



AN APPRAISAL OF THE FOSSIL RECORD FOR THE CIROLANIDAE (MALACOSTRACA: PERACARIDA: ISOPODA: CYMOTHOIDA), WITH A DESCRIPTION OF A NEW CIROLANID ISOPOD CRUSTACEAN FROM THE EARLY MIOCENE OF THE VIENNA BASIN (WESTERN CARPATHIANS)

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Abstract: Isopod crustaceans are rarely preserved in the fossil record. Herein, an appraisal of the fossil record for the cirolanid isopods is presented. Five genera are briefly discussed, including *Bathynomus*, *Brunnaega*, *Palaega*, *Pseudopalaega* and *Cirolana*. A key for the cirolanid genera known to date from the fossil record is provided based mostly on pleotelson characters. From the early Miocene of the Slovak part of the Vienna Basin, *Cirolana feldmanni* sp. nov. is described being only the fifth fossil *Cirolana* species known to date and one of the few with preserved appendages. The material exhibits preservation suggesting biphasic moulting;

the mode of preservation suggests a rather short time between shedding the posterior and anterior parts of the exoskeleton instead of hours or even days known in extant taxa. As no subsequent transport or physical disturbance was inferred, the specimens can be stated as *in situ* preservation. From the palaeoecological point of view, it is concluded that *Cirolana feldmanni* sp. nov. is the first unequivocal fossil deep-water *Cirolana* as suggested by the accompanied fauna.

Key words: Isopoda, Cirolanidae, early Miocene, the Vienna Basin, moulting, deep-water environment.

ISOPODS are an extremely diverse order and include the largest peracaridan crustaceans. They are often common and important members of a variety of marine, freshwater and terrestrial habitats (Kensley and Schotte 1989) and occur in all habitats on all continents with the exception of the terrestrial Antarctica and Arctic ice surfaces. Because of the delicate nature of their exoskeleton, the isopod fossil record is poor in comparison with the known present-day diversity. Fossil isopods are usually poorly preserved without any appendages, visible eyes or mouthparts (compare Guinot *et al.* 2005; Vega *et al.* 2005; Feldmann 2009; Wilson *et al.* 2011), all of which are critical in isopod classification (Wägele 1989; Brandt and Poore 2003).

The Miocene deposits of the Vienna Basin have yielded many decapod crustacean remains (Reuss 1859; Glaessner 1928; Bachmayer and Küpper 1952; Bachmayer 1953*a, b*, 1954, 1962; Bachmayer and Tollmann 1953; Hyžný and

Schlögl 2011), but few isopods (Bachmayer 1947; Tauber 1950). The material presented here adds new data to the isopod fossil record and is the first reported occurrence of a cirolanid isopod from the Vienna Basin. It is considered also to be the first known Miocene occurrence of the genus *Cirolana* Leach, 1818.

The only known occurrences of fossil isopods from the Vienna Basin represent findings from the first half of the 20th century. Three species have been described from the Miocene deposits: *Cymodoce oroszyi* Bachmayer, 1947, *Sphaeroma weinfurteri* Bachmayer, 1947, and *S. bachmayeri* Tauber, 1950. All of these were placed within the family Sphaeromatidae Latreille, 1825, members of which are usually capable of rolling into a ball. Interestingly, the specimens described by Bachmayer (1947) and Tauber (1950) are preserved enrolled or nearly enrolled. This type of preservation of sphaeromatid isopods was reported also

by De Angeli and Lovato (2009) from the late Eocene of Italy. Sphaeromatid isopods differ markedly from members of the family Cirolanidae Dana, 1852. Cirolanids are predators or scavengers, whereas sphaeromatids exhibit herbivorous habits (Brusca *et al.* 2007). All mentioned occurrences of sphaeromatid fossils (Bachmayer 1947; Tauber 1950; De Angeli and Lovato 2009) were found within shallow-water carbonate facies with abundant bryozoans and red algae, *Teredo* borings and corals, respectively. The cirolanid specimens described herein come from much deeper-water facies without any reefal structures in the surroundings.

GEOLOGICAL SETTING

The Cerová-Lieskové locality, which yielded the present specimens, is situated at the foothills of the Malé Karpaty Mountains, located in the north-eastern part of the Vienna Basin (Slovakia) (Fig. 1). During the Miocene, it was a part of the Central Paratethyan Sea. At the study site, Karpatian (latest Burdigalian) sediments of the Lakšárska Nová Ves Formation (Špička and Zapletalová 1964) are well exposed in a former claypit. These are characterized by massive, locally laminated calcareous clay and clayey silt with thin tempestites (up to 5 mm thick) with plant remains and several thin sandstone layers in the uppermost part of the section. The section is more than 15 m thick, the lower part is actually covered by a large debris cone; thus, only the upper part some 10 m thick is accessible.

Macrofossil assemblages comprise vertebrates (fishes, bathyal sharks) and a wide spectrum of invertebrates (bivalves, gastropods, cephalopods, scaphopods, decapods and isopods, regular and irregular echinoids, ophiuroids,

siliceous sponges and rare corals). Microfossil suites include both benthic and planktonic foraminifera, radiolarians, sponge spicules, ostracods, crinoid ossicles, fish otoliths and, in places, extremely abundant Bacillariophyta. Published systematic accounts are so far focused on molluscs (Harzhauser *et al.* 2011; Schlögl *et al.* 2011) and crustaceans (Hyžný and Schlögl 2011; Harzhauser and Schlögl 2012).

Age assignment of these deposits relies on the co-occurrence of the foraminifera *Uvigerina graciliformis* Papp and Turnovsky, 1953 and *Globigerinoides bisphericus* Todd in Todd, Cloud, Low and Schmidt, 1954 and the absence of the genus *Praeorbulina* Olsson, 1964. The first appearance datum (FAD) of *U. graciliformis* marks the base of the Karpatian Stage (e.g. Piller *et al.* 2007), while that of *G. bisphericus* is within Zone M4b of Berggren *et al.* (1995), correlating with the upper Karpatian. The appearance of *Praeorbulina* marks the start of the middle Miocene. The regional Paratethyan Karpatian Stage has consistently been considered to be the time equivalent of the latest Burdigalian (Piller *et al.* 2007).

The deep-water conditions are suggested by the chondrichthyans (Ch. Underwood, pers. comm. February 2011), decapod crustaceans (Hyžný and Schlögl 2011) and molluscs (Harzhauser *et al.* 2011), and palaeodepths based on foraminiferal faunas were estimated following the two-step depth equations developed by Hohenegger (2005). Analyses (evaluated for the 2.4-m-thick interval between samples no. 14 to no. 20) allow to estimate water depths of 240–330 m with extreme values ranging from 149 to 498 m. Spezzaferri *et al.* (2002) suggested deposition at a depth around 300 m for a similar foraminiferal association from the ‘Steirischer Schlier’ of the Styrian Basin in Austria.

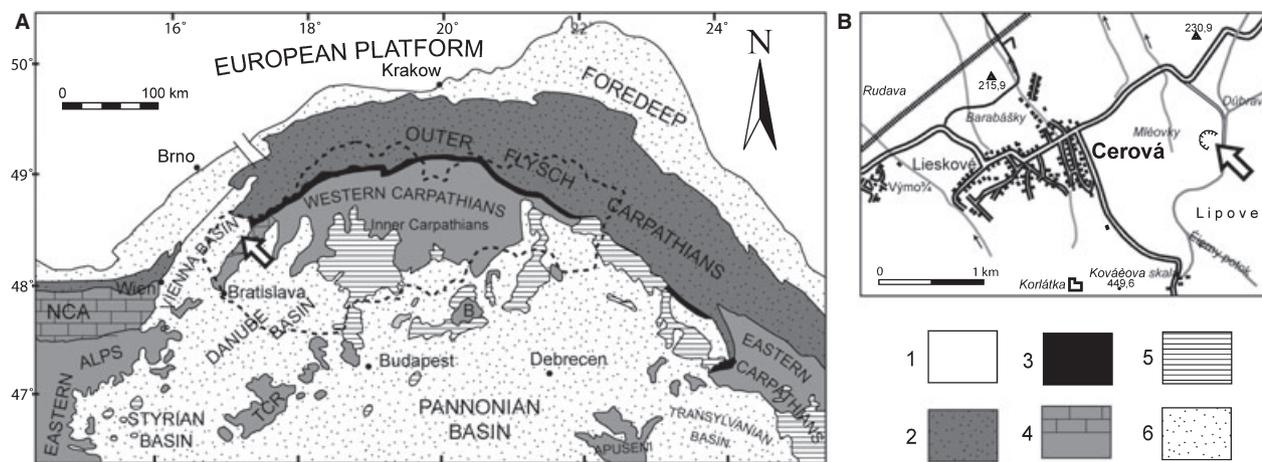


FIG. 1. Geographical position of the studied area. A, Position of the Vienna Basin in the Carpathian–Pannonian system (simplified from Kováč 2000), locality indicated with arrow; B, location of the Cerová-Lieskové, the type locality of *Cirolana feldmanni* sp. nov. Legend: 1, European platform units; 2, Carpathian-Alpine externides; 3, Pieniny Klippen Belt; 4, Alpine-Carpathian-Dinaride and Pannonian internides; 5, Neogene volcanics; 6, Neogene basins; B, Bükk; NCA, Northern Calcareous Alps; TCR, Transdanubian Central Range.

SYSTEMATIC PALAEOLOGY

Repository. Studied material is deposited in the Department of Geology and Paleontology, Comenius University in Bratislava (KGP-MH) and the Natural History Museum SNM, Bratislava, Slovakia (SNM-Z).

Higher-rank classification follows Ahyong *et al.* (2011). The species description and diagnosis were prepared from *Cirolana* character set using the program DELTA (Dallwitz *et al.* 1997). Family-level and genus-level character states as given by Bruce (e.g. 1986, 2003) and Brusca *et al.* (1995) are excluded from the species description and should be regarded as implicit.

Class MALACOSTRACA Latreille, 1802
Order ISOPODA Latreille, 1817

Remarks. The higher classification of isopods is based on somatic characters such as pleon and pleotelson morphology, morphology of the pleopods and the morphology and articulation of the uropods. In the Cymothoidea, the morphology of the mouthparts is critical in defining families (Wägele 1989; Brandt and Poore 2003), but these appendages are rarely preserved in the fossil record. Moreover, accurate identification may require dissection and microscopic examination of appendages (Brusca *et al.* 2007). Several authors (Basso and Tintori 1994; Wilson 1998; Polz *et al.* 2006; Hansen and Hansen 2010) have argued that generic or even species assignment may be based on characters shown by the cephalothorax or pleotelson. Although fossil taxa can be described, defined and named, it is usually not possible to distinguish them from most extant congeners as the taxonomy of fossil taxa relies largely or entirely on somatic characters, while extant genera are defined on both somatic and appendage morphology and in some cases can be separated only by appendage morphology. The greatest difficulties in the classification of fossil specimens are encountered when fossil specimens are preserved only as posterior parts of dorsal exoskeleton. This issue was widely discussed by Wieder and Feldmann (1989), Feldmann and Goolaerts (2005), Feldmann and Rust (2006) and Hansen and Hansen (2010).

We consider the apparent paucity of fossil cirolanid records partly to be a consequence of fossil isopods usually not retaining their appendages and so precluding definitive generic and family determination. Thus, only taxa with distinct somatic morphology can be identified in the fossil record. Another difficulty is interpretative: genera (and families) distinguished by mouthpart differences may be lumped into only one observable morphotype (the fossil genus *Palaega* Woodward, 1870 may be a case, see below). Many other genera may simply be too fragile to be represented in the fossil record or they inhabit environments

with low chance to be preserved in sedimentological record (e.g. caves). Moreover, predation and scavenging of corpses as well as exuviae reduce the number of remains that would be buried and preserved.

Wieder and Feldmann (1992, p. 959) discussed in detail the assignment of fossils to isopod genera and concluded that 'by making some generalizations based upon those parts preserved, one can effectively limit the possibilities and, thus, place fossil isopods in probable taxa'. Somatic morphology (pereonite 1 length, pleonite 5 with free lateral margins or overlapped by 4, pleonite 1 visible or largely concealed) is usually consistent within a genus. Contrary to that, somatic ornamentation such as the presence of nodules or carina and is not necessarily of generic merit.

Suborder CYMOTHOIDA Wägele, 1989
Family CIROLANIDAE Dana, 1852

Diagnosis. Body ovoid to semicylindrical; eyes lateral; all seven pereonites distinct, coxae well developed on pereonites 2–7, extending to posterior margin of pereonite, not extending significantly beyond pereonite; those of pereonites 5–7 with distinct posteroventral angle; pleon composed of pleonites 1–5 distinct or rarely fused; pleonite 6 fused to telson to form pleotelson; pleotelson flat or weakly vaulted, entire, never perforate or strongly vaulted; uropods biramous, articulating ventrolaterally, dorsoventrally flattened (occasionally round in section) and forming caudal fan, endopod not fused to peduncle.

Remarks. Diagnoses given by Brandt and Poore (2003, p. 917) for the Cymothoidea Wägele, 1989, the superfamilies Cymothoidea Leach, 1814 and Cirolanoidea Dana, 1852 all effectively also diagnose the family Cirolanidae in the absence of appendages. The family has been revised by Hansen (1890, 1905), Monod (1930), Bruce (1986) and Brusca *et al.* (1995). The diagnosis presented here reflects those characters that are likely to be seen in fossils and is therefore not directly compatible with those diagnoses used for extant families, notably failing to differentiate Cirolanidae from Corallanidae Hansen, 1890 and Tridontellidae Bruce, 1984. The detail of coxal morphology will, for the most part, separate Cirolanidae from Cymothoidea, which usually have short, rounded ('reniform') coxae that do not extend to the posterior of the pereonite; the exception being that some species of *Nerocila* Leach, 1818 have large and acute coxae. Until now, only one fossil taxon has been attributed to the Cymothoidea: *Cymatoga jazykowi* von Eichwald, 1863 from the Upper Cretaceous of Russia: re-examination of the type material, considered lost by Van Straelen (1928, p. 18), is necessary to confirm or reject its familial status. Hessler (1969, p. R380) sug-

gested possible morphological affinity of *C. jazykowi* to *Palaega*. Concerning other possible fossil cymothoids, Monod (1926) suggested strong cymothoid affinities are shown by the fossil genus *Urda* Münster, 1840 currently classified within its own family. Hessler (1969, p. R387) and Taylor (1972, p. 102) discussed the affinities of *Urda* and the family Urdidae Kunth, 1870. The genus is still treated as a separate family in Feldmann *et al.* (1994) and Brandt *et al.* (1999), although its status may be questioned, as some *Urda* species exhibit characters typical for Cirolanidae, for example, *Urda mccoysi* (Carter, 1889). Moreover, we consider the interpretation of eyes in *Urda rostrata* Münster, 1840 and *U. punctata* Münster, 1840 depicted by Kunth (1870, pl. figs 1–3) as erroneous. The systematic revision of the Urdidae is, however, beyond the scope of present contribution; therefore, we refrain to discuss this issue more in detail and for the time being we classify *Urda* as a member of its own family.

A broad tridentate mandibular incisor is one of the most important and readily observed characters in defining and identifying the Cirolanidae; associated with that character are the large mobile anteriorly toothed ‘triangular’ molar process and the morphology of the spine row (e.g. see Bruce 1986; Brusca *et al.* 1995; Brandt and Poore 2003). In the absence of antennae, mouthparts or pereopods, one cannot confidently differentiate the isopod families Cirolanidae, Aegidae White, 1850, Corallanidae and Tridentellidae from each other. Critical and ‘key’ characters defining these families are primarily found in the mouthparts and secondarily in the pereopods. Corallanidae and Tridentellidae have what may be described as ‘sucking’ or ‘piercing’ mouthparts, forming a narrow buccal cone, with a narrow mandible incisor, and consequently, they have proportionally slightly narrower heads (see Delaney 1989). Aegidae, similarly, have ‘sucking’ mouthparts, but often have wide heads with large eyes that occupy more than 30 per cent of the head width (Bruce 2009). The present Vienna Basin specimens have rather wide head without large eyes. Therefore, placement among Cirolanidae is most appropriate.

The Cirolanidae is one of the most diverse marine isopod families. There are 62 accepted extant genera in Cirolanidae (Schotte *et al.* 2010), with five fossil genera explicitly attributed to the family: *Brunnaega* Polz, 2005 (see Bruce 2009, p. 15; Wilson *et al.* 2011; transferred to Cirolanidae), *Cirolana*, *Palaega*, *Pseudopalaega* Mezzalana and Martins-Neto, 1992 and *Bathynomus*, which is both extant and known as a fossil (Imaizumi 1973; Wieder and Feldmann 1989; Obata and Omori 1993; Karasawa *et al.* 1995; Takakuwa 2004). The status of *Palaega* remains ambiguous and probably represents several taxa. Bowman (1971) demonstrated how *Palaega lamnae* Bowman, 1971 could be placed with equal merit into the Cymothoidea or Cirolanidae. For discussion on this issue, a reference is

made to Feldmann and Goolaerts (2005), Feldmann and Rust (2006) and Feldmann (2009); see also below.

Genus BATHYNOMUS Milne Edwards, 1879

Type species. *Bathynomus giganteus* Milne Edwards, 1879, by monotypy.

Remarks. Species of *Bathynomus* can be seen to form two groups (Lowry and Dempsey 2006), the so-called giants represented by, for example, *B. immanis* Bruce, 1986 and the ‘supergiants’ represented by *B. giganteus* Milne Edwards, 1879. Giants are usually <150 mm in body length and have flat pleotelson spines that do not curve dorsally; supergiants have long pleotelson spines, which in several species, are round in section and curve dorsally (Lowry and Dempsey 2006). Several fossil species are attributed to *Palaega* (e.g. *P. goedertorum* Wieder and Feldmann, 1989; *P. undecimspinosus* Karasawa, Nobuhara and Matsuoka, 1992), which possess pleotelson characters identical to those of *Bathynomus* as stated in the presented key (Table 1). If confirmed to be congeneric with *Bathynomus*, these fossils appear to be ‘giants’ rather than ‘supergiants’ *sensu* Lowry and Dempsey (2006). The ICZN ruling (Anonymous 1992; Opinion 1668) gives the name *Bathynomus* precedence in any cases of nomenclatural conflict. *Bathynomus* has been explicitly recorded as fossil by Obata and Omori (1993), Karasawa *et al.* (1995) and Takakuwa (2004).

Stratigraphic range. *Palaega goedertorum* from the late Eocene and early Miocene of the USA (Washington State) seems to be the oldest representative of the genus if its generic assignment to *Bathynomus* is confirmed.

Genus BRUNNAEGA Polz, 2005

Type species. *Brunnaega roeperi* Polz, 2005, by monotypy.

Remarks. The genus *Brunnaega* was originally attributed to the family Aegidae. Bruce (2009, p. 15) and Hansen and Hansen (2010, p. 141) cast doubts on this assignment, as no explanation was given for placing the genus in the Aegidae by Polz (2005). Bruce (2009, p. 15) argued that *Brunnaega* is better placed in the Cirolanidae.

Wilson *et al.* (2011), in again formally transferring *Brunnaega* to the Cirolanidae, also provided a detailed diagnosis of the genus, based on excellently preserved and abundant specimens of *Brunnaega tomhurleyi* Wilson *in* Wilson, Paterson and Kear, 2011, from Queensland (Australia), which in several specimens showed details of appendages rarely seen in the fossil specimens. Wilson *et al.* (2011, p. 1056) stated that ‘Although we do not

TABLE 1. Key to fossil Cirolanidae (excluding *Pseudopalaega* Mezzalana and Martins-Neto, 1992) and Urdidae.

1	Pleotelson without distinct spines or denticulation on posterior margin	2
	Pleotelson quadrate or semicircular with distinct spines or denticulation on posterior margin	4
2	Pleotelson shorter than or as long as pleon, semicircular, lateral margins subparallel, with median dorsal ridge	<i>Urda</i> (Urdidae)
	Pleotelson longer than pleon, ovate to subtriangular, without median dorsal ridge	3
3	Pleonite 5 with free lateral margins	<i>Brunnaega sensu</i> Polz, 2005
	Pleonite 5 laterally overlapped by pleonite 4	<i>Cirolana</i>
4	Pleotelson lateral margins serrated, posterior margin with large central spine and several smaller additional spines positioned laterally	<i>Palaega sensu</i> Woodward, 1870
	Pleotelson lateral margins not serrated, weakly sinuous; posterior margin with spines small or large, approximately subequal in size laterally	5
5	Pleotelson posterior margin with 7–13 large distinct spines	<i>Bathynomus</i>
	Pleotelson posterior margin with minute denticulation	<i>Palaega sensu lato</i>

The key is based on posterior exoskeleton parts, that is, pleon and pleotelson, as these are of greatest fossilization potential and are commonly preserved in isopod fossils.

have evidence for many features (present authors = diagnostic characters) included in the diagnosis for the type species, the shared anatomical similarity between it and the new species described below supports extension of the generic diagnosis. Implicitly therefore, the revised generic concept now rests with *B. tomhurleyi* and not the type species.

If a genus diagnosis is based on other than the type species, the generic concept may then belong to another taxon. The several characters stated by Wilson *et al.* (2011) that allow recognition of *Brunnaega* are as follows: smooth dorsal surfaces, elongate distally rounded coxae, elongate uropods with subtriangular endopods and a pleotelson lacking carina or marginal denticles. Most of these characters are widely distributed and sometimes polymorphic among cirolanid genera. *Brunnaega roeperi* Polz, 2005, the type species, differs on three of these four characters – the pleon dorsal surfaces are nodular, the coxae are posteriorly acute and the uropods are elongate and distally rounded (not subtriangular). In addition, the pleon morphology of *B. tomhurleyi* differs significantly from that of the type species. *Brunnaega roeperi* has a ‘short’ pleon with pleonite 5 having free lateral margins, not overlapped by pleonite 4; *Brunnaega tomhurleyi* has pleonite 5 laterally overlapped by pleonite 4 and has a ‘long’ pleon. Pleonite 5 morphology is consistent in cirolanid genera and distinguishes a major difference in the family, namely the division between the ‘Eurydicinae’ and ‘Cirolaninae + Conilerinae’ of Kensley and Schotte (1989).

Bowman (1975) gave a useful illustrated summary of pleon morphology (see also Bruce 1981, 1986; Brusca *et al.* 1995; Riseman and Brusca 2002). This difference in pleonite 5 morphology is of generic significance, and *Brunnaega tomhurleyi* needs to be assigned to another, possi-

bly new, genus. For all these reasons, the original descriptive data given by Polz (2005) should be used to identify the genus.

Stratigraphic range. *Brunnaega roeperi* was described from the late Kimmeridgian of Germany (Polz 2005). *Brunnaega tomhurleyi* from the latest middle to late Albian of Queensland, Australia (Wilson *et al.* 2011) is removed from the genus.

Genus PALAEGA Woodward, 1870

Type species. *Palaega carteri* Woodward, 1870, by monotypy.

Remarks. The taxonomy of the genus *Palaega* is complex. Concerning the possible synonymy with the genus *Bathynomus* A. Milne Edwards, 1879 reference is made to Polz *et al.* (2006, p. 4), who provided detailed account on this issue (see also Martin and Kuck 1990), and the ICZN ruling (Anonymous 1992; Opinion 1668).

Several authors have already emphasized the nature of *Palaega* as a ‘form genus’ representing a mixture of several independent genera or even families (Hessler 1969, R380; Feldmann and Goolaerts 2005, p. 1032; Feldmann and Rust 2006, p. 412). Hessler (1969) recognized two morphological groups within the genus based on the structure of the head region and the placement of the eyes. Feldmann and Goolaerts (2005) further developed this idea and recognized three distinct morphologies within *Palaega*, a point of view with which we agree. In our key (Table 1), we distinguished only *Palaega sensu* Woodward, 1870 and *Palaega sensu lato* as it is beyond the scope of present article to revise all the species of the genus *Palaega*. Feldmann and Rust (2006, p. 412)

provided a list of named species referred to *Palaega* together with their stratigraphic and geographic distribution, although they cast doubt on the generic assignment of a number of those species. Since then, three more species have been assigned to this genus (Karasawa *et al.* 1992, 2008; Polz *et al.* 2006).

The list published by Feldmann and Rust (2006) contains information about the morphology of pleotelson (and other features) when preserved and examined. The pleotelson posterior margin varies in the general shape from triangular through subquadrate to broadly rounded or semicircular. Moreover, some species of *Palaega* possess large spines on the posterior margin of pleotelson (e.g. *P. kakatahi* Feldmann and Rust, 2006), whereas others have a rather crenulated pleotelson posteriorly without distinct spines (e.g. *P. nusplingensis* Polz, Schweigert and Maich, 2006). In this respect, the terminology is not uniform and what is referred to as spination in Rathbun (1935) is crenulation in Polz *et al.* (2006). The number of posterior spines varies from 7 to more than 20 (*P. williamsonensis* Rathbun, 1935 has 24 minute spines); when a large number of small spines occurs this is better interpreted as crenulation or serration. Some species lack posterior spines. We suggest that species without spines on posterior margin of the pleotelson should not be considered as belonging to the genus *Palaega*, as this character was among the strongest morphological characteristic defined by Woodward (1870). On the basis of the type species, *P. carteri*, Woodward (1870), named an axial keel (or median ridge), plicae (or serrations) along the lateral borders and spines on the posterior margin as diagnostic to the genus. Woodward (1870) described the pleotelson of *P. carteri* as semicircular, but many other species do not fit this shape. As pointed out by Polz *et al.* (2006, p. 4), there are species of *Palaega*, which do not exhibit the characteristic features of the pleotelson attributed to the type species. While *Palaega* is generally accepted as belonging to the Cirolanidae, some species with prominently serrated or spinose pleotelson posterior margin (e.g. *P. carteri* and *P. kakatahi*) could equally be placed in the Aegidae, the pleon and pleotelson morphology being similar to extant species such as *Aega angustata* Whitledge, 1901 and *A. komai* Bruce, 1996 (see Bruce 2009).

Palaega sensu Woodward (1870) can be therefore characterized by semicircular pleotelson posterior margin, with a median dorsal ridge, serration along the lateral margins and spines on the posterior margin. Other morphologies should be considered as belonging to other genera. In this respect, a complete re-evaluation of the type material of all species currently referred to *Palaega* is strongly needed.

Stratigraphic range. The oldest representative of the genus is *P. suevica* Reiff, 1936 from the early Pliensbachian of Germany.

Palaega kessleri Reiff, 1936 from the same strata does not possess spines on the pleotelson; thus, its generic assignment is doubtful. Many Oligocene and Miocene species assigned to *Palaega* cannot be accommodated within *Palaega sensu* Woodward, 1870.

Genus PSEUDOPALAEGA Mezzalira and Martins-Neto, 1992

Type species. *Pseudopalaega granulifera* Mezzalira and Martins-Neto, 1992, by original designation.

Remarks. The genus was erected by Mezzalira and Martins-Neto (1992) to accommodate several species of Permian age from Brazil. Three species are known (Martins-Neto 2001). Mezzalira and Martins-Neto (1992, p. 52) stated that the genus can be diagnosed by the presence of a semicircular cephalon that is not completely surrounded by pereonite 1; dorsal eyes; elongate, oval body; seven similarly sized free pereonites and five slightly narrower free pleonites; and well developed coxae. According to Martins-Neto (2001, p. 239), the genus possesses a relatively faint median ridge on the pleotelson and is therefore similar to the genus *Palaega*. Such a difference is insufficient to distinguish it from other cymothoid genera. It should be noted that most cymothoids possess lateral eyes, whereas dorsal eyes are characteristic of, for example, serolids, some sphaeromatids and asellotans. It can be concluded that either the description by Mezzalira and Martins-Neto (1992) does not agree with rather poorly figured specimens of *Pseudopalaega* or that the genus is not related to the Cirolanidae. Mezzalira and Martins-Neto (1992) initially left the genus as *incerta sedis*; later Martins-Neto (2001) classified it within the family Cirolanidae. Poor preservation of this material with insufficient species descriptions calls for a revision of the genus to assess its familial status. If the dorsal position of eyes is confirmed, it should be removed from Cirolanidae (see diagnosis above). For this reason, we omitted this genus in the key (Table 1).

Stratigraphic range. Three species are known, *P. granulifera* Mezzalira and Martins-Neto, 1992, *P. microcelata* Mezzalira and Martins-Neto, 1992 and *P. iratiensis* Martins-Neto, 2001, all from the Permian of Brazil.

Genus CIROLANA Leach, 1818

Type species. *Cirolana cranchii* Leach, 1818, by monotypy.

Diagnosis. Cephalon reniform, distinctly narrower than pereonite 1, anterior margin evenly rounded or with small rostral point. Pereonite 1.5–1.8 as long as pereonite 2. Pleon 11–17 per cent total body length (usually 11–14 per cent); pleonite 1 often largely concealed by pereonite 7; pleonite 5 lateral margins encompassed by those of

pleonite 4. Pleotelson without median dorsal ridge, posterior margin without evident spines or deep serrations. Antennular peduncle article 3 longest. Antennal peduncle articles 4–5 longest. Frontal lamina flat, about twice as long as wide, clypeus sessile. Pereopods 1–3 with anterodistal margins of ischium and merus not produced. Uropodal peduncle posteriorly acute produced along mesial margin of endopod.

Remarks. When dealing with fossils, it is important not to make a familial or generic assignment on the basis of a single character. It is better to consider a set of characters, especially if only somites are preserved. Wieder and Feldmann (1992) argued that the combination of the characters as reniform shape of the cephalon and its impression beneath the first pereonite, the size and position of the eyes, the number, shape and proportions of free pereonites and pleonites, the broad shape of the pleotelson and the overall body shape can justify assignment to *Cirolana*. It should be noted that morphology of pleon, pleotelson and uropods may be generally similar between some cirolanid, such as *Cirolana* and *Natatolana* Bruce, 1981. Thus, the two genera may not be distinguishable on these characters. These are the most speciose cirolanid genera with 128 and 74 nominal extant taxa, respectively (Schotte *et al.* 2010). *Natatolana* in general has relatively broad posterior pereopods, which are often highly setose and have somewhat flattened proximal segments (Keable 2006), and also the robust setae tend to be more elongate and acute than in *Cirolana*. Both genera may present distally acute or rounded uropodal rami; in *Natatolana* the apices of the rami are defined by robust setae, whereas in *Cirolana* the apices may be bifid or sub-bifid, and the endopod ranges from acute to broadly rounded. The material presented herein has what appear to be ambulatory pereopods, with similar proportions to *Cirolana*, notably a more robust basis, indicating that *Cirolana* is more appropriate than *Natatolana*. The relatively short pleon (Figs 2, 3) with pleonite 1 largely concealed by pereonite 7 further supports placement in *Cirolana*.

Cirolana is one of a group of genera that have a similar somatic morphology but differ in mouthpart morphology. Genera similar to *Cirolana* are *Neocirolana* Hale, 1925, *Baharilana* Bruce and Svavarsson, 2003, and the monotypic freshwater genus *Saharolana* Monod, 1930. *Neocirolana* has distally narrowed mandibles, and typically, the head appears proportionally narrower than in *Cirolana*. *Baharilana* differs from *Cirolana* in pleopod, pereopod and some mouthpart morphology, the only somatic difference is that no species of *Baharilana* has any form of rostral point, while most species of *Cirolana* do have a rostral point. The distinction between *Cirolana* and *Saharolana* is not clear and is open to question. The broad head in the species described here again supports inclusion in *Cirolana*.

Stratigraphic range. *Cirolana* is known from several occurrences (for review see Feldmann 2009). The oldest species is *Cirolana enigma* Wieder and Feldmann, 1992 from the Lower Cretaceous of South Dakota (Wieder and Feldmann 1992). This study reports the first Miocene occurrence of the genus worldwide.

Cirolana feldmanni sp. nov.

Figures 2A–G, 3A–F, 4A–G, 5.

2011 ‘cirolanid isopods’ Hyžný and Schögl, p. 344.

Derivation of name. The epithet honours Prof. Rodney M. Feldmann (Kent State University, Ohio) who has contributed much to knowledge of the fossil Isopoda.

Holotype. SNM-Z 35102 (Fig. 2), a near-complete specimen with preserved exoskeleton parts and remains of appendages.

Paratypes. SNM-Z 24873–24875, 35103–35104 and 35529.

Additional material. KGP-MH CL001, a fragmentary specimen with well preserved pleonites.

Specimens were distributed within the studied section without any clear pattern. They exhibit a good state of preservation, although partially compressed and slightly deformed. In almost all specimens, original cuticle with distinct ornamentation is present. Nearly all specimens can be identified as apparent moults.

Diagnosis. Body lateral margins subparallel; rostral point minute or absent; pereonites 2–7 similar in form, lateral margins with prominent coxal plates, most prominent and acute on pereonite 7; pleonites similar in length and width; pleonite 1 concealed under pereonite 7 in dorsal view; pleonite 5 overlapped marginally by pleonite 4; pleotelson slightly wider than long, tapering to narrowly rounded posterior margin lacking obvious spines or notch; uropods ovoid in shape, longitudinally elongated, tapering proximally; uropodal endopod extending to but not beyond posterior margin of pleotelson.

Description. Body 1.2–1.6 times as long as greatest width, dorsal surfaces smooth. Supposed eyes sessile, moderately large. *Pereonite 1* and coxae 2–3 each with posteroventral angle rounded; coxae 5–7 with entire oblique carina, posteriorly acute; posterior margins of pereonites 5–7 smooth, except for row of tiny pits extending along posterior margin. *Pleon* with pleonite 1 largely concealed by pereonite 7 (Figs 3D–E, 4A–E); pleonites 3–5 posterior margin smooth; posterolateral angles of pleonite 2 forming acute point, not posteriorly produced; pleonite 3 with posterolateral margins not extending to posterior margin of pleonite 5, acute; not extending beyond posterior margin of pleonite 5, posterolateral margin of pleonite 4 acute; pleonite 5 with posterolateral angles overlapped by lateral margins of pleonite 4 (Figs 3D–F, 4A–E). *Pleotelson* 0.8 times as long as anterior width, dorsal surface without longitudinal carina; lateral margins convex, margins smooth, posterior margin evenly rounded, without median

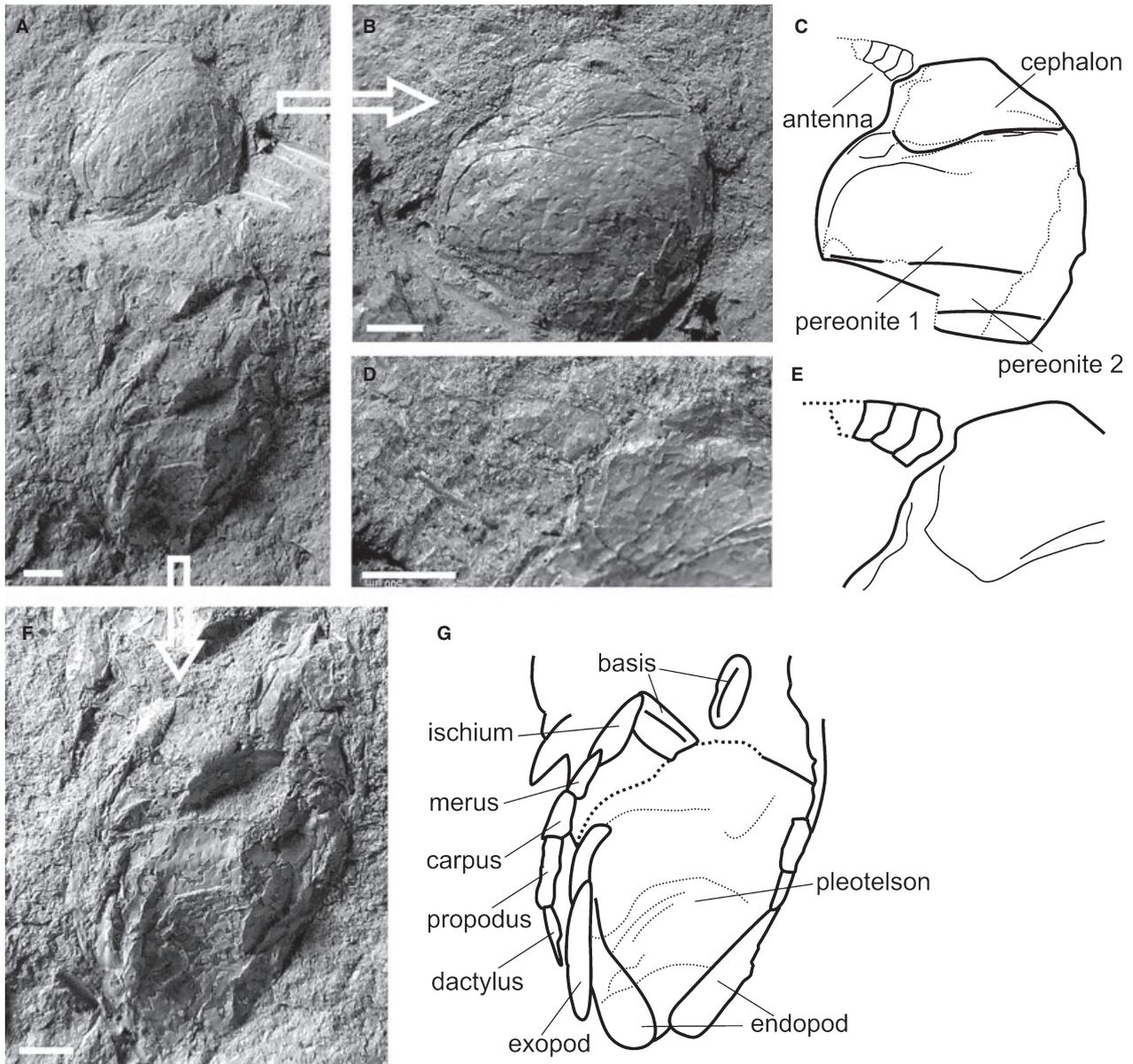


FIG. 2. *Cirolana feldmanni* sp. nov., SNM-Z 35102 (holotype). A, near-complete specimen. Note that posterior exoskeleton part is preserved in ventral aspect. B–C, head region and its interpretive drawing. D–E, close-up of the putative basal antennal segments. F–G, posterior exoskeleton part in ventral aspect and its interpretive drawing showing preserved pereopod 7. Scale bar represents 1 mm.

point (Figs 3D–F, 4A–C). *Pereopod 7* basis 2.0 times as long as greatest width, superior margin weakly convex; ischium 1.0 times as long as basis; 3.6 times as long as wide; carpus 0.6 as long as ischium, 1.4 times as long as wide; propodus 0.9 as long as ischium, 3.6 times as long as wide (Fig. 2F–G). *Uropod* peduncle posterior lobe about one-third as long as endopod (obscure); rami extending to pleotelson apex, apices narrowly rounded. *Endopod* apically not bifid; lateral margin weakly convex, without prominent excision; mesial margin weakly convex (Figs 3D–E, 4A–B). *Exopod* not extending to end of endopod, 3.6 times as long as greatest width, 0.8 as long as exopod, apically not bifid; lateral margin weakly convex; mesial margin sinuate, proximally concave (Figs 3D–E, 4A–B).

Body length estimated to be 1.3–2.0 cm.

Type locality. Cerová-Lieskové (north-eastern part of the Vienna Basin, Slovakia); Lakšárska Nová Ves Formation (late Karpatian, latest Burdigalian in the Mediterranean scale).

Discussion. *Cirolana feldmanni* sp. nov. differs from all currently known fossil species of *Cirolana* in having slender uropods and a narrowly rounded pleotelson apex. All fossil *Cirolana* species can be differentiated from each other on the basis of their pleotelson morphology. *Cirolana enigma* has a broad pleotelson that is wider than long and a

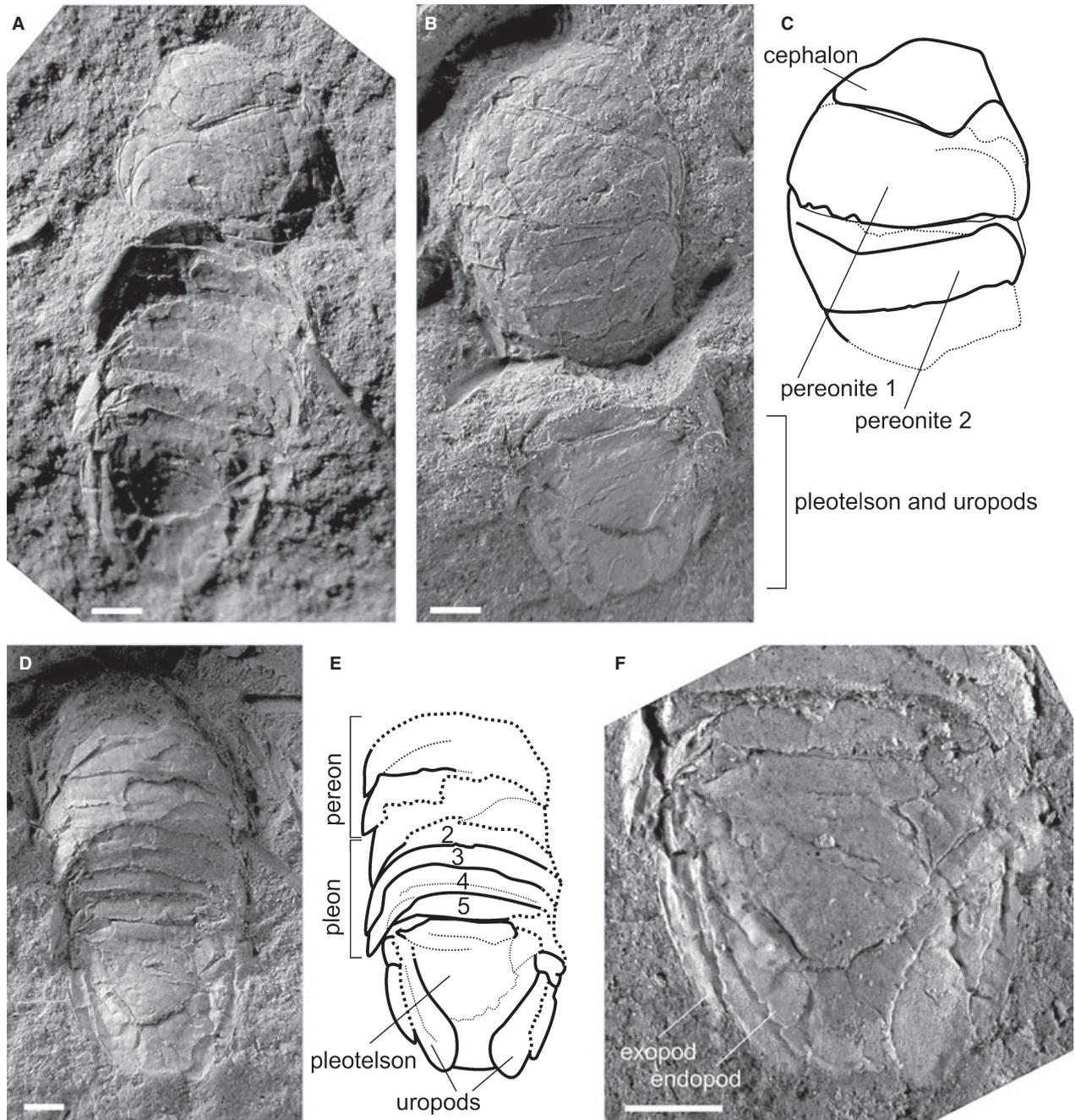


FIG. 3. *Cirolana feldmanni* sp. nov., SNM-Z 24873 (paratype). A–B, near-complete specimen. Anterior exoskeleton part is preserved as counterpart in A and as part in B, whereas posterior exoskeleton part is preserved *vice versa*. C, interpretive drawing of B. D–E, prepared posterior part with preserved pleotelson and uropods and its interpretive drawing. F, Detail of pleotelson and uropods. Scale bar represents 1 mm.

distinctly rounded posterior margin. *Cirolana fabianii* De Angeli and Rossi, 2006 from the lower Oligocene of Italy has a subtriangular pleotelson with convex lateral margins possessing two small spines on each side. *Cirolana makihiki* Feldmann, Schweitzer, Maxwell and Kelley, 2008 from the Pliocene of New Zealand has a small and triangular pleotelson. The pleotelson of *C. garassinoi* Feldmann, 2009 from

the Santonian of Lebanon is about as wide as long, and its posterior margin (Feldmann 2009, fig. 2A) is deeply indented and furthermore has broadly rounded uropod rami. The pleotelson of *Cirolana feldmanni* sp. nov. is longer than wide and the posterior margin is more acute, although not forming a distinct tip. There are additional character differences in the uropods. Uropods are preserved

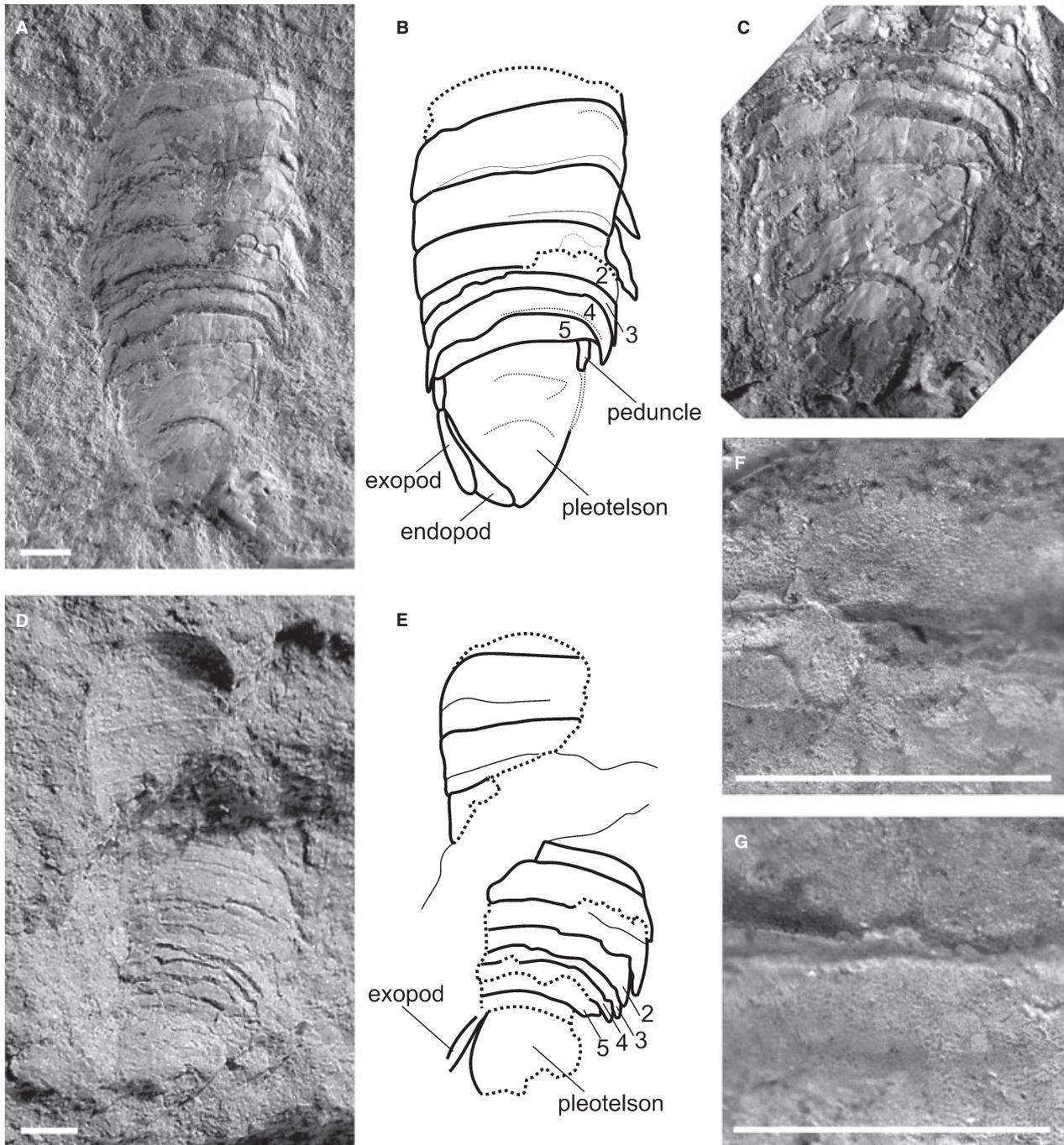


FIG. 4. *Cirolana feldmanni* sp. nov. A–B, posterior exoskeleton part and its interpretive drawing (paratype SNM-Z 24874). C, detail of pleotelson and uropods of A. D–E, fragmentary anterior and posterior exoskeleton parts preserved in different planes (paratype SNM-Z 35103). Note that anterior exoskeleton part is preserved as counterpart (imprint). F–G, close-up of preserved cuticle on pleonites of SNM-Z 24874. Scale bar represents 1 mm.

in *C. fabianii*, *C. garassinoi* and *C. feldmanni* sp. nov. In *C. fabianii*, they are ovoid in overall shape, and in *C. garassinoi*, they are broad with a distinctly triangular endopod. *Cirolana feldmanni* sp. nov. has relatively narrow, elongate uropods tapering proximally to a broadly rounded apex.

One specimen of *Cirolana feldmanni* has retained pereopods 7 (SNM-Z 35102). The basis is relatively broad with an evident carina present (Fig. 2F–G). Species of *Natatolana* may have a fine longitudinal carina on the lateral margin of the posterior pereopods, and this fine

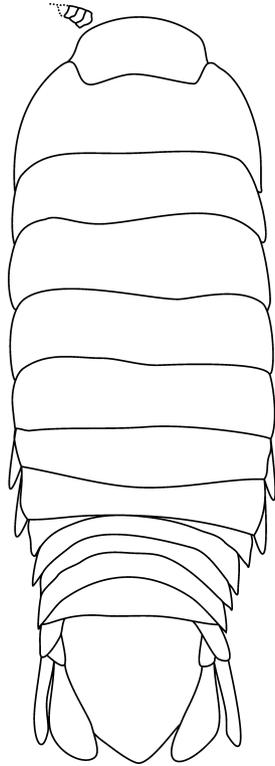


FIG. 5. *Cirolana feldmanni* sp. nov., reconstruction of the exoskeleton in dorsal aspect.

carina is generally well developed and centrally positioned (see Keable 2006), while in *Cirolana* it is absent (see Bruce 1986, 2004; Brusca *et al.* 1995). On balance, the position of the carina and relative width of the basis lead us to place this species into *Cirolana* rather than *Natatolana*.

REMARKS ON TAPHONOMY

Isopods characteristically exhibit biphasic moulting (e.g. Schöbl 1880; Tait 1917; Vernet and Charmantier-Daures 1994), in which the posterior part of the exoskeleton (pleon and posterior three pereonal somites) is always shed prior to the anterior half. The moult of the anterior part is followed within a few hours or even days, and then, it usually breaks up into small fragments that would be nearly impossible to interpret in the fossil record (Wieder and Feldmann 1992; Feldmann and Rust 2006; Polz *et al.* 2006). Most fossil isopods are therefore represented only by the posterior exoskeleton (e.g. Feldmann and Goolaerts 2005; Feldmann and Rust 2006; Polz *et al.* 2006; Feldmann *et al.* 2008; Hansen and Hansen 2010); only a few are based on the entire or near-entire preserved body (e.g. Bachmayer 1947; Tauber 1950; Feldmann *et al.* 1998; Polz *et al.* 2006; Feldmann 2009).

Most isopod specimens described herein exhibit characteristics of biphasic moulting. In three cases, only the posterior part is preserved: SNM-Z 24874 (Fig. 4A–C), SNM-Z 24875 and SNM-Z-35529. In another five specimens, SNM-Z 24873 (Fig. 3), SNM-Z 35102 (Fig. 2), SNM-Z 35103 (Fig. 4A–E), SNM-Z 35104 and KGP-MH CL001, both anterior and posterior parts are preserved in close proximity to each other. In all those specimens, the anterior part is upturned relative to the posterior part. Assuming that the posterior part was shed first, it can be concluded that, the anterior part was upturned after shedding, retaining its anterior–posterior orientation. We assume that the period between moulting of the posterior and anterior part had to be rather short (possibly minutes), as in all five specimens retaining both parts, they are preserved at the same place.

A good state of preservation of the original cuticle (Fig. 4F–G) in nearly all cases and preservation of the basal segments of antenna (antennal peduncle) (Fig. 2B–E) together with complete pereopod 7 (Fig. 2F–G) on the holotype specimen (SNM-Z 35102) favours the interpretation of rapid burial of the moults. Interestingly, as the anterior part of the moults did not break apart the presence of consequent physical disturbance after shedding, the exoskeletons can be excluded. The specimens come from various parts of the section within an interval of at least 2 m, suggesting an absence of stronger physical disturbance (e.g. bioturbation) after the sediment was deposited. Post-mortem transport or any other physical modification to the specimens can be excluded as virtually all faunal elements described from the section (Hyžný and Schlögl 2011; Schlögl *et al.* 2011; unpublished data of MH and JS) point to an autochthonous assemblage. The preservation of fragile parts in the associated decapod fauna (Hyžný and Schlögl 2011) supports this conclusion.

The interpretation of studied isopod specimens as moults seems to be most probable. Although the body may break in two pieces in similar way to that, resembling moults, it is rather unlikely that the arrangement of exoskeleton parts would be roughly the same in all specimens as presented herein. This and also the completeness of the specimens exclude the possibility of interpreting the specimens as remains from predation or scavenging.

PALAEOECOLOGICAL AND PALAEOBIOGEOGRAPHICAL IMPLICATIONS

Most cirolanid isopods are free-living predators or carnivorous scavengers (Brusca *et al.* 1995 and references therein; see also Brusca *et al.* 2007). Cirolanids are capable swimmers that also spend much time burrowed in sand, under rocks or in crevices; they can also be found

in any suitable refugium such as mussel beds, massed intertidal worm tubes, kelp holdfasts or burrows of other animals (Brusca *et al.* 1995).

Cirolanids most commonly inhabit shallow-water environments (continental rise to the intertidal) where they reach their greatest abundance. Cirolanids are also known from many other environments, such as from anchialine and freshwater caves, open freshwater (rarely) and oceanic deep-water habitats. The majority of species live at depths of <500 m (Brusca *et al.* 1995). The greatest documented diversity for the family is to be found in the south-western Pacific region bounded by eastern Australia, New Zealand northwards to New Caledonia and the Coral Sea, this region having 144 (36 per cent) of the 395 marine species. It is also known that cirolanids are highly diverse on coral reefs, and the true extent of tropical diversity remains to be documented.

Extant members of the genus *Cirolana* have worldwide distribution and are known predominantly from depths ranging from the intertidal zone to about 200 m, and there are very few deep-water species, with only five species extending beyond 500 m of depth, to a maximum depth of 1544 m. The majority of the 126 described extant *Cirolana* species (Schotte *et al.* 2010) are known from the Indo-Pacific Ocean with only one, *C. cranchii* Leach, 1818, known from the Mediterranean (Europe) (Brusca *et al.* 1995).

Cirolana feldmanni sp. nov. stems from a deep-water setting, which is characterized by bathyal molluscs (Harzhauser *et al.* 2011), rather deep-water decapods (Hyžný and Schlögl 2011) and bathyal sharks. Concerning the previously described *Cirolana* fossils, the environment of *C. fabianii* from the Oligocene of Italy (Perarolo) has been reconstructed as the shallow lagoon of the coral barrier (De Angeli, pers. comm. March 2011). *Cirolana makihiki* from the Pliocene of New Zealand comes from a shallow marine environment too (Feldmann *et al.* 2008, p. 45). Little is known about the environment and bathymetry of other fossil *Cirolana* species. Concerning *C. enigma* from the Cretaceous of South Dakota (USA), Wieder and Feldmann (1992, p. 961) stated: 'The uncertainty introduced by the unreliable collection information makes it difficult to determine the exact environment in which these isopods existed'. Something similar can be stated also for *C. garassinoi* from the Cretaceous of Lebanon, as there is a lack of sedimentological studies and no accompanying invertebrate fossils have been found in association with the only isopod specimen (A. Garassino, pers. comm. March 2011). Thus, we can conclude that *C. feldmanni* sp. nov. is the first report of unequivocal fossil deep-water *Cirolana*.

Low diversity of the genus *Cirolana* in today's Mediterranean compared to other regions (e.g. Indo-Pacific) could be a consequence of the Messinian salinity crisis

(Hsü *et al.* 1978; see also Harzhauser *et al.* 2007 and references therein). Today's Caribbean has also a relatively low diversity of isopods (Poore 2002 for Australia; Kensley and Schotte 1989 for the Caribbean; Schotte *et al.* 2010). *Cirolana feldmanni* sp. nov. documents presence of the genus in the Paratethyan realm, so it can be concluded that *Cirolana* also inhabited the Mediterranean as there were sea connections between these two palaeobiogeographic areas during the Miocene (Rögl 1998, 1999; Harzhauser *et al.* 2007).

CONCLUSIONS

From an appraisal of the cirolanid fossil record presented herein, several conclusions can be drawn:

1. *Palaega sensu* Woodward (1870) is characterized by semicircular pleotelson posterior margin, with a median dorsal ridge, serration along the lateral margins and spines on the posterior margin. Other morphologies should be considered as belonging to other genera. For instance, several fossil species attributed to extinct genus *Palaega* demonstratively possess pleotelson characters identical to those of extant *Bathynomus*. *Bathynomus* does not possess serration along the lateral margins and therefore should not be treated as junior subjective synonym of *Palaega*. In this respect, a complete re-evaluation of the type material of all species currently referred to *Palaega* is strongly needed.
2. *Brunnaega tomhurleyi* from the Early Cretaceous of Australia differs in pleonite 5 morphology (which is considered of generic significance) from the type species of the genus *B. roeperi* from the Late Jurassic of Germany. As a result, *B. tomhurleyi* needs to be assigned to another, possibly new, genus.
3. The familial status of *Pseudopalaega* from the Permian of Brazil is obscure. If the dorsal position of eyes is confirmed as stated in its description, it should be removed from Cirolanidae.

From the fossil isopod material described herein, the following conclusions can be drawn.

1. *Cirolana feldmanni* sp. nov. from the early Miocene of the Slovak part of the Vienna Basin represents only the fifth fossil *Cirolana* species known to date and one of few with preserved appendages. It represents the first record of cirolanid isopod crustacean from the Neogene of the Vienna Basin.
2. The material exhibits preservation suggesting biphasic moulting. The mode of preservation suggests rather short time between shedding the posterior and anterior parts of the exoskeleton instead of hours or even days known in extant taxa so far. We presume that preservation of moults was secured with rapid burial

and no subsequent transport or physical disturbance and therefore can be stated as *in situ* preservation.

3. The material stems from deep-water settings as suggested from accompanied fauna. As a conclusion, *C. feldmanni* sp. nov. is considered herein to be a first report of unequivocal fossil deep-water *Cirolana*.

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NOTE ADDED IN PROOF

During processing of the present manuscript, an additional extinct species of *Cirolana* has been identified. Roger (1946) introduced the name *Ibacus cottreaui* Roger, 1946 for what he interpreted as a scyllarid decapod from the Santonian of Lebanon. The material has recently been reassigned to *Cirolana* by Feldmann and Charbonnier (2011). Although *Cirolana cottreaui* stems from the same locality that has also yielded *C. garassinoi*, these taxa differ in a number of characters, as discussed by Feldmann and Charbonnier (2011). *Cirolana cottreaui* differs from *Cirolana feldmanni* sp. nov. in possessing large eyes that occupy almost the entire width of the cephalon and in having a different shape of the pleotelson, more reminiscent of *C. garassinoi*.

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