

LEPADIFORM AND SCALPELLIFORM BARNACLES FROM THE OLIGOCENE AND MIOCENE OF THE PARATETHYS SEA

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Abstract: A review on the Oligocene and Miocene stalked barnacles of the Paratethys Sea is presented. The fauna comprises two lepadiform and eight scalpelliform species. Only two species are known from Oligocene deposits, four are documented from Lower Miocene formations, and another four species occur in the Middle Miocene. Only one Oligocene and one Miocene species occur in two different Paratethyan basins in roughly coeval environments, and only a single Middle Miocene species is also known from the adjacent Mediterranean Sea. This low degree of biogeographical similarity is probably a result from the still low number of publications dealing with this group. Stalked barnacles are

often indicating bathyal or at least deep sublittoral environments. Especially, the abundance of the benthic deep-water lepadiform *Poecilasma* in evaporitic deposits of the Middle Miocene Badenian Salinity Crisis may serve as new evidence for a deeper marine depositional environment. *Scalpellum paratethyanum* sp. nov. and *Lepas sattmanni* sp. nov. are described as new species; *Arcoscalpellum renevieri* (Mayer and Gümbel in Gümbel, 1861) is introduced as new combination.

Key words: Lepadiformes, *Poecilasma*, Scalpelliformes, *Scalpellum*, Paratethys Sea, bathyal faunas.

EUROPEAN late Cainozoic lepadomorph barnacles are a somewhat neglected group in palaeontology. A first boom followed during the late 19th century after the jump start by the monographs of Darwin (1851*a, b*, 1854). Several studies dealt at least partly with fossil Thoracica from Austria, Poland, Italy, Malta and France (e.g. Gümbel 1861*a, b*; Reuss 1864, 1867; Des Moulins 1875; Seguenza 1876; Fischer 1886; Weithofer 1887; De Alessandri 1894, 1897, 1906; Joleaud and Joleaud, 1914). During the 20th century, the interest of the community was declining and only few papers appeared (e.g. Tièche 1905; De Alessandri 1922; Szörényi 1934). Finally, a major review of most of the Cainozoic taxa was carried out by Withers (1953); however, this review has been neglected by most palaeontologists (Prieur and Philippe 1984; Mañé and Calzada 1994). Even today, this overview is a great base for new studies but suffers from outdated stratigraphic concepts which obscure the distribution of several species. Most Tortonian occurrences in Withers (1953) are in fact of Langhian or Serravallian age, corresponding to the Badenian of the regional stratigraphic scheme (Piller *et al.* 2007; see Harzhauser *et al.* 2003 for a discussion on the erroneous use of

‘Tortonian’ in the older Paratethys literature). Moreover, owing to the complex political history of central and south-eastern Europe, the historical locality names, listed by Withers (1953), are partly misspelled or are ambiguous, as the name may refer to several different villages. These drawbacks will be cleared in this paper, and new species and data from the Paratethys are presented.

During the Oligocene and Miocene, the Paratethys was a huge epicontinental sea. It formed a northern satellite sea of the Western Tethys (= Proto-Mediterranean) and came into existence during the latest Eocene owing to the rising Alpine island chains consisting of the Alps, Dinarids, Hellenids, Pontids and the Anatolian Massif (Rögl 1998). During its maximum extent, it spread from the Rhône Basin in France towards Inner Asia. The newly formed Paratethys was separated into two large geotectonic units which underwent different environmental histories owing to differently timed geotectonic events and global sea-level fluctuations (Popov *et al.* 2004). The smaller western part consists of the Western and the Central Paratethys being opposed by the larger Eastern Paratethys. Herein, only the Thoracica assemblages of the smaller western part are considered. The connections to

the western, central and eastern Mediterranean Sea were extremely variable throughout the Miocene. Especially within the mollusc faunas, geodynamically driven phases of isolation often resulted in strongly increasing endemicity levels, whilst Mediterranean faunas took over during phases with open marine connections (e.g. Studencka *et al.* 1998; Harzhauser and Piller 2007). A comparable critical evaluation of the lepadiform and scalpelliform Thoracica of the Paratethys with focus on stratigraphy and geodynamic is missing so far. Therefore, this paper tries to integrate new and existing data on Oligocene and Miocene lepadiform and scalpelliform barnacles from the Paratethys.

MATERIAL AND LOCALITIES

This synthesis is based on the collections of the Natural History Museum Vienna (Austria) and the Museum of the Sternwarte Kremsmünster (Austria). All illustrated specimens are stored in these institutions. Further data are utilized from material stored in the collections of the Natural History Museum in London as described by Withers (1953). The newly studied material derives from the Oligocene of the Inneralpine Molasse of the Lower Inn Valley (Austrian Alps), the Lower Miocene of the North Alpine Foreland Basin (Pucking, Ottnang, Kremsmünster; Austria) and the Vienna Basin (Cerová; Slovakia). Middle Miocene specimens come from the Carpathian Foredeep (Podjarkow at Hanachivka; Ukraine, Wieliczka; Poland, Opava; Czech Republic) and the Vienna Basin (Steinebrunn, Vienna; Austria). In the fol-

lowing, an updated stratigraphy of the sections is given and a geographical overview is presented in Figure 1.

1. *Bad Häring in Tyrol (Austria)*. This is situated in the Lower Inn Valley of the Inneralpine Molasse. The grey marls of the Paisslberg Formation belong to the Kiscellian stage (= Rupelian) and correspond to the nannoplankton zone NP 22 (Löffler and Nebelsick 2001).
2. *Budapest Ujlak brickyard (Hungary)*. This is a clay pit at Budapest with pelites of the Kiscell Formation of the upper Kiscellian stage (= upper Rupelian) corresponding to the early nannoplankton zone NP 24 (Báldi 1986).
3. *Pucking locality (Austria)*. Pucking was a temporary outcrop in the vicinity of Pucking in Upper Austria. The silty clays are part of the Ebelsberg Formation (Krenmayr and Schnabel 2006) and belong to the North Alpine Foreland Basin. They are part of the upper Egerian stage (= Aquitanian) and correspond to the nannoplankton zone NN2 (Gregorova *et al.* 2009; Grunert *et al.* 2010a).
- 4–5. *Ottang-Schanze (Austria)* in the North Alpine Foreland Basin of Upper Austria represents the holostratotype for the regional Ottnangian stage. It is located 500 m N of the village Ottnang in Upper Austria; *Kremsmünster* is located 32 km in the east of Ottnang. Both localities represent mica-rich grey-brown clayey-sandy silt of the Ottnang Formation in the North Alpine Foreland Basin. The age corresponds to the middle Burdigalian, and nannoplankton zone NN3 was detected (Grunert *et al.* 2010b).



FIG. 1. Geographic position of the localities mentioned in the text.

6. *Belpberg (Switzerland)*. This is a section south-east of Bern. The mica-rich, fine- to medium-grained sandstones are of late Eggenburgian to early Otnangian age (= middle Burdigalian) (Schoepfer 1989; Pfister and Wegmüller 1994; Gruner 2001). The area was part of the Western Paratethys which formed a transition between the Rhône Basin in the west and the North Alpine Foreland Basin in the east.
7. *Cerová-Lieskové (Slovak Republic)*. The outcrop is at the western slope of the Malé Karpaty Mts. at the eastern margin of the Vienna Basin. The deposits of the abandoned clay pit are calcareous clay and clayey silt of the Lakšárska Nová Ves Formation (Špička and Zapletalová 1964). The age of the Cerová section is late Karpatian (= late Burdigalian) (Hyžný and Schlögl 2011).
8. *Grünes Kreuz (Austria)*. *Grünes Kreuz* at Nussdorf in Vienna is a famous but abandoned and vanished outcrop from where numerous foraminifers and bryozoans have been described. The so-called *Amphistegina* marls are sandy marls, interbedded in coralline limestones and belong to the Middle Badenian *Spiroplectamina* Zone (= late Langhian) (Schmid 1989).
9. *Steinebrunn (Austria)*. An outcrop at the western margin of the Vienna Basin. The outcrop Milchhaus, where exceptionally mollusc-rich sandy marls of the Middle Badenian *Spiroplectamina* Zone (= late Langhian) were outcropping (Grill 1968), is not existing anymore.
10. *Pfaffstätten (Austria)*. The outcrop was close to the village Pfaffstätten c. 11 km S of Vienna in Austria; the sandy marls and coralline limestones are situated at the western margin of the Vienna Basin. Based on the detailed lists and descriptions of Karrer (1877), they belong to the lower or middle Badenian stage (Langhian or lower Serravallian).
- 11–12. *Borač and Kralice nad Oslavou (Czech Republic)* are villages near Brno in Moravia (Brno-venkov and Třebíč districts). The pelitic deposits are isolated relics of the Carpathian Foredeep preserved on crystalline rocks of the Bohemian Massif and are of early Badenian age (= Langhian) (Buday *et al.* 1965).
13. *Sudice (Czech Republic)* near Knínice u Boskovic (District Blansko) also belongs to the Carpathian Foredeep; there, the Pre-Neogene basement is formed by Permo-Carboniferous rocks of the Boskovic Furrow. The age is early Badenian (= Langhian) (pers. comm. S. Nehyba, Masaryk University, Brno; note that there is also a Sudice near Brno and a Sudice near Opava in the Czech Republic which both bear Miocene deposits).
14. *Opava-Kateřinky (NE Czech Republic)* is situated in the Carpathian Foredeep. The pelitic deposits are rich in gypsum and formed during the Badenian Salinity Crisis in the middle Badenian (= latest Langhian to earliest Serravallian) (Buday *et al.* 1965; de Leeuw *et al.* 2010).
15. *Hanachivka-Podjarkow (Ukraine)* and *Wieliczka (SE Poland)*. They represent parts of the Carpathian Foredeep. The sections are famous for the evaporitic deposits with salt and gypsum of the middle Badenian Salinity Crises (= latest Langhian, earliest Serravallian) (Kasprzyk 2003; Peryt 2006; de Leeuw *et al.* 2010).

SYSTEMATIC PALAEOLOGY

Remarks. The systematic hierarchy follows Chan *et al.* (2010) and Di Geronimo (2010) and references therein. Basic terms are shown in Figure 2.

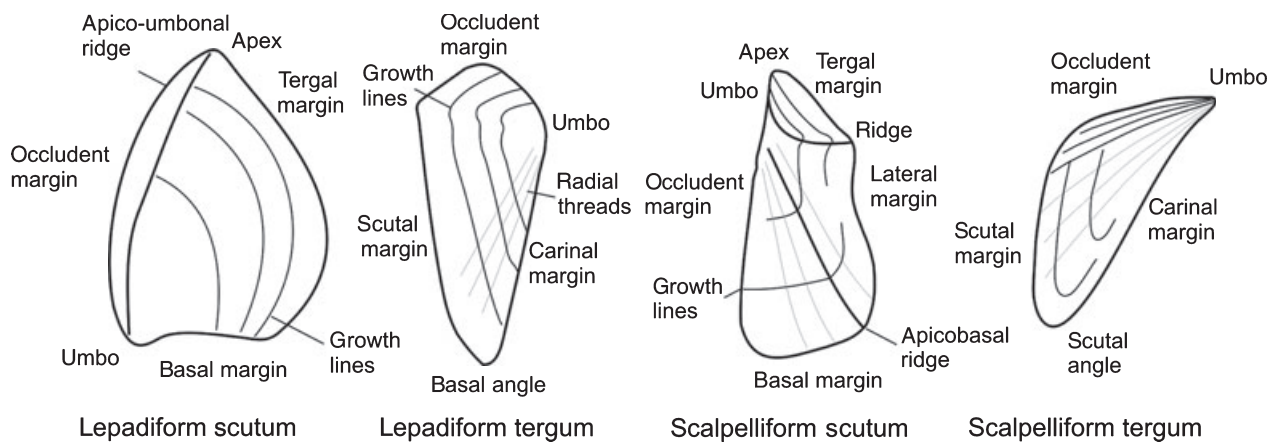


FIG. 2. Simplified drawings of lepadiform and scalpelliform scuta and terga with indication of the terms used herein. The terminology follows Withers (1953).

Superorder THORACICA Darwin, 1854
 Order LEPADIFORMES Buckeridge and Newman, 2006
 Suborder LEPADOMORPHA Pilsbry, 1916
 Family POECILASMATIDAE Annandale, 1909

Genus POECILASMA Darwin, 1851

Type species. Poecilasma kaempferi Darwin, 1851.

Poecilasma miocaenica Reuss, 1864
 Figures 3A–E, 4

1864 ?*Poecilasma miocaenica* m. Reuss, p. 230, pl. 2, fig. 12.
 1867 *Poecilasma miocaenica* Rss.; Reuss, p. 172, pl. 8,
 figs 4–6.
 1953 *Trilasmis (Poecilasma) miocaenicum* (Reuss); Withers,
 p. 340, pl. 56, figs 6–8.

Holotype. Specimen NHMW1859/45/555 from Podjarkow at Hanachivka, Ukraine; Middle Miocene, Badenian.

Material. Numerous scuta and few terga (Podjarkow at Hanachivka: NHMW1859/45/555, Wieliczka: NHMW1867/7/97, 1867/7/96, Opava: NHMW1866/8/8, Vienna Nussdorf: NHMW2010/0084/0001).

Remarks. The scuta are quite variable in shape and size, ranging from 3 to 7 mm in length; the occludent margin is slightly convex to nearly straight; basal margin short and feebly concave; tergal margin also straight or slightly concave. Especially, the apico-umbonal ridge varies from crest-like to rounded.

This small-sized species is especially abundant in gypsum- and salt-bearing deposits of the Carpathian Foredeep, which developed during the Badenian Salinity Crisis (de Leeuw *et al.* 2010).

Distribution. This species is documented from Podjarkow at Hanachivka (Ukraine), Wieliczka (Poland), Kateřinky at Opava (Czech Republic), Sudice (Czech Republic), Steinebrunn (Austria) and Vienna Grünes Kreuz (Austria). All these occurrences are of middle Badenian age corresponding to the latest Langhian and earliest Serravallian and suggest some biostratigraphic value of *Poecilasma miocaenica* (note that Withers (1953) erroneously listed some of the localities as Tortonian, Late Miocene; see Harzhauser *et al.* (2003) for a discussion on the erroneous use of ‘Tortonian’ in the Paratethys literature).

Family LEPADIDAE Darwin, 1851

Genus LEPAS Linnaeus, 1758

Type species. Lepas anatifera Linnaeus, 1758.

Lepas sattmanni sp. nov.
 Figures 5A–H, 6B–C

Derivation of name. In honour of Helmut Sattmann, zoologist at the Natural History Museum Vienna.

Holotype. Natural History Museum Vienna, NHMW 2003z0026/0487, (Fig. 5B), left scutum, length: 14.5 mm.

Paratypes. Natural History Museum Vienna, NHMW 2003z0026/0487, (Fig. 5A, C–D), left scutum, length: 15.2 mm, left and right terga length: 14.4 mm, carina length: 14.2 mm.

Material. Two slabs of clay with numerous disarticulated valves (NHMW 2003z0026/0487, NHMW 2003z0026/0296); >20 scuta of different stages of growth, two terga, one carina.

Type locality and age. Pucking in Upper Austria; Lower Miocene (Aquitanean, = upper Egerian), Ebelsberg Formation.

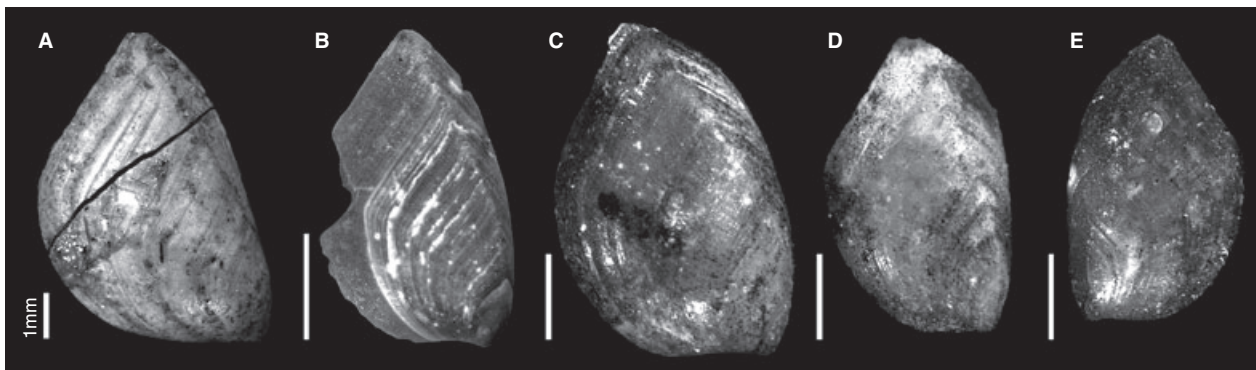


FIG. 3. *Poecilasma miocaenica* Reuss, 1864; scuta (Middle Miocene, Badenian). A, Holotype. NHMW1859/45/555, Podjarkow at Hanachivka, Ukraine. B, NHMW2010/0084/0001, Vienna, Austria. C–E, NHMW1867/7/97, Wieliczka, Poland, illustrated in Reuss, 1867 (pl. 8, figs 4–6). All scale bars represent 1 mm.

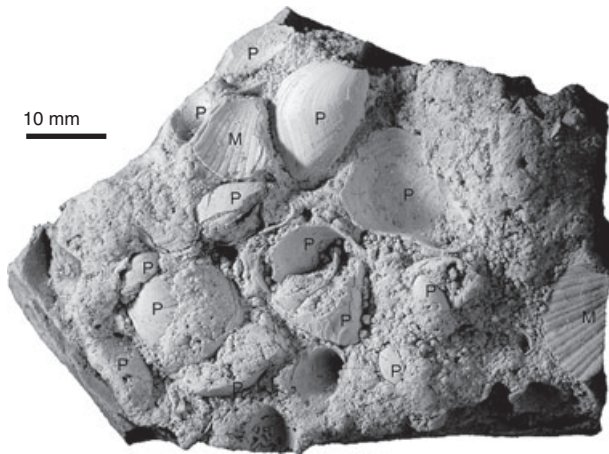


FIG. 4. *Poecilasma coquina* from Kateřinky at Opava (NE Czech Republic) in gypsum-rich pelites of middle Badenian age (NHMW1866/8/8). P, *Poecilasma*, M, molluscs, Scale bar represents 10 mm.

Diagnosis. Medium-sized *Lepas* with narrow, elongate carina with prominent growth lines; scuta elongate subtriangular with broad basal margin, weak apico-umbonal ridge and blunt rim close to the basal margin in the inner surface. Terga long, narrow, angulated and nearly smooth.

Description. Carina elongate and narrow and only moderately bowed inwards. Umbo in apical position; narrow parietes, covered by distinct, irregular, ridge-like growth lines. Tectum strongly convex close to the apex but nearly flat towards the rounded base. Sculpture consisting of prominent and slightly wavy growth lines. Scutum elongate subtriangular with nearly straight and long basal margin. This grades into the weakly convex tergo-lateral margin via rather abrupt curve in subadult valves but becomes widely rounded in adult ones. The occludent margin is initially straight, forming an angle of c. 70–80 degrees with the basal margin, and becomes convex in later stages. The apex is slightly protruding, well defined and accentuated by a rounded apico-umbonal ridge. The growth lines form thread-like ridges and are somewhat irregular at the intersections with the apico-umbonal ridge. Juvenile shells display a very weak radial sculpture originating at the umbo. Inner side of scutum bears a broad and prominent rounded rim parallel to the basal margin.

Generally, the convexity of the valves decreases during ontogeny and nearly flat increments are added along the tergo-lateral margin in latest stages of growth. Tergum elongate and thin; scutal and carinal margins area straight-sided and form a rounded basal angle of c. 25 degrees. Occludent margin convex, forming an angle of c. 120 degrees with the scutal margin. A very weak fold extends from the umbo towards this scutal angle. This fold is mainly documented by an indentation of the growth lines. Numerous very delicate radial threads radiate from the umbo towards the lower scutal margin.

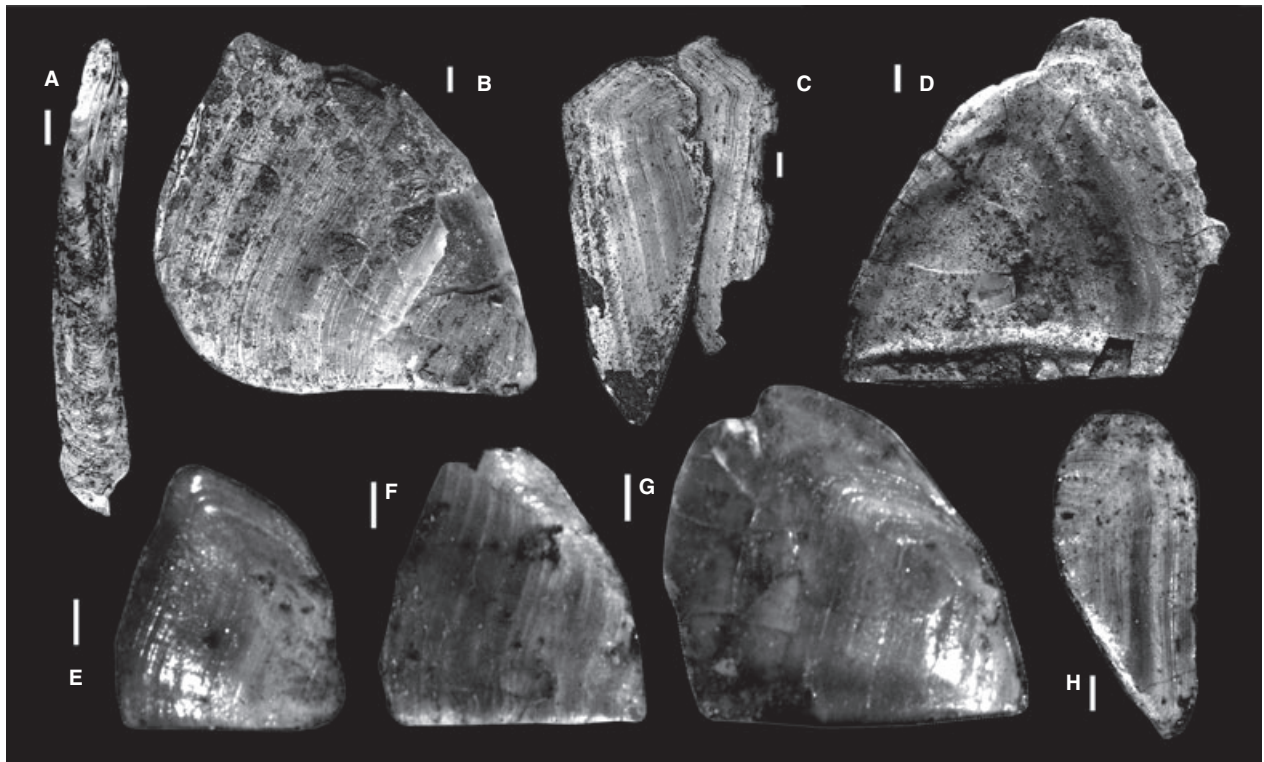


FIG. 5. A–H, *Lepas sattmanni* sp. nov. (Pucking, Upper Austria, Lower Miocene, Aquitanian). A, carina, paratype, NHMW 2003z0026/0487 (probably same individual as holotype). B, left scutum, holotype, NHMW2003z0026/0487. C, terga, paratype, NHMW2003z0026/0487. D, left scutum, paratype NHMW2003z0026/0487. E–G, left scuta in different stages of growth, NHMW2003z0026/0296. H, left tergum, NHMW2003z0026/0296. All scale bars represent 1 mm.

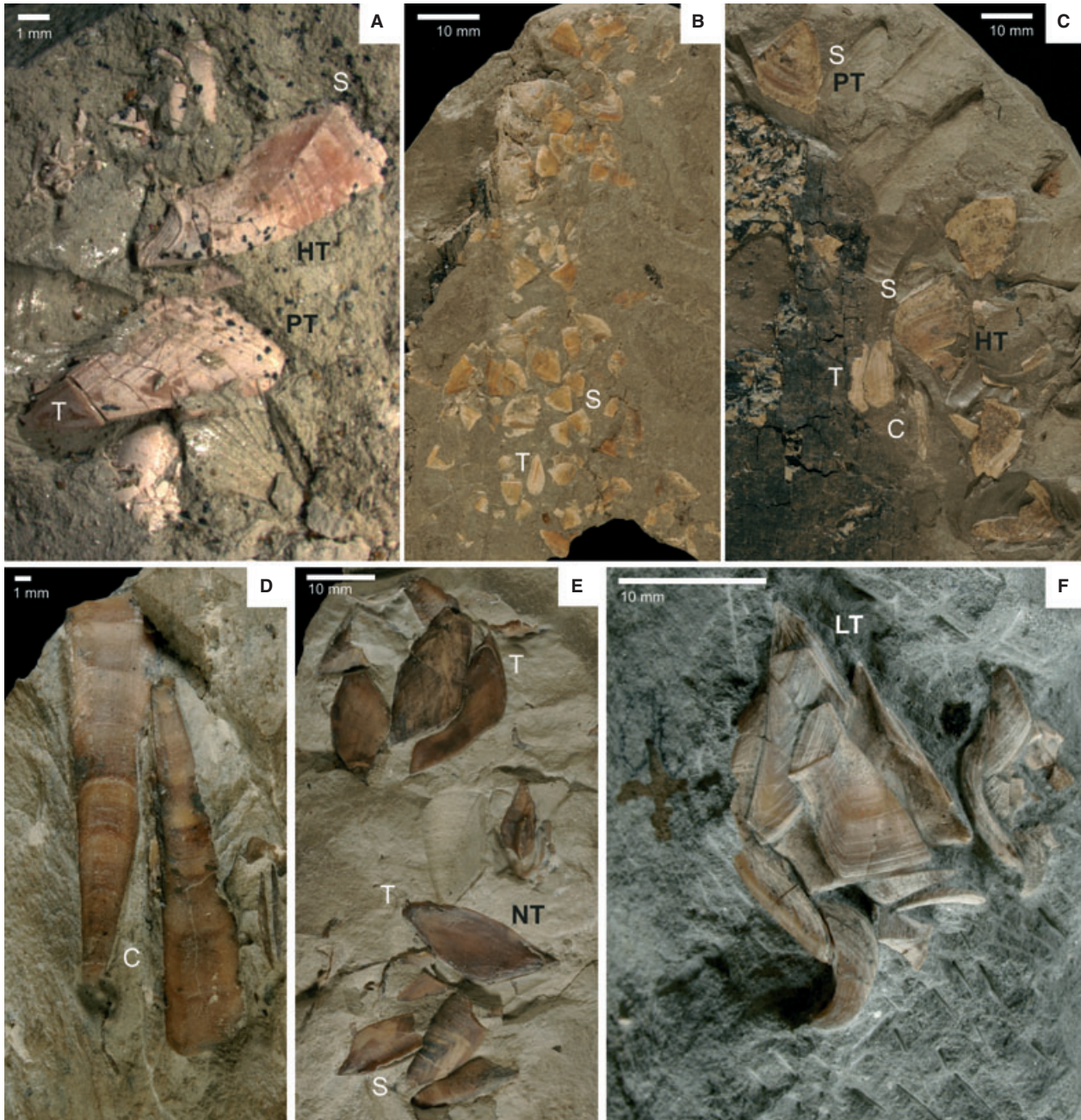


FIG. 6. A, *Scalpellum paratethyanum* sp. nov. (Cerová-Lieskové, Slovak Republic; Lower Miocene, Karpatian). B–C, *Lepas sattmanni* sp. nov. (Pucking, Upper Austria, Lower Miocene, Aquitanian). B, subadult colony attached to driftwood, NHMW2003z0026/0296. C, fully grown colony attached to driftwood, NHMW2003z0026/0487. D–E, *Arcoscalpellum renevieri* (Mayer and Gümbel in Gümbel, 1861) (Bad Häring in Tyrol, Austria, Lower Oligocene, Kiscellian). D, carinae, NHMW1884/0500/2730. E, scuta and terga, neotype, NHMW2010/0085/0001. F, capitulum of *Scalpellum pfeifferi* Weithofer, 1887 (Kremsmünster, Lower Miocene, Ottnangian), lectotype, collection of the Sternwarte Kremsmünster. Photograph: Dr. P. Amand Kraml, Sternwarte Kremsmünster, Austria. Scale bar represent 1 mm or 10 mm. Abbreviations: C, carina; S, scutum; T, tergum; HT, holotype; PT, paratype; NT, neotype; LT, lectotype.

Remarks. Among the European Miocene *Lepas*, only *Lepas rovasendai* De Alessandri, 1894 (*sensu* Withers 1953) from the Aquitanian, Burdigalian and Langhian of the Turin Hills in Italy, is reminiscent of *L. sattmanni* at first view. Nevertheless, it is much higher because of its longer

occludent and tergal margins and the comparatively shorter basal margin. Moreover, it develops a stronger apico-umbonal ridge. The angle between basal and occludent margins is obtuse in *L. rovasendai* throughout ontogeny but decreases strongly in *L. sattmanni*. The

carina of the Italian species differs strongly from *L. sattmanni* in its short, broad and waisted shape. Especially, the flared basal portion of the carina of *L. rovasendai* allows a clear distinction. The Late Miocene *Lepas mallandriniana* Seguenza, 1876, from Sicily, develops a concave tergal margin. *Lepas orbigny* Fischer, 1886 and *Lepas aquitanica* Fischer, 1886 from the Early Miocene of France, bear strong radial ridges on scuta and terga. The long basal margin and the comparatively short tergo-lateral margin distinguish *Lepas sattmanni* also from the extant *Lepas anatifera* Linnaeus, 1758 and *L. anserifera* Linnaeus, 1767. The extant *Lepas pectinata* Spengler, 1792 is reminiscent in this feature but differs significantly in its sculpture consisting of radial striae and grooves and even spines (Hinojosa *et al.* 2006; Di Geronimo 2010). The rim close to the basal margin of the scutum is slightly reminiscent of the internal basal shoulder of *Pristinolepas* Buckeridge, 1983 from the Oligocene to Middle Miocene of New Zealand. This shoulder is very broad and extends to the margin in *Pristinolepas*. In contrast, the rim of *L. sattmanni* is clearly separated from the basal margin.

Two colonies are documented; both are attached to lignitic driftwood. One consists of numerous juveniles, whilst the second comprises few adult, disarticulated valves. Recently, the Pucking section achieved more scientific attention owing to its outstanding fossils. Gregorova *et al.* (2009) described several huge sunfishes, and Grunert *et al.* (2010a, pl. 5, fig. 5) illustrated the holotype of the newly described species and provided a survey of the rich macro- and microfauna of this 'konservat lagerstätte' proposing a dysoxic depositional environment in the outer shelf.

Distribution. Known so far only from the Aquitanian of the North Alpine Foreland Basin.

Order SCALPELLIFORMES Buckeridge and Newman, 2006

Family SCALPELLIDAE Pilsbry, 1916

Subfamily ARCOSCALPELLINAE Zevina, 1978

Genus ARCOSCALPELLUM Hoek, 1907

Type species. *Scalpellum michelottianum* Seguenza, 1876.

Arcoscalpellum renevieri (Mayer and Gümbel in Gümbel, 1861) comb. nov.

Figure 6D–E

1861b *Pollicipes Renevieri* Mayer et Guembel; Gümbel, p. 675.

1934 *Scalpellum loczyi* Szörényi, p. 276, pl. 17, figs 1–6, 14–16.

1953 *Arcoscalpellum loczyi* (Szörényi); Withers, p. 218, pl. 31, figs 1–8.

Neotype. Natural History Museum Vienna, NHMW2010/0085/0001, text-fig. 6E, right tergum, length: 25.5 mm.

Material. Four marl slabs with 10 terga, five scuta and four carinae (NHMW 1884/0500/2730, NHMW 2010/0085/0001, NHMW 2010/0085/0002, NHMW 2010/0085/0003) from Bad Häring in Tyrol, Austria; Lower Oligocene, Kiscellian stage.

Remarks. Gümbel (1861a) introduced this species as *nomen nudum*. In the same year, he discussed this species again without illustration but provided a valid description (Gümbel 1861b). This was overlooked by Szörényi (1934) who described the same species from the Hungarian Oligocene as *Scalpellum loczyi*. Schlosser (1923) and Schachl (1939) mentioned *Pollicipes renevieri* in their lists as well without illustration. Withers (1953) was not aware of the first description from Bad Häring and designated a lectotype of the Hungarian *Arcoscalpellum loczyi*. A comparison of the Austrian material with the Hungarian specimens in the collections of the Hungarian National History Museum in Budapest clearly proves that both taxa are conspecific, and thus, *Pollicipes Renevieri* gains priority. No holotype was designated by Gümbel (1861b) who referred to a private collection. Therefore, in accordance with the ICZN Article 25.d.5, the specimen illustrated as Text-figure 6E, coming from the original type locality, is designated herein as neotype of *Arcoscalpellum renevieri*. A very detailed description of the species is given in Withers (1953). Only the carina of the Hungarian material is untypical as it is slightly misshapen and small, whilst the carinae from the type locality range 24–35 mm in length and 5–6 mm in width. Generally, the sculpture of the terga and scuta of the Austrian valves is slightly weaker than in the Hungarian specimens; for example, the apicobasal ridges are less distinct. The scutal interior surface is visible only in a single incomplete specimen, which does not show a ledge for complementary males as typical for several arcoscalpellids. The generic placement is based on the high similarity with the plate morphology of the type species *Arcoscalpellum michelottianum* (Seguenza, 1876). A separation from *Anguloscalpellum* Zevina, 1978 is difficult as the distinctive peduncular plates are unknown (cf. Young, 2001a). The angulate outlines of the upper latus and infra-median latus of *A. renevieri*, as illustrated by Withers (1953), correspond better to *Arcoscalpellum* than to *Anguloscalpellum*.

Distribution. *Arcoscalpellum renevieri* (Mayer and Gümbel in Gümbel, 1861) is known so far only from the Early Oligocene of the Paratethys. It is documented from the Hungarian Kiscell Formation and the Austrian Paisslberg Formation.

Subfamily Scalpellinae Pilsbry, 1907

Genus SCALPELLUM Leach, 1817

Type species. Lepas scalpellum Linnaeus, 1767.*Scalpellum paratethyanum* sp. nov.

Figures 6A, 7A–O

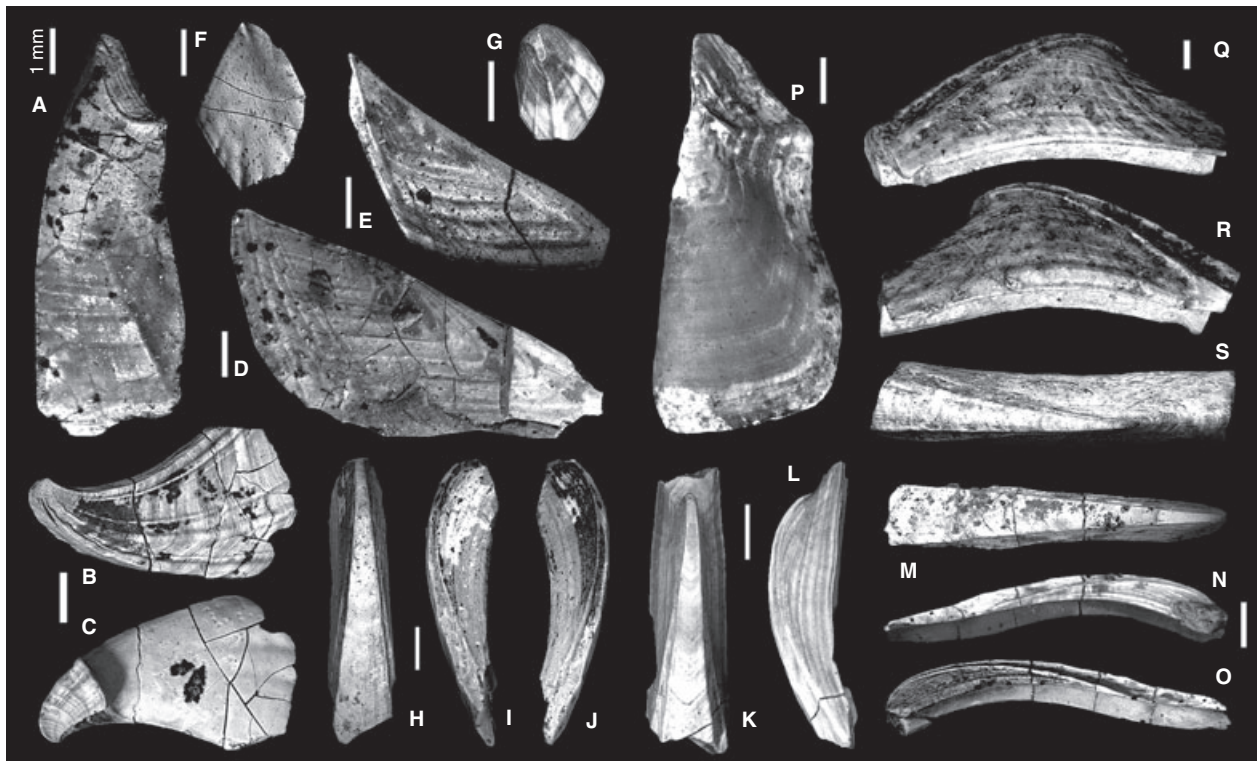
Derivation of name. After the Paratethys Sea.*Holotype.* Natural History Museum Vienna, NHMW2010/0086/0001, (Fig. 7A), right scutum, length: 8.9 mm, right tergum, length: 8.7 mm.*Paratypes.* NHMW2010/0086/0002, (Fig. 7D), right tergum length: 6.3 mm; NHMW 2010/0086/0003, text-fig. 7F, upper latus maximum diameter: 3.7 mm.*Material.* One slab with a right tergum and a right scutum, one isolated right tergum, one isolated upper latus, three carinae, two carinal lati.*Type locality and age.* Cerová-Lieskové N 48 35.284 E 17 24.126, Slovak Republic; Early Miocene, late Burdigalian; Karpatian stage; grey calcareous silt of the Lakšárska Nová Ves Formation.*Diagnosis.* A *Scalpellum* characterized by a rather slender scutum with prominent and strongly curved ridge between occludent margin and tergo-lateral angle and a distinct apico-basal ridge; upper latus elongate hexagonal.*Description.* Scutum slender elongate trapezoidal; umbo situated close to the weakly convex occludent margin. Lateral margin straight in the lower part but slightly concave close to the slightly projecting tergo-lateral angle. Tergal margin straight to feebly concave terminating in a narrow, rounded apex. Close below the apex starts a distinct ridge that extends in a strongly bent curve towards the tergo-lateral angle. Strong ridge-like growth lines cover the area between the ridge and the tergal margin. A distinct apico-basal ridge is accompanied by numerous delicate longitudinal riblets. Tergum obtusely triangular with confluent upper and lower carinal margins. Occludent margin nearly straight in young specimens and slightly convex in adults; strong ridges are developed during growth parallel to the occludent margin crossing the distinct but weaker growth lines of the scutal margin. Scutal angle

FIG. 7. A–O, *Scalpellum paratethyanum* sp. nov. (Cerová-Lieskové, Slovak Republic; Lower Miocene, Karpatian). A, right scutum, holotype, NHMW2010/0086/0001. B–C, left carinal latus. D, right tergum, paratype (probably from the same individual as holotype) NHMW2010/0086/0002. E, right tergum. F, upper latus, paratype NHMW2010/0086/0003. G, upper latus. H–J, K–L and M–O three carinae in left, right and plan views. P, *Scalpellum burdigalense* Des Moulins, 1875, right scutum, NHMW1858/18/5 (Salles, France, Serravallian). Q–S, *Scalpellum dalpiazii* Withers, 1953, carina in left, right and plan views (Pfaffstätten, Lower Austria, Middle Miocene, Badenian), NHMW2010/0087/0001. All scale bars represent 1 mm.

broadly rounded. Carina elongate, narrow and only moderately curved. Tectum flat with very weak longitudinal threads, distinct growth lines and a weak ridge along each margin. Parietes narrow, slightly concave and bounded by another longitudinal ridge. Intraparietes narrow but wider than the parietes; covered by numerous ridges which are caused by growth lines. Inner surface deeply concave. Carinal latus short triangular, moderately curved along the lower margin and concave along the upper margin. Outer surface flat, sculptured by 4–6 strong ridges. The ridges close to the margins are most prominent. Lateral end separated into two more or less straight edges separated by an obtuse angle. Inner side smooth aside from the strongly thickened boss at the carinal termination which bears several strong growth lines forming transversal ridges. Upper latus elongate and irregular hexagonal; furrows on the inner surface, which correspond to surface sculpture, suggest at least seven strong radial ridges in fully grown specimens.

Remarks. Withers (1953) mentions nine species of *Scalpellum* from the Early and Middle Miocene of Europe: *S. burdigalense* Des Moulins, 1875, *S. pfeifferi* Weithofer, 1887, *S. dalpiazzi* Withers, 1953, *S. molinianum* Seguenza, 1876, *S. lovisatoi* De Alessandri, 1894, *S. moraviense* Withers, 1953, *S. studeri* Tièche, 1905, *S. formae* De Alessandri, 1906 and *S. avenionense* Joleaud and Joleaud, 1914. None of these is conspecific with the specimens from Cerová. The scutum of *Scalpellum paratethyanum* is reminiscent of that of *Scalpellum burdigalense* in its general shape and the marked concave ridge between umbo and tergo-lateral angle (Fig. 7P). A major difference, however, is the distinct apico-basal ridge of the species from Cerová, whilst scuta of *S. burdigalense* are evenly convex. A clear difference is also the upper latus of *S. burdigalense* which is elongate ovoid with convex edges and smooth inner side, whereas the upper latus of *S. paratethyanum* is polygonal and displays deep furrows on the inner side. The morphology of that element is closer to *Scalpellum pfeifferi*. The latter species is distinguished from *S. paratethyanum* by its scutum. This develops a straight ridge between umbo and tergo-lateral angle and the tergal margin is straight. Whilst the terga of both species are very similar in shape and sculpture, the scutum of *S. pfeifferi* is broader and lacks the distinct apico-basal ridge. The carinal latus of *S. paratethyanum* is shorter, and wider. *S. dalpiazzi*, from the Burdigalian of the Turin Hills in Italy, develops a completely different scutum of wide trapezoidal shape. *S. molinianum*, from the Early Miocene to Pliocene of the Mediterranean area, differs in its broad and low tergal area, the straight part of the ridge close to the tergo-lateral area and the point of maximum concavity of that ridge which is close to the occludent margin in *S. molinianum* but closer to the lateral margin in *S. paratethyanum*. *S. lovisatoi*, from the Mediterranean Miocene, differs in its aberrant scutum with narrow and elongate apical part. *S. moraviense*, from the Middle Miocene of Moravia, bears a prominent sculpture of longitudinal ridges on scutum and tergum. Finally, *Scalpellum*

studeri is known from the Burdigalian of Belpberg near St. Gallen in Switzerland. This species differs from *S. paratethyanum* in its extraordinary large size with a carina length of more than 30 mm.

Distribution. This species is known only from the upper bathyal deposits of the proto-Vienna Basin, which was part of the Paratethys Sea during the late Early Miocene.

Scalpellum dalpiazzi Withers, 1953

Figure 7Q–S

1953 *Scalpellum dalpiazzi* Withers, p. 278, pl. 45, figs 3–15, pl. 46, figs 1–9, text-fig. 97.

Material. One carina, NHMW 2010/0087/0001, length: 14 mm, height: 6 mm; Pfaffstätten in Lower Austria, Vienna Basin; Badenian, Middle Miocene.

Remarks. The only specimen known so far from the Paratethys area is a very robust, elongate cup-shaped carina. Its umbo is removed far from the apex and apically bent. The tectum is nearly flat with a faint sculpture of longitudinal ridges, separated from the slightly concave and narrow parietes by two blunt ridges. Another very strong ridge demarcates the parietes from the extremely wide intraparietes. These form a deep concavity below the umbo and are covered by wide radial ridges with flat tops. The growth lines form comparable ridges and cause an irregular cancellate pattern together with the radial ridges.

Withers (1953) mentions only three species from the Mediterranean Miocene which develop comparable carinae. The exceptional cup-like shape is reminiscent of the strongly sculptured *Scalpellum avenionense* Joleaud and Joleaud, 1914. Nevertheless, this species from the Miocene of the Rhône Basin is clearly distinguished by the deep furrow on the tectum. *Scalpellum formae* De Alessandri, 1906, from the Burdigalian of the Turin Hills, develops even stronger but narrower radial ribs and the intraparietes are narrower. *Scalpellum lovisatoi* De Alessandri, 1894, from the Early and Middle Miocene of Italy and Malta, develops a much higher number of densely spaced longitudinal ridges.

Distribution. *Scalpellum dalpiazzi* is known from the Aquitanian and Burdigalian of the Turin Hills. A Langhian occurrence from the same area is mentioned from the Monte di Cappuccini by Withers (1953). This species was not known so far from the Paratethys where it is now documented from Badenian deposits.

Scalpellum pfeifferi Weithofer, 1887

Figure 6F

1887 *Scalpellum Pfeifferi* Weithofer, p. 373, pl. 15, figs 1–19.

1953 *Scalpellum pfeifferi* Weithofer; Withers, p. 264, pl., 41, figs 1–7, text-fig. 87.

Material. The capitulum, illustrated by Weithofer (1887, pl. 15, fig. 1), was designated as lectotype by Withers (1953). In addition, numerous isolated elements and partly preserved capitula are stored in the collection of the Sternwarte Kremsmünster. Ottnang Formation; Early Miocene, middle Burdigalian, Ottnangian.

Remarks. Withers (1953) provided a detailed re-description of the species but erroneously proposed a Middle Miocene age. The occurrence of *Scalpellum pfeifferi*, however, seems to be restricted to the Ottnangian stage (= middle Burdigalian) of the Paratethys. Owing to restrictions from the Mediterranean Sea, the endemism within the marine mollusc fauna was strongly increasing in the Paratethys at that time (Rögl 1998; Harzhauser and Piller 2007; Landau *et al.* 2009). The high number of valves and the record from two separate coeval sections suggests that this species was a quite common element.

Distribution. Only known from the Lower Miocene deposits at Ottnang and Kremsmünster in Upper Austria.

DISCUSSION

Diversity and stratigraphic ranges

Additional taxa recorded by Withers (1953) but not encountered during this study are the following: *Calantica sulci* Withers, 1953 from Borač and Sudice (Czech Rep., Badenian, Middle Miocene), *Scalpellum hungaricum* Szörényi, 1934 from Budapest (Hungary, Kiscellian, Early Oligocene), *Scalpellum studeri* Tièche, 1905 from Belpberg at Bern (Switzerland, Burdigalian, Early Miocene) and *Scalpellum moraviense* Withers, 1953 from Borač, Kralice and Sudice (Czech Rep., Badenian, Middle Miocene). Thus, in total, there are now 10 species of stalked barnacles known from the Paratethys Sea. The oldest taxa are *Scalpellum hungaricum* and *Arcoscalpellum renevieri* which occurred during the Early Oligocene (Kiscellian). Only the latter one is documented from two localities in Hungary and Austria, indicating a wide distribution. No records are known so far from the Late Oligocene. Most mollusc assemblages from that time in Hungary and Austria reflect shallow marine and littoral settings or even estuarine brackish conditions (Báldi 1973; Harzhauser and Mandić 2002) explaining the scarceness of lepadiform and scalpelliform barnacles. *Lepas sattmanni* sp. nov. is the only lepadid found during the early Early Miocene (Aquitanian), and two species occurred during the middle Burdigalian (*Scalpellum studeri* and *Scalpellum pfeifferi*)

and one during the late Burdigalian (*Scalpellum parathyianum* sp. nov.). Repeated phases of open marine connections towards the western Mediterranean via the North Alpine Foreland Basin, deep marine basins and upwelling settings provided habitats for the establishment of stalked barnacles in the Paratethys. None of the many species described by Withers (1953) from the Aquitanian and Burdigalian of the Turin Hills is documented from the Paratethys. This is surprising in respect to the otherwise tight biogeographical relations of the Mediterranean mollusc faunas with those of the Early Miocene Paratethys (Harzhauser *et al.* 2002; Harzhauser and Piller 2007). Therefore, the poor affinities to coeval faunas from the Mediterranean Sea are probably an artefact owing to the insufficient knowledge of lepadiform and scalpelliform taxa. The highest diversity is observed during the early Middle Miocene when four species occurred in the Paratethys Sea. Only *Scalpellum dalpiazii* is also known from the Mediterranean, where it appears already during the Early Miocene (Withers 1953). In addition, *Scalpellum moraviense*, *Calantica sulci* and *Poecilasma miocaenica* settle the Paratethys during the Langhian and earliest Serravallian (early and middle Badenian). The diversity drops distinctly during the Serravallian, and no scalpelliform and lepadiform barnacles are described so far from the late Badenian. Interestingly, only *Poecilasma miocaenica* occurred also in the Carpathian Foredeep during the Badenian Salinity Crisis and seems to have bloomed there.

Concluding, the fossil stalked barnacles of the Paratethys are usually documented by rather isolated findings. Only *Arcoscalpellum renevieri* and *Poecilasma miocaenica* are known from more than one section or basin. The biostratigraphic value is thus hard to evaluate. The abundance and distribution of *Poecilasma miocaenica*, however, may point to an acme during the middle Badenian. The Paratethyan diversity patterns are comparable with those reported from adjacent bioprovinces, indicating a similar level of knowledge. The number of reported taxa ranges between one and three in the Aquitanian and Langhian of the Mediterranean and the Burdigalian and Serravallian of the Eastern Atlantic (Withers 1953). A clear exception is the Burdigalian of the Turin Hills in Italy from where Withers (1953) documents at least 10 species.

Palaeoecology

Stalked barnacles are not common in littoral environments. Therefore, their occurrence in the fossil record may bear important information for palaeobathymetry estimates. In total, five genera are recorded from the Paratethys Sea.

Of these, *Lepas sattmanni* is the only pelagic barnacle. Extant representatives of *Lepas* are settling on floating objects on the sea surface and display very wide geographical distributions. Findings of *Lepas* in deep-water deposits are thus explained by sunken flotsam such as driftwood (Green *et al.* 1994; Di Geronimo 2010; Inatsuchi *et al.* 2010). The animals can become washed ashore and may thus also occur in shallow marine deposits. At Pucking, the two colonies are attached to lignitified driftwood and occur in fish-bearing pelites (Fig. 6B–C). The palaeoenvironment is interpreted by Grunert *et al.* (2010a) as outer shelf environment with low oxygen levels.

The most abundant lepadomorph in the Paratethys was *Poecilasma miocaenica*. Extant species of *Poecilasma* are benthic deep-water barnacles living mainly attached to crabs (Green *et al.* 1994; Pinho *et al.* 2001) but also to other decapods, echinoderms (Williams and Moyses 1988) and even on plastic (Lampitt 1990). Up to 1000 individuals may be attached to a single host (Williams and Moyses 1988). All records reviewed by Young (2001b) range between 217- and 1386-m water depth. Paratethyan occurrences may thus indicate deep marine and oxygenated conditions. Sediment samples from Opava in the Carpathian Foredeep even contain *Poecilasma coquinas* (Fig. 4). In contrast, only isolated elements are found in the Vienna Basin. This may point to a blooming of this species in the restricted and species-poor marine environment of the Carpathian Foredeep during the evaporitic event. Moreover, the abundance of this deep-water lepadomorph in evaporitic successions clearly hints to a deeper marine depositional environment. The potential host crabs are unknown so far.

Arcoscalpellum is a benthic deep-water dweller which lives attached to other benthos, such as bamboo corals, gastropods and rocks, in water depths between 60 and 5100 m (Young 2001b; Buhl-Mortensen and Høeg 2006; Chan *et al.* 2009). The Oligocene *Arcoscalpellum renevieri* is documented from the Kiscell and Paisslberg formations which both represent deep sublittoral to upper bathyal depositional environments (Báldi 1986; Löffler and Nebelsick 2001). Báldi (1986) suggests a water depth of 200–1000 m for the Kiscell clay which is thus in accordance with the occurrence of *Arcoscalpellum*.

Scalpellum lives benthic and is attached to polychaetes, gorgonians, molluscs, decapods and echinoderms (Nilsson-Cantell 1978; Chan *et al.* 2009; Di Geronimo 2010). It occurs already in shallow sublittoral environments below low water mark and ranges down to bathyal settings (Nilsson-Cantell 1978; Bradshaw *et al.* 2001; Buhl-Mortensen and Høeg 2006; Southward 2008). The various Paratethyan *Scalpellum* species, too, derive from quite different settings. Therefore, the occurrence of this genus cannot be interpreted in terms of palaeobathymetry without consideration of the associated faunas. Nonbathyal

conditions in <200-m water depth can be postulated as habitat of *Scalpellum pfeifferi* based on the foraminifers from the Ottnang section (Grunert *et al.* 2010b). In contrast, the mollusc faunas associated with *Scalpellum hungaricum* and *Scalpellum paratethyanum* suggest upper bathyal conditions (Báldi 1986; Schlögl *et al.* 2011). Finally, *Scalpellum dalpiazi* is associated with the otherwise very rare bamboo coral *Keratoisis melitensis* (Goldfuss, 1826), which points to deep marine conditions (Noé *et al.* 2008). The palaeogeographical position of the section, close to the shores formed by Mesozoic limestones of the Alps, indicates a steep, shaded, submarine scarp with bamboo corals.

CONCLUSIONS

Oligocene and Miocene lepadiform and scalpelliform barnacles of the circum-Mediterranean area are still poorly known. The records are isolated and spotty. This synthesis is a first step since the milestone publication of Withers (1953) to evaluate the stalked barnacles of the Paratethys Sea. There, the diversities during the Oligocene and Miocene remain low and range from one to four species. A slight increase during the Langhian might be correlated with the Mid-Miocene climate optimum but could also be simply related to the larger extant of Middle Miocene deposits (Kroh 2007).

The low biogeographic relation of the Paratethyan stalked barnacles with the more diverse and better known Mediterranean ones is surprising. Only a single species occurs in both areas. This, too, seems to be caused by the insufficient knowledge of the fossil Thoracica as such marked biogeographic separation is absent in other marine groups during the Miocene.

The palaeoecological settings are generally in agreement with the habitat requirements of extant relatives. This implies that especially scalpelliform barnacles can be used for rough palaeobathymetric estimates for deep sublittoral to bathyal palaeoenvironments. Most taxa are recorded by isolated valves, single capitula or rare colonies. Only *Poecilasma miocaenica* occurs in large numbers and is widespread in the Paratethys during the middle Badenian. The most outstanding occurrences are *Poecilasma coquinas* in the evaporates of the Badenian Salinity Crisis. As extant *Poecilasma* are deep-water dwellers, these occurrences are important proxies for deep marine basins in the Carpathian Foredeep during the Middle Miocene.

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