

Paleoecological control of ostracode distribution in a Pennsylvanian Auernig cyclothem of the Carnic Alps, Austria

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Abstract

Pennsylvanian (Kasimovian) ostracodes from the lower part of the Auernig Group, Carnic Alps, Austria, inhabited a shallow-marine and open-marine environment. Paleontological investigations of two ostracode faunas brought significant differences between the ostracode assemblage of the *Anthracoporella* (dasycladalean algae) mound environment and the one from the overlying nodular limestone. Additionally paleoecological data are obtained from the overall microfacies of mound and mound-cover rocks and from their respective fossil associations. These data are used to interpret ostracode environments.

Mound ostracode assemblages show a smaller number of dominant species, contain remarkably tiny forms (for example the bolliid *Solleikope parva* Fohrer, 1991), and are dominated by smooth-shelled to less ornamented carapaces. This is probably because large size and sculpture elements such as spines and thorns would have been restricting for a life in an *Anthracoporella* "jungle". Some species, for example *Carnizzia auricula* Fohrer, 1997b, are adapted to the mound environment because of their morphological features, and are very rare to absent outside of the *Anthracoporella* mounds.

Ostracode faunas collected from the overlying nodular limestone are completely different. They are characterized by a higher number of dominant species and show a broad variety of morphological features. These faunas are dominated by the highly ornamented members of the families Amphissitidae, Scrobiculidae, Kirkbyidae, Kellettinidae, and Paraparchitidae.

Representatives of the family Bairdiidae, e.g., *Bairdia*, are the most abundant species in *Anthracoporella* mounds and in the mound-cover rocks. This group of ostracodes requires open-marine and shallow-marine conditions, but within these parameters there is a high paleoecological tolerance. With regard to these paleoecological limits *Bairdia* is an opportunistic species.

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Anthracoporella mound ostracodes of other Pennsylvanian shelf regions have so far not been reported. As to the mound-cover ostracodes there are close relationships of the Carnic Alps ostracodes to those of the Cantabrian Mountains, Spain.

Keywords: *Anthracoporella* mounds; Austria; Carnic Alps; Cyclothems; Ostracodes; Paleoecology; Pennsylvanian; Upper Carboniferous

1. Introduction

Cyclic sedimentation patterns caused by glacio-eustatic sea-level changes are a common phenomenon in Upper Paleozoic strata nearly worldwide. The Pennsylvanian strata of the Carnic Alps (Auernig Group and Lower Pseudoschwagerina Limestone, each consisting of several formations) are characterized by such cyclothems (Figs. 1, 2).

A common type of cyclothem in the Auernig Group begins with siliciclastics at the base. Bedded limestone containing phylloid algae follows upward, merging into algal mounds constructed largely by *Anthracoporella* and *Archaeolithophyllum*. The mounds are overlain by nodular limestone containing selectively silicified organisms. Siliciclastics follow above, before the next cyclothem begins.

Ostracodes are prominent components in Late Carboniferous and Early Permian carbonates of the Carnic Alps and were the subject of several papers (Ruggieri, 1966; Ruggieri and Siveter, 1975; Becker and Fohrer, 1990; Fohrer, 1991, 1997a,b; Sánchez de Posada and Fohrer, 2001). The present paper focuses on the oldest known ostracode faunas and their paleoecological implications of the entire Auernig Group and Rattendorf Group.

Research on ostracodes in Pennsylvanian Auernig Group limestones is governed by the occurrence of selectively silicified organisms including ostracodes (e.g., Fohrer, 1991, 1997a). Otherwise it is very difficult, if not impossible, to extract the ostracodes from the limestones. In general this kind of silicification occurs in the nodular limestones that overlie algal mounds. The massive mounds, which contain algae, are commonly not affected by silicification except for one cyclothem in the Pizzul Formation, where parts of massive algal mound rocks are silicified. The latter has been studied in order to compare ostracodes adapted to *Anthracoporella* mound environments with ostracode faunas

obtained from the overlying (mound-cover) nodular limestones.

Ostracode data from *Anthracoporella* mounds of other Pennsylvanian shelf regions have so far not been reported. However, ostracodes of the nodular limestone that overlies mounds bear a striking resemblance to ostracode faunas from the Cuera Limestones (Moscovian) in the Cantabrian Mountains, Spain (Sánchez de Posada and Fohrer, 2001; Sánchez de Posada and Bless, 1999). Thus, comparison of mound versus mound-cover ostracodes in the present paper may give clues to the paleoecological control of ostracode distribution in Pennsylvanian rocks.

2. Location, geological context, and stratigraphic scheme

Basins formed by Variscan orogenic movements (late Namurian to middle Westphalian) in the Carnic Alps, on the present Austrian–Italian border (Fig. 1), were filled with mid-Carboniferous to Early Permian age sediments. These sediments form the Pennsylvanian to Early Permian age Auernig, Rattendorf, and Trogkofel Groups (Figs. 1, 2). The Auernig Group is subdivided, from base to top, into the Meledis, Pizzul, Corona, Auernig, and Carnizza Formations. The measured section (Fig. 3) is from the Pizzul Formation. Sediments of the Auernig Group are cyclic deposits (Auernig Rythmus sensu Kahler, 1955) with quartz-rich conglomerates, sandstone (usually cross-bedded at the base), bioturbated siltstone (with trace fossils), and limestone (Fig. 3). The environments range from deltaic and shoreface to shallow-marine (Venturini, 1990, p. 13). The Rattendorf Group is subdivided into the Lower Pseudoschwagerina Limestone, the Grenzland Formation, and the Upper Pseudoschwagerina Limestone. The overlying Trogkofel Group (Fig. 1, not on Fig. 2) includes the Trogkofel Lime-

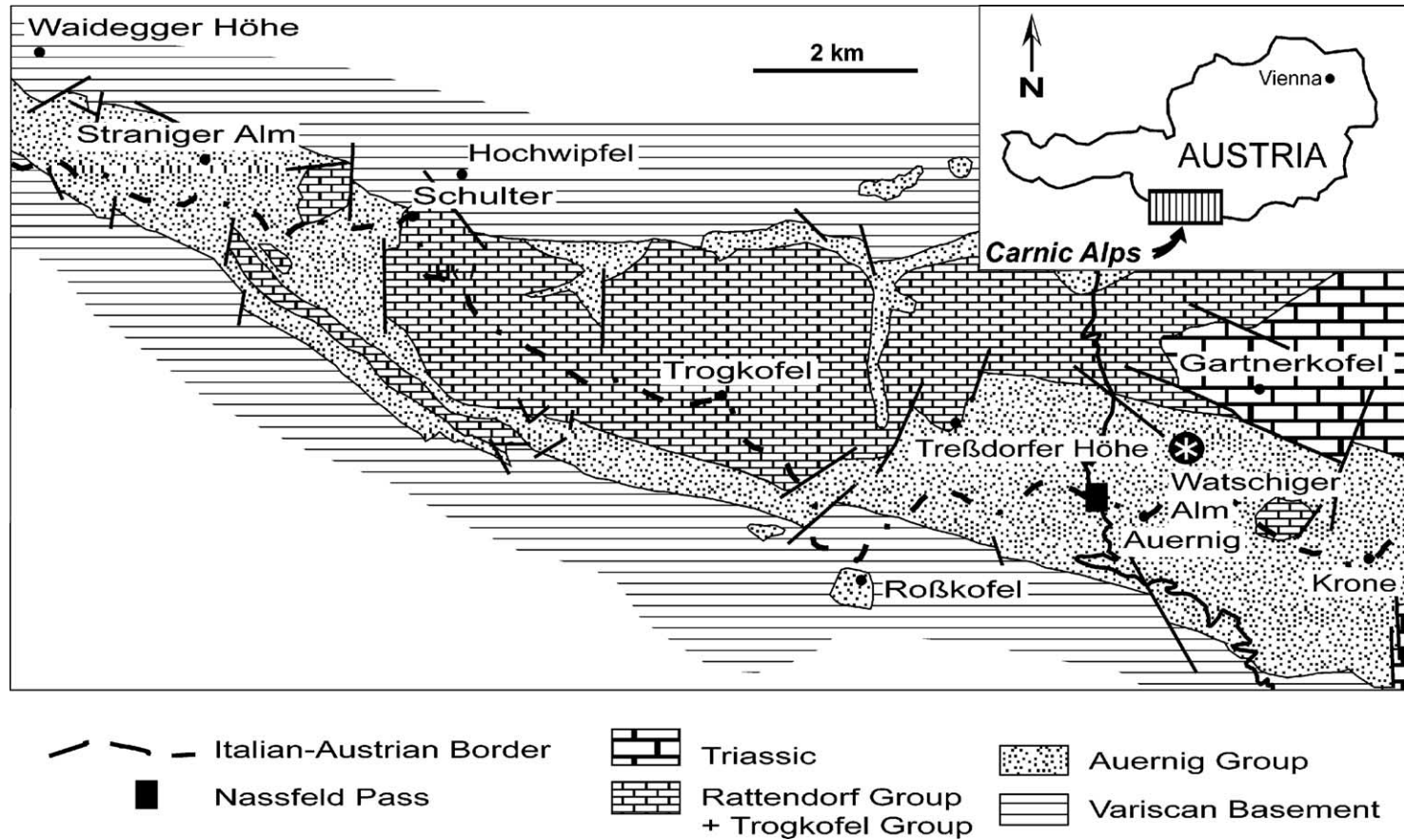


Fig. 1. Location of measured section Watschiger Alm (WA/P; asterisk) within the Carnic Alps in the Nassfeld Pass area, at the Italian–Austrian border. Vertically marked zone in Carnic Alps field (upper right rectangle) indicates the enlarged area.

Stratigraphy		Units of the study area	
L.- Permian	Sakmarian	RATTENDORF GROUP	Upper Pseudoschwagerina Limestone
	Asselian		Grenzland Formation
Pennsylvanian	Gzhelian		AUERNIG GROUP
		Carnizza Formation	
		Auernig Formation	
	Corona Formation		
	Pizzul Formation		
	Kasimovian	Meledis Formation	

Fig. 2. Stratigraphic scheme of the Pennsylvanian and Lower Permian units in the Carnic Alps. The measured section belongs to the Pizzul Formation (asterisk), Auernig Group, and is Kasimovian in age.

stone, composed of massive reef carbonates, as well as some isolated, and stratigraphically younger units (Tressdorf and Goggau Limestones). The Trogkofel units are overlain by breccia beds (Tarvis Breccia), which occur throughout the southern Alps (Buggisch and Flügel, 1980).

The measured section (Watschiger Alm, WA/P) is situated 1.2 km NE from Nassfeld Pass (Fig. 1). The hiking trail from Nassfeld Pass to Gartnerkofel crosses the limestone bed (huge “stairs”) close to a little stream 0.1 km SE of Watschiger Alm mountain hut.

3. Sedimentology

3.1. Facies

A common cyclothem type in the Auernig Group begins with siliciclastics at the base, followed by bedded limestone that merge into algal mounds. The mounds are overlain by nodular limestone containing selectively silicified organisms. Siliciclastics follow above, before the next cyclothem begins (Fig. 3). A

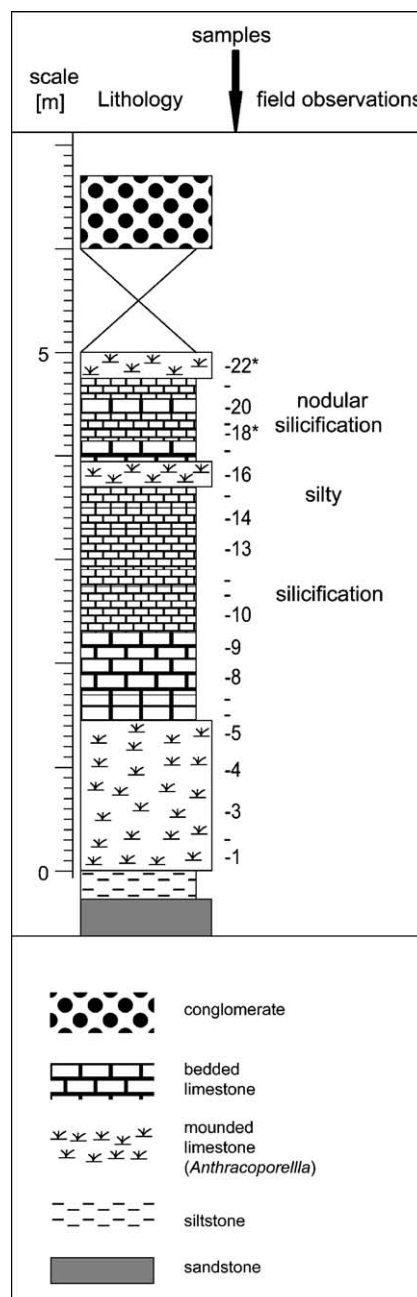


Fig. 3. Log of the measured section. The cyclothem pattern with conglomerate, sandstone, siltstone, algal mounded limestone, and nodular bedded limestone is characteristic of all Auernig Group formations.

summary description of the cyclothem units is given below, with a particular emphasis on mound and mound-cover facies.

Conglomerates are up to 20 m thick in the Auernig Group, with large-scale cross bedding and common fining-upward sequences. Quartz is the dominant component, along with sandstone and siltstone clasts. Sandstones vary from a few centimeters to 50 m in thickness. Cross bedding is common. The matrix is predominantly siliciclastic (quartz and mica), with carbonate less common and coal layers rare. Plant remains, concretions, and trace fossils are common. Siltstones are thinner (commonly less than 2 m) than conglomerates and sandstones. Exceptionally thick siltstone layers occur in the Pizzul Formation (up to 3.2 m), where they contain fossil-rich limestone layers (e.g., productid brachiopodes; [Heritsch, 1935](#)) and common plant remains, concretions, and bioturbation. About 40 to 120 cm of bedded limestone commonly overlies siltstones, but with individual limestone beds rarely exceeding 20 cm in thickness. The mounded facies is a few centimeters to 6 m thick in the Auernig Group, but it is only approximately 30 to 140 cm thick in the measured section ([Fig. 3](#)). The top of the measured section also contains smaller, juxtaposed mound bodies. The mound cover is composed of nodular bedded limestone that may contain silty and marly layers. The nodular facies may reach 5 m in thickness in the Pizzul and Auernig Formations, but does not exceed 2 m in the measured section. Silicification is a common feature of this facies throughout the Auernig cyclothem (Fohrer, 1991, 1997a; Samankassou, 1997). Exceptionally, fossils in both, the algal mound and mound cover of the measured section, are silicified.

3.2. Microfacies of mound rocks

The mound core is composed of *Anthracoporella* algal boundstone ([Fig. 4a](#)). Algae built a delicate framework as indicated by nearly unbroken upright *Anthracoporella* thalli enclosing constructional pores and the lack of collapse or compactional structures ([Fig. 4a](#)). Cavities between, and sheltered by algal thalli are filled with lime mud, cements, and/or peloidal clotted structures. The well-preserved, branched in situ algae are partly encrusted and bound by

micritic cements and *Tubiphytes* ([Fig. 4a](#)). The space between the thalli also seems to have provided small habitats for other organisms such as foraminifers, ostracodes (see below), bryozoans, and some molluscs. Skeletal grains, *Tubiphytes*, small foraminifers, and gastropodes are sparse where enclosed within the peloid-dominated areas. Skeletal grains within the non-peloidal cavities are more diverse, and composed of fusulinids, small foraminifers, gastropodes, brachiopodes and other bioclasts.

3.3. Microfacies of mound-cover rocks

The dark gray, nodular limestones covering the mounds are composed of wackestone and packstone. Algal constructional features (boundstone, cavities, cements, peloidal clotted areas) are absent. Highly diverse fossils in the mound-cover facies ([Fig. 4b](#) and [c](#)) include bryozoans ([Kodsi, 1967](#)), ostracodes ([Fohrer, 1991, 1997a](#); see below), *Archaeolithophyllum* red algae, brachiopodes ([Heritsch, 1935](#)), *Tubiphytes*, gastropodes, foraminifers, and, rarely, trilobite and crinoid fragments. Fossils are commonly silicified. Compactional features (e.g., stylolites) are common.

3.4. Interpretation, depositional environment

3.4.1. Mounds

This microfacies lacks winnowing- and wave-generated sedimentary structures, flanking grainstone, and coarse bioclastic grainstone, indicating a quiet-water environment below storm-wave base for the development of *Anthracoporella* mounds (cf. [Samankassou, 1998](#)). The diversity in *Anthracoporella* mounds of the measured section is relatively higher than that in comparable mounds of the Auernig Group and Lower Pseudoschwagerina Limestone (see [Samankassou, 1998](#)).

3.4.2. Mound cover

The red algae *Archaeolithophyllum*, fusulinid, and benthic smaller foraminifers are indicative of shallow water ([Toomey et al., 1977](#); [Beauchamp, 1994](#)). The environment was obviously favorable to biota, as indicated by the highly diverse fossil association. Input of cool-water may have influenced the fossil association, which is particularly rich in red algae and

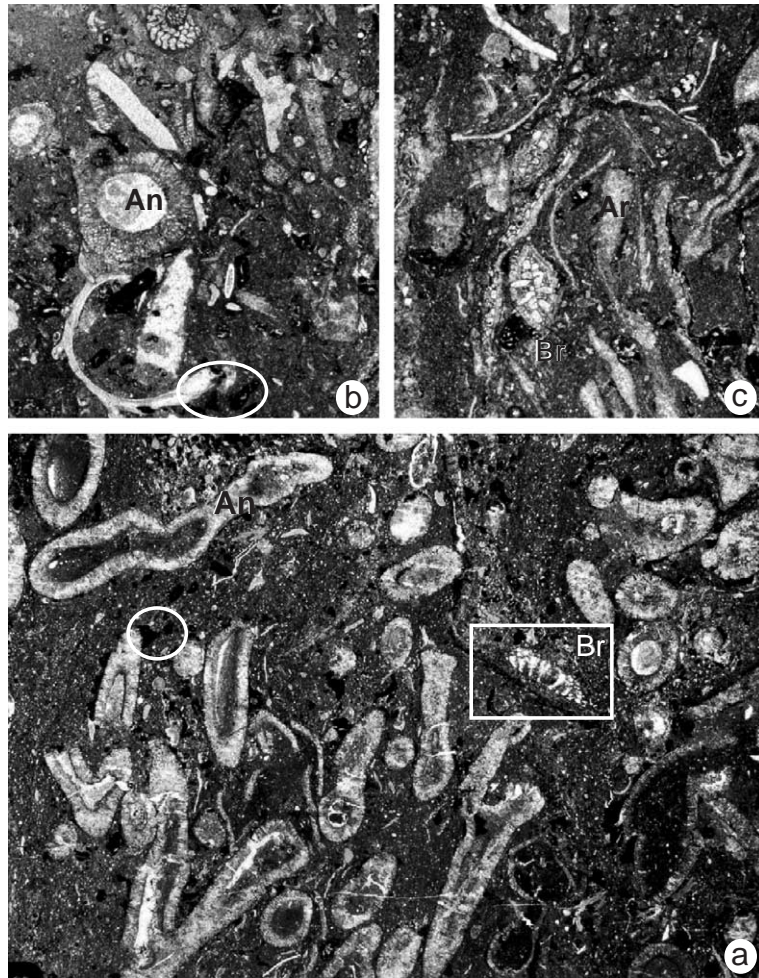


Fig. 4. (a) Mound facies. *Anthracoporella* boundstone. Most of *Anthracoporella* thalli (An) are unbroken. Branching of thalli is recognizable. Fossil diversity is low, with *Tubiphytes* (encircled), rare bryozoans (rectangle), and smaller foraminifers. Picture is 6.4 cm wide. (b) and (c) Mound-cover facies. Bioclastic wackestone and packstone. Fossils are more diverse than in the mound facies and include brachiopodes, bryozoans (Br), fusulinids (upper center in b), *Tubiphytes* (encircled), fragments of algal thalli [*Archaeolithophyllum* (Ar) and, rarely, *Anthracoporella* (An)], and smaller foraminifers. Algal constructional structures are absent. Pictures b and c are 1.4 cm wide, respectively.

bryozoans and lacking in ooids and peloids (Saman-kassou, 2002).

4. Paleontology

4.1. Materials

The silicified ostracodes were dissolved from the limestones using formic acid. All micropaleontological samples are housed in the collections of Institut für

Paläontologie, Universität Erlangen-Nürnberg, Germany. The catalogue numbers (prefix O) are given in the caption of Fig. 5.

4.2. Results

This study is based mainly on two ostracode faunas, which were obtained from the Watschiger Alm section (WA/P) in the Nassfeld Pass area (Fig. 1). In total 22 limestone samples were collected from the measured section (Fig. 3). All samples were con-

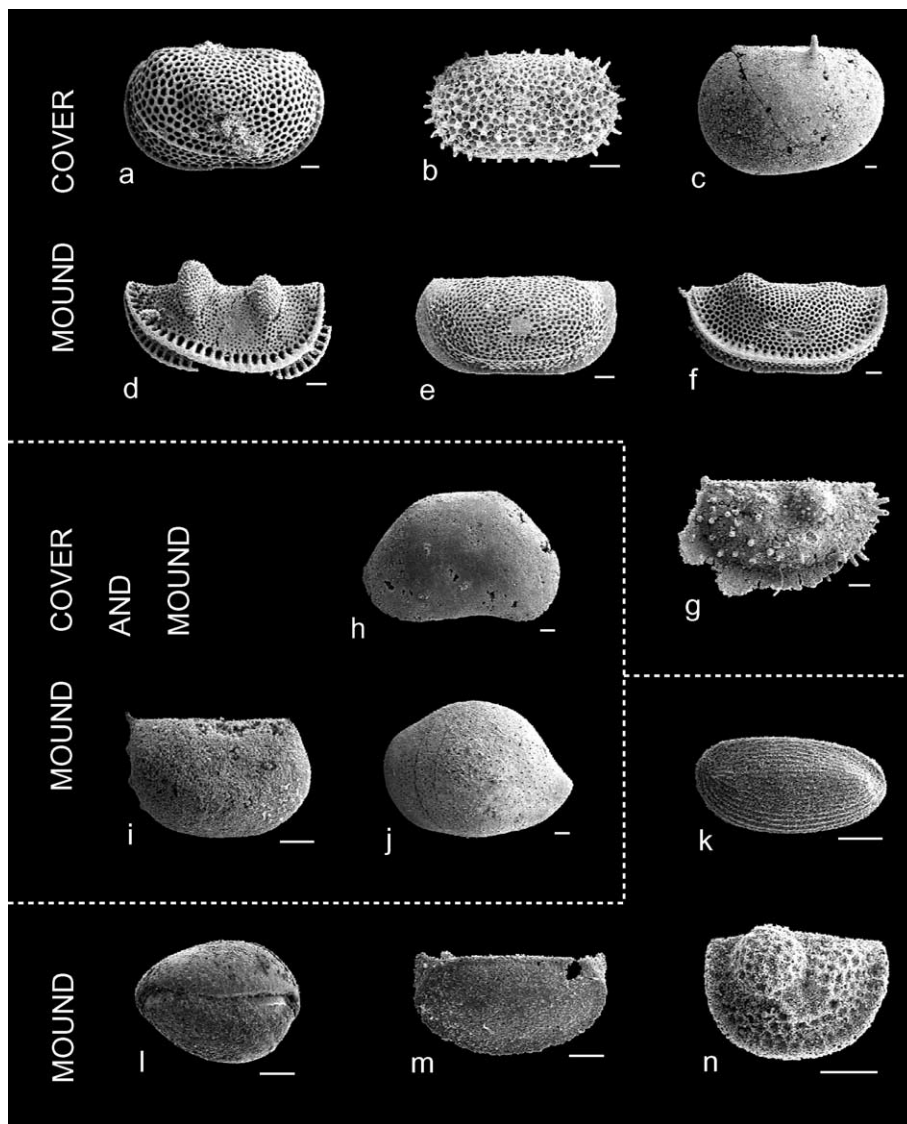


Fig. 5. (a)–(h) Mound and mound-cover ostracodes of the Pennsylvanian Pizzul Formation, Carnic Alps, Austria. (a) *Shleesha* cf. *punguis* (Ulrich and Bassler, 1906), lateral view of a right valve, O 2904/8/4-1. (b) *Roundyella simplicissima* (Knight, 1928), lateral view of a left valve, O 2904/24/1-1. (c) *Shivaella* sp., lateral view of a left valve, O 2904/23/3-1. (d) *Kelletina carnica* Ruggieri and Siveter, 1975, lateral view of a right valve, O 2906/9/1-1. (e) *Knightina* sp., lateral view of a left valve, O 2904/7/11-1. (f) *Aurikirkbya hispanica* Becker et al., 1977, lateral view of a right valve, O 2904/7/3-1. (g) *Hollinella* (*Keslingella*) aff. *radiata* (Jones and Kirkby, 1886), lateral view of a left valve, O 2904/6/3-1. (h) *Bairdiocypris* sp., lateral view of a right valve, O 2904/15/1-1 (reproduced with permission from Fohrer 1997a, pl. 15, fig. 4). (i) *Coryellina* aff. *ventricornis* (Jones and Kirkby, 1886), lateral view of a right valve, O 2904/2/1-1. (j) *Bairdia* sp., lateral view of a right valve, O 2904/13/1-1. (k) *Richterina* (*Richterina*) aff. *striatula* (Richter, 1848), lateral view of a right valve, O 2904/21/1-1. (l) *Microcheilinella* sp., ventral view to a carapace, O 2904/16/2-1. (m) *Carnizzia auricula* Fohrer, 1997b, lateral view of a left valve, O 2906/25/1-1. (n) *Solleikope parva* Fohrer, 1991, lateral view of a right valve, O 2904/4/1-1. Each scale bar is 100 μm long.

sidered for microfacies analysis but only a few for ostracode extraction. Especially in the lower part of the section (sample 1–9) the limestones lack silicifica-

tion of organisms. Beginning with sample 10 the limestones are weakly silicified, resulting in rare ostracodes (5–10 specimens per sample) in residues

and poor preservation of specimens. The most intensive silicification occurs in the upper part of the section (samples 18–22). But only samples 18 (355 specimens) and 22 (398 specimens) are characterized by intensive silicification, good preservation, and abundance of ostracodes, therefore we focused on these two samples. The number of specimens per species in each sample and their relative abundance as percentages are given in Table 1.

4.3. Ostracodes

In the following section key morphological features of mound and mound-cover species are described. Measurements are given in millimeters; *L* refers to the length of the ostracode, *H* stands for height.

4.3.1. Mound ostracodes

Order: Palaeocopida Henningsmoen, 1953.

Family: Bolliidae Boucek, 1936.

Genus: *Solleikope* Becker, 1978.

Solleikope parva Fohrer, 1991.

S. parva (Fig. 5n) with its semi-circular outline and its very pronounced posterior and reduced an-

Table 1
Quantitative evaluation of mound (sample WA/P/22) and mound cover (sample WA/P/18) ostracode faunas of the Pennsylvanian Pizzul Formation, Carnic Alps, Austria

Species	Mound (WA/P/22)		Mound cover (WA/P/18)	
	<i>N</i>	Percent	<i>N</i>	Percent
<i>Shleesha</i> cf. <i>pinguis</i>	7	1.8	76	21.4
<i>Solleikope parva</i>	47	11.8	0	0.0
<i>Carnizzia auricula</i>	39	9.8	0	0.0
<i>Richterina</i> (<i>Richterina</i>) aff. <i>striatula</i>	35	8.8	12	3.4
<i>Roundyella simplicissima</i>	5	1.3	35	9.9
<i>Microcheilinella</i> sp.	34	8.5	3	0.8
<i>Shivaella</i> sp.	0	0.0	29	8.2
<i>Kelletina carnica</i>	4	1.0	21	5.9
<i>Knightina</i> sp.	3	0.8	20	5.6
<i>Aurikirkbya hispanica</i>	3	0.8	17	4.8
<i>Coryellina</i> aff. <i>ventricornis</i>	16	4.0	16	4.5
<i>Bairdiocypris</i> sp.	11	2.8	8	2.3
<i>Hollinella</i> (<i>Keslingella</i>) aff. <i>radiata</i>	0	0.0	7	2.0
<i>Bairdiidae</i>	183	46.0	98	27.6
Others	11	2.8	13	3.7
TOTAL	398	100.0	355	100.0

terior lobe is one of the smallest ostracode species of the entire Pennsylvanian Carnic Alps material. Measurements of Fig. 5n (adult): *L*=0.33 mm, *H*=0.23 mm.

So far the genus is described from Westphalian limestones of the Cantabrian Mountains in Spain (*Solleikope sollei* Becker, 1978) and from Kasimovian and Gzhelian carbonates in the Carnic Alps, Austria (*S. parva* Fohrer, 1991). The Spanish species has a much more pronounced anterior lobe than *S. parva*.

Family: Punciidae? Hornibrook, 1949.

Genus: *Carnizzia* Fohrer, 1997b.

Carnizzia auricula Fohrer, 1997b.

C. auricula (Fig. 5m) is a smooth-shelled small- to medium-sized ostracode with ovate lateral outline. Left valves are provided with ear-like triangular processes at the cardinal corners. Dorsal and ventral margins are in a deeply notched position. Measurements of Fig. 5m (adult): *L*=0.57 mm, *H*=0.28 mm.

This ostracode species is so far recorded from the Pennsylvanian Auernig Group in the Carnic Alps.

Several morphological features such as ear-like protrusions at the cardinal corners, size, and shape resemble very much that of the punciid ostracode genus *Manawa* described by Hornibrook (1949, 1963) and Swanson (1989a,b) from modern New Zealand shelf regions. There is possibly an affiliation to the family Punciidae. A detailed discussion on the relation of *C. auricula* with the Punciidae is beyond the scope of this paper.

Order: Myodocopida Sars, 1866.

Family: Entomozoidae Pribyl, 1950.

Genus: *Richterina* Gürich, 1896.

Richterina (*Richterina*) aff. *striatula* (Richter, 1848).

This small ostracode (Fig. 5k) with an ovate lateral outline is characterized by delicate anastomosing parallel ridges on its lateral surface similar to fingerprint patterns. Measurements of Fig. 5k (juvenile): *L*=0.43 mm, *H*=0.22 mm, adult specimens are 0.50 to 0.55 mm in length.

There is a striking resemblance to *R. (R.) striatula* from the Upper Devonian of the Holy Cross

Mountains in Poland (Olempska, 1992). However, it is most unlikely that this ostracode is conspecific with the Carnic Alps material because of the lower and middle Carboniferous gap between the fossil record of *R. (R.)* aff. *striatula* and *R. (R.) striatula*.

Most authors have described entomozoaceans as typically pelagic ostracodes, which rarely occur on shelf areas (Groos-Uffenorde and Schindler, 1990; Bless, 1983). Gooday (1983) indicated the possibility of a planktonic and benthic life mode for entomozoan ostracodes. Casier (1987) pointed out that even a shallow water benthic life style is possible.

R. (R.) aff. *striatula* predominantly occurs in *Anthracoporella* mounds. As *Anthracoporella* mounds grew in shallow water environments, our data support Casier's (1987) interpretation.

Order: Podocopida Müller, 1894.

Family: Pachydomellidae Berdan and Sohn, 1961.

Genus: *Microcheilinella* Geis, 1933.

Microcheilinella sp.

Microcheilinella sp. (Fig. 5l) is a very tiny, ovate to egg-shaped, smooth-shelled ostracode. The left valve strongly overlaps the right one, especially along the ventral margin. Measurements of Fig. 5l (adult): $L=0.48$ mm, $H=0.36$ mm.

Some specimens show "ventrale Inzisuren", small openings along the free margin in antero- and postero-ventral positions. According to Becker (1988) "ventrale Inzisuren" are typical for *Microcheilinella*.

4.3.2. Mound-cover ostracodes

Order: Palaeocopida Henningsmoen, 1953.

Family: Amphissitidae Knight, 1928.

Genus: *Shleesha* Sohn, 1961.

Shleesha cf. pinguis (Ulrich and Bassler, 1906).

The lateral outline of *S. cf. pinguis* (Fig. 5a) is ovate to sub-rectangular. The ostracode is characterized by a distinct posterodorsal shoulder and reticulated surface, with reticulation more fine-grained on the central lobe. Measurements of Fig. 5a (adult): $L=1.09$ mm, $H=0.67$ mm.

In lateral view it is similar to the specimens described by Sohn (1961, pp. 135–136). In ventral

and dorsal views, however, the width of the carapaces and the shape of the central lobes differ.

The species is very common in most of the mound-cover limestones of the Auernig Group and occurs rarely in the *Anthracoporella* mound.

Order unknown

Family: Scrobiculidae Posner, 1951.

Genus: *Roundyella* Bradfield, 1935.

Roundyella simplicissima (Knight, 1928).

The reticulated surface of ovate-rectangular *R. simplicissima* (Fig. 5b) is covered with many short spines. In most of the specimens the spines are more or less broken. Measurements of Fig. 5b (juvenile): $L=0.61$ mm, $H=0.36$ mm, adult specimens are about 0.8 mm in length.

This species is widespread in most mound-cover limestones of the Auernig Group.

Order unknown

Family: Paraparchitidae Scott, 1959.

Genus: *Shivaella*. Sohn, 1971.

Shivaella sp.

Shivaella sp. (Fig. 5c) is a preplete, very large, smooth-shelled ostracode with a large spine in mid-/posterodorsal position on each valve. Measurements of Fig. 5c (adult): $L=1.64$ mm, $H=1.14$ mm.

Morphological features to distinguish *Shivaella* from the similar *Paraparchites*, such as development of the dorsal margin and the dorsal spines are given in a revision of the paraparchitaceans by Sohn (1971).

Shivaella sp. is common in mound-cover limestones of Pizzul Formation. It is less common in the Auernig Formation.

Order: Palaeocopida Henningsmoen, 1953.

Family: Kellettinidae Sohn, 1954.

Genus: *Kellettina* Swartz, 1936.

Kellettina carnica Ruggieri and Siveter, 1975.

K. carnica (Fig. 5d) with its reticulated surface is dominated by two prominent lobes and two fence-like frills. The more marginal frill is ventrally drawn in. Measurements of Fig. 5d (adult): $L=1.00$ mm, $H=0.47$ mm.

The species is common in all mound-cover limestones of the Auernig Group.

Family: Kirkbyidae Ulrich and Bassler, 1906.

Genus: *Knightina* Kellett, 1933.

Knightina sp.

The predominant morphological character in this large kirkbyacean ostracode (Fig. 5e) is the reticulated surface. There is a lack of intensive lobation and the frills are weakly developed. Measurements of Fig. 5e (juvenile): $L=1.01$ mm, $H=0.5$ mm, adult specimens are about 1.30 mm in length.

Outside *Anthracoporella* mounds *Knightina* sp. is common in the Auernig Group and Rattendorf Group, inside the mounds it is rare.

Genus: *Aurikirkbya* Sohn, 1950.

Aurikirkbya hispanica Becker et al., 1977.

Another very large kirkbyacean ostracode is *A. hispanica* (Fig. 5f). It is characterized by a reticulated surface, a large posterior lobe, two clearly developed frills, and a small posterior cardinal spine. Measurements of Fig. 5f (adult): $L=1.30$ mm, $H=0.60$ mm.

Its distribution in the Carnic Alps sediments is similar to that of *Knightina* sp. Outside the Carnic Alps *A. hispanica* is reported from Upper Carboniferous limestones of the Cantabrian Mountains and Pyrenees in Spain.

Family: Hollinellidae Bless and Jordan, 1971.

Genus: *Hollinella* Coryell, 1928.

Subgenus: *Hollinella* (*Keslingella*) Bless and Jordan, 1970.

Hollinella (*Keslingella*) aff. *radiata* (Jones and Kirkby, 1886).

The lateral surface of this medium-sized hollinellid species is covered with distinct papillae. The posterior lobe is moderate and the posterior margin is provided with several spines. The prominent adventral structure in females and the slightly smaller ones in males are susceptible for destruction during preparation processes (Fig. 5g). Measurements of Fig. 5g (adult): $L=0.85$ mm, $H=0.42$ mm.

There is a striking resemblance to specimens of *H. (K.) radiata* described by Bless and Jordan (1972) from the Menard Formation (upper Chester) of Illinois. It remains unclear if these specimens are conspecific with the poorly preserved Austrian material or not.

H. (K.) aff. *radiata* is limited to the mound-cover limestones of the Pizzul Formation.

4.3.3. Mound and mound-cover ostracodes

Order: Palaeocopida Henningsmoen, 1953.

Family: Leperditellidae Ulrich and Bassler, 1906.

Genus: *Coryellina* Bradfield, 1935.

Coryellina aff. *ventricornis* (Jones and Kirkby, 1886).

This small-sized smooth-shelled species (Fig. 5i) is characterized by three regularly arranged spines at the posterior margin and a moderate posterior cardinal spine. Measurements of Fig. 5i (adult): $L=0.54$ mm, $H=0.36$ mm.

C. aff. ventricornis mostly resembles the specimens of *C. ventricornis* described by Sohn (1962) from upper Mississippian strata of U.S.A. and Great Britain. They mainly differ from the Carnic Alps material in a more prominent median sulcus. This sulcus is weak to absent in the specimens from Pizzul Formation.

C. aff. ventricornis is limited to the mound and mound-cover limestones of the Auernig Group.

Order: Podocopida Müller, 1894.

Family: Bairdiocyprididae Shaver, 1961.

Genus: *Bairdiocypris* Kegel, 1932.

Bairdiocypris sp.

Bairdiocypris sp. (Fig. 5h) is a large smooth-shelled ostracode with rounded anterior and posterior ends. Measurements of Fig. 5h (adult): $L=1.40$ mm, $H=0.82$ mm.

The species occurs in the Auernig Group and Rattendorf Group. This species and closely related forms are common ostracodes in Upper Carboniferous shallow-marine environments worldwide.

Family: Bairdiidae Sars, 1888.

Genus: *Bairdia* McCoy, 1844.

Bairdia sp.

Bairdia sp. (Fig. 5j) is a very large smooth-shelled punctate ostracode with a subspherical lateral outline. Measurements of Fig. 5j (adult): $L=1.35$ mm, $H=0.98$ mm.

Bairdia sp. is one of about three or four different species of *Bairdia*, all of them occur in the mound and mound-cover limestones in similar proportions. Bairdiacean ostracodes are the most abundant faunal elements in all Auernig Group and Rattendorf Group limestones.

5. Discussion

The evaluation of ostracode association, coupled with micofacies analysis, indicates obvious differences in species abundance, size, and ornaments in ostracode faunas obtained from *Anthracoporella* mounds (sample WA/P/22, Fig. 5k–n, Table 1) and faunas from mound covering strata (sample WA/P/18, Fig. 5a–g, Table 1). There is no difference between mound and mound cover in terms of salinity, water depth, or siliciclastic input (Samankassou, 2002).

- Fully marine biota occur in mound and mound-cover strata.
- Biota in both parts point to shallow water and low-energy conditions.
- No major difference in the terrigenous content of mound and mound-cover rocks was reported.

Sorting of dead carapaces by currents is unlikely. According to Samankassou (2003) *Anthracoporella* mounds in the Carnic Alps grew in a low-energy environment below wave base. Differences in ostracode abundance, size, and ornament are thus linked to other factors than those listed above.

5.1. Abundance of species

Specimens of only a few ostracode species (*S. parva*, *C. auricula*, *Richterina* (*Richterina*) aff. *striatula*, and *Microcheilinella* sp.; see Fig. 5k–n, Table 1) obviously well adapted to the mound environment, occur in large numbers in the mound facies. However, most of the remaining species are represented by very few specimens. Different and fewer

species dominate the mound assemblage. This lower relative abundance fits well the results of microfacies analysis: in general, the diversity of organisms is lower in *Anthracoporella* mounds compared to the mound cover.

The species distribution is much more balanced in the mound-cover fauna. Most species occur in considerable numbers. Moreover, members of the families Amphissitidae (*S. cf. pinguis*, Fig. 5a), Kirkbyidae (*Knightina* sp., Fig. 5e and *A. hispanica*, Fig. 5f), Scrobiculidae (*R. simplicissima*, Fig. 5b), and Kellettinidae (*K. carnica*, Fig. 5d), widespread in the mound cover, are rare in the mound facies.

Bairdiacean ostracodes and species like *Bairdiocypris* sp. and *C. aff. ventricornis* occur in both environments, the *Anthracoporella* mound and mound cover. Moreover the representatives of the genus *Bairdia* are the predominant group of ostracodes in both milieus. In general *Bairdia* can tolerate environmental changes, it only requires open-marine and shallow-marine conditions. This may explain why Pennsylvanian shallow- and open-marine ostracode faunas are dominated by bairdiaceans worldwide (e.g., Bless, 1983; Kaesler and Denver, 1988).

5.2. Size

Differences between mound and mound-cover ostracode sizes are striking. The four dominant mound ostracodes are small in size (see Fig. 5k–n, all pictured specimens with the exception of Fig. 5k are adults, for measurements see Section 4.3.1). The smallest ostracode species found to date in the entire Pennsylvanian deposits of the Carnic Alps, *S. parva*, is predominant in the mound environment. Thus, small size seems to be an advantage for life in the *Anthracoporella* “jungle”.

In the mound-cover ostracode sizes vary, ranging from the tiny *Microcheilinella* (0.48 mm) to the large *Shivaella* (1.66 mm).

The size of ostracodes occurring in the mound and mound cover varies. *C. aff. ventricornis* is small to medium-sized, whereas the smooth-shelled species of *Bairdia* and *Bairdiocypris* sp. belong to the largest ostracodes of the two assemblages. Possibly the latter inhabited the ground or even the upper part of

the sediment. According to Sohn (1960) mud dwelling is the common life style for *Bairdia*. The fact that many specimens of the above-mentioned genera (*Bairdia* and *Bairdiocypris*) occur as complete carapaces supports this interpretation. Palaeocopid ostracodes, which are assumed to have epibenthic life mode, are mostly recorded as single valves.

5.3. Ornament

Mound ostracodes differ from those of mound cover through their ornament. All common mound species lack projecting spines, intensive lobation, and fence-like adventral structures. Smooth-shelled species or species with reduced, delicate ornamentation are predominant. In spite of its robust ornamentation *S. parva* (Fig. 5n) is a common element in the mound fauna, possibly because of its tininess. In mound-cover faunas, however, a high diversity of sculptural elements can be observed (Fig. 5).

The ostracode *C. auricula* illustrates very well the role of morphology in distribution and adaptation or paleoecological constraints. *C. auricula* (Fig. 5m) is extremely rare in mound-cover samples, but quite numerous in mound sample WA/P/22 together with the dasycladalean alga *Anthracoporella spectabilis*. Fohrer (1997b) discussed the morphological peculiarities of *C. auricula* as adaptation to a life in this very special algal-mound environment. When active the ostracode had opened valves. In this position the “ears” of the left valves give a smooth, ovate outline in dorsal view to the ostracode (Fohrer, 1997b, p. 369). This shape may have facilitated locomotion in an *Anthracoporella* “jungle”. *C. auricula* with its particular morphology was obviously well adapted to the particular mound environment.

6. Conclusions

Ostracode distribution in a Pennsylvanian Auernig cyclothem of Pizzul Formation appears to be controlled by paleo-environmental parameters. Ostracode assemblages differ as a result of the completely different *Anthracoporella* mound milieu and

mound-cover environment. There are several striking tendencies:

1. *Anthracoporella* mound ostracode faunas show smaller number of dominant species than mound-cover faunas
2. Tiny ostracodes occur predominantly in the mound milieu
3. Extremely ornamented ostracodes, common in the mound cover, are rare to absent in the mound milieu
4. Ostracodes of particular morphology, e.g., *C. auricula*, occur only in *Anthracoporella* mounds.

Ostracodes in mound-cover rocks from other Auernig cyclothem (e.g., Auernig Formation) described in Fohrer (1991, 1997a) are similar to those of the Pizzul Formation described in the present paper. Because all cyclothem of the Auernig Group have similar patterns with algal mound and mound-cover rocks, the distribution patterns of ostracodes in the Pizzul Formation cyclothem may be representative for the other Auernig Group cyclothem. The results of the present study, if confirmed in coeval basins, may contribute to explain ostracode distribution in Pennsylvanian sequences and to understand the paleoecological parameters that controlled the associations.

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References

- Beauchamp, B., 1994. Permian climatic cooling in the Canadian Arctic. In: Klein, G.D. (Ed.), *Paleoclimate, Tectonics, and Sedimentation During Accretion, Zenith, and Breakup of a Supercontinent*, Special Paper, vol. 288. Geological Society of America, pp. 229–246.
- Becker, G., 1978. Flachwasser-Ostracoden aus dem hohen Westfal Asturiens (Kantabrisches Gebirge, N-Spanien): 1. Palaeocopida. *Senckenb. Lethaea* 59, 37–69.
- Becker, G., 1988. Ventrale Inzisuren bei paläozoischen Podocopida (Ostracoda) und ihre funktionelle Deutung. *Paläontol. Z.* 62, 277–284.
- Becker, G., Fohrer, B., 1990. Schließmuskel-Feld eines kirkbyiden Ostracoden aus dem hohen Oberkarbon. *Neues Jahrb. Geol. Paläontol., Monatsh.* 1990 (6), 329–335.
- Becker, G., Bless, M.J.M., Sánchez de Posada, L.C., 1977. Ostracoden. In: Requadt, H., Becker, G., Bless, M.J.M., Eickhoff, G., Sánchez de Posada, L.C. (Eds.), *Mikrofaunen aus dem Westfal der spanischen Westpyrenäen (Ostracoda, Conodonta, Foraminifera)*. *Neues Jahrb. Geol. Paläontol., Abh.*, vol. 155, pp. 65–107.
- Berdan, J.M., Sohn, I.G., 1961. Family Pachydomellidae Berdan & Sohn, n. fam. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part Q, Arthropoda. 3. Crustacea, Ostracoda*. Univ. Kansas Press, Lawrence, pp. 373–374.
- Bless, M.J.M., 1983. Late Devonian and Carboniferous ostracode assemblages and their relationship to the depositional environment. *Bull. Soc. belge Géol.* 92, 31–53.
- Bless, M.J.M., Jordan, H., 1970. Stratigraphical and taxonomical remarks on the ostracode genus *Hollinella* Coryell. *Med. Rijks Geol. Dienst, Nieuwe Serie* 21, 81–91.
- Bless, M.J.M., Jordan, H., 1971. Classification of palaeocopid ostracodes belonging to the families Ctenoloculinidae, Hollinidae and Hollinellidae. *Bull. Centre de Recherches Pau-SNPA* 5, 869–890.
- Bless, M.J.M., Jordan, H., 1972. Ostracodes of the family Hollinellidae. *Med. Rijks Geol. Dienst, Serie C* 3, 1–155.
- Boucek, B., 1936. Die Ostracoden des böhmischen Ludlows. *Neues Jahrb. Mineral. Geol. Paläontol., Abt. B* 76, 31–98.
- Bradfield, H.H., 1935. Pennsylvanian Ostracoda of the Ardmore Basin, Oklahoma. *Bull. Am. Paleontol.* 22, 1–173.
- Buggisch, W., Flügel, E., 1980. Die Trogkofel-Schichten der Karnischen Alpen: Verbreitung, geologische Situation und Geländebefund. *Carinthia II, Sonderh.* 36, 13–50.
- Casier, J.-G., 1987. Etude biostratigraphique des ostracodes du récif de Marbre Rouge du Hautmont à Vodelée (Partie supérieure du Frasnien, Bassin de Dinant, Belgique). *Rev. Paléobiol.* 6, 193–204.
- Coryell, H.N., 1928. Some new Pennsylvanian Ostracoda. *J. Paleontol.* 2, 87–94.
- Fohrer, B., 1991. Verkieselte Flachwasser-Ostracoden und ihre Begleitfauna und flora aus dem Oberkarbon der Karnischen Alpen (Naßfeld-Region, Kärnten, Österreich). *Abh. Geol. Bundesanst.* 46 (107 pp.).
- Fohrer, B., 1997a. Ostracoden aus dem Oberkarbon und Unterperm der Karnischen Alpen (Österreich): Systematik, Biostratigraphie und Palökologie. *Jahrb. Geol. Bundesanst.* 140, 99–191.
- Fohrer, B., 1997b. *Carnizzia auricula* n. g., n. sp. aus dem Oberkarbon der Karnischen Alpen (Österreich): Eine außergewöhnliche Ostracode mit einer außergewöhnlichen Lebensweise. *Geol. Bl. Nordost-Bayern Angrenz. Geb.* 47, 367–380.
- Geis, H.L., 1933. *Microcheilinella*, a new name for the ostracode genus *Microcheilus*. *J. Paleontol.* 7, 112.
- Gooday, A.J., 1983. Entomozoacean ostracods from the Lower Carboniferous of south-western England. *Palaeontology* 26, 755–788.
- Groos-Uffenorde, H., Schindler, E., 1990. The effect of global events on entomozoacean ostracoda. In: Whatley, R., Maybury, C. (Eds.), *Ostracoda and Global Events*. Chapman and Hall, London, pp. 101–112.
- Gürich, G., 1896. Das Paläozoikum im polnischen Mittelgebirge. *Verh. Russ. Kaiserl. Mineral. Ges.* 32, 1–539.
- Henningsmoen, G., 1953. Classification of Paleozoic straight-hinged ostracods. *Nor. Geol. Tidsskr.* 31, 185–288.
- Heritsch, F., 1935. Neue Versteinerungen aus den Na(feld)schichten der Karnischen Alpen. *Sitzungsberichte der Akademie der Wissenschaften in Wien, Mathem.-naturw. Klasse, Abteilung I* 144 (7. und 8.), 349–373.
- Hornibrook, N. de B., 1949. A new family of living ostracoda with striking resemblances to some Palaeozoic Beyrichiidae. *Trans. Roy. Soc. N.Z., Bot.* 77 (4), 469–471.
- Hornibrook, N. de B., 1963. The New Zealand ostracode family Punciidae. *Micropaleontology* 9 (3), 318–320.
- Jones, T.R., Kirkby, J.W., 1886. Notes on the Paleozoic bivalved Entomostraca. No. XXII. On some undescribed species of British Carboniferous Ostracoda. *Ann. Mag. Nat. Hist.* 106, 249–269.
- Kaessler, R.L., Denver, L.E., 1988. Nearshore ostracoda in the early Permian. In: Hanai, T., Ikeya, N., Ishizaki, K. (Eds.), *Evolutionary Biology of Ostracoda*. Elsevier, Amsterdam, pp. 671–683.
- Kahler, F., 1955. Entwicklungsräume und Wanderwege der Fusulinen im Euroasiatischen Kontinent. *Geologie* 4, 179–188.
- Kegel, W., 1932. Zur Kenntnis paläozoischer Ostrakoden: 2. Bairdiidae aus dem Mitteldevon des Rheinischen Schiefergebirges. *Jahrb. Preuss. Geol. Landesanstalt zu Berlin* 52, 245–250.
- Kellett, B., 1933. Ostracodes of the Upper Pennsylvanian and the Lower Permian strata of Kansas: 1. The Aparchitidae, Beyrichiidae, Glyptopleuridae, Kloedenellidae, Kirkbyidae, and Youngiellidae. *J. Paleontol.* 7, 59–108.
- Knight, J.B., 1928. Some Pennsylvanian ostracodes from the Henrietta Formation of eastern Missouri. Part I. *J. Paleontol.* 2, 229–267.
- Kodsi, M.G., 1967. Die Fauna der Bank s des Auernig (Oberkarbon; Karnische Alpen, Österreich): 1. Teil: Fenestella Lonsdale 1839. *Carinthia II* (157), 59–81.

- McCoy, F., 1844. A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland (Dublin, 207 pp.).
- Müller, G.W., 1894. Die Ostracoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. Fauna und Flora des Golfes von Neapel und der angrenzenden Meeresabschnitte, Zoologische Station zu Neapel 21, 404 pp.
- Olempska, E., 1992. Shell structure of the entomozoceans: allegedly planktonic ostracodes of the Palaeozoic. *Acta Palaeontol. Pol.* 36, 373–398.
- Posner, V.M., 1951. Stratigrafiya i mikrofauna nizhnego Karbona zapadnogo krila podmoskovnoi kotlovini. Trudi vsesoyuznogo neftyanogo nauchno-issledovatel'skogo geologo-razvedochnogo instituta (VNIGRI), Novaya Seriya 56, 1–108.
- Pribyl, A., 1950. On the Bohemian Ostracoda of the families Entomozoidae and Entomoconchidae. *Bull. Intern. Acad. Tcheque Sci.* 50, 101–128.
- Richter, R., 1848. Beitrag zur Paläontologie des Thüringer Waldes: Die Grauwacke des Bohlens und des Pfaffenberges bei Saalfeld. Dresden, Leipzig (48 pp.).
- Ruggieri, G., 1966. Nuovo genere di ostracode del Carbonifero superiore delle Alpi Carniche. *Riv. Ital. Paleontol.* 72, 1–8.
- Ruggieri, G., Siveter, D.J., 1975. On *Kellettina carnica* Ruggieri and Siveter sp. nov. *Stereo-Atlas Ostracod Shells* 2, 215–222.
- Samankassou, E., 1997. Muster und Kontrollfaktoren der zyklischen Sedimentation im Jungpaläozoikum (Oberkarbon-Untermesozoikum) der Karnischen Alpen, Österreich: Eine integrierte Untersuchung. PhD Thesis, University of Erlangen-Nürnberg, Erlangen. 397 pp.
- Samankassou, E., 1998. Skeletal framework moulds of dasycladalean alga *Anthracoportella*, Upper Paleozoic, Carnic Alps, Austria. *Palaios* 13, 297–300.
- Samankassou, E., 2002. Cool-water carbonates in a paleoequatorial shallow-water environment: the paradox of the Auernig cyclic sediments (Upper Pennsylvanian, Carnic Alps, Austria-Italy) and its implications. *Geology* 30, 655–658.
- Samankassou, E., 2003. Upper Carboniferous-Lower Permian buildups of the Carnic Alps, Austria-Italy. In: Ahr, W.M., Harris, P.M., Morgan, W.A., Somerville, I.D. (Eds.), *Permian-Carboniferous Carbonate Platforms and Reefs*. SEPM Special Publication 78 and AAPG Memoir 83, pp. 201–217.
- Sánchez de Posada, L.C., Bless, M.J.M., 1999. Hollinellidos del Moscovense superior (Carbonífero) del este de Asturias (N de España). *Rev. Esp. Paleontol.*, 29–41 (no° extr. Homenaje al Prof. J. Truyols).
- Sánchez de Posada, L.C., Fohrer, B., 2001. Kirkbyoid ostracodes (Upper Carboniferous) from the Cantabrian Mountains (Spain) and Carnic Alps (Austria and Italy). *J. Paleontol.* 75 (5), 972–984.
- Sars, G.O., 1866. Oversigt af Norges marine Ostracoder. *Norske Vidensk.-Akad. Forhandl.* (130 pp.).
- Sars, G.O., 1888. Nye bidrag til kundskaben om middlehavets invertebratfauna. 4. Ostracoda mediterranea. *Arch. Math. Naturvidensk.* 12, 173–324.
- Scott, H.W., 1959. Type species of *Paraparchites* Ulrich and Bassler. *J. Paleontol.* 33, 670–674.
- Shaver, R.H., 1961. Family Bairdiocyprididae. In: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part Q, Arthropoda. 3. Crustacea, Ostracoda*. Univ. Kansas Press, Lawrence, pp. 364–367.
- Sohn, I.G., 1950. Growth series of ostracodes from the Permian of Texas. *U.S. Geol. Surv. Prof. Pap.* 221-C, 33–43.
- Sohn, I.G., 1954. Ostracoda from the Permian of the Glass Mountains, Texas. *U.S. Geol. Surv. Prof. Pap.* 264-A, 1–24.
- Sohn, I.G., 1960. Paleozoic species of *Bairdia* and related genera — revision of some Paleozoic ostracode genera. *U.S. Geol. Surv. Prof. Pap.* 330-A, 1–105.
- Sohn, I.G., 1961. *Aechminella*, *Amphissites*, *Kirkbyella*, and related genera — revision of some Paleozoic ostracode genera. *U.S. Geol. Surv. Prof. Pap.* 330-B, 107–160.
- Sohn, I.G., 1962. Stratigraphic significance of the Paleozoic ostracode genus *Coryellina* Bradfield, 1935. *J. Paleontol.* 36, 1201–1213.
- Sohn, I.G., 1971. New Late Mississippian ostracode genera and species from Northern Alaska. A revision of the Paraparchitacea. *U.S. Geol. Surv. Prof. Pap.* 711-A, 1–24.
- Swanson, K., 1989a. Ostracod phylogeny and evolution — a Manawan perspective. *Cour. Forsch.-Inst. Senckenberg* 113, 11–20.
- Swanson, K., 1989b. *Manawa staceyi* n. sp. (Punciidae, Ostracoda), soft anatomy and ontogeny. *Cour. Forsch.-Inst. Senckenberg* 113, 235–259.
- Swartz, F.M., 1936. Revision of the Primitiidae and Beyrichiidae, with new Ostracoda from the Lower Devonian of Pennsylvania. *J. Paleontol.* 10, 541–586.
- Toomey, D.F., Wilson, J.L., Rezak, R., 1977. Evolution of Yucca Mound complex, Late Pennsylvanian phylloid algal buildup, Sacramento Mountains, New Mexico. *Am. Assoc. Pet. Geol. Bull.* 61, 2115–2133.
- Ulrich, E.O., Bassler, R.S., 1906. New American Paleozoic Ostracoda. Notes and descriptions of Upper Carboniferous genera and species. *Proc. U.S. Natl. Mus.* 30, 149–164.
- Venturini, C., 1990. Field workshop on Carboniferous to Permian sequence of the Pramollo-Nassfeld Basin (Carnic Alps) (September 2–8, 1990), Guidebook, Udine. 159 pp.