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Ivana Karanovic^a & William F. Humphreys^{bcd}

^a Department of Life Science, Hanyang University, Seoul, South Korea, 133-791 & Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, 7001, Australia

^b Western Australian Museum, Collections and Research, 49 Kew Street, Welshpool, WA, 6106, Australia

^c School of Earth and Environmental Sciences, The University of Adelaide, South Australia 5005

^d School of Animal Biology, University of Western Australia, Nedlands, Western Australia, Australia

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Research Article

Phylogeny and diversity of Timiriaseviinae ostracods (Podocopida, Cytheroidea) with description of one new species from arid Western Australia

IVANA KARANOVIC¹ & WILLIAM F. HUMPHREYS^{2,3,4}

¹Department of Life Science, Hanyang University, Seoul, South Korea, 133–791 & Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Tasmania, 7001, Australia

²Western Australian Museum, Collections and Research, 49 Kew Street, Welshpool, WA, 6106, Australia

³School of Earth and Environmental Sciences, The University of Adelaide, South Australia 5005

⁴School of Animal Biology, University of Western Australia, Nedlands, Western Australia, Australia

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Gomphodella De Deckker, 1981 belongs to the subfamily Timiriaseviinae, and it inhabits almost exclusively subterranean waters of Western Australia. We describe the ninth species of the genus, *G. alexanderi* sp. nov., from bore-holes in the Pilbara region. The species is closely related to *G. yandii* Karanovic, 2009 and *G. quasihirsuta* Karanovic, 2009, but can be distinguished by its shell morphology, appearance of the hemipenis, and chaetotaxy of the antenna. We also report on *G. yandii* and *G. cf. martensi* Karanovic, 2009, collected sympatrically with the new species, indicating some new characters not mentioned in the original descriptions. We show for the first time that *Gomphodella* has an inverse lophodont hinge, instead of a lophodont one as previously believed. The significance of the hinge structure, sulci, and other shell characters in the systematics of Timiriaseviinae are discussed. In addition, the posterior extension on the female body, the so-called ‘forked organ’, is here reported for the first time in the genus *Gomphodella*. Because these characters provide a new insight into the phylogenetic relationships of Timiriaseviinae we performed two cladistic analyses: one including only nine genera with living representatives, the other including 17 genera. They resulted in one and 23 equally parsimonious trees respectively. Inclusion of the fossil taxa significantly changes the tree topology, but on both trees the Gondwanan lineage, *Cytheridella* Daday, 1905/*Gomphocythere* Sars, 1924/*Gomphodella* is strongly supported, as well as a close connection between the South American semi-terrestrial and some fossil genera. Another well-supported clade is formed by the genera *Kovalevskiella* Klein, 1963, *Frambocythere* Colin, 1980 and *Rosacythere* Colin, 1980. Maps of distribution of Recent genera and geological age of Timiriaseviinae are also presented here.

<http://zoobank.org/urn:lsid:zoobank.org:pub:E3041FDD-7233-4733-841C-98549108FE61>

Key words: Australia, cladistics, fossil ostracods, Limnocytheridae, subterranean waters, systematics

Introduction

Timiriaseviinae is the most adaptable non-marine subfamily of the superfamily Cytheroidea, although the superfamily itself is not very successful in non-marine ecosystems in comparison to other ostracods. Today, there are around 2000 Recent non-marine ostracods described (Karanovic, 2012), and they are divided into three main superfamilies: Cypridoidea, Darwinuloidea and Cytheroidea. Whereas Darwinuloidea are exclusively freshwater organisms, of the other two Cytheroidea is by far more

successful in marine environments and is much less diverse in fresh water than Cypridoidea. Cytheroidea has only about 400 species in continental waters, compared with more than 4000 in the sea (Horne *et al.*, 2002). Of these 400 species about 140 belong to the family Limnocytheridae (which includes Timiriaseviinae), and the rest to the families Cytherideidae, Entocytheridae, Kliellidae, Leptocytheridae and Loxoconchidae. Today, they inhabit a different range of non-marine habitats (Table 1). Ancient lakes are generally known to hold 25% of the entire freshwater ostracod diversity (Martens *et al.*, 2008), but in the case of cytherids, the percentage is much higher (Table 1). While Cytherideidae, Leptocytheridae and Loxoconchidae are much more diverse in marine waters, the

Correspondence to: Ivana Karanovic. E-mail: ivana.karanovic@utas.edu.au

Table 1. Number of living species in cytherid families in different freshwater ecosystems (some species inhabit multiple ecosystems)

Family	Ancient lakes	Subterranean waters	Other lakes and freshwater bodies	Semi-terrestrial	Commensal on freshwater crustaceans
Cytherideidae	71	—	2	—	—
Enthocytheridae	—	—	—	—	200
Kliellidae	—	—	2	—	—
Leptocytheridae	3	—	4	—	—
Limnocytheridae	32	14	84	7	—
Loxococonchidae	—	2	4	—	—
TOTAL	106	16	96	7	200
Grand total			425		

other three are distributed almost exclusively in fresh water, with Limnocytheridae occasionally found in brackish waters.

Limnocytheridae is by far the most successful of the six non-marine cytheroid families. It lives in all types of freshwater ecosystems, and it is the only one with several representatives in semi-terrestrial habitats, such as leaf litter and bromeliad cups (Danielopol, 1975; Pinto *et al.*, 2008). It is divided in two subfamilies: Limnocytherinae and Timiriaseviinae. Timiriaseviinae is more ecologically diverse than Limnocytherinae and it has 51 living species in nine genera: *Afrocythere* Klie, 1935, *Cytheridella* Daday, 1905, and *Metacypris* Brady & Roberston, 1870 live mostly in open freshwater bodies; *Gomphocythere* Sars, 1924 is today almost exclusively found in the African Rift Lakes, with a couple of exceptions known from other lake-type ecosystems; *Dolekiella* Gidó, Artheau, Colin, Danielopol & Marmonier, 2007, *Gomphodella* De Deckker, 1981, and *Kovalevskiella* Klein, 1963 are subterranean taxa (with only one *Gomphodella* species found in surface waters, see Karanovic, 2006); while *Elpidium* Müller, 1880 and *Intrepidocythere* Pinto, Rocha & Martens, 2008 are found in semi-terrestrial environments. Until Martens (1995) showed their phylogenetic relationship, it was thought that *Cytheridella*, *Gomphocythere* and *Gomphodella* did not belong to the subfamily Timiriaseviinae (see Colin & Danielopol, 1980), but rather to the tribe Cytheridellini of the subfamily Limnocytherinae (Danielopol *et al.*, 1990).

Timiriaseviinae are distinguished by the swollen shell shape which is due to the brooding chamber developed in the posterior part of the female carapace. Park & Martens (2001) cite the brooding as one of the factors affecting the success of this lineage in Lake Tanganyika. Another shell character which is present in almost all genera is a dorso-ventral sulcus. It gives the shell a medially constricted appearance when seen from dorsal view, and it clearly marks the start of the brooding pouch in females. The sulcus can be a 'true' one, clearly visible from the inside of the shell, or 'false' (or pseudosulcus, Colin *et al.*, 2000) when it is not reflected on the inside of the shell. Timiriaseviinae have three different hinge types:

adont, lophodont and inverse lophodont. The lophodont hinge is probably a plesiomorphic character, based on the result of the 18S analysis of 16 cytheroid families (Yamaguchi, 2003), and several hinge types evolved from it.

The oldest fossil record attributed to this subfamily dates back from the Late Triassic (Colin & Carbonel, 1996; Gidó *et al.*, 2007) and belongs to the genus *Timiriasevia* Mandelstam, 1947. Beside *Timiriasevia* another eight exclusively fossil genera have been assigned to Timiriaseviinae: *Abrotocythere* Zhao, 1987, *Frambocythere* Colin, 1980, *Progomphocythere* McKenzie, Engelbresten, Archer & Price, 2004, *Rosacythere* Colin, 1980, *Sinometacypris* Yu, 1978, *Sinuocythere* Colin, Cabral, Dépêche & Mette, 2000, *Theriosynoecum* Branson, 1936 and *Vecticypris* Keen, 1972. More than 400 fossil species of Timiriaseviinae have been named so far (see lists in Kempf, 1980, 1997). With the exception of *Dolekiella*, *Gomphodella*, *Elpidium* and *Intrepidocythere*, other Recent genera also have some fossil record. The ecology of the fossil genera was largely the same as today, with the exception of *Timiriasevia* which could have been found in marine environments (Colin & Danielopol, 1980). According to Gidó *et al.* (2007) it is possible that *Abrotocythere* even inhabited caves.

Until now, no fossilized soft parts of any Timiriaseviinae have been described, and we can only rely on what can be observed in the living species. Based on this, it can be concluded that there is very little variability within species and that genera are well-defined and very conservative. Palaeontologists face a number of difficulties in the taxonomy of the group. The most obvious one is that the shell shape and ornamentation of Recent genera can be very variable. *Gomphodella* is a good example of how ornamentation can strongly vary within one genus of Timiriaseviinae with the shell of some species being almost smooth while others are strongly ornamented with deep and shallow pits, etc. (Karanovic, 2006, 2009). Similarly with *Gomphocythere* although there are no smooth shells and often strong protuberances occur especially amongst the Lake Tanganyika species flock (see Park & Martens, 2001). On the other hand, all living *Kovalevskiella* have the same, rosette type of ornamentation,

Cytheridella has more or less developed pits, *Elpidium* and *Metacypris* species are smooth to lightly pitted (see Colin & Danielopol, 1980). Amongst exclusively fossil genera, *Theriosynoecum* seems to have the most variable shell ornamentation, and some species have prominent lateral protuberances (see Pinto & Sanguinetti, 1962) like *Gomphocythere*. *Rosacythere* also shows a great variability, from smooth shells to ‘raspberry-type’ ornamentation (see Colin & Carbonel, 1996) and clear fossae. Colin & Carbonel (1996) consider raspberry-type shell ornamentation as ancestral to rosette-type, found in most *Frambocythere* and *Kovalevskiella*. Although the hinge type does not seem to vary amongst the Recent species of one genus, often fossil species with different hinge types have been assigned to the same genus (see discussion in this paper).

There have been several attempts to resolve the phylogenetic relationships of Timiriaseviinae using modern methods such as cladistics. Park *et al.* (2002) tested the phylogenetic relationship amongst the Lake Tanganyika *Gomphocythere* and found that the shell characters are far more homoplastic than the soft parts characters. Although not all branches were resolved, the authors were able to define several small lineages within the lake. Gidó *et al.* (2007) tested phylogenetic relationships between nine genera (they excluded *Afrocythere*, *Gomphocythere*, *Gomphodella*, *Elpidium*, *Progomphocythere*, *Sinometacypris* and *Theriosynoecum*) using 14 characters of the shell. The single tree they presented clearly indicates two main lineages, one supporting the close relationships between *Kovalevskiella*, *Frambocythere* and *Rosacythere*, and of their newly described genus *Dolekiella* and *Abrotocythere*. The other clade supports a close relationship between *Metacypris* and other fossil genera included in the analysis. Savatnalinon *et al.* (2008) tested phylogenetic relationships amongst Recent genera, each genus represented with one or two species. The result of their analysis supported a close relationship between *Afrocythere*, *Gomphocythere* and *Cytheridella*. A previously postulated (Colin & Danielopol, 1980) close relationship between *Afrocythere* and *Elpidium* was not supported, while the position of *Gomphodella* remained questionable. Finally, Karanovic (2009) performed a cladistic analysis of all described living Timiriaseviinae using mostly characters of soft parts. The tree presented in that paper has two major clades, one comprising only *Gomphocythere*. Karanovic (2009) also performed a cladistic analysis of the genus *Gomphodella*, but this tree was largely unresolved.

Gomphodella was originally monospecific, with *Gomphodella maia* De Deckker, 1981 distributed in south and south-west Australia. Seven species belonging to *Gomphodella* have been described from arid Western Australia (Karanovic, 2006, 2009) together with a high diversity of Candoninae (see Karanovic, 2007). In the present paper we describe another species collected from the subterranean waters of the Pilbara region. Study of

the details of its shell and soft parts revealed some interesting characters previously overlooked, or misinterpreted both in the original description (De Deckker, 1981) and subsequently (Karanovic, 2006, 2009). These characters shed a new light on the relationships between *Gomphodella* and other living and fossil genera. They also raise the question of how to use some shell characters in ostracod palaeontology. We here discuss this and perform two cladistic analyses, one comprising only the Recent genera and another including the fossil ones, in order to assess affinities between living and fossil Timiriaseviinae.

Materials and methods

Collecting methods

Sampling of groundwater sites through bores followed EPA Guidance Statements 54 and 54a (EPA 2003, 2007). Modified weighted plankton nets of 70 μm mesh with mouth diameters of 50 mm or 100 mm were hauled through the full length of the water column multiple times and also after gently agitating the bottom of the bore. Samples were sorted under a dissecting microscope (Olympus SZ40 and SZ61, magnification up to 40 \times) in the field and preserved in 100% ethanol.

Taxonomic methods

Specimens were dissected and mounted on microscope glass slides in CS-10 medium. The dissected appendages were then covered with a coverslip and the valves of each specimen were transferred to a micropalaeontological slide. The dissection was done under a Leica L2 stereoscopic microscope, and the appendages were observed under a Leica DM 2500 compound microscope equipped with N-Plan objectives. The line drawings were prepared with the aid of the drawing tube attachment. Scanning Electron Micrographs (SEM) were taken with a Hitachi S-4700 scanning electron microscope at Eulji University (Seoul).

The examined material is deposited at the Western Australian Museum (WAM), Perth. Abbreviations used in text and figures: A1, antennula; A2, antenna; UR, uropodal ramus; H, height; L, length; LV, left valve; Md, mandible; Mx, maxillula; RV, right valve; L5, L6, L7, first, second and third thoracopods; W, width.

Cladistic methods

Two analyses of the subfamily Timiriaseviinae based on 19 morphological characters were performed; one with only nine Recent Timiriaseviinae genera and the other with 17 genera using an heuristic search. The matrix (Appendix 1, see online supplemental material, which is available from the article’s Taylor & Francis Online page

at <http://dx.doi.org/10.1080/14772000.2014.882870>) was created using WinClada, version 1.00.08 (Nixon, 2002) and then analysed using NONA, version 2 (Goloboff, 1999). All characters were equally weighted in both analyses. In both analyses the fossil genus *Sinometacypis* Yu, 1978 was excluded because of an insufficient description. *Limnocythere* Brady, 1867 (subfamily Limnocytherinae) was used as an outgroup taxon.

The list of characters used in the analysis were: 0. Brood chamber in females: absent (0), present (1); 1. Hinge: adont (0), lophodont (1), inverse lophodont (2); 2. Dorso-ventral sulcus: absent (0), present (1); 3. Additional anterior sulcus: absent (0), present (1); 4. Pseudo-sulcus: absent (0); present (1); 5. Sieve pores: absent (0), reduced (1), present (2); 6. Surface of the shell: mostly smooth, or poorly ornamented (0); mostly harshly ornamented (1); 7. Ventral ridges on the shell: absent (0), present (1); 8. Rosette/Raspberry type of ornamentation: absent (0), present (1); 9. Shell in lateral outline: more or less elliptical (0), more globular to angular (1); 10. Vento-lateral expansion (alar prolongation): absent (0), present (1); 11. Lateral alae or tubercles: absent (0), present (1); 12. Seta on the second segment of A1: apically positioned (0), medially positioned (1), missing (2); 13. Md-palp: with clearly divided segments (0); with partly fused segment (1), with completely fused segments, except the terminal (2); 14. Penultimate segment of Md-palp: normal (0), dilated (1); 15. Mx1-palp: with clearly separated segments (0), with segments fused but still distinguishable (1), no remnant of the second segment remaining (2); 16. Extension on the distal lobe of hemipenis: absent (0), present (1); 17. Distal lobe of the hemipenis: wide (0), elongated (1); 18. Forked organ: absent (0), present (1).

Results

Order Podocopida Sars, 1899

Superfamily Cytheroidea Baird, 1850

Family Limnocytheridae Klie, 1938

Subfamily Timiriaseviinae Mandelstam, 1960

Genus *Gomphodella* De Deckker, 1981

Amended diagnosis (modified after Karanovic, 2006). Hinge inverse lophodont. Surface often harshly ornamented. Sieve pores present. Sexual dimorphism pronounced, with females having posteriorly enlarged carapace with brooding pouch. A1 5- or 6-segmented, no seta on second segment. A2 with three distal claws. Md with all segments separated, and with setae on last two segments transformed into enlarged claws. Mx1 palp with second segment fused with first. No sexual dimorphism in thoracopods. Female with forked organ. Hemipenis with trunk-like extension on distal lobe.

Gomphodella alexanderi sp. nov.

(Figs 1–5)

HOLOTYPE. male (dissected on one slide – WAM C51867).

ALLOTYPE. female (dissected on one slide – WAM C51868).

PARATYPES. male (in alcohol – WAM C51869), one RV of a female (on SEM stub).

TYPE LOCALITY. Australia, Western Australia, Pilbara region, 85.5 km NW of Newman, stygofauna haul net, borehole Mar01-0611-02, 22°46'50''S, 119°10'47''E, 23 June 2011, collector J. Alexander (BES: 17009).

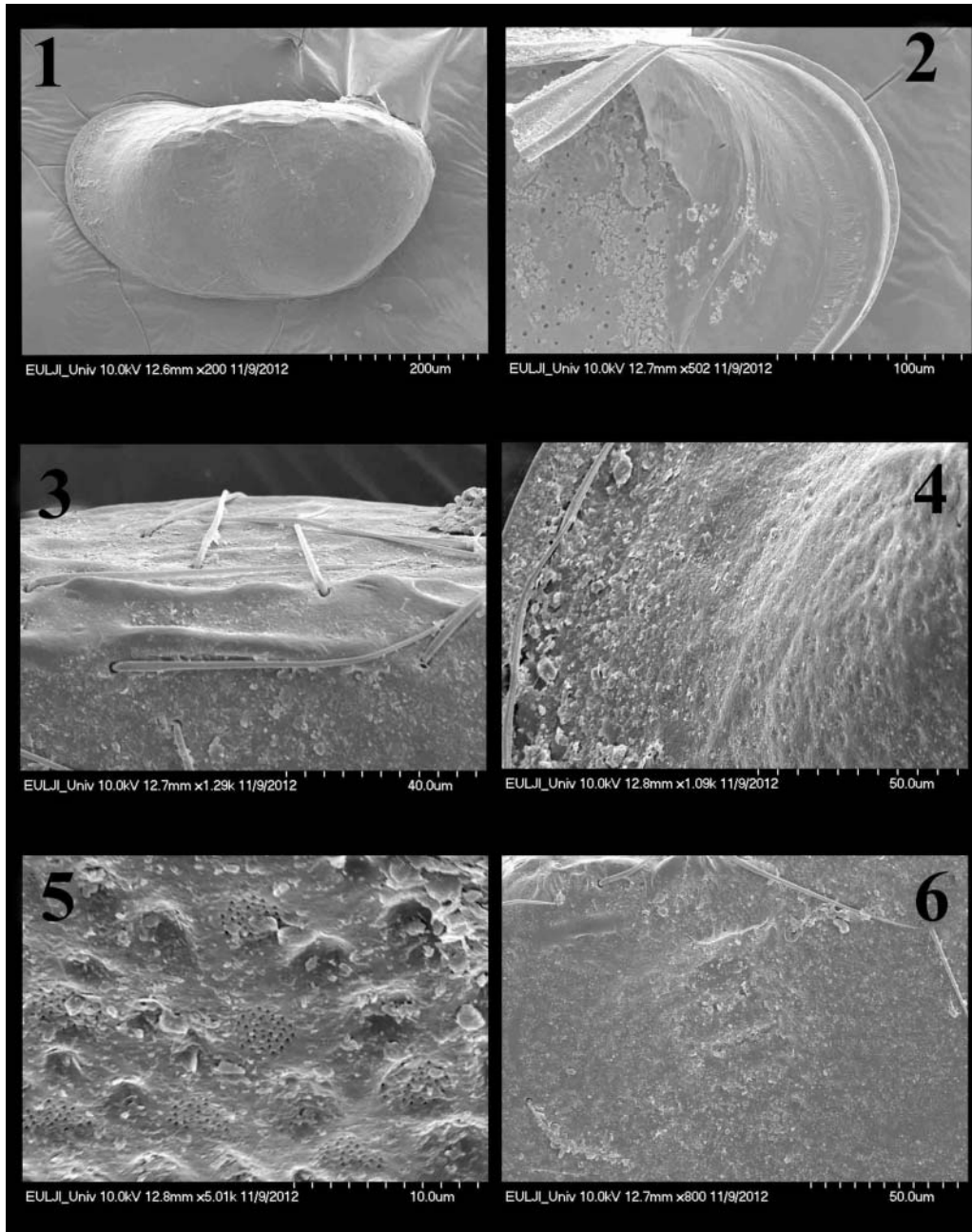
ADDITIONAL MATERIAL. One male (dissected on one slide – WAM C51870), 1 female (dissected on one slide – WAM C51871), from Australia, Western Australia, Pilbara region, 85.5 km NW of Newman, stygofauna haul net, borehole Marillana01–504, 22°46'50''S, 119°10'47''E, 23 August 2011, collector J. Alexander (BES: 17001); one juvenile (in alcohol – WAM C51872), from Australia, Western Australia, Pilbara region, 75 km NW of Newman, stygofauna haul net, borehole YMCCA-502, 22°46'22''S, 119°12'30''E, 24 August 2011, collector J. Alexander (BES: 17007).

ETYMOLOGY. The species is named after Mr Jason Alexander from the BIOTA Environmental Sciences Company Pty Ltd., who collected the material. The name is to be treated as a noun in the genitive singular.

DIAGNOSIS. Carapace with brooding chamber present (Fig. 1). Marginal pore canals straight and relatively dense anteriorly (Fig. 2). Ventral margin with unequally long longitudinal ridges (Fig. 3). Surface covered with very shallow pits (Fig. 4) and small bumps (Fig. 5). Sieve pores present (Fig. 5). Adductor muscle scar with vertical row of four scars (Fig. 6). Two types of surface setae present: one shorter and exiting from hemmed-like area, and other longer and stiff, exiting from normal pore-holes (Fig. 7) Hinge inverse lophodont (Figs 8–10) with medial bar present on the RV and negative parts anteriorly and posteriorly. LV with a medial groove, and poorly developed cardinal and caudal teeth. A1 clearly 6-segmented. One long, postero-medial seta present on second segment of A2. Md and Mx1 typical for the genus. L5 and L6 without setae on second segment. Hemipenis with proximal (basal) part of distal lobe subdivided in two long triangular processes. UR with two hirsute lobes. FO organ present.

Description

MALE. Carapace almost rectangular in lateral view (Fig. 11). L = 0.43 mm. Dorsal margin very slightly curved and gently sloping towards posterior end. Anterior and posterior margins rounded, posterior slightly narrower than anterior one. Flange wide on the posterior end. Anteriorly selvage wide. Greatest H situated frontally and

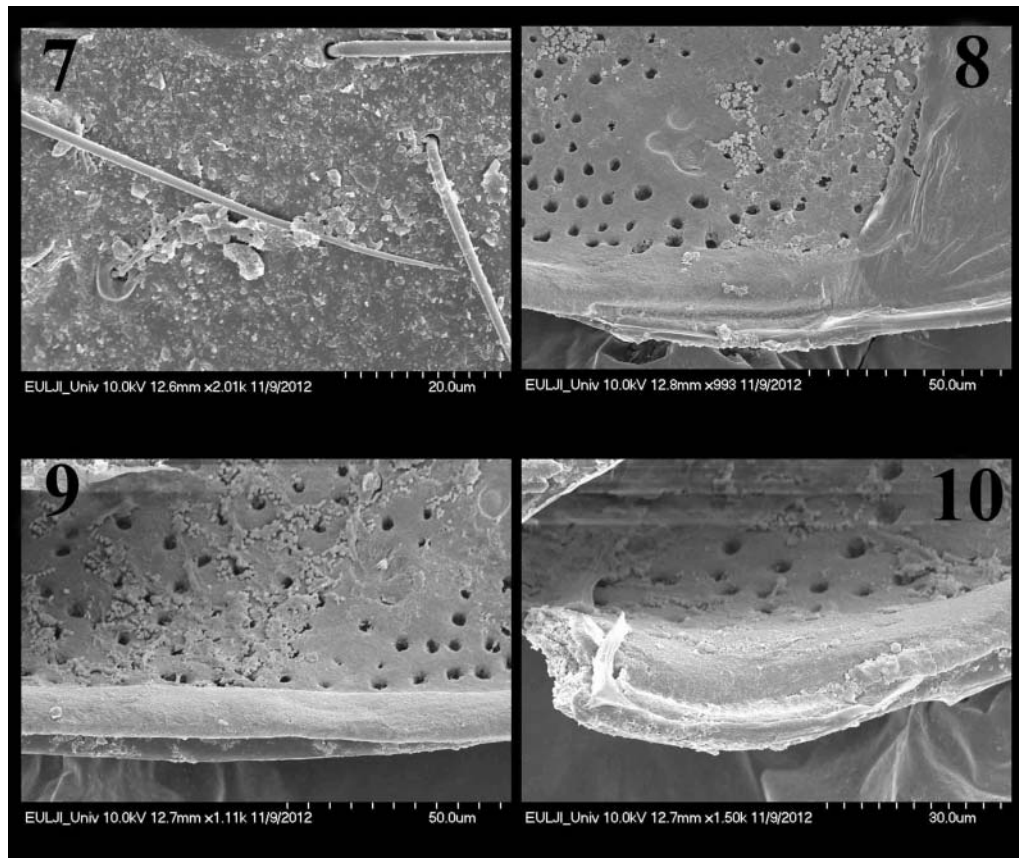


Figs 1–6. *Gomphodella alexanderi* sp. nov. SEM photographs. 1, 3–6: paratype female; 2: allotype female: 1: RV, lateral view from the outside; 2: RV, inside view of the anterior margin; 3: RV, part of the ventro-lateral margin, outside view; 4: RV, part of the anterior margin, outside view; 5: details of the surface with sieve-pore canals; 6: muscular scar imprints.

equalling 58% of L. Inner calcified lamella narrow. In dorsal view (Fig. 14) anterior end cuneiform and protruding, posterior end rounded. Generally, shell ball-like in dorsal view. Greatest width situated around middle and equalling 70% of L. Dorsally and ventrally, LV overlaps RV. Ventral surface covered with few unequally long longitudinal ridges. Surface of the carapace roughly ornamented but without any prominent pits, only small bumps. Sieve pore canals present. Some patchy

colouration present on the carapace. Surface also covered with long stiff setae. Two types of surface setae present: one shorter and exiting from hemmed-like area; other exiting from normal pore-holes.

A1: 6-segmented (Fig. 18), each segment clearly separated from neighbouring ones. First and second segments without any seta. Second segment with fringe of hair-like. Third segment with one serrulate seta, not reaching distal end of fifth segment. Fourth segment with two short



Figs 7–10. *Gomphodella alexanderi* sp. nov. SEM photographs. 7: paratype female; 8–10: allotype female: 7: detail of the surface showing two types of setae; 8: RV, anterior part of the hinge; 9: medial part of the hinge; 10: posterior part of the hinge.

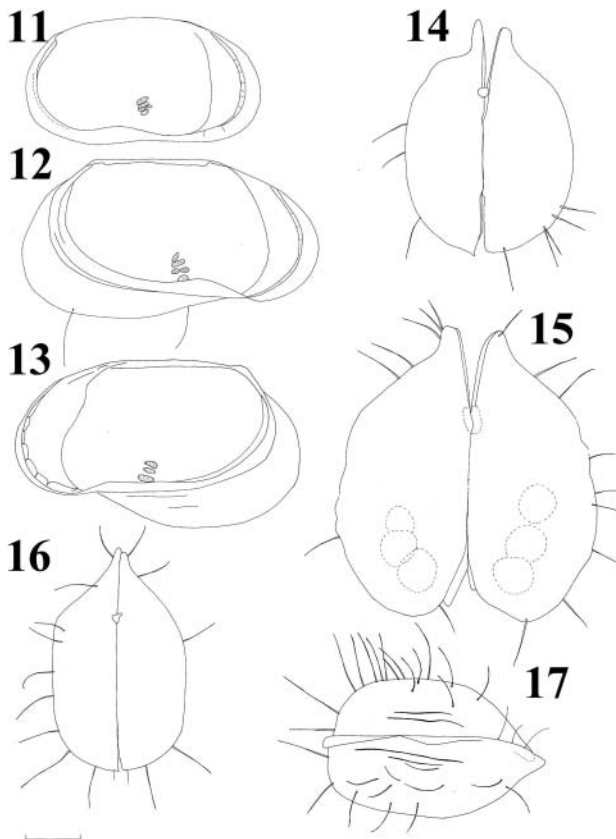
serrulate setae, both slightly exceeding distal end of penultimate segment. Fifth segment with three anterior setae, one serrulate (and being the shortest of the three) and two apparently smooth setae; one of the smooth setae slightly longer than the serrulate seta of the same segment, other smooth seta at least two times longer and exceeding distal end of terminal segment. Fifth segment posteriorly with one seta, serrulate around middle and almost as long as, smooth seta situated anteriorly. Terminal segment with total of four setae: one representing aesthetasc, and proximally fused with one smooth setae, which is longer than aesthetasc. Fusion very short. Other two setae on terminal segment, both apparently smooth, one situated more anteriorly and shorter than other situated more centrally. Length ratio between five segments: 3.3 : 1.7 : 1 : 1.5 : 3.3.

A2: 4-segmented (Fig. 23). First segment bare. Second segment short and with one posteriorly situated serrulate seta (reaching middle of following segment). Same segment with tufts of hair-like setulae. Third segment long proximally with tufts of setulae. Two (or one) setae situated around middle of third segment posteriorly, one normal smooth seta not reaching distal margin of third segment, other aesthetasc and just reaching distal margin. Third segment postero-distally with one plump, serrulate

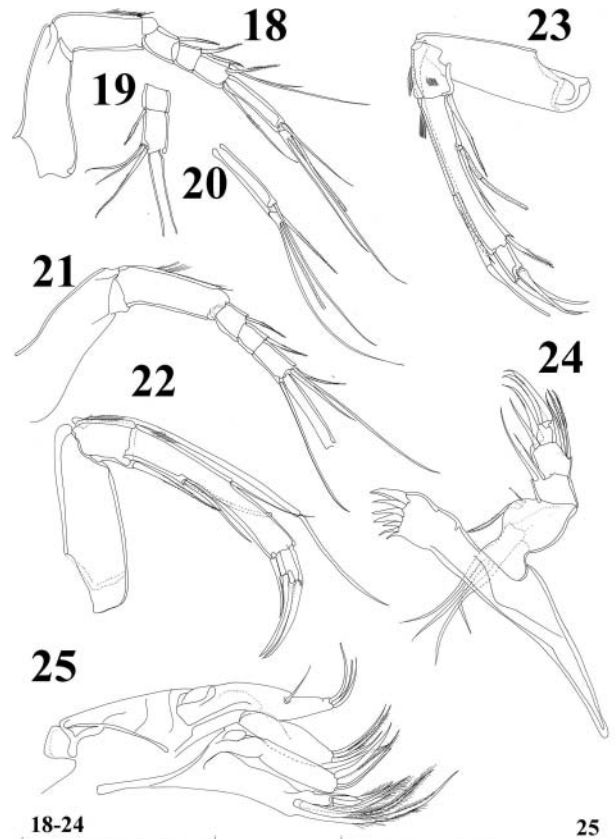
seta, which reaching first one third of terminal claws. Finally, third segment with smooth and thin seta situated posteriorly, below middle L of the segment and slightly exceeding distal margin of the segment. Terminal segment short and with three curved, slender claws, all equally long. Exopod rod-like (exit of excretory gland), with apparently two ‘segments’: first long and reaching middle of terminal segment, second short and reaching until middle of distal claws. Length ratio between second, third and fourth segments equalling: 1 : 4.5 : 1.

MXL: Vibratory plate with one recurved seta. Palp with not well-defined segment (Fig. 25). Proximal part longer than distal. Palp with three long pappose setae situated laterally on first segment. Second segment with three pappose setae distally, and one short, smooth seta medially. All endites on Mx1 long, and each carrying 3–4 strong setae, some being serrulate, some smooth. The shortest endite with one smooth seta situated medially.

MD: Palp 4-segmented (Fig. 24). First segment with two setae internally on the appendage, one very short and smooth, other longer and serrulate. Second segment with two smooth setae situated internally, one shorter than the other. Following segment with three equally long, serrulate setae externally, and two setae internally; one of the



Figs 11–17. *Gomphodella alexanderi* sp. nov. 11 & 14: holotype male; 12, 13 & 15: allotype female; 16, 17: juvenile (WAM C51872); 11 & 12: LV, lateral view from the inside; 13: RV, lateral view from the outside; 14–16: carapace, dorsal view; 17: carapace, ventral view. Scale = 0.1 mm.



Figs 18–25. *Gomphodella alexanderi* sp. nov. 18, 23–25: holotype male; 19: male (WAM C51870); 20–22: allotype, female: A–A1; 19: last three distal segments of A1; 20: terminal segment of A1; 21: A1 without apical setae; 22 & 23: A2; G, Md; 25: MxI-palp and endites. Scales = 0.1 mm.

internal setae transformed into distally curved and serrate claw. Terminal segment with two claws, both distally curved and serrate. Vibratory plate with four almost equally long setae.

L5: 4-segmented (Fig. 26). First segment dorsally with total of four serrulate setae. Two proximal setae longer and both slightly exceeding distal end of same segment. Two other setae short, also serrulate and situated apically on the segment. First segment with one long, ventral serrulate seta. Second segment with one short, serrulate seta situated anteriorly. Third segment without any seta. Terminal segment with short, smooth, relatively thick claw. Length ratio between last three segments 1.5 : 1 : 1.1. Tufts of hair-like setulae present on borders between second and third, and third and fourth segments.

L6: 4-segmented (Fig. 27). First segment with three dorsal setae, all serrulate, distal one being the shortest. Same segment with one ventral, serrulate seta. Other segments without any setae, and only with rows of short hair-like setulae along margins. Distal segment with one claw, which more slender than on L5. Length ratio between second, third and fourth segments equalling 2.2 : 1 : 1.25.

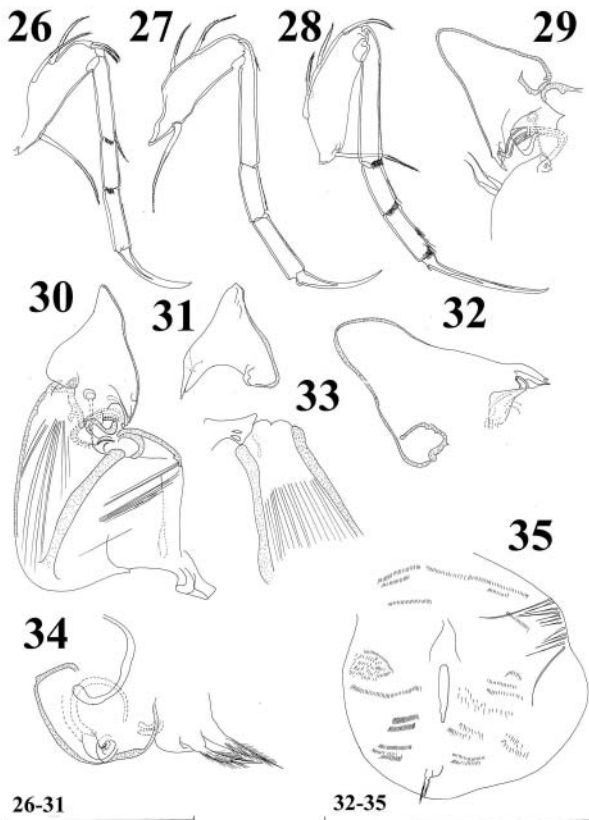
L7: 4-segmented (Fig. 28). Leg similar to L6 except more densely covered with tufts of hair-like setulae and terminal claw very slender compared with both L5 and L6 terminal claws. Length ratio between second, third and fourth segments equalling 2.5 : 1 : 1.1.

HEMIPENIS. Body not very muscular, but distal lobe prominent and articulated (Figs 30, 31). Distal lobe triangular, pointed distally. Dorsal margin sinusoid with square basal part. Ventral margin also sinusoid but basal part subdivided in two long triangular parts. Copulatory process straight and relatively short.

FEMALE. In lateral view (Figs. 12, 13) with brooding chamber prominently overhanging valve margins. L (measured together with the overhanging part) = 0.53 mm. In dorsal view (Fig. 15) much wider than males, with prominent brooding chamber, greatest W = 90% of total L. Eggs visible inside the chamber. Other details of the shell (ornamentation and calcified inner lamella) similar to male.

A1: Similar to male, but fourth segment with only one seta (Figs 20, 21).

A2: Similar to male, but exopod with more pointed tip, and terminal claws less curved (Fig. 22).



Figs 26–35. *Gomphodella alexanderi* sp. nov. 26–28, 30, 31 & 33: holotype male; 29 & 32: male (WAM C51870); 34 & 35: allotype, female; 26: L5; B, L6; C, L7; 29: distal lobe of hemipenis; 30: hemipenis; 31: distal lobe of hemipenis; 32: distal part of hemipenis; 33: connecting part between two hemipenis; 34: genital lobe with UR setae; 35: distal end of the body with caudal seta and FO organ. Scales = 0.1 mm.

GENITAL FIELD AND UR. Genital field rounded and sclerotized along margins, UR with two lobes represented by thick, pappose setae (Fig. 34).

END OF THE BODY. Caudal seta, short and appose. Entire caudal end covered with rows of spinules or fine setulae. Some longer hair-like setae also present. FO organ cylindrical (Fig. 35).

JUVENILE. In dorsal and ventral views with more angular margins (Figs 16, 17).

VARIABILITY. The fourth segment of the A1 can be posteriorly armed with one seta, or rarely two setae. The case of two setae was noticed only on one A1 in the holotype male, while allotype female and all other observed specimens have one seta at that position. Another observed variability concerns the proximal end of ventral margin of the distal lobe of hemipenis. One male (WAM C51870) from the same area, but not the type locality, has slightly different morphology of this part (Figs 29, 32). Namely one of the long triangular processes may be additionally subdivided distally.

REMARKS AND AFFINITIES. Majority of *Gomphodella* species were described from both sexes, the only exceptions being *G. aura* Karanovic, 2009 known after females, and *G. martensi* known after males. The former species can be easily distinguished from *G. alexanderi* sp. nov. by a characteristic appearance of the shell, which in dorsal view has a translucent fringe. Females of this species also have three hirsute lobes on the UR, contrary to the new species which has only two. The morphology of the hemipenis seems to be one of the most important features for discrimination between species. This mostly concerns the appearance of the distal lobe of the hemipenis with its characteristically shaped, usually tapering ventro-proximal (basal) part. The new species is in this regard most closely related to *G. quasihirsuta* Karanovic, 2009 and *G. yandii* Karanovic, 2006. Both species have this part of the hemipenis subdivided in two or three long processes. Interestingly, in all three species there seems to be a small variability in the number of processes (two or three) and the depth of the incisures. In other species this part is very poorly divided (*G. glomerosa* Karanovic, 2006), not divided by an incisure (*G. hirsuta* Karanovic, 2006), the tapering process is very short (*G. martensi*), or it is very complex with an additional hanging structure (*G. maia* De Deckker, 1981). The second very important characteristic is the shape and ornamentation of the shell. Each of the described *Gomphodella* species has a distinctive shape and ornamentation. The shell of the new species is most similar to *G. quasihirsuta*, both having a relatively simple shell compared with other species, and they also have some colour pigmentation. *Gomphodella quasihirsuta* has more prominent brooding chamber and a more cuneiform anterior end when seen from dorsal view. In addition, *G. quasihirsuta* has narrower posterior margin, and has more prominent pits on the surface (especially around the muscle scar imprints). *Gomphodella alexanderi* is obviously most closely related to *G. quasihirsuta*, but beside a similar shell shape and the hemipenis morphology they can be distinguished also based on chaetotaxy: the antero-medial seta on the penultimate segment of A2 is very short in *G. quasihirsuta* (even hardly visible), while in the new species it reaches distal margin of the same segment. In addition, all thoracopods of *G. quasihirsuta* are armed with one seta on the second segment, while this seta is only present on L5 in *G. alexanderi*.

***Gomphodella cf. martensi* Karanovic, 2006**
(Fig. 6A, B)

MATERIAL EXAMINED. Two valves from Australia, Western Australia, Pilbara region, 55.1 km NW of Newman, stygofauna haul net, borehole WW3-0611-01, 22°49'45"S, 119°16'26"E, 21 June 2011, collector J. Alexander (BES: 17005).

REMARKS. The present finding is identified as *G. cf. martensi* because only empty valves were collected, and because there are some differences in the ornamentation of the shell between it and the original description. Namely, the surface fossae are much deeper in the original description, but the protuberances from which surface setae exit are less developed. This species also has two types of surface setae like *G. alexanderi*. Two types of setae were not mentioned in the original description (Karanovic, 2009).

***Gomphodella yandii* Karanovic, 2006**
(Fig. 6C, D)

Gomphodella yandii sp. nov. – Karanovic (2006), p. 125, Figs 72–91; 94B–D.

MATERIAL EXAMINED. Nine females, 1 male from Australia, Western Australia, Pilbara region, 85.5 km NW of Newman, stygofauna haul net, borehole Mar01-0611-02, 22°46'50"S, 119°10'47"E, 23 June 2011, collector J. Alexander (BES: 17009); 10 females, 1 male, 1 juvenile from Australia, Western Australia, Pilbara region, 85.5 km NW of Newman, stygofauna haul net, borehole

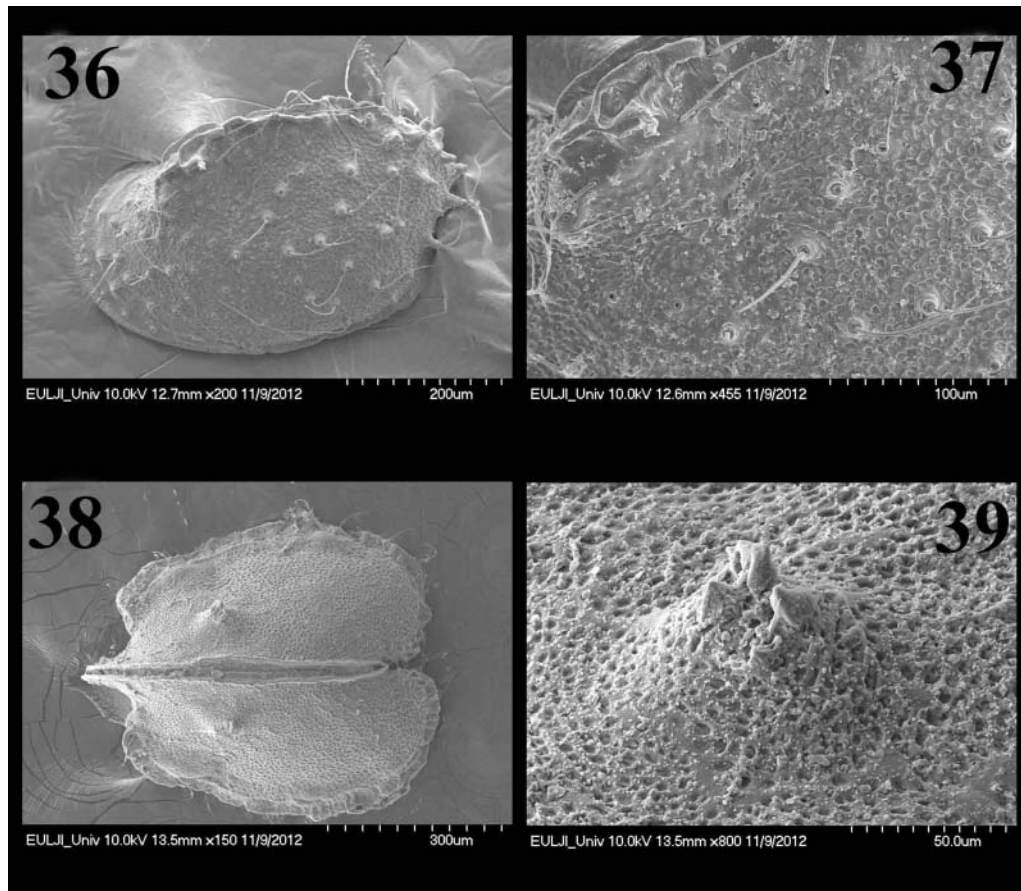
Marillana01–504, 22°46'50"S, 119°10'47"E, 23 August 2011, collector J. Alexander (BES: 17001).

REMARKS. This finding is almost identical with the original description, both regarding the shell ornamentation and shape and the soft part morphology. The only difference noticed are the two peculiar ocular buds (Fig. 38), clearly seen from the view. These buds were not mentioned in the original description. Each of the two buds carries only one small seta (Fig. 39), maybe having a sensory function.

Discussion

Morphology of Timiriaseviinae

De Deckker (1981) labelled the hinge of *Gomphodella* as lophodont, stating that the cardinal and caudal teeth are on the left valve, which is in fact the characteristic of the inverse lophodont hinge type. Study of the new material proves that *Gomphodella* indeed has an inverse lophodont hinge. This puts the genus much closer to *Gomphocythere*. Other Timiriaseviinae genera with the inverse lophodont



Figs 36–39. SEM photographs. 36 & 37: *Gomphodella martensi* Karanovic, 2008; 38 & 39: *Gomphodella yandii* Karanovic, 2006: 36: RV, lateral view from the outside; 37: detail of the surface; 38: carapace, dorsal view from the outside; 39: detail of the ocular part of the carapace.

hinge are: *Frambocythere*, *Rosacythere*, *Kovalevskiella* and *Progomphocythere*. According to Martens (1995), inverse lophodont is only a variation of the lophodont hinge type and in some other Timiriaseviinae genera, such as *Metacypris* (see the cladistic analysis in Gidó *et al.*, 2007) both hinge types can be found. According to Colin & Danielopol (1980), inversion from lophodont to inverse lophodont can be found in fossil species of *Theriosynoeicum*, *Timiriasevia*, *Frambocythere* and *Kovalevskiella*. A reversal of the hinge type has also been recorded in the living species *Elpidium purperi* Danielopol, 1980 (in Colin & Danielopol, 1980), which seems to have a lophodont hinge, in contrast to its congeners where it is adont. *Elpidium purperi* has a very distinct hemipenis compared with other species of the same genus (very elongated, compared with more robust in other species), which may indicate that it belongs to a different lineage, but *Elpidium* is relatively briefly described, so this would need to be studied further. It is interesting to note that the lophodont hinge, with all elements clearly developed, is found almost exclusively in fossil Timiriaseviinae species. The only exceptions are the two living species of *Metacypris* and a monospecific genus *Dolekiella*. Also, it seems that amongst living species there are no cases of variability in the hinge type, only in the level of development of cardinal and/or posterior teeth, such as in some *Gomphocythere* (see Martens, 2003). The monospecific genus *Intrepidocythere* has more or less adont to lophodont hinge type, with a medial bar on the LV and posterior tooth on the RV.

The presence of one or two true sulci has been traditionally used to distinguish *Rosacythere* (one sulcus) from *Frambocythere* (two sulci) (see Colin & Danielopol, 1980). However, some unnamed species of *Rosacythere* [such as *R. sp. 2* and *R. sp. 3* from Colin & Carbonel (1996)] and *R. carpathica* Pipik, Sýkora, Colin & Havrila, 2008 have been described without sulci. As for the *Frambocythere*, at least one species (*F. valeroni* Tambareau, 1991 (in Tambareau *et al.*, 1991)) has a single sulcus. Colin & Carbonel (1996) consider shell without any sulcus as a more primitive form, which is supported by the fact that *Rosacythere sp. 1.* and *R. sp. 2* are the oldest records of the genus, dating from the Middle Jurassic, while one sulcus forms of *Rosacythere* date from the Early Cretaceous. *Metacypris*-like forms without any sulci also have one of the oldest records of all Timiriaseviinae (see Colin & Danielopol, 1980), as does *Timiriasevia* Mandelstam, 1947. Some late (from the Early Eocene) *Frambocythere* have one sulcus, which Colin & Carbonel (1996) also use as an example of more advanced forms. *Rosacythere carpathica* is the most recent fossil record of the genus (Pipik *et al.*, 2008), and in this case sulci-less form appears again in the Late Cretaceous, after it was lost in the Middle Cretaceous. Further on, the only living *Frambocythere* species, *F. relicta* Smith, Lee, Choi, Chang & Colin, 2012, recently described from South Korea (Smith *et al.*, 2012),

has two sulci. Although Smith *et al.* (2012) recently described the first living representative of *Frambocythere* from South Korea, we strongly doubt this systematic arrangement, because the soft part morphology is indistinguishable from *Kovalevskiella*. What is remarkable about their discovery is the first description of the males, never discovered before in *Kovalevskiella*. The morphology of the hemipenis additionally supports the close relationship of *Kovalevskiella* (or *Frambocythere*) with Timiriaseviinae. Smith *et al.* (2012) incorrectly use the term atavistic instead of plesiomorphic when discussing the presence of males and the presence of two sulci on the carapace as reasons for describing the species in the genus *Frambocythere*, instead of *Kovalevskiella*, although they acknowledge a strong similarity in the soft parts. Parthenogenesis is a common way of reproduction in ostracods, and some genera are known to have rare males. One of the most drastic examples is the presence of extremely rare males in 'ancient asexuals', such as Darwinulidae (Smith *et al.*, 2006). The variability of number of sulci has been confirmed both for *Frambocythere* and other Timiriaseviinae (see above) and the two sulci seems in this case to be a plesiomorphic character state contrary to Colin & Carbonel's (1996) opinion (see above). Most *Gomphocythere* have a true sulcus, and only in the two Middle East species does it seem to be absent.

Another very important character of the shell is the presence of sieve-pores in all *Gomphodella*, *Gomphocythere* and *Cytheridella*, and reduced ones in some *Metacypris* (see Martens, 1995). None of the fossil records of Timiriaseviinae mentions sieve pores, but this does not necessarily mean that they are absent. Sieve pores are, according to Park *et al.* (2002) sensory organs, and they have occurred many times in different ostracod lineages. Two types of the so-called trichoid sensilla (Hanai & Tabuki, 1995) are often found in cytherids but this is the first record in *Gomphodella* (Figs 7, 37). Peculiar sensillae were also observed at the apex of ocular protuberances in *G. yandii* Karanovic, 2009 (Figs 38, 39) and they would belong to the c-type sensillae of Hanai & Tabuki (1995). McKenzie *et al.* (2004) mention two types of normal surface pores in the monospecific fossil genus *Progomphocythere* which may indicate a presence of two types of sensillae. This Mesozoic genus, described from Queensland, Australia, is very similar to *Gomphodella*, as expressed in a strongly developed ventro-lateral prolongation (alar prolongation) present in many *Gomphodella* species. In fact, McKenzie *et al.* (2004) point out a different hinge type as the major difference between the two genera, an observation attributable only to the erroneous description of this character by De Deckker (1981) (see above). In our opinion it is very likely that the two genera are synonyms.

A close relationship between *Gomphocythere* and *Gomphodella* is reflected in the similar soft part morphology, especially the appearance of the hemipenis. It was not

noticed previously that, like *Gomphocythere*, species of *Gomphodella* also have a fork-like organ (Fig. 35). This organ was thought to be the second UR in *Gomphocythere* (see Park & Martens, 2001), which was later on clarified when it was realized that the UR is paired in this genus (Martens, 2003). If the observations are correct, *Cytheridella tepida* Victor, 1987, described from Nigeria (Victor, 1987) does not have the UR. It was also believed that *Cytheridella* species lack the UR, and have a two-forked organ instead (see Karanovic, 2007), which is not true. Namely, Purper (1974) redescribed the type species of the genus, *C. illosvayi* Daday, 1905 and clearly drew two UR, both consisting of an elongated shaft and two basally fused setae (which could have been confused with a forked organ). The forked organ is in this species clearly set dorsally to the caudal seta and easily distinguished from the UR. *Cytheridella* also has similar hemipenis to *Gomphocythere* and *Gomphodella* (see Karanovic, 2009), and all three share quite similar Mxl palp, consisting of two fused segments. Beside other distinguishing characters, *Cytheridella* has a peculiar L7 and a transformed Md-palp, the latter it shares with a monospecific genus *Afrocythere* Klie, 1935 and, to some extent, with *Metacypris* (see fig. 3 in Smith & Hiruta, 2004). On the other hand, and contrary to *Gomphocythere*, *Gomphodella* and *Cytheridella*, Mxl palp in *Metacypris*, *Kovalevskiella*, *Dolekiella*, *Intrepidocythere* and presumably *Afrocythere*, does not have any trace of the second segment. Here we point out that *Intrepidocythere* has a similar hemipenis to *Gomphodella* and *Cytheridella*, with extended trunk on the distal lobe of hemipenis, and although it has separated segments on the Md palp, they are very wide and do resemble the Md palp of *Cytheridella*.

Adaptations to subterranean waters

Contrary to the subfamily Candoninae, which is the most dominant ostracod group in subterranean water, Timiriaseviinae do not have prominent adaptations to life in subterranean waters, such as elongated segments, long claws, very long sensory organs on appendages (see Danielopol, 1978). In subterranean *Gomphodella* species even the eye is fully developed as well as the shell pigmentation. The only, potentially indicative, adaptation is a slightly longer aesthetasc on the second antenna in the subterranean species compared with the only surface water representative, *G. maia* De Deckker, 1981. The lack of elaborate adaptation in *Gomphodella* may indicate a relatively recent colonization of the subterranean waters, probably since Pliocene, timing coinciding with a period of aridity in Australia. *Kovalevskiella* and *Dolekiella* are two exclusively subterranean genera. They have completely lost their eyes and pigmentation, and often display a loss of segments on the antennula, and in the latter genus the loss

of a claw on the antenna. This may indicate a longer period of time since these lineages colonized subterranean waters. According to Gidó *et al.* (2007), *Sinuocythere*, which is apparently closely related to *Dolekiella*, may have been living in the subterranean waters of China since Middle Jurassic or Late Cretaceous. *Kovalevskiella* is a much younger genus (Eocene/Oligocene), and there is no indication that the fossil species may have been living in subterranean waters. However, the fact that *Gomphodella* still has a representative which is common in open water bodies, while *Kovalevskiella* is rarely to be found in phreatic waters (see Colin & Danielopol 1980), may indicate a much more prolonged occupation of subterranean waters of the latter genus.

Diversity, distribution, and age of Timiriaseviinae

Of living genera the most diverse timiriaseviin is *Gomphocythere*, with 24 Recent species described (see Karanovic, 2012). Most of these species are from Africa, with significant species flocks in the Great Rift Valley lakes (Park & Martens, 2001; Martens, 2003 (Fig. 40)). The northern-most record of the genus is from the Middle East (Martens, 1993; Boomer & Gearey, 2011), and one species is known from New Zealand and Australia (Hornibrook, 1955; Barklay, 1968; Hussainy, 1969). With the exception of *G. gearayi* Boomer & Gearey, 2011, which is very similar to the recent *G. ortali* Martens, 1993, it is hard to tell if other *Gomphocythere*-like forms do belong to this genus or to *Cytheridella*. Whatley *et al.* (2003) acknowledge this difficulty, but they also say that: 'The former (*Gomphocythere*) has a reversed lophodont hinge, with the terminal bars in the LV, while the latter (*Cytheridella*) has normal lophodont hingement.' This, according to the definition of *Cytheridella* based on the soft parts as well, is not correct, because Recent *Cytheridella* have an adont hinge, although one may observe some remnants of lophodont hinge (such as very small teeth posteriorly on the RV) in the illustrations of some Recent species. The authors further state that: 'There is something of a convention that, with fossil taxa, Mesozoic species are usually referred to *Gomphocythere*, while Cenozoic species are placed in *Cytheridella*.' This is also not completely correct, because some authors (Bhandari, 1998; Sharma *et al.*, 2008) place species recovered from the Palaeocene and even Eocene to *Gomphocythere*. Therefore, the real known diversity, as well as the age of *Gomphocythere* is not certain. Since some fossil species assigned to *Gomphocythere* can be found in India, and today only one species can be found as far north as the Middle East, we can assume that the genus never had a wider distribution, in contrast to *Cytheridella* where fossils can be found in Europe but from where the genus disappeared in the Miocene.

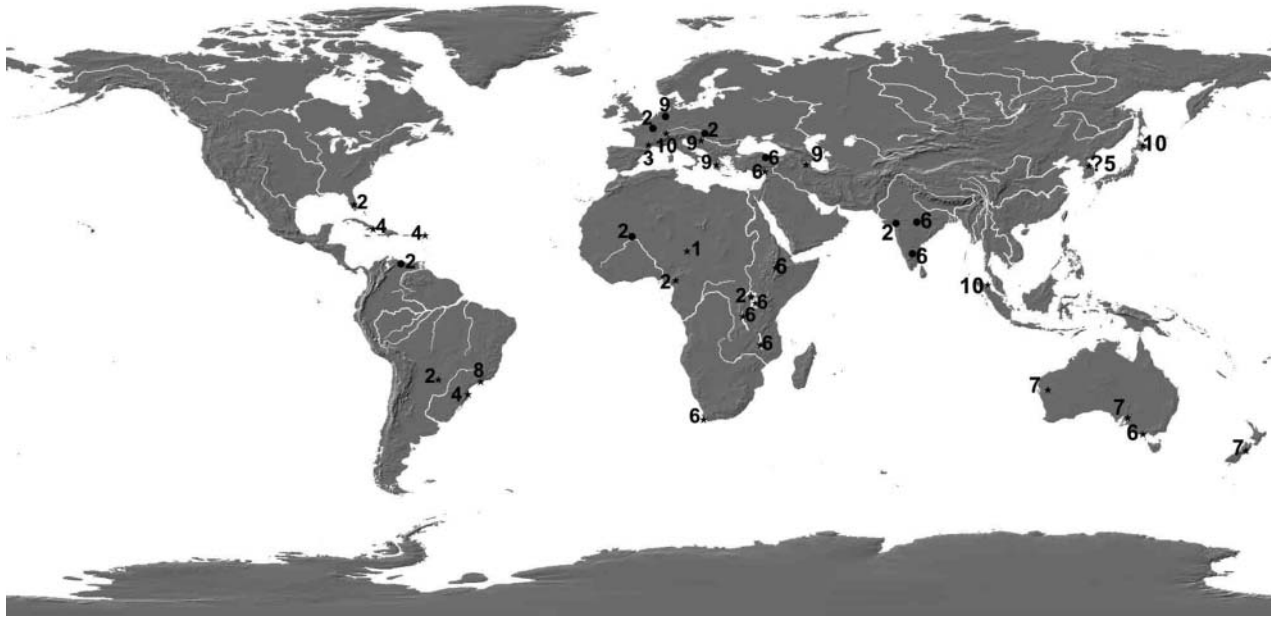


Fig. 40. Distribution of the genera of the subfamily Timiriaseviinae with living representatives of: 1. *Afrocythere* Klie, 1935; 2. *Cytheridella* Daday, 1905; 3. *Dolekiella* Gidó, Artheau, Colin, Danielopol & Marmonier, 2007; 4. *Elpidium* Müller, 1880; 5. *Frambocythere* Colin, 1980; 6. *Gomphocythere* Sars, 1924; 7. *Gomphodella* De Deckker, 1981; 8. *Intrepidocythere* Pinto, Rocha & Martens, 2008; 9. *Kovalevskiella* Klein, 1963; 10. *Metacypris* Brady & Robertson, 1880. Stars refer to the Recent species, circles to the fossil finding. Note that geographically very close localities of *Kovalevskiella* are not included on the map.

Cytheridella has four recent species distributed in Africa and Central and South America (Fig. 40). Park *et al.* (2002) mentioned that it can also be found in Australia, although there are no published records to support this. There are three fossils assigned to *Cytheridella* species reported from the Palaeogene of Europe and India (Monostori, 1993). Colin *et al.* (1997) reported *C.* sp. from the Late Cretaceous from Mali (Africa), indicating this as the oldest record of the genus and a proof that the genus originated in Africa. The Late Cretaceous record is considered to belong to *Gomphocythere* by Whatley *et al.* (2003), and both *Gomphocythere* and *Cytheridella* are indicated to have started from the Late Cretaceous (Fig. 41).

Elpidium has six and *Metacypris* three Recent species. The latter genus dates back to the Early Cretaceous (Fig. 41). It is very hard to say if all species described in this genus really belong there. According to Kempf (1980, 1997) *Metacypris* has around 170 named species and subspecies. A very similar fossil genus, *Vecticypris* Keen, 1972 has been described from the Oligocene of Great Britain (Keen, 1972), but Colin *et al.* (2000) consider some Cretaceous 'primitive' *Metacypris* from Europe, Africa and South America to belong to this genus as well, which, considering the geological age from which *Vecticypris* was described, is a rather long stretch in time and space. If we accept the present systematics, then *Metacypris* was known from the Palaeocene to Recent, and today

three species are distributed in Japan (Smith & Hiruta, 2004), Thailand (Savatenalinton *et al.*, 2008) and Europe (Meisch, 2000) (Figs 40, 41).

The second largest Recent genus is *Gomphodella*, with nine species, all endemic to Australia (Karanovic, 2006, 2009) (Fig. 40). So far, there is no fossil record of this genus, although the Miocene *Progomphocythere* is very closely related and may even be its junior synonym. *Kovalevskiella* fossils are known from the Oligocene of Europe (Fig. 40) and today the genus has five Recent species in Europe, Central Asia and, if one accepts that the record from Korea is actually *Kovalevskiella*, one representative from the Far East. *Afrocythere*, *Dolekiella* and *Intrepidocythere* are monospecific and so far known only from their type localities: Senegal (Klie, 1935), France (Gido *et al.*, 2007) and Brazil (Pinto *et al.*, 2008) respectively (Fig. 40).

All other genera of the subfamily are known only as fossils, and of these *Theriosynoecum* is the most diverse. It has 100 species and subspecies (Kempf, 1980, 1997) and a fossil record dating from the Middle Jurassic to the Late Cretaceous (Fig. 41), and an almost worldwide distribution. The oldest of all genera is *Timiriasevia*, with the earliest record from the Late Triassic and includes 88 named species (Kempf, 1980, 1997). *Rosacythere*, with seven species, and *Sinuocythere* with three species, also date from the Middle Jurassic, being lost from the fossil record by the Late Cretaceous and the end of Jurassic

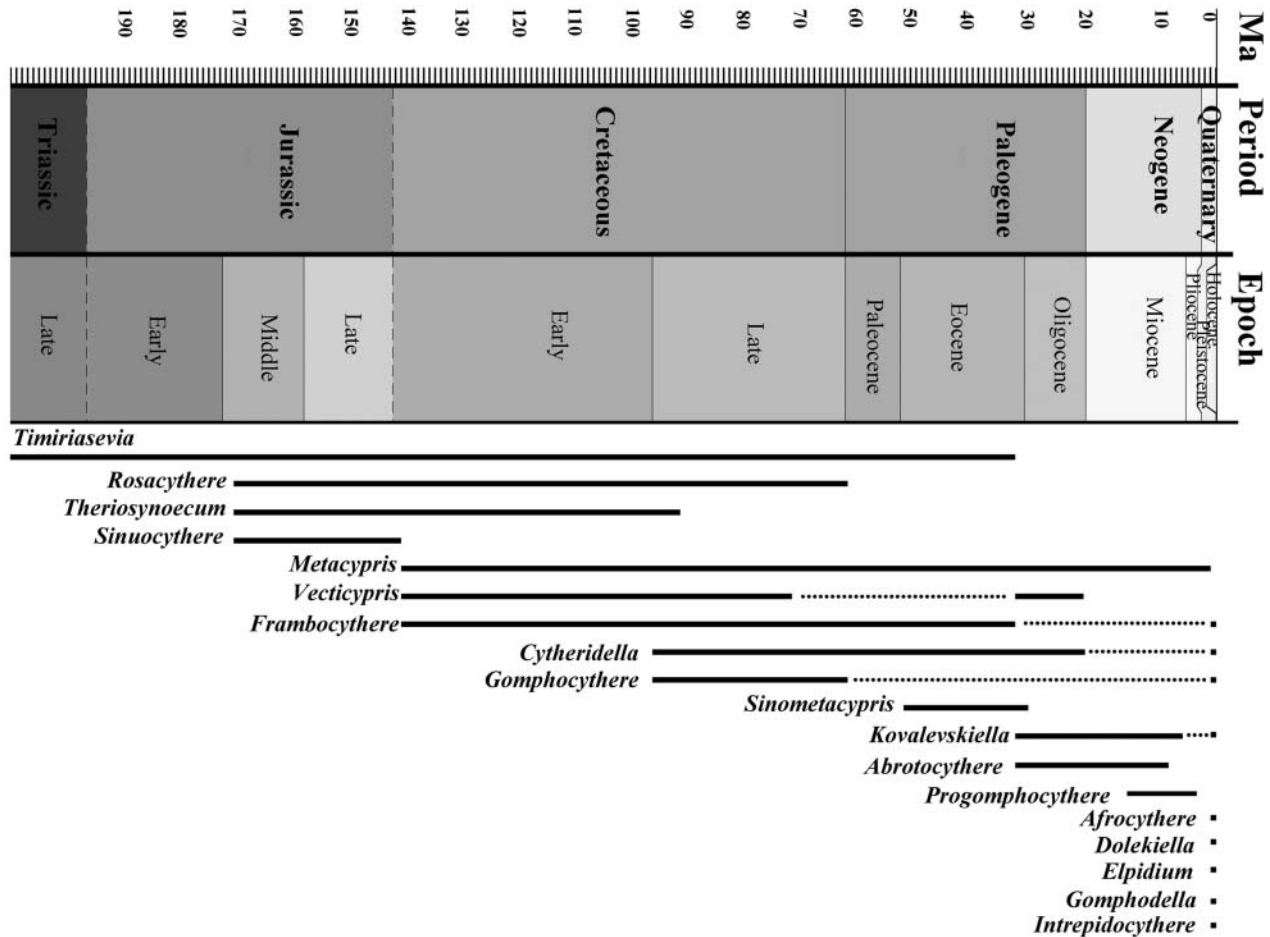


Fig. 41. Geological age of Timiriaseviinae.

respectively (Fig. 40). Species of *Sinuocythere* are known from the southern Tethyan Realm – Tunisia, Morocco and Portugal (Colin *et al.* 2000). *Rosacythere* was distributed in Europe.

Frambocythere has four fossil species: *F. tumiensis* Helmdach, 1978, *F. pustulosa* (Grekoff, 1957), *F. valeroni* Tambareau, 1991, and *F. colini* Bhandari, 1998. The earliest record is of *F. pustulosa* from the Early Cretaceous of Chad, and Colin (2011) states that it had a Gondwana distribution, although it has never been reported from its other parts. Other species are known from the Late Cretaceous to Eocene in Europe, China, India and Iran (Colin & Danielopol, 1980; Bhandari, 1998, Whatley *et al.*, 2003; Colin, 2011; Colin *et al.*, 2012). Although the genus is sometimes hard to distinguish from *Rosacythere* (see above), authors working on this genus have a tendency to describe several subspecies of the same species, with very clear differences in the morphology, distribution and age. There are five or six subspecies of *F. tumiensis*, with distribution range from India, Iran and Europe and ages from the Late Cretaceous to the Palaeocene. The differences

reported sometimes concern even a different valve overlap (see the comment on the difference between *Frambocythere tumiensis anjarensis* Bhandari & Colin, 1999 and *Frambocythere tumiensis lakshmiai* Whatley & Bajpai, 2000 in Whatley *et al.* 2003).

Two youngest exclusively fossil genera are the monospecific *Sinometacypris* Ye, 1978 from the Eocene and *Abrotocythere* with two Oligocene/Miocene species from China (Fig. 41).

Phylogenetic relationships

The first cladistic analysis resulted in one tree (Fig. 42), 28 steps long, with the consistency index (Ci) of 71 and the retention index (Ri) of 71. The tree is divided into two major clades: one consisting of *Gomphodella*, *Gomphocythere*, *Afrocythere* and *Cytheridella*. The other comprises *Kovalevskiella*, *Dolekiella*, *Metacypris*, *Elpidium* and *Intrepidocythere*. In comparison to the phylogenetic tree in Karanovic (2009) and Savatentalinton *et al.* (2008),

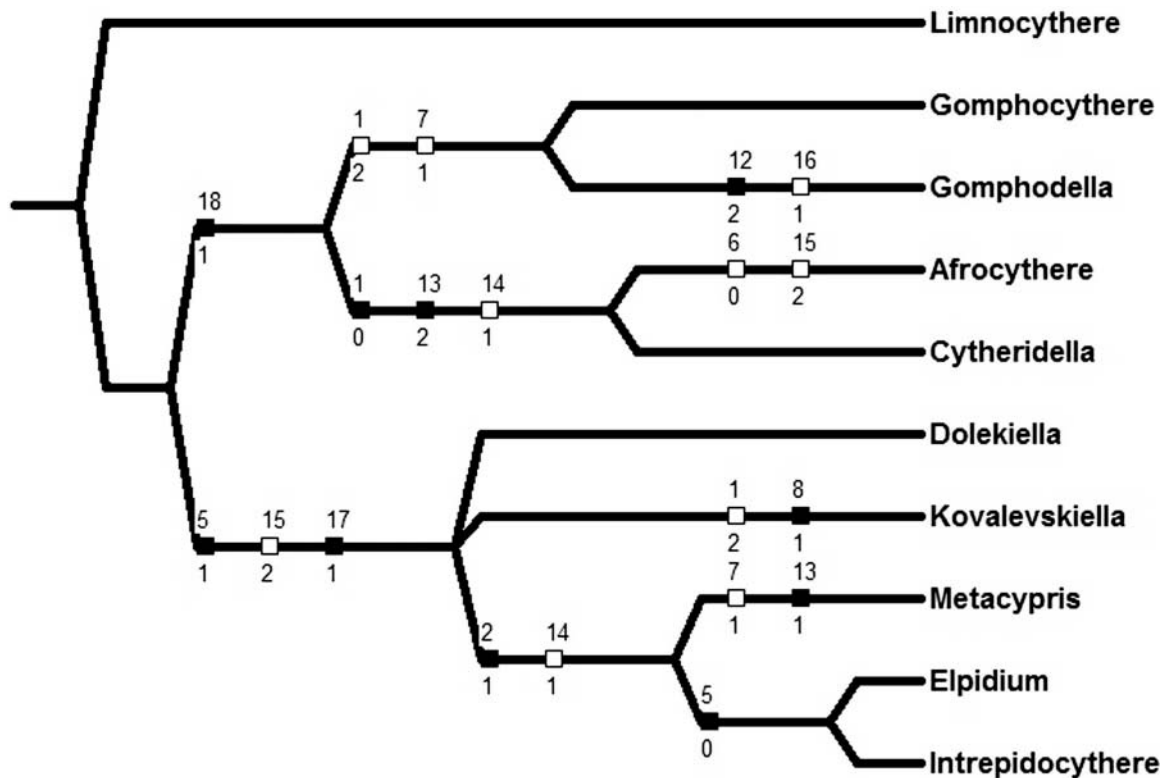


Fig. 42. Cladistic tree resulting from the analysis of 19 morphological characters, scored for nine genera of the Recent Timiriaseviinae and *Limnocythere* as an outgroup. Unsupported nodes had collapsed. Nodes labelled with characters (above node number corresponds to the character number, number below to its state). Black squares indicate apomorphic characters, white ones either plesiomorphic or homoplastic characters.

Gomphodella is now much more closely related to *Gomphocythere*, which is supported by the newly discovered characters (see above). These genera and *Cytheridella* clearly form a lineage, defined as the tribe Cytheridellini (Danielopol *et al.*, 1990). This group has an obvious Gondwana distribution. In contrast to Colin & Danielopol (1980) and Savatnalinton *et al.* (2008) and in accordance with Karanovic (2009), *Afrocythere* and *Cytheridella* seem to be closely related; this can be supported with similar morphology of the mandibular palp, but not with other details of their morphology. Colin & Danielopol (1980) postulate a close relationship between *Elpidium* and *Afrocythere*, while the cladistic tree of Savatnalinton *et al.* (2008) supports the clade *Afrocythere* and *Gomphocythere*. The topology of *Afrocythere* on our tree can be misleading, because many characters are still unknown for the genus, such as hemipenis and morphology of the posterior end of the body in females.

Elpidium and *Intrepidocythere* form the most terminal clade on the tree, with *Metacypris* being basal to it. A close phylogenetic relationship between the two genera as well as between *Metacypris* and *Elpidium* has been reported elsewhere (see Colin & Danielopol, 1980; Pinto *et al.*, 2008; Karanovic, 2009).

The second tree (Fig. 43) is the majority rule of 23 equally parsimonious trees (40 steps, $Ci=64$, $Ri=72$), and it is 40 steps long, with $Ci=55$ and $Ri=59$. The major difference in the topology between the previous tree and this one is that it is much less resolved and that the grouping of *Afrocythere* with the Gondwana lineage is not supported on the second tree. The first difference can be explained with the fact that the soft part morphology is not known in the fossil genera, and that fossil taxa display an intrageneric variability in characters such as hinge type and number of sulci, this is also reflected in the very low Ci and Ri values for the majority rule. The position of *Afrocythere* is not resolved and this can only be explained by the lack of known characters. The Gondwana lineage *Cytheridella*, *Gomphocythere* and *Gomphodella* is well supported on the second cladogram and here it is joined by *Progomphocythere*, a genus very similar to *Gomphodella*. It is interesting to note that *Cytheridella* is basal on the Gondwana clade, supported by a primitive character such as the adont hinge. The clade *Elpidium*/*Intrepidocythere* is also well supported, but it is interesting that *Metacypris* is not part of this clade, in contrast to the first tree (Fig. 42). This is not surprising, since the fossils of *Metacypris* are

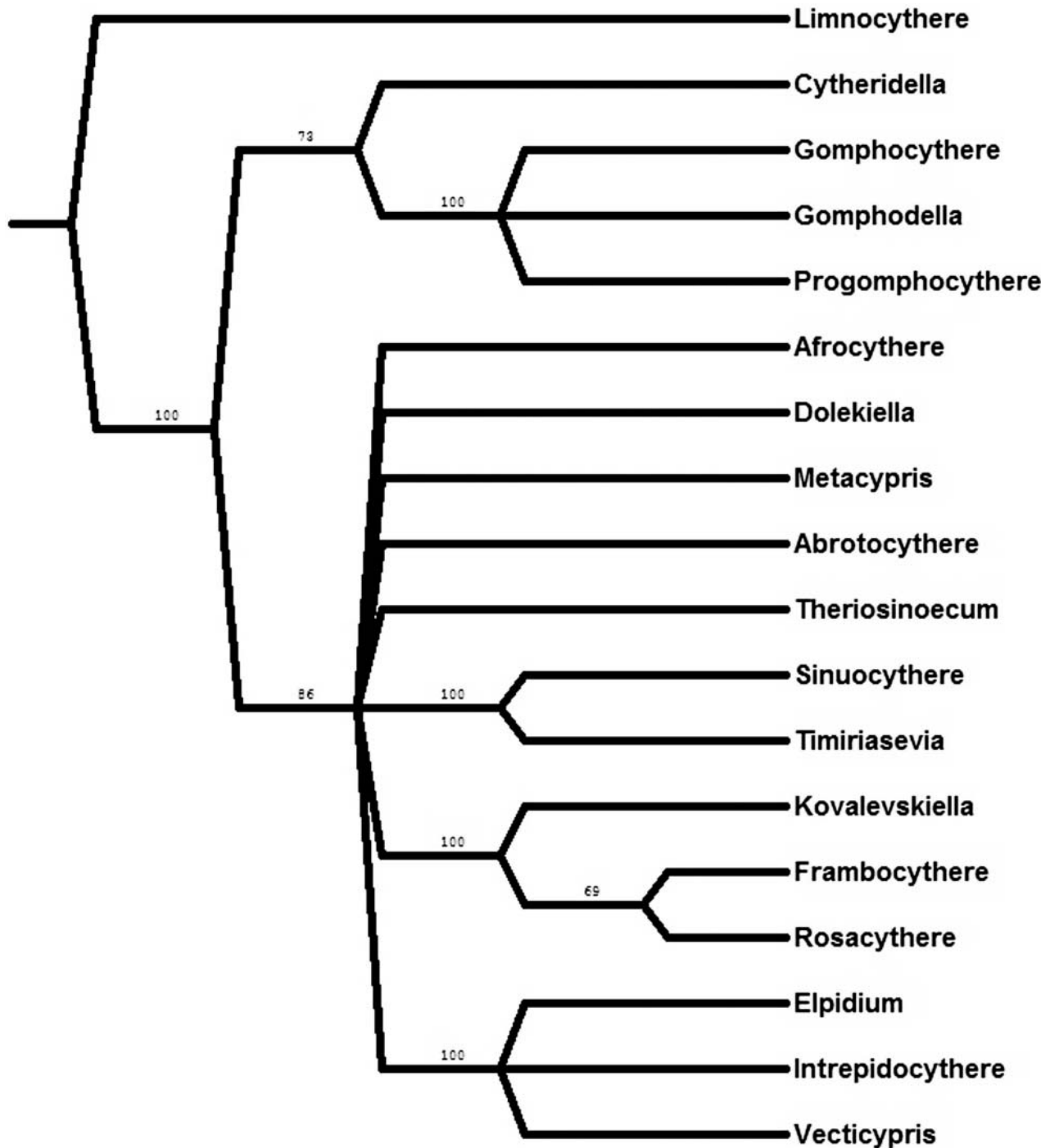


Fig. 43. Majority rule consensus of 23 equally parsimonious cladograms resulting from the analysis of 19 morphological characters, scored for 17 genera of the subfamily Timiriaseviinae and *Limnocythere* as an outgroup. Unsupported nodes had collapsed. Support for each branch shown as a percentage.

variable in many regards, one being the hinge (see above). In our opinion, there may have been two lineages of *Metacypris*: one giving rise to *Elpidium* and *Intrepidocythere* in South America, and the other to the present day *Metacypris*. In fact, the Late Cretaceous fossils assigned to *Vecticypris* found in South America

(Carignano & Varela, 2011) may be ancestral to this lineage, and this genus indeed forms a clade with *Elpidium* and *Intrepidocythere*. It is hard to tell if *Vecticypris* from South America are the same as the one found in the Oligocene of Europe. Soft part morphology indicates that *Elpidium* and *Intrepidocythere* have more

characters in common (including a peculiar seta on A1, see Pinto *et al.*, 2008), than each does with *Metacypris*.

The position of *Theriosynoecum*, in our opinion, does not indicate a true phylogeny. Since there are some cases of variability in the hinge, it may be that the lineage with the inverse lophodont type gave rise to *Cytheridella*/*Gomphocythere*/*Gomphodella*. *Sinuocythere*–*Timiriasevia* lineage is characterized by an ellipsoidal shape and this lineage does not seem to have descendants today. On the cladistic tree of Gidó *et al.* (2007), the two genera form a clade with *Metacypris* and *Vecticypris*, both having distinctly globular shell shape. *Abrotocythere* is, according to Gidó *et al.* (2007), closely related to *Dolekiella* but this is not supported on our cladogram. However, it must be pointed out that amongst all Timiriaseviinae genera *Dolekiella* is indeed most closely related to *Abrotocythere* because they share very similar shell ornamentation and the hinge structure, while the main difference is that the fossil genus has a sulcus, while *Dolekiella* does not.

This paper is one of the first attempts to resolve the phylogeny of Timiriaseviinae, and we believe that a rigorous revision of described fossil taxa is necessary to its success. That revision should bear in mind the following: the soft part morphology is very conservative amongst genera; the shape and ornamentation varies to a certain degree; and there are practically no hinge inversions in the hinge type amongst the living taxa.

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Supplemental data

Supplemental data for this article can be accessed here.

Appendix 1. Character matrix used in the cladistic analysis: 0, 1, 2 – character states; * \$ – ambiguous character state; ? – unknown character state.

References

- BARKLEY, M. H. 1968. Additions to the freshwater ostracod fauna of New Zealand. *New Zealand Journal of Marine and Freshwater Research* **2**, 67–80.
- BHANDARI, A. 1998. Non-marine Ostracoda from subsurface of the Cambay Shale (Eocene) of Gujarat, India and their paleoecological significance. *Revista Española de Micropaleontología* **30**, 1–10.
- BOOMER, I. & GEAREY, B. 2011. The occurrence of a new species of *Gomphocythere* (Ostracoda, Limnocytheridae) in the Holocene of SE Turkey: the northernmost record for the genus. *Journal of Micropaleontology* **29**, 115–118.
- CARIGNANO, A. & VARELA, J. A. 2011. Ostrácodos (Crustacea) de la Formación Allen (Cretácico Tardío), Cuenca Neuquina, Argentina. *Revista Brasileira de Paleontologia* **14**, 167–178.
- COLIN, J. P. 2011. From light to darkness: from *Frambocythere* Colin, 1980 to *Kovalevskiella* Klein, 1963 (Limnocytheridae, Timiriaseviinae). *Joannea - Geologie und Paläontologie* **11**, 44–47.
- COLIN, J. P. & CARBONEL, P. 1996. Middle Jurassic record of the limnic ostracode genus *Rosacythere* (Limnocytheridae, Timiriaseviinae): implications on the origin and evolution of the *Kovalevskiella* group. *Journal of Micropaleontology* **15**, 187–191.
- COLIN, J. P., CABRAL, M. C., DÉPÊCHE, F. & METTE, W. 2000. *Sinuocythere* n. gen. (Ostracoda, Limnocytheridae, Timiriaseviinae), a new genus of limnic ostracode from southern Tethyan Middle and Upper Jurassic. *Micropaleontology* **46**, 123–134.
- COLIN, J. P. & DANIELOPOL, D. L. 1980. Sur la morphologie, la systématique, la biogéographie et l'évolution des ostracodes Timiriaseviinae (Limnocytheridae). *Paleobiologie continentale* **11**, 1–51.
- COLIN, J. P., TAMBAREAU, Y. & KRASHENINNIKOV, V. A. 1997. An early record of the genus *Cytherevidella* Daday, 1905 (Ostracoda, Limnocytheridae, Timiriaseviinae) from the Upper Cretaceous of Mali, West Africa: palaeobiogeographical and palaeoecological considerations. *Journal of Micropaleontology* **16**, 91–95.
- COLIN, J. P., VAZIRI-MOGHADDAM, H., SAFARI, H. & SHARIARI-GRAI, S. 2012. Presence of *Frambocythere* COLIN, 1980, (limnic ostracode) in the Maastrichtian of the Zagros Mountains, Iran: a newly recognized link between southern Europe and the Far East. *Carnets de Géologie [Notebooks on Geology]*, Letter 2012/02 (CG2012_L02), 173–181.
- DANIELOPOL, D. L. 1975. Remarques sur la diversification morphologique de trois nouvelles espèces d'*Elpidium* (Ostracoda) a Cuba. *Bulletin of American Paleontology* **65**, 47–60.
- DANIELOPOL, D. L. 1978. Über die Herkunft und Morphologie der Süßwasser-hypogaeischen Candoninae (Crustacea, Ostracoda). *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse, Abteilung I* **187**, 1–162.
- DANIELOPOL, D. L., MARTENS, K. & CASALE, L. M. 1990. Revision of the genus *Leucocythere* Kaufmann, 1892 (Crustacea, Ostracoda, Limnocytheridae) with description of a new species and two new tribes. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* **59**, 63–94.
- DE DECKKER, P. 1981. Taxonomy and ecology notes of some ostracods from Australian inland waters. *Transactions of the Royal Society of South Australia* **105**, 91–138.
- EPA. 2003. Consideration of Subterranean Fauna in Groundwater and Caves during Environmental Impact Assessment. Guidance Statement No. 54. Environmental Protection Authority, Perth, Australia.
- EPA. 2007. Sampling methods and survey considerations for subterranean fauna in Western Australia. Guidance Statement No. 54a. Environmental Protection Authority, Perth, Australia.
- GIDÓ, Z., ARTHEAU, M., COLIN, J. P., DANIELOPOL, D. L. & MARMONIER, P. 2007. Description of the stygobiotic crustacean *Dolekiella europaea* gen. nov. sp. nov. (Ostracoda, Limnocytheridae) from southern France. *Vie et Milieu* **57**, 109–116.

- GOLOBOFF, P. 1999. *NONA* (No Name) version 2, published by the author, Tucumán, Argentina.
- HANAI, T. & TABUKI, R. 1995. Shell structure of *Promanawa* – discussion on the Bauplan of podocopid Ostracoda. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institute* **92**, 259–272.
- HORNE, D. J., COHEN, A. & MARTENS, K. 2002. Taxonomy, morphology and biology of Quaternary and living Ostracoda. In: Holmes, J. A. & Chivas, A. R., Eds., *The Ostracoda, applications in Quaternary research*. Geophysics Monographs. Washington DC. **131**, 5–36.
- HORNIBROOK, N. K. 1955. Ostracoda in the deposits of Pyramid Valley swamp. *Records of the Canterbury Museum* **6**, 267–277.
- HUSSAINY, S. U. 1969. A new species of *Gomphocythere* (Limnocytheridae, Ostracoda) from Australia. *Proceedings of the Royal Society of Victoria, (New Series)* **82**, 299–303.
- KARANOVIC, I. 2006. On the genus *Gomphodella* (Crustacea: Ostracoda: Limnocytheridae) with descriptions of three new species from Australia and redescription of the type species. *Species Diversity* **11**, 99–135.
- KARANOVIC, I. 2007. Candoninae (Ostracoda) from the Pilbara region in Western Australia. *Crustaceana Monographs* **7**, 1–433.
- KARANOVIC, I. 2009. Four new species of *Gomphodella* De Deckker, with a phylogenetic analysis and a key to the living representatives of the subfamily Timiriaseviinae. *Crustaceana* **82**, 1133–1176.
- KARANOVIC, I. 2012. *Recent freshwater ostracods of the World*. Crustacea, Ostracoda, Podocopida, Springer-Verlag, Berlin, Germany, pp. 1–608.
- KEEN, M. C. 1972. The Sannoisian and some other Upper Palaeogene Ostracoda from north-west Europe. *Palaeontology* **15**, 267–325.
- KEMPF, E. K. 1980. Index and bibliography of nonmarine Ostracoda. 1. Index A. *Geologisches Institut der Universität zu Köln, Sonderveröffentlichungen* **35**, 1–188.
- KEMPF, E. K. 1997. Index and bibliography of nonmarine Ostracoda. 6. Index A. Supplement 1. *Geologisches Institut der Universität zu Köln, Sonderveröffentlichungen* **109**, 1–142.
- KLIE, W. 1935. Ostracoda aus dem tropischen Westafrika. *Archiv für Hydrobiologie* **38**, 35–68.
- McKENZIE, K. G., ENGELBRETTSEN, M., ARCHER, M. & PRICE, E. 2004. Ostracoda from the Miocene, Riversleigh World Heritage deposits, Queensland, including *Progomphocythere* n. gen., with discussion of palaeoenvironments and age. *Bolletino della Società Paleontologica Italiana* **43**, 321–330.
- MARTENS, K. 1993. On the taxonomy and zoogeography of the genus *Gomphocythere* Sars, 1924 (Crustacea, Ostracoda), with the description of a new species from Nahal Dan (Israel). *Belgian Journal of Zoology* **123**, 39–54.
- MARTENS, K. 1995. On the validity and taxonomic position of the Cytheridellini (Crustacea, Ostracoda, Limnocytheridae). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institute* **92**, 273–280.
- MARTENS, K. 2003. On the evolution of *Gomphocythere* (Crustacea, Ostracoda) in Lake Nyassa/Malawi (East Africa), with the description of 5 new species. *Hydrobiologia* **497**, 121–144.
- MARTENS, K., SCHÖN, I., MEISCH, C. & HORNE, D. J. 2008. Global diversity of ostracods (Ostracoda, Crustacea) in freshwater. *Hydrobiologia* **595**, 185–193.
- MEISCH, C. 2000. *Freshwater Ostracoda of western and central Europe*. *Süßwasserfauna von Mitteleuropa* 8/3, Spektrum Akad. Vlg. Gustav Fischer, Heidelberg, Berlin, Germany, pp. 1–522.
- MONOSTORI, M. 1993. The genus *Cytheridella* in the Palaeogene of Eastern Europe. *Revista Española de Micropaleontología* **25**, 107–112.
- NIXON, K. C. 2002. *WinClada* version 1.00.08, published by the author, Ithaca, New York, USA.
- PARK, L. & MARTENS, K. 2001. Four new species of *Gomphocythere* (Crustacea, Ostracoda) from Lake Tanganyika, East Africa. *Hydrobiologia* **450**, 129–147.
- PARK, L. E. & MARTENS, K. & COHEN, A. S. 2002. Phylogenetic relationships of *Gomphocythere* (Ostracoda) in Lake Tanganyika, East Africa. *Journal of Crustacean Biology* **22**, 15–27.
- PINTO, D. I. & SANGUINETTI, Y. T. 1962. *A complete revision of the genera Bisulcoocypris and Theriosynoeum (Ostracoda) with the world geographical and stratigraphical distribution (including Metacypris, Elpidium, Gomphocythere and Cytheridella)*, Escola de Geologia de Pôrto Alegre, Porto Alegre, Brasil, pp. 1–164.
- PINTO, R. L., ROCHA, C. E. F. & MARTENS, K. 2008. On the first terrestrial ostracod of the Superfamily Cytheroidea (Crustacea, Ostracoda): description of *Intrepidocythere ibipora* n. gen. n. sp. from forest leaf litter in São Paulo State, Brazil. *Zootaxa* **1828**, 29–42.
- PIPIK, R., SYKORA, M., COLIN J. P. & HAVRILA. 2008. A new phytal limnic ostracod *Rosacythere carpathica* sp. nov. from the Upper Cretaceous of the Western Carpathians: implications for evolution of Timiriaseviinae. *Cretaceous Research* **30**, 465–476.
- PURPER, I. 1974. *Cytheridella boldi* Purper, sp. nov. (Ostracoda) from Venezuela and a revision of the genus *Cytheridella* Daday, 1905. *Anais da Academia Brasileira da Ciências* **46**, 435–662.
- SAVATENALINTON, S., BORGONIE, G. & MARTENS, K. 2008. On *Thaicythere srisumona* n. gen., n. sp. (Ostracoda) from Thailand, with notes on the phylogeny of the subfamily Timiriaseviinae Mandelstam, 1960. *Crustaceana* **81**, 411–432.
- SHARMA, R., BAIPAI, S. & SINGH, M. P. 2008. Freshwater Ostracoda from the Paleocene-Age Deccan Intertrappean Beds of Lalitpur (Uttar Pradesh), India. *Journal of the Palaeontological Society of India* **53**, 177–183.
- SMITH, R. J. & HIRUTA, S. I. 2004. A new species of *Metacypris* (Crustacea: Ostracoda: Cytheroidea: Limnocytheridae) from Hokkaido, Japan. *Species Diversity* **9**, 37–46.
- SMITH, R. J., KAMIYA, T. & HORNE, D. J. 2006. Living males of the ‘ancient asexual’ Darwinulidae (Ostracoda: Crustacea). *Proceedings of the Royal Society, Biological Sciences* **273**, 1569–1578.
- SMITH, R. J., LEE, J., CHOI, Y. G., CHANG, C. Y. & COLIN, J. P. 2012. A Recent species of *Frambocythere* Colin, 1980 (Ostracoda, Crustacea) from a cave in South Korea; the first extant representative of a genus though extinct since the Eocene. *Journal of Micropalaeontology* **31**, 131–138.
- TAMBAREAU, Y., GRUAS-CAVAGNETTO, C., FEIST, M. & VILLATTE, J. 1991. Flores et faunes continentales ilardiennes du versant sud de la Montagne Noire et de la Montagne d’Alaric. *Revue de Micropalaeontologie* **34**, 69–90.
- VICTOR, R. 1987. A new species of the genus *Cytheridella* (Crustacea, Ostracoda) from Nigeria, West Africa. *Journal of Natural History* **21**, 893–902.

- WHATLEY, R. C., BAJPAI, S. & WHITTAKER, J. 2002. Freshwater ostracoda from the Upper Cretaceous Intertrappean beds at Mamoni (Kota district), southeastern Rajasthan, India. *Revista Española de Micropaleontología* **35**, 75–86.
- YAMADA, S. 2007. Ultrastructure of the carapace margin in the Ostracoda (Arthropoda: Crustacea). *Hydrobiologia* **585**, 201–211.
- YAMAGUCHI, S. 2003. Morphological Evolution of Cytherocopine Ostracods Inferred from 18S Ribosomal DNA Sequences. *Journal of Crustacean Biology* **23**, 131–153.

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