Switzerland, Luterbacher & Premoli Silva (1962), in (m) umbilical, (n) edge and (o) spiral view. SEM image available on the online Mesozoic Planktonic Foraminiferal Taxonomic Dictionary at http://portal.chronos.org/gridsphere?cid1/4res_taxondb. (p–r) *Thalmanninella gandolfii*, sample 1050C-26R-5, 18–20 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (p) umbilical, (q) edge and (r) spiral view. (s–u) *Thalmanninella brotzeni*, sample 1050C-26R-3, 15–17 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (s) umbilical, (t) edge and (u) spiral view. (v–x) *Thalmanninella globotruncanoides*, sample 1050C-26R-3, 15–17 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (v) umbilical, (w) edge and (x) spiral view. Scale bars = 100 μm .

margin acute and marked by a keel in all chambers of the last whorl; on spiral side 2.5–3 whorls, with 6–8 chambers in the last whorl, increasing gradually in size as added, crescentic in shape at least twice longer than wide except the last two chambers that become

more petaloid; intercameral sutures curved backwards marked by slightly raised, finely beaded keel; on umbilical side chambers subtriangular to subtrapezoidal, initially slowly increasing in size, the last two chambers slightly larger and inflated; intercameral sutures fairly

curved backwards marked by a very slightly raised keel to flush with test surface except the last one lying within a gentle depression that may mask the raised suture; intercameral keels extend to the umbilical edge forming a more raised periumbilical ridge, except on the last chamber that exhibits only an adumbilical inflation; umbilicus rather small and deep; primary aperture umbilical-extraumbilical as a medium high arch; a few supplementary apertures, bordered by a thin lip, are visible within the umbilical area; wall macroperforate and smooth.

Distinguishing features. *Thalmanninella brotzeni* differs from *Th. globotruncanoides* by having an almost equally biconvex profile, a rather compact less lobate outline, more crescentic chambers separated by strongly backwards-curved intercameral sutures in spiral view growing slowly in size, less prominent periumbilical ridges, a smaller and deeper umbilicus, and supplementary apertures only umbilical in position.

Remarks. This species has been regarded for a long time as a junior synonym of *Th. globotruncanoides* (Wonders, 1978, 1980; Robaszynski *et al.* 1994, 2008; Robaszynski & Caron, 1995; Gale *et al.* 1996; Gonzalez-Donoso, Linares & Robaszynski, 2007).

Stratigraphic distribution. Uppermost part of the *Th. appenninica* Zone to the lower upper Cenomanian.

Geographical distribution. Algeria, Tunisia, Morocco, France, Central Italy, Israel and the western Atlantic Ocean.

Thalmanninella globotruncanoides (Sigal, 1948),
emended

Figure 2h–j (holotype MNHN F6 0840, Sidi Aissa, Algeria); Figure 2k–m (paratype, Morocco); Figure 4a–f (Mont Risou, France); Figure 4v–x (ODP 1050, Blake Nose Plateau, NW Atlantic Ocean).

1948 *Rotalipora globotruncanoides* Sigal, pl. I, fig. 4a–c, refigured in Sigal, 1952, fig. 24 (Sidi Aissa, Algeria).

1993 *Rotalipora (Thalmanninella) globotruncanoides* (Sigal); Gonzalez-Donoso & Linares in Robaszynski *et al.*, pl. XIX, figs 2, 4, 5, 9 (Tunisia).

2002 *Rotalipora globotruncanoides* Sigal; Bellier & Moullade, pl. 2, fig. 4–7 (Blake Nose Plateau, NW Atlantic Ocean).

2004 *Rotalipora globotruncanoides* Sigal; Kennedy *et al.*, fig. 8, parts 13–15 (Mont Risou, France).

2007 *Thalmanninella globotruncanoides* (Sigal); Ando & Huber, pl. A1, fig. 1a–c (metatype USNM 387929, Sidi Aissa, Algeria).

2007 *Thalmanninella globotruncanoides* (Sigal); Caron & Premoli Silva, pl. 1, fig. 2a–c (topotype, Sidi Aissa, Algeria).

Emended description. Test coiled in a low trochospire, umbilico-convex; equatorial outline subcircular to ovoid, spiral side almost plane with inner spire very slightly elevated, peripheral margin acute in edge view and keeled on all chambers of the last whorl; on spiral side 2.5–3 whorls, with 6–7 chambers on the last whorl, initially crescentic then they become slightly petaloid, enlarging rather rapidly in size; surface of the last two chambers slightly concave in the central part giving an almost plane aspect to the trochospire; intercameral sutures curved and marked by a beaded keel slightly raised on the first chambers of the last whorl and becoming smoother in the last two chambers; spiral suture of the first whorls, possibly keeled, located in a gentle depression; on umbilical side chambers enlarging gradually but rather rapidly in size, subtrapezoidal with flat surface in the first three to four, the last three chambers becoming gradually more inflated; intercameral sutures initially gently curved and oblique with respect to the equatorial margin, then increasingly more oblique and markedly depressed; sutural beaded keels slightly visible and flush with test surface along the first four sutures, each extending to form a periumbilical ridge; sutural keels not visible or absent between the last two chambers; the last two more inflated chambers exhibit a prominent smooth fold of the chamber surfaces, located in the inner part of each chamber, that bifurcates from the umbilicus half way towards the periphery; primary aperture umbilical-extraumbilical as a medium high arch; umbilicus rather large and shallow, partially covered by a triangular, long porticus extending from the last chamber; supplementary apertures, bordered by a thin lip, are umbilical in the early outer chambers, then they progressively migrate out of the umbilicus along the inner part of the suture in the last three chambers, the last one being sutural; wall macroperforate and smooth.

Distinguishing features. *Thalmanninella globotruncanoides* differs from *Th. brotzeni* in having a more lobate outline and a faster growth rate, a folded surface in the last two inflated and more petaloid chambers, a larger and shallower umbilicus, and supplementary apertures migrating along the sutures and out of the umbilical area through ontogeny. It differs from *Th. greenhornensis* in having fewer chambers in the last whorl, an umbilico-convex profile, raised umbilical sutures only in the first chambers of the last whorl, and supplementary apertures migrating progressively out of the umbilical area, the last one being sutural. *Th. greenhornensis* is well differentiated by its numerous elongated chambers in the last whorl that curve backwards both in the spiral and umbilical sides and by having a symmetrically biconvex profile as discussed by Ando & Huber (2007).

Remarks. Kennedy *et al.* (2004) illustrated two specimens as *Rotalipora globotruncanoides* from Mont Risou (fig. 8, parts 8–12 and 13–15): the specimen in figure 8, parts 13–15, although distorted in spiral view,

is close to the type material of *Th. globotruncanoides* (see also Ando & Huber, 2007), while the second specimen illustrated in figure 8, parts 10–12, being also distorted, is less convincing.

Stratigraphic distribution. Base of the Cenomanian to the lower upper Cenomanian.

Geographical distribution. Algeria, Tunisia, Morocco, France, Central Italy, Spain and the western Atlantic Ocean.

3. Equivocal species concept of

Pseudothalmanninella tehamaensis

The appearance level of *Pseudothalmanninella tehamaensis* (= *Rotalipora tehamaensis* Marianos & Zingula, 1966) is a secondary criterion for placing the Albian/Cenomanian boundary (Kennedy *et al.* 2004). *Pseudothalmanninella tehamaensis* was described by Marianos & Zingula (1966) from Dry Creek in California from a single Albian level yielding *Planomalina buxtorfi* and *Pseudothalmanninella ticinensis*. In our opinion the primary and secondary types (Fig. 5a–f), although poorly preserved, fit well with Marianos & Zingula's original drawing and description of the species: 'Test trochoid, biconvex, nearly circular, periphery only weakly lobate, single-keeled; chambers compressed, thickest at the umbilicus, early chambers of last whorl pustulose, later ones smooth, 6–8 in last whorl, increasing slowly in size, normally overlapping dorsally; spiral sutures curved, raised and thickened, curved back at the periphery forming a keel; umbilical sutures radial, depressed near outer edge, becoming raised and thickened near umbilicus, and in some specimens having a thickened ridge around the umbilicus connecting adjacent sutures; umbilicus narrow, deep; primary aperture a high umbilical-extraumbilical arch showing a lip; one secondary aperture, having a lip, per suture in the umbilicus. Dimensions: Greatest diameter of holotype 0.34 mm; least diameter 0.30 mm; thickness 0.16 mm' (Marianos & Zingula, 1966, p. 339).

Our identification of *Ps. tehamaensis* across the Albian/Cenomanian boundary interval at Mont Risou (Fig. 5g–i), and in the equivalent and well-preserved planktonic foraminiferal associations recorded at the Blake Nose Plateau (Fig. 5j–r) strictly follow the original description.

Remarkably, over the years the species concept of *Ps. tehamaensis* has changed and been erroneously interpreted probably because of its similarity with companion species and in the absence of SEM images of the type material (now available at the CHRONOS website, www.chronos.org). In fact, *Ps. tehamaensis* was either included in the range of variability of *Rotalipora greenhornensis* (Douglas, 1969; Masters, 1977) or of *Ps. ticinensis* (Barr, 1972) or of *Rotalipora evoluta* (Pessagno, 1967). Consequently, the species was not considered valid by the European Working Group

on Planktonic Foraminifera in the preparation of the Atlas (Robaszynski & Caron, 1979).

Afterwards, Gonzalez-Donoso & Linares *in* Robaszynski *et al.* (1994) called *Ps. tehamaensis* high-spired forms occurring at Kalaat Senan (Tunisia), in a short stratigraphic interval immediately above the appearance level of *Th. globotruncanoides*. These authors questioned the validity of the species, it being either very similar to *Ps. ticinensis* (Fig. 5s–x) or a possible intrapopulation morphotype within the *Th. globotruncanoides* species-group. The specimen illustrated as *Ps. tehamaensis* by Gonzalez-Donoso & Linares *in* Robaszynski *et al.* (1994, plate 20, fig. 1) is characterized by having straight and raised umbilical sutures, except on the ultimate chambers, and by possessing a distinctive periumbilical ridge and a slightly elevated trochospire. The validity of *Ps. tehamaensis* was reaffirmed by Caron *in* Kennedy *et al.* (2004, p. 30) and its lowest occurrence was used as a secondary marker for the identification of the base of the Cenomanian Stage at the Mont Risou GSSP. The specimen illustrated as *Ps. tehamaensis* (Kennedy *et al.* 2004, fig. 8, parts 7–9) is only in partial agreement with the *Ps. tehamaensis* species concept adopted by Gonzalez-Donoso & Linares *in* Robaszynski *et al.* (1994), as it shows raised umbilical sutures only on the first two chambers of the ultimate whorl, a slightly developed periumbilical ridge and a high trochospire asymmetrically biconvex. However, since *Ps. tehamaensis* is a biconvex form and does not possess a high trochospire, its identification at Mont Risou is here revised. Moreover, to stabilize the species concept of *Ps. tehamaensis* we provide an emended description as follows.

Genus *Pseudothalmanninella* Wonders, 1978, emended Gonzalez-Donoso, Linares & Robaszynski, 2007

Type species. *Globotruncana ticinensis* forma tipica Gandolfi, 1942

Pseudothalmanninella tehamaensis (Marianos & Zingula, 1966), emended
Figure 5a–c (holotype USMN 641551, Dry Creek, Tehama County, California); Figure 5d–f (paratype 1, USMN 641552, Dry Creek, Tehama County, California); Figure 5g–i (Mont Risou, France); Figure 5j–r (ODP 1050, Blake Nose Plateau, NW Atlantic Ocean).

1966 *Rotalipora tehamaensis* Marianos & Zingula, pl. 38, fig. 4a–c (Dry Creek, Tehama County, California).

not 1994 *Pseudothalmanninella tehamaensis* (Marianos & Zingula); Gonzalez-Donoso & Linares *in* Robaszynski *et al.*, pl. 20, fig. 1 (Kalaat Senan, Tunisia).

not 2004 *Rotalipora tehamaensis* Marianos & Zingula; Caron *in* Kennedy *et al.*, fig. 8, parts 7–9 (Mont Risou, France).

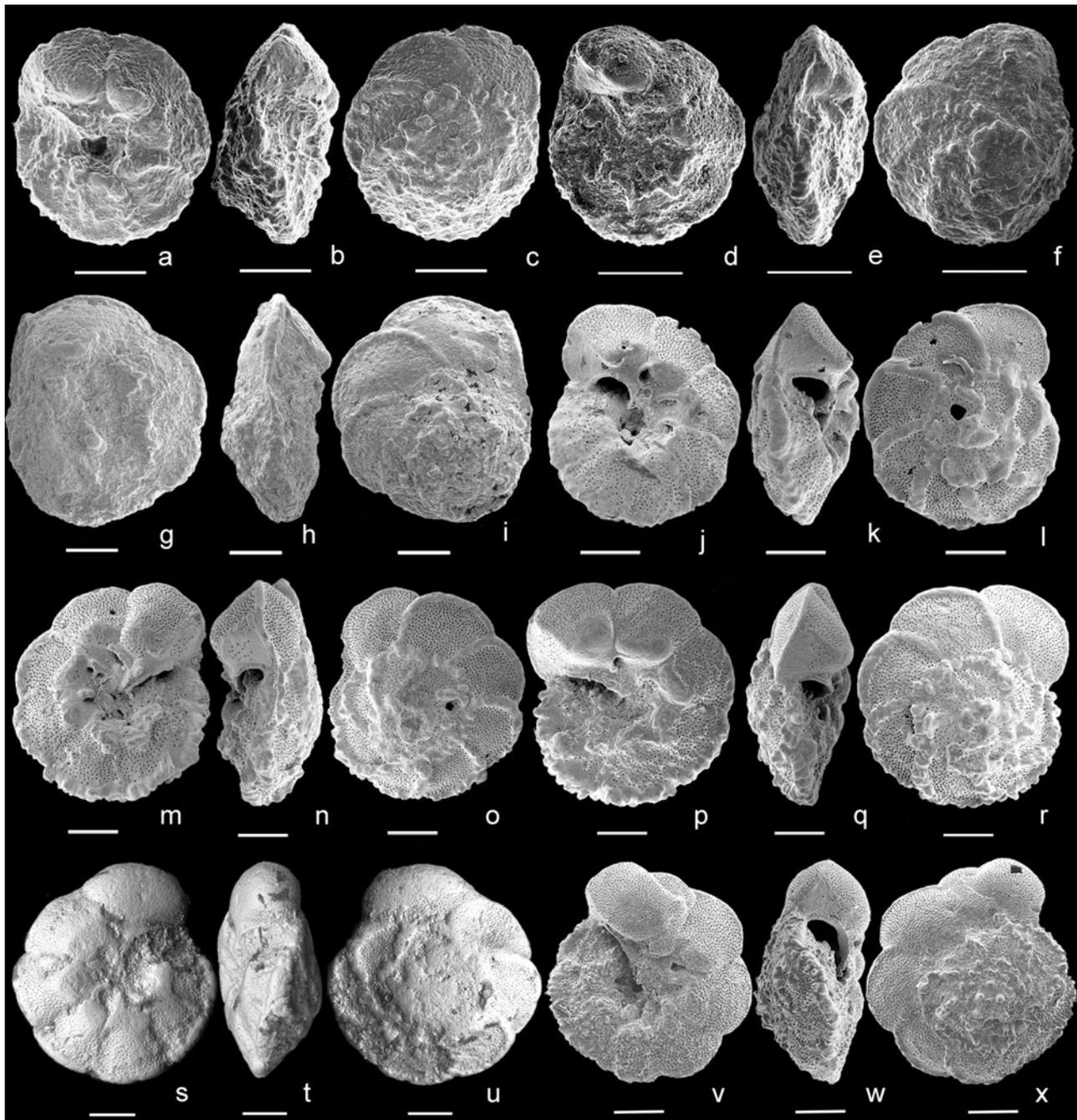


Figure 5. (a–c) *Pseudothalmaninella tehamaensis*, holotype USNM 641551, Marianos & Zingula, 1966, Tehama County, California, Albian, in (a) umbilical, (b) edge and (c) spiral view. (d–f) *Pseudothalmaninella tehamaensis*, paratype 1 USNM 641552, Marianos & Zingula, 1966, Tehama County, California, Albian, in (d) umbilical, (e) edge and (f) spiral view. SEM images of *Ps. tehamaensis* type material available on the online Mesozoic Planktonic Foraminiferal Taxonomic Dictionary at http://portal.chronos.org/gridsphere?cid1/4res_taxondb. (g–i) *Pseudothalmaninella tehamaensis*, sample –27 m, Mont Risou, Hautes-Alpes, France, in (g) umbilical, (h) edge and (i) spiral view. (j–l) *Pseudothalmaninella tehamaensis*, sample 1050C-27R-3, 8–10 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (j) umbilical, (k) edge and (l) spiral view. (m–o) *Pseudothalmaninella tehamaensis*, sample 1050C-27R-2, 103–105 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (m) umbilical, (n) edge and (o) spiral view. (p–r) *Pseudothalmaninella tehamaensis*, sample 1050C-27R-2, 103–105 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (p) umbilical, (q) edge and (r) spiral view. (s–u) *Pseudothalmaninella ticinensis*, in (s) umbilical, (t) edge and (u) spiral view; specimen illustrated by Gandolfi (1942), pl. 4, fig. 11, bed 30, Breggia section, Ticino, Switzerland and deposited at the NHM in Basel. SEM image courtesy of B. T. Huber (Smithsonian Institution). (v–x) *Pseudothalmaninella ticinensis*, sample 1050C-27R-1, 73–76 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (v) umbilical, (w) edge and (x) spiral view. Scale bars = 100 μ m.

Emended description. Test trochospiral with a moderately elevated spire; equatorial outline circular, very weakly lobate, peripheral margin acute throughout with one keel; 2.5–3 whorls with 7–9 chambers in final whorl, uniformly and slowly increasing in size, trapezoidal on the umbilical side, petaloid to slightly crescentic in the last ones on the spiral side; in edge view peripheral margin initially close to spiroconvex passing to symmetrically biconvex in adult; on the umbilical side the first chambers of the last whorl are compressed and display a flat or even depressed surface, whereas the last two or three become progressively thicker and characteristically triangular in shape towards the umbilicus; straight and raised umbilical sutures on most chambers except between the last two where raised sutures, if present, may be lying within a gentle depression (raised sutures possibly masked and not visible); raised sutures on the spiral side curved and bending sharply backwards at the peripheral margin; umbilicus small and deep bordered by a distinctive periumbilical ridge; primary aperture umbilical-extraumbilical as a medium arch, supplementary apertures within the umbilical area; wall macroporulate and smooth.

Distinguishing features. *Pseudothalmanninella tehamaensis* differs from *Ps. ticinensis* (Fig. 5s–x) by having raised umbilical sutures and a distinctive periumbilical ridge and by possessing flattened instead of inflated chambers on the umbilical side. It differs from *Pseudothalmanninella klausii* (Lehmann, 1966; see emendation by Spezzaferri & Caron, 2008) in having a more compact equatorial outline, a lower trochospire, and raised keeled umbilical sutures in the early chambers of the last whorl, tending to form an extended periumbilical ridge instead of depressed sutures throughout and a faint periumbilical ridge confined to the early chambers.

Remarks. The specimen illustrated as *Ps. tehamaensis* by Gonzalez-Donoso & Linares in Robaszynski *et al.* (1994) shares most of the characters with the holotype and mainly conforms to the emended description; however, it possesses a last chamber that is too inflated and apparently not keeled. It may be interpreted either as an ancestral or an aberrant form of *Ps. tehamaensis*. Concerning the specimen illustrated by Caron in Kennedy *et al.* (2004), it is keeled throughout but in edge view it is more compressed than the type material, exhibits raised umbilical sutures only in the first two chambers and the periumbilical ridge is less prominent. On the basis of these observations, it may be interpreted as an ancestral form to *Ps. tehamaensis* or a juvenile specimen.

Phylogenetic relationships. *Pseudothalmanninella tehamaensis* is inferred to represent the final member of the *Pseudothalmanninella* lineage (Gonzalez-Donoso, Linares & Robaszynski, 2007). It is interpreted to have evolved from *Ps. ticinensis* (Fig. 5s–x) by acquiring

raised umbilical sutures, developing a distinctive periumbilical ridge and by flattening the chambers on the umbilical side.

Stratigraphic distribution. Uppermost part of the *Th. appenninica* Zone to the lowermost part of the *Th. globotruncanoides* Zone. According to Marianos & Zingula (1966), the holotype co-occurs with *Planomalina buxtorfi* in a single level dated as Albian.

Geographic distribution. California, the western Atlantic Ocean, Tunisia and France.

4. Planktonic foraminifera index species at Mont Risou and Blake Nose Plateau

The planktonic foraminiferal assemblages across the GSSP boundary interval at Mont Risou have been restudied to document the stratigraphic distribution of *Th. globotruncanoides*, *Th. brotzeni* and *Ps. tehamaensis* using the species concepts revised in this study. We confirm the first appearance level of *Th. globotruncanoides* (Fig. 4a–f) at –36 m as in Kennedy *et al.* (2004), and document the first appearance of *Th. brotzeni* and *Th. gandolfii* (Luterbacher & Premoli Silva, 1962) (Fig. 4g–l) at sample –64 m. However, we have to remark that *Th. brotzeni* occurs discontinuously up-section and *Th. globotruncanoides* is rare in sample –36 m and, in agreement with previous data (Kennedy *et al.* 2004), it becomes more common from sample –27 m up-section.

Planomalina buxtorfi and *Pseudothalmanninella ticinensis* disappear at –116 m and –60 m, respectively. *Thalmanninella appenninica* and *Th. balernaensis* occur discontinuously from the base to the top of the section studied. *Pseudothalmanninella tehamaensis* is very rare and shows a very short stratigraphic range (from sample –27 m to –19 m), whereas common transitional morphotypes between *Ps. ticinensis* and *Ps. tehamaensis* occur from sample –116 m to –27 m (Fig. 6).

To test the reproducibility of the data, the sequence of bioevents observed across the Albian/Cenomanian boundary at Mont Risou is compared with that found throughout the equivalent stratigraphic interval at Blake Nose Plateau (ODP Leg 171B, North Western Atlantic Ocean) where the planktonic foraminiferal associations are better preserved (Petrizzo & Huber, 2006a). In general, at Blake Nose the transitional morphotypes from *Ps. ticinensis* to *Ps. tehamaensis*, *Th. gandolfii* (Fig. 4p–r), *Th. brotzeni* (Fig. 4s–u) and *Th. globotruncanoides* (Fig. 4v–x) appear in the same stratigraphic order (Fig. 7) documented at Mont Risou. An exception is represented by *Ps. tehamaensis*, which is first recorded below the lowest occurrence of *Th. globotruncanoides*. This discrepancy is likely assignable to the rarity and poor preservation of specimens of *Th. tehamaensis* at Mont Risou preventing the accurate identification of its lowest appearance.

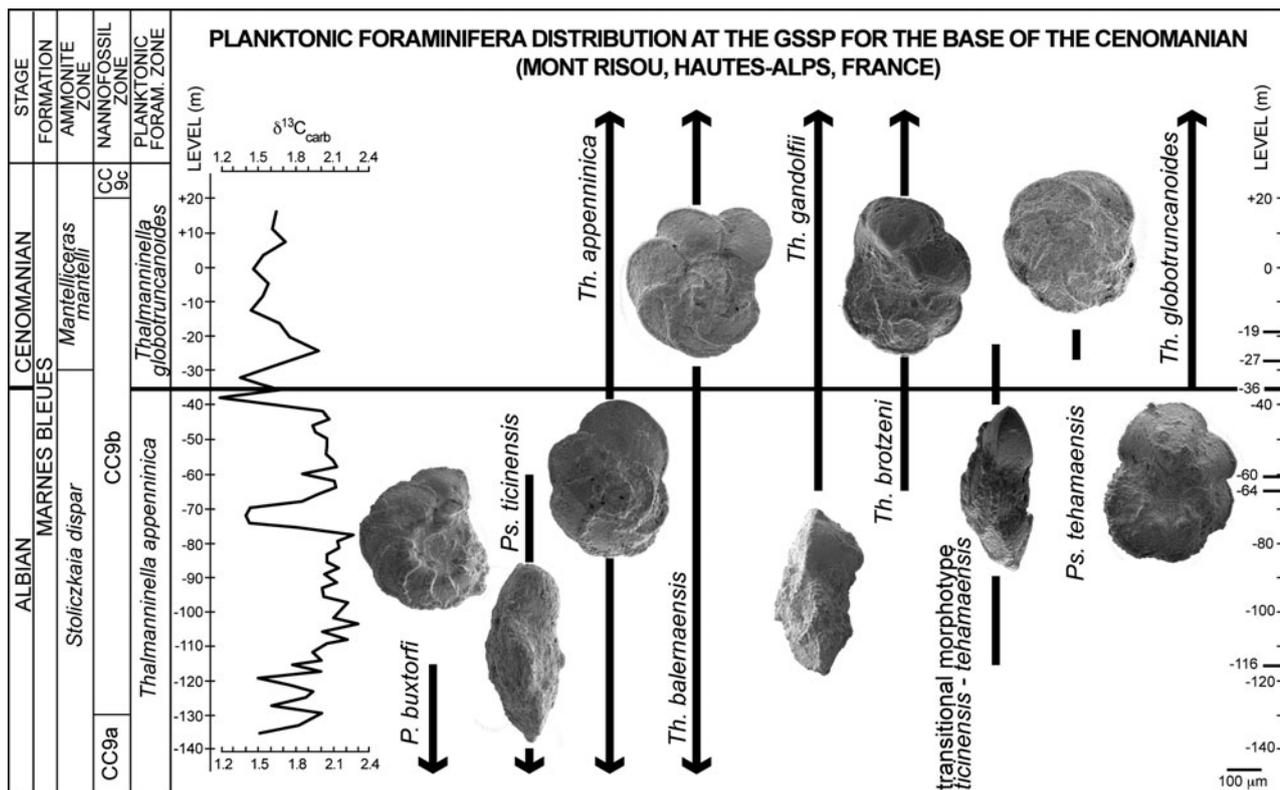


Figure 6. Distribution of selected planktonic foraminifera at the GSSP for the base of the Cenomanian Stage at Mont Risou (Hautes-Alps, France). Ammonite and nannofossil zonations according to Kennedy *et al.* (2004). Carbon isotope curve from Gale *et al.* (1996).

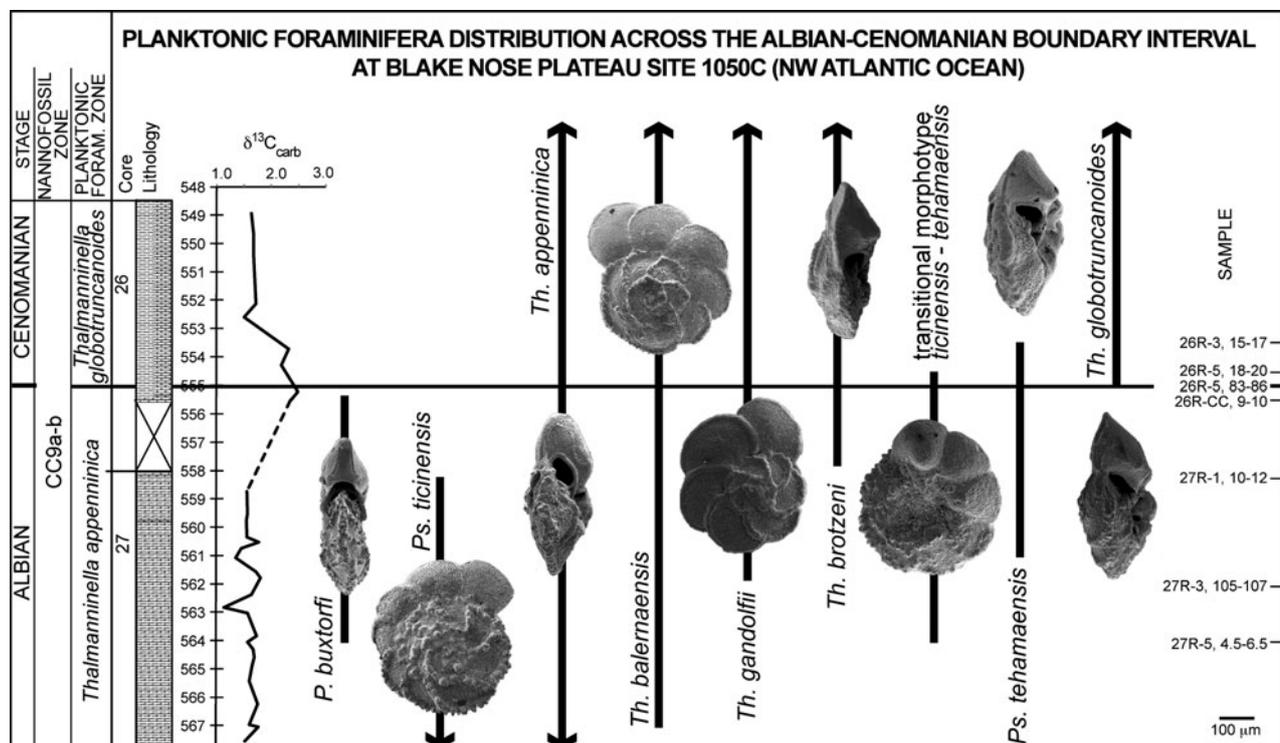


Figure 7. Distribution of selected planktonic foraminifera across the Albian/Cenomanian boundary interval at Hole 1050C Blake Nose Plateau (NW Atlantic Ocean). Nannofossil zonation from Watkins & Bergen (2003). Carbon isotope data according to Petrizzo *et al.* (2008).

However, the most relevant difference between the two localities is the different stratigraphic range shown by *P. buxtorfi*: at Blake Nose all the relevant planktonic foraminiferal appearances except for *Th. globotruncanoides* fall in stratigraphic levels still containing specimens of *P. buxtorfi*, whereas at Mont Risou *P. buxtorfi* shows an earlier disappearance and only co-occurs with the transitional *Ps. ticinensis* – *Ps. tehamaensis* morphotypes (Figs 6, 7).

Significantly, this finding highlights the diachroneity of the disappearance level of *P. buxtorfi* and confirms its unreliability for regional and global correlations. In fact, the extinction of *P. buxtorfi* was originally reported to fall above the appearance levels of *Th. brotzeni* and *Th. globotruncanoides* by Sigal (1977) in his biozonal scheme of the Mediterranean area and by Collignon, Sigal & Grekoff (1979) from North Madagascar. These observations were later confirmed by Robaszynski *et al.* (2008) in their study of the planktonic foraminiferal assemblages across the upper Albian – lower Cenomanian stratigraphic interval in Central Tunisia.

Specimens similar to the paratype of *Th. brotzeni* (Fig. 2d–g) and paratype 3 of *Th. globotruncanoides* (Fig. 2n–q) here interpreted as related to *Th. greenhornensis*, have not been observed in the assemblages across the Albian/Cenomanian boundary at Mont Risou and Blake Nose.

A summary of the main morphological features of *Th. brotzeni*, *Th. globotruncanoides*, *Th. gandolfii*, *P. ticinensis* and *P. tehamaensis* is presented in Table 1 to clarify the species concepts adopted in this study.

The development of a continuous umbilical ridge and raised umbilical sutures is the basis for distinguishing *Ps. tehamaensis* from *Ps. ticinensis*; however, a consistent distinction between the two species is not always easy at Mont Risou, especially because *Ps. tehamaensis* shows a short stratigraphic range and is rare, whereas the transitional forms have a longer stratigraphic distribution and dominate in the assemblage (Fig. 6). The evolutionary transition from *Ps. ticinensis* to *Ps. tehamaensis* observed at Mont Risou is better documented at Blake Nose (Fig. 7). The transitional specimens from *Ps. ticinensis* to *Ps. tehamaensis* are characterized by showing the periumbilical ridge only on the first chambers of the last whorl and/or having the last two chambers slightly inflated so that the sutures seem depressed (Fig. 8a–r). Since the specimen illustrated as *Ps. tehamaensis* in Kennedy *et al.* (2004, fig. 8, parts 7–9) shows raised umbilical sutures only on the first two chambers of the ultimate whorl and a slightly developed periumbilical ridge, it could likely represent a transitional form in between *Ps. ticinensis* and *Ps. tehamaensis* similar to the specimen observed at Blake Nose (Fig. 8d–f).

Distinctive high-spired morphotypes (Fig. 8s–x) have been observed close to the disappearance level of *P. buxtorfi* at Mont Risou (sample –116 m) and associated with common *P. buxtorfi* at Blake Nose (sample ODP 1050C-27R-3, 8–10 cm). These morphotypes are similar to the high-spired *Ps. klausii* described

Table 1. Summary of the main morphological features of the single-keeled species occurring across the Albian/Cenomanian boundary interval.

	<i>Th. brotzeni</i>	<i>Th. globotruncanoides</i>	<i>Th. gandolfii</i>	<i>Ps. ticinensis</i>	<i>Ps. tehamaensis</i>
Peripheral margin	Almost equally biconvex, keeled	Umbilico-biconvex, inner spine very slightly elevated, keeled	Plano-convex, keeled	Biconvex, keeled except on the last chamber	Spiroconvex to biconvex, keeled
Equatorial outline	Subcircular to slightly lobate	Subcircular to ovoid, slightly lobate	Subcircular, lobate	Circular	Circular to subcircular
Growth rate	Gradual, rather slow	Gradual, faster in last chambers	Gradual, rather slow	Uniformly very slow	Uniformly very slow
Spiral chambers	Crescentic to petaloid	Crescentic to petaloid	Petaloid	Trapezoidal	Petaloid to slightly crescentic
Spiral sutures	Curved strongly backwards and raised	Curved and raised	Curved and raised	Curved and raised	Curved and bending sharply backwards, raised
Umbilical chambers	Subtriangular to subtrapezoidal; last two chambers slightly inflated	Subtrapezoid with flat surface, last two chambers more inflated; fold of the chamber surfaces that bifurcates in the inner part of each chamber	Trapezoidal, last chamber rather inflated	Triangular and inflated, last chamber more inflated	Triangular with flat surface
Umbilical sutures	Curved backwards and raised, last suture slightly depressed	Initially curved and raised then become oblique and depressed	Straight to curved becoming depressed	Straight and depressed	Straight and raised, then flush with the chamber surface or slightly depressed on the last chamber with lip
Supplementary apertures	Completely umbilical, apertures with lip	Umbilical, then migrate out of the umbilical area and become sutural on the last chambers, apertures with lip	Completely umbilical	Completely umbilical	Completely umbilical, apertures with lip
Periumbilical ridges	Present except on the last chambers	Present except on last two folded chambers	Present only on the first 2–3 chambers	Present only on the first 2–3 chambers	Present on all chambers

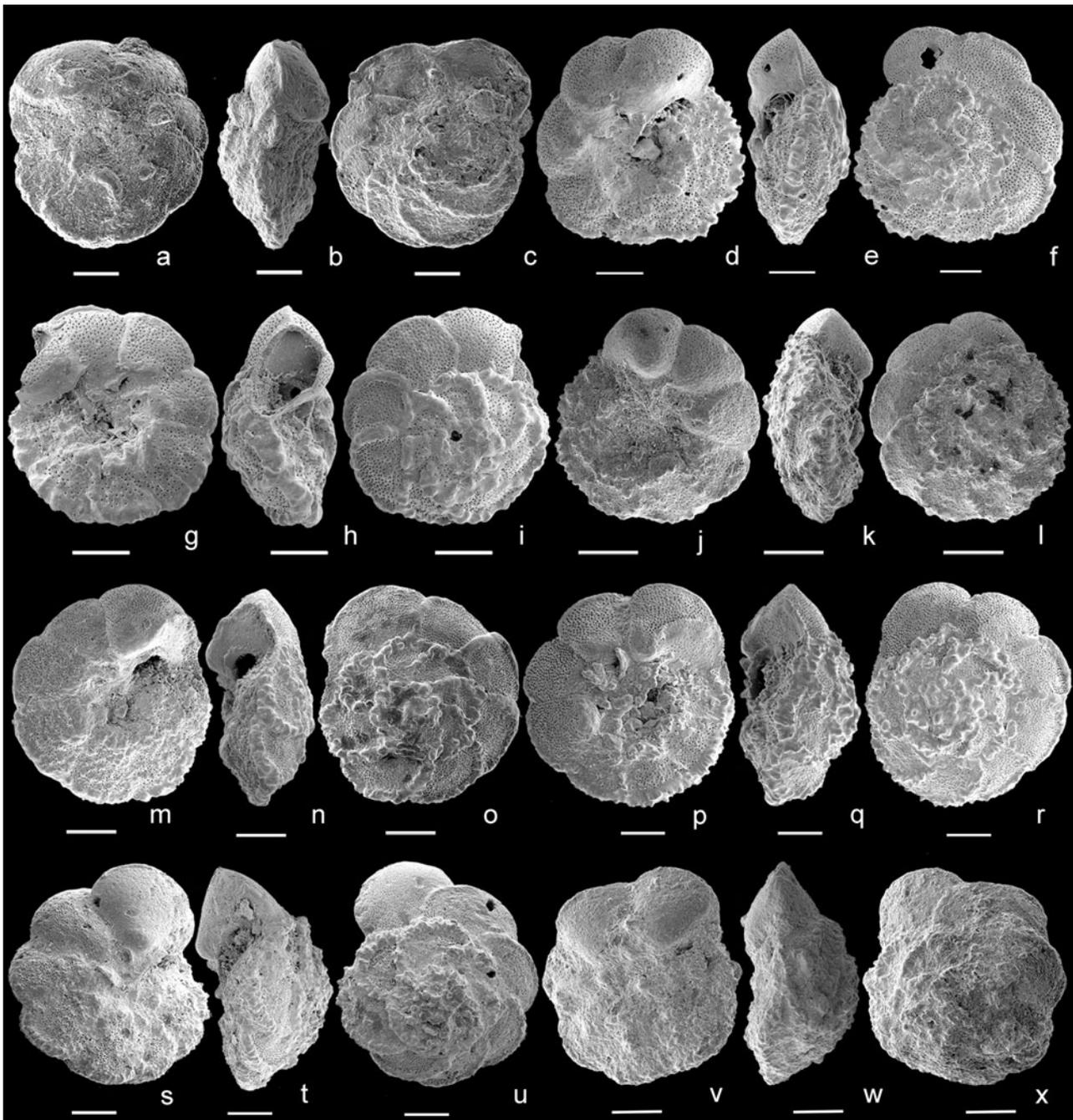


Figure 8. Transitional morphotypes between *Ps. ticinensis* and *Ps. tehamaensis*. Specimens with the periumbilical ridge developed only on the first chambers of the last whorl and slightly inflated chambers: (a–c) sample –27 m, Mont Risou, Hautes-Alpes, France, in (a) umbilical, (b) edge and (c) spiral view; (d–i) sample 1050C-27R-2, 103–105 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (d, g) umbilical, (e, h) edge and (f, i) spiral view; (j–l) sample 1050C-27R-3, 105–107 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (j) umbilical, (k) edge and (l) spiral view; (m–o) sample 1050C-27R-5, 4.5–6.5 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (m) umbilical, (n) edge and (o) spiral view; (p–r) sample 1050C-26R-5, 18–20 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (p) umbilical, (q) edge and (r) spiral view.

High-spired specimens included in the variability of *Ps. ticinensis*: (s–u) sample 1050C-27R-3, 8–10 cm, Leg 171B Blake Nose Plateau, NW Atlantic Ocean, in (s) umbilical, (t) edge and (u) spiral view; (v–x) sample –116 m, Mont Risou, Hautes-Alpes, France, in (v) umbilical, (w) edge and (x) spiral view. Scale bars = 100 μ m.

by Lehmann (1966) and recently revised and illustrated by SEM by Spezzaferri & Caron (2008), but differ in the absence of the periumbilical ridges. Moreover, *Ps. klausii*, tentatively considered as an intermediate form between *P. ticinensis* and *P. tehamaensis* (see Gonzalez-Donoso, Linares & Robaszynski, 2007), has not been

observed in the studied assemblages. We believe that the high-spired morphotypes observed at Mont Risou and Blake Nose strongly resemble *Ps. ticinensis*, being characterized by having depressed umbilical sutures throughout. To date, we include the high-spired specimens within the *Ps. ticinensis* population as they are

rare and do not show a significant distribution, being unrelated to precise stratigraphic levels.

5. Conclusions

Re-examination of the planktonic foraminiferal assemblages across the GSSP of the base of the Cenomanian Stage at Mont Risou allows revision of the sequence of appearances of the planktonic foraminifera index taxa, as follows (Fig. 6):

(1) The evolutionary transition from *Ps. ticinensis* to *Ps. tehamaensis* is very distinctive and is documented from the disappearance of *P. buxtorfi* to the lower range of *Th. globotruncanoides*;

(2) *Th. brotzeni* appears 28 m below the appearance level of *Th. globotruncanoides*; *Th. brotzeni* and *Th. globotruncanoides* are consistently identified as separate species, but the latter is very rare at the beginning of its stratigraphic range.

The species identifications and their stratigraphic distributions at Mont Risou are in good agreement with the data collected from Blake Nose Plateau in the North Western Atlantic Ocean. An exception is the disappearance level of *P. buxtorfi* that falls in a stratigraphic level already containing the transitional morphotype *Ps. ticinensis* – *Ps. tehamaensis*, *Th. gandolfii* and *Th. brotzeni* (Fig. 7) at Blake Nose. This observation causes additional uncertainty regarding the reliability of the last occurrence level of *P. buxtorfi* for regional and global correlations. A second exception is the lowest appearance of *Ps. tehamaensis*: at Blake Nose it precedes the lowest occurrence of *Th. globotruncanoides*, whereas at Mont Risou it appears 9 m above the appearance of *Th. globotruncanoides* and shows a very short stratigraphic distribution. This discrepancy, probably related to the rarity and poor preservation of *Th. tehamaensis* specimens at Mont Risou, confirms its unreliability for correlations. Therefore, *Th. tehamaensis* should not be used anymore as a secondary criterion for placing the Albian/Cenomanian boundary.

Finally, the outstanding question regarding the accurate identification of the index species *Th. globotruncanoides* is here solved. However, we have to remark on the difficulties related to the identification of the first representative of a new species when it is very rare and shows morphological characters clearly visible only in well-preserved specimens.

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