Tadeusz Namiotko*,[1], Dan L. Danielopol[2], Soumaya Belmecheri[3,4], Martin Gross[5] and Ulrich von Grafenstein[4]

[1]Laboratory of Limnozoology, Department of Genetics, University of Gdańsk, Kładki 24, 80–822 Gdańsk, Poland; e-mail: namiotko@biotech.ug.gda.pl
[2]Commission for the Stratigraphical and Palaeontological Research of Austria, Austrian Academy of Sciences, c/o Institute for Earth Sciences (Geology and Palaeontology), Karl-Franzens University, Heinrichstraße 26, A-8010 Graz, Austria
[3]Department of Meteorology, Earth and Environmental Systems Institute, The Pennsylvania State University, 416 Walker Building, University Park, PA-16802, USA
[4]Laboratoire des Sciences du Climat et de l'Environnement, Orme des Merisiers, Bâtiment 701, F-91191 Gif-sur-Yvette, France
[5]Department for Geology and Palaeontology, Universalmuseum Joanneum, Weinzöttlstraße 16, A-8045 Graz, Austria

Research Paper

On the Leptocytheridae Ostracods of the Long-Lived Lake Ohrid: A Reappraisal of their Taxonomic Assignment and Biogeographic Origin

key words: morphology, biosystematics, palaeobiogeography, redescription of *Leptocythere karamani* Klie, 1939

Abstract

Leptocythere karamani Klie, one of few non-marine species of the family Leptocytheridae (Ostracoda), is redescribed from specimens recently collected from the long-lived Lake Ohrid on the Albanian-Macedonian border. Detailed morphologies of valves and limbs of this species were compared with those of other Ohrid-Prespa leptocytherids, of some recent marine representatives of the genera *Leptocythere* Sars and *Callistocythere* Ruggieri from the Mediterranean, Irish and Baltic seas as well as with that of fossil non-marine species from the Miocene palaeo-Lake Pannon belonging to the genera *Amnicythere* Devoto and *Euxinocythere* Stancheva. Comparison with other species of Leptocytheridae inhabiting fresh to brackish waters of the Black-Azov, Caspian and Aral seas were also carried out using descriptions provided in the literature. Based on the comparative morphological studies it is shown that *L. karamani* and other Ohrid leptocytherids have a number of characters distinguishing them from other members of the genus *Leptocythere* but demonstrating a relationship with species of the genus *Amnicythere*. The most reliable of these characters are: a) anterior valve vestibulum from where mostly uni-ramified pore canals start, b) the entomodont hinge type with a strong anterior anti-slip tooth, a smooth posterior anti-slip bar on the left valve, and c) the hemipenis with underdeveloped lateral lobe and reduced clasping organ. From this strong evidence, the Ohrid leptocytherid species are allocated to the genus *Amnicythere*. Finally, a biogeographic scenario on the origin of the Ohrid leptocytherids is proposed which matches the "Lake Pannon derivate hypothesis". Close relationship of the Ohrid *Amnicythere* species with the non-marine leptocytherid taxa from the Neogene lakes of Central and Eastern Europe and with extant taxa from the Black and Caspian seas may indicate that the Ohrid *Amnicythere* derived from Lake Pannon species which were able to colonise lakes in Southern Europe through a stepping-stone process and subsequently to adapt to freshwater environment.

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* Corresponding author

1. Introduction

Lake Ohrid located in south-eastern Europe (Albania/Macedonia) is a classic ancient lake, whose origin is estimated to have occurred 2–5 million years ago. The lake displays one of the highest diversities of organisms in the world (STANKOVIĆ, 1960; ALBRECHT and WILKE, 2008). Intense modern research activities are carried not only on strictly biological aspects, like those related to the origin of the high number of endemic species (review in ALBRECHT and WILKE, 2008) but also on topics belonging to limnology and palaeolimnology of the lake (MATZINGER *et al.*, 2006; BELMECHERI *et al.*, 2009; WAGNER *et al.*, 2009; BELMECHERI *et al.*, 2010).

One of the puzzling aspects of ancient lakes is the presence of species which apparently are closely related to animal groups widely spread in the marine environment (MARTENS, 1987). This is also the case with the ostracod family Leptocytheridae of Lake Ohrid. This group is represented by more than two hundred recent and fossil species, distributed all around the marine world (HARTMANN, 1975; WHATLEY and MAYBURY, 1981) but with few species living at present in the non-marine environment (MARTENS and SAVATENALINTON, 2011). Three species belonging to the most common marine group of the Leptocytheridae, the genus *Leptocythere* SARS, were described by KLIE (1939) from Lake Ohrid: *L. angulata* KLIE, *L. karamani* KLIE and *L. proboscidea* KLIE, and a fourth one, *L. prespensis* PETKOVSKI (here named *L.* aff. *prespensis*), originally described from Lake Prespa, was also found in Lake Ohrid by PETKOVSKI and KEYSER (1992). The presence of these species in this long-lived lake was used as an argument for a possible connection of the Ohrid to a marine system in the past (WAGNER *et al.*, 2009; LORENSCHAT *et al.*, 2011). The alternative hypothesis on the origin of the present-day leptocytherids in Lake Ohrid is that non-marine leptocytherids existed in limnic systems and from there they colonised Lake Ohrid. This latter hypothesis was briefly discussed by us at the 7th European Ostracod Meeting in Graz (NAMIOTKO *et al.*, 2011a). Here we provide *in extenso* arguments for the non-marine origin of the Ohrid leptocytherids and for their assignment to a different genus, namely *Amnicythere* DEVOTO.

We first review basic morphological traits of Leptocytheridae valves and redescribe *Leptocythere karamani* using living specimens recently sampled by two of us (S.B. and U.G.). We will further compare our Ohrid leptocytherids with extant marine *Leptocythere* and *Callistocythere* RUGGIERI species from the Mediterranean, Irish and Baltic seas together with information existing on living leptocytherids from the Caspian and Black seas as well as from the Balkan Prespa Lake. Additionally, we will use for comparative purposes non-marine fossil species from the Miocene palaeo-Lake Pannon. These latter taxa belong to the genera *Amnicythere* and *Euxinocythere* STANCHEVA. Based on these data it is possible to better characterise and further to verify the taxonomic assignment of the *Leptocythere* ostracods from Lake Ohrid. We will additionally propose for them a palaeo-biogeographical scenario which should further stimulate studies on evolutionary aspects of Recent and fossil Leptocytheridae.

2. Material and Methods

Material of *Leptocythere karamani* used in this study was collected by two of us (S.B. and U.G.) from the Albanian part of Lake Ohrid in June 2008. The sample was taken by dragging the 40-m-deep bottom at a site OH023 of latitude 40°54′42.44″ N and longitude 20°39′53.61″ E, close to the coring site JO2004-1 (100 m depth) used for palaeolimnological studies (*cf.* BELMECHERI *et al.*, 2009; BELMECHERI *et al.*, 2010). The sampling site ecologically and bathymetrically corresponds to the sublittoral "shell zone"-sand/silt zone transition, as defined by ALBRECHT and WILKE (2008). In the field the sample was preserved in 70% ethanol. In the laboratory, specimens were sorted and dissected under a stereoscopic binocular microscope at a magnification of 20–60×. The dissected specimens were mounted

in glycerine on slides with valves stored dry in micropalaeontological slides, whereas entire specimens were preserved in 97% ethanol in glass tubes. The dissection and slide-preparation were performed according to NAMIOTKO *et al.* (2011b). Both valves and soft parts were examined, measured, photographed and drawn using a transmitted light compound microscope (TLM) fitted with a *camera lucida* at magnifications of 100× to 1000× (oil immersion). Scanning electron micrographs (SEM) were also taken to illustrate the structure details of valves and soft parts. We tried as much as possible to examine the same valve on both sides and with both TLM and SEM techniques. For the SEM analysis of the soft parts, specimens were dehydrated by the critical-point-drying method prior to examination. The numbers accompanying the illustrated valves of *L. karamani* (No. 8259–8261) are those of the catalogued material deposed in the collection of the Universalmuseum Joanneum (Dept. Palaeontology), Graz. Other specimens used for the present paper are housed in the collections of T.N. (Univ. Gdańsk).

The following additional Leptocytheridae specimens were used as comparative material:

Leptocythere pellucida (BAIRD) – one female right valve (No. 8264) photographed in both TLM and SEM; sampled by D. J. HORNE on 23 February 1980 on the sandy substrate of the beach of Walney Island, Irish Sea, U.K.

Leptocythere lacertosa (HIRSCHMANN) – three males photographed in TLM; sampled on 26 July 1981 by M. OLEŃSKA and T. SYWULA from the littoral of Gdańsk Bay off Rewa (the Baltic Sea) (site 3C in OLEŃSKA and SYWULA 1988).

Leptocythere prespensis PETKOVSKI – one male right valve (No. 5646) photographed in TLM; sampled by H. LÖFFLER from the littoral of Lake Prespa (Macedonia); for location of the site see LÖFFLER *et al.* (1998: Fig. 1).

Leptocythere ramosa ROME – one left valve (No. 6213) photographed in TLM; sampled by N. PUGLIESE in the Adriatic Sea off Trieste.

Callistocythere adriatica MASOLI – one left valve (No. 6222) photographed in TLM; sampled by N. PUGLIESE in the Adriatic Sea off Trieste.

Amnicythere tenuis (REUSS) – male left valves (No. 2879) from the AC layer and one female left valve (No. 8229) from Core 5 of the Hennersdorf section in Lower Austria, near Vienna, Late Miocene (Pannonian E) (*cf.* DANIELOPOL *et al.*, 2011a: Fig. 6).

Amnicythere nodosa (*sensu* SOKAČ, 1972) – left male valve (No. 8228) from the Hennersdorf section, same location and sample as for *A. tenuis* specimen No. 8229.

Euxinocythere lacunosa (REUSS) – left male valve (No. 8227) from same location and sample as *A. tenuis* specimen No. 8229.

Comparisons with other species belonging to the family Leptocytheridae were carried out using the descriptions provided in the literature. We analysed the shape of various leptocytherid valves using the computer programme *Morphomatica* (LINHART *et al.*, 2007) and protocols for geometric morphometrics reviewed in NEUBAUER and LINHART (2008) and BALTANÁS and DANIELOPOL (2011).

Here we present also an innovative method for the sex identification of adult leptocytherid valves. This approach is necessary because sexual dimorphism for many leptocytherid species is poorly expressed, especially in the case of dead assemblages with isolated valves. The superposition of valves in *Morphomatica* using the standardised algorithm for surface shape comparison allows such identification. Figure 2 documents such an approach: Figure 2A and B show that the shape of female valves does not markedly differ while in Figure 2C to F the differences between female and male valves are clearly shown. As an example we offer the precise case of the unique right valve of *Leptocythere prespensis* (No. 5646) for which the sex at the beginning of the investigation could not be determined. Superposed on the outlines of the valves published for living specimens by PETKOVSKI and KEYSER (1992: Plate 1, Figures 5 and 7) it becomes clear that our valve belongs to a male specimen.

Most of the acronyms used for the description of valve details follow those used in classic publications like HANAI (1961), VAN MORKHOVEN (1962), ATHERSUCH *et al.* (1989), HORNE *et al.* (2002), YAMADA and KEYSER (2010), SAMES (2011): A – "attached area", At – anterior tooth of LV located on the inter-cardinal anti-slip bar, f – fossa, fmz – fused marginal zone, H – height of valves, Hmax/h$_{75}$ – height index (the ratio between the maximal valve height and the height measured at 75% of the valve length), im – inner margin, L – length of valves, Lk – "*Leptocythere*" knob, loc – line of concrescense, LV – left valve, om – outer margin, ot – ocular tubercle, pr – principal reticulation, prc – partial marginal canal (used instead of "false marginal canal"), pvc – postero-ventral carina, rc – radial marginal canal, RV – right valve, se – selvage, sr – secondary reticulation, V – vestibulum.

Names for the limbs were used according to MEISCH (2000). The setal formula for the first podomere of the walking legs follows the model of ATHERSUCH *et al.* (1989). The terminology developed for

Limnocytheridae by MARTENS (1990) and DANIELOPOL *et al.* (1990), as generalised for Cytheroidea by MARTENS (1998), was used for the hemipenis morphology. Abbreviations and symbols pertaining to the limbs used in the text and figures: A1 – antennule (first antenna), A2 – antenna (second antenna), CR – caudal ramus (= uropod, furca), GL – female genital lobe, HP – hemipenis, Md – mandible, Mdp – mandibular palp, Mx1 – maxillule, Mx1p – maxillular palp, T1 – first thoracopod, T2 – second thoracopod, T3 – third thoracopod.

3. Results

3.1. General Aspects of the Morphology of Leptocytheridae

Leptocytheridae are remarkable within the Cytheroidea because of several morphological traits of the valves and limbs which are here presented briefly in order to facilitate identification necessary for research on comparative morphology and/or systematics of this family.

1. The shape of the valves varies from elongated and more-or-less rectangular (*e.g.* Fig. 1A, C) to triangular shapes (*e.g.* Figs. 1F, 2A, 6A). This latter shape is due to the process of paedomorphosis, where the adult valves resemble those of juvenile stages (*cf.* Fig. 5B).

2. The anterior vestibule and the anterior radial-pore canals build a functional unit (Fig. 1B, D). Towards the valve inside the vestibulum is delineated by the inner margin of the calcified inner lamella, and distally by the so-called line of concrescence. This latter forms a dendritiform space which still belongs to the vestibulum. The dendritiform space narrows towards the outer valve margin and the digitiform tubes define the radial canals.
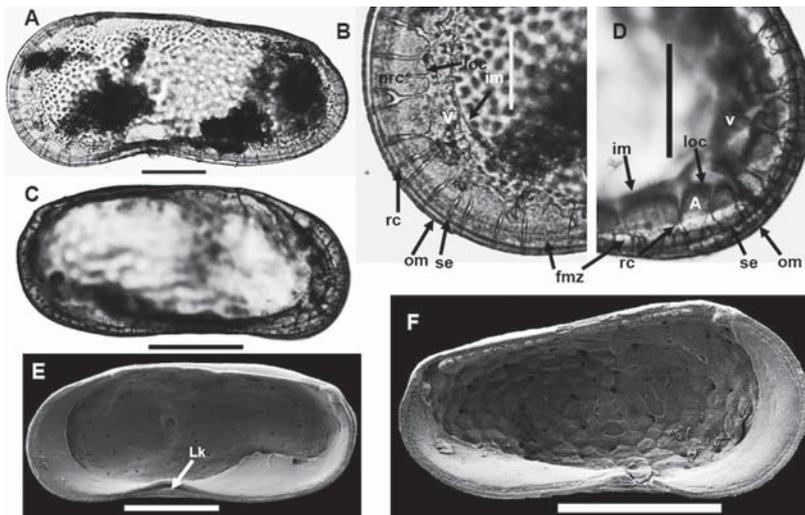

Figure 1. A–B – *Leptocythere prespensis* PETKOVSKI, Recent, Lake Prespa littoral, RV, specimen 5646, TLM internal view; A – general view, B – detail of anterior part from A; C–E – *Leptocythere pellucida* (BAIRD), Recent, Walney Island, beach (U.K.), RV, specimen 8264; C – TLM external view, general aspect; D – detail from C; E – SEM general internal view; F – *Euxinocythere lacunosa* (REUSS), fossil, Late Miocene, stage Pannonian E, Hennersdorf, Vienna Basin, LV, specimen 8227, SEM general internal view. For the explanations of the abbreviations see Material and Methods section. Scale bars: A, D – 0.1 mm, B – 0.05 mm, C, E, F – 0.2 mm.

Some of them open between the selvage and the outer margin, others open outside submarginally (hence we named these as partial radial canals).

The size of vestibulum delineated in this way is variable, ranging from a wide area in *Leptocythere* species to a reduced in the representatives of *Amnicythere*. It is not visible in species belonging to *Euxinocythere*, such as *E. lacunosa* and/or in the genus *Tavanicythere* BOSSIO (GLIOZZI *et al.*, 2005). The vestibulum in species belonging to *Callistocythere* is reduced to two wide spaces delineated by the line of concrescence (BONADUCE *et al.*, 1975).

The fused marginal zone, the calcified area existing between the outer and the inner lamellae, is traversed by the radial pore canals. In the *Amnicythere* species the radial pore canals are simple, digitiform and seldom bifurcate (see Fig. 6C), while in the *Leptocythere* species these canals are short and united in a comb-like shape starting from anterior funnel-shape spaces (Fig. 1C, D).

Between the digitiform areas and the fused marginal zone (Fig. 1D) one notices attached areas (A) similar to those described by VAN MORKHOVEN (1962) for *Caudites nipeensis* VAN DEN BOLD.

3. In the middle of the ventral peripheral area of the valves, between the selvage and the outer margin there is a simple lock system, *i.e.*, the so-called "*Leptocythere* knob" of the right valve (Fig. 1E) fits a less visible excavation on the left valve, the so-called "snap pit". This complex trait characterises the family Leptocytheridae HANAI, 1957 (*cf.* GLIOZZI *et al.*, 2005).
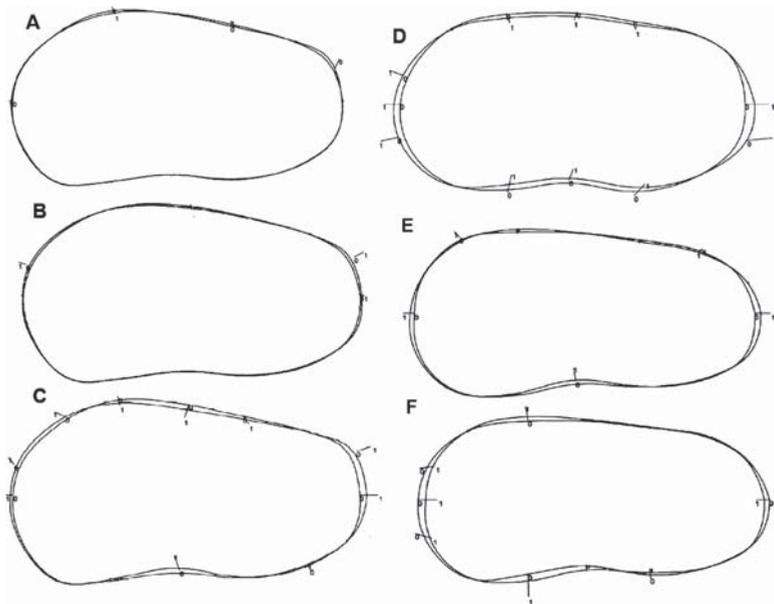

Figure 2.   Comparative analysis of the shape of the *Leptocythere* valves using the standardized algorithm for surface of *Morphomatica* program ver. 1.6 by the superposition of one valve (1) on the reference valve (0); A – *Leptocythere karamani*, female LV (0), specimen 8259 and RV (1), specimen 8260; B – *L. karamani*, female RV (0), specimen 8260 and female RV (1) figured by PETKOVSKI and KEYSER (1992: Fig. 19); C – *L. karamani*, female LV (0), specimen 8259 and male LV (1), specimen 8261; D – *Amnicythere tenuis* (REUSS, *sensu lato*), female LV (0), specimen 8229 and male (1), specimen 2879; E – *Leptocythere prespensis* PETKOVSKI, RVs from Lake Prespa figured by PETKOVSKI and KEYSER (1992: Figs. 12 and 21), female (0) and male (1); F – *L. prespensis*, RVs, specimen 5646 assumed as male (0) and female valve (1) from Lake Prespa from PETKOVSKI and KEYSER (1992: Fig. 12).

4. The hinge of Leptocytheridae is of entomodont type (*cf.* HANAI, 1961; ATHERSUCH *et al.*, 1989) with well developed cardinal teeth on the right valve and an inter-cardinal bar (Fig. 1E). The inter-cardinal anti-slip bar of the left valve has either teeth (Fig. 1F) or is smooth. The structure of this complex trait is characteristic for the various genera of Leptocytheridae (STANCHEVA, 1968; GLIOZZI *et al.*, 2005). *Leptocythere* and *Euxinocythere* species display a denticulated anti-slip inter-cardinal bar (Fig. 1F), and sometimes an anterior tooth is separated from more posterior positioned denticules by a diastema. Species of the genus *Amnicythere* have a smooth inter-cardinal anti-slip bar with a well developed anterior tooth separated from the bar by a diastema (DEVOTO, 1965; STANCHEVA, 1968; see our Figs. 4A–E and 6D-F). This latter tooth displays sexual dimorphism in *Amnicythere* species being longer in the male and shorter and slightly inflated on the female valve (see our Figs. 4A, B, D; 6D).

5. The sexual dimorphism of the carapace shape in dorsal view, and that of the valves in lateral view helps to identify the sex for the valves when no limbs exist. Females have usually a shorter and wider carapace as compared to the male (*cf.* ATHERSUCH *et al.*, 1989). When only the isolated valves exist, the valves shorter and higher in the anterior third may be identified as belonging to females. These differences are clearly visible by superposition of valves and analysis with the morphometric methods (Fig. 2C–F) as previously described.

6. Soft parts diagnosis mainly after HARTMANN and PURI (1974) and ATHERSUCH *et al*. (1989). A1 five-segmented and stout. A2 four-segmented with two terminal claws and 2-jointed spinneret bristle well developed in both sexes. Mdp short, 2nd podomere not larger than other podomeres, exopodal vibratory plate with a main and a secondary ray. Mx1 branchial plate with one type of ray. T1-T3 enlarging progressively towards the rear of the body with setal formula of protopods as: $(1 + 1 : 2 : 1) (1 + 1 : 1 : 1) (1 : 1 : 1)$. CR with two setae. Distal part of HP with two lobes.

3.2. Redescription of *Leptocythere karamani* KLIE, 1939

Valves

In lateral view the left and right valves closely resemble each other in shape, but the left one is slightly higher at the anterior and posterior dorsal corners (Fig. 2A). Slight sexual dimorphism of valve shape and size. Male valves are more elongated and have lesser height than those of the female, especially in the anterior and posterior portions (compare Figs. 2C, 3A and 3D or 4A and 4D). Male carapace length ranges 0.61–0.63 mm, while that of females 0.60–0.65 mm (see measurements below). Maximal height of the valves located in the anterior third represents in the female 53–54% while in the male 51–52% of the maximal length. The height index Hmax/h_{75} in percentage represents 84–85% for females and 83–84% for the males.

The inner lamella is well developed on the anterior and the postero-ventral sides (Figs. 3A–E, 4A and D). A small vestibulum is visible in TLM (Fig. 3A–C). Anterior radial canals long and simple, seldom bi- or tri-furcated with bulbous enlargement located near the fused marginal zone (Fig. 3A–B). The radial canals open within the furrow made by the selvage and the outer margin, while the partial radial canals open sub-marginally on the outer peripheral surface of the valve (Fig. 3B).

Selvage located close to the outer margin and running parallel to this latter except along the central part of the ventral side where it diverges inward. Living specimens display a thin sclerified lamella which protrudes slightly over the outer margin of the valve. The "*Leptocythere*" knob visible on the right valve (Fig. 3E and 4G), while the snap-pit on the left valve is barely visible (Fig. 3H).

The hinge is represented by two elongated cardinal teeth on the right valve. The posterior tooth L-shaped and divided into 5 cusps which decrease in strength from the posterior to the
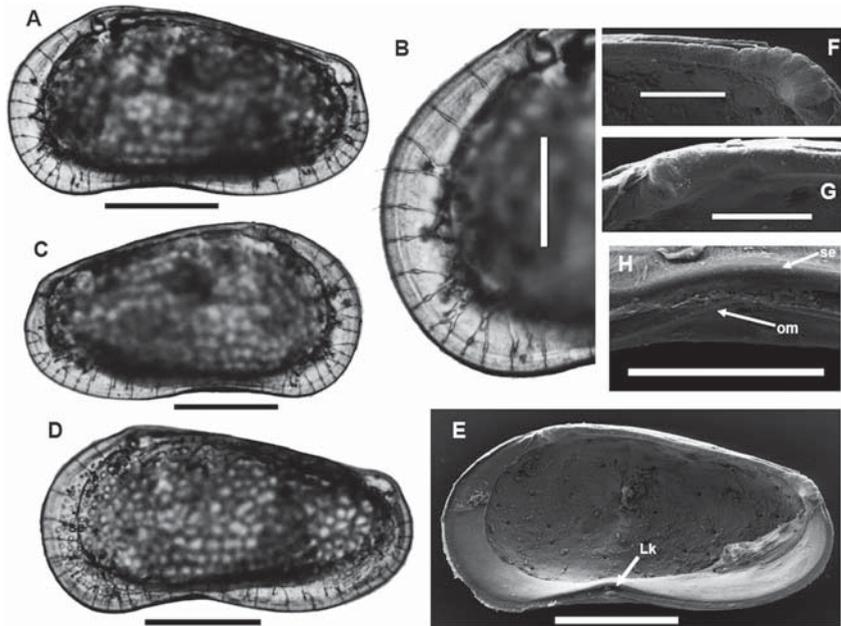
Figure 3. *Leptocythere karamani* Klie, Recent, Lake Ohrid, adult valves; A – female LV, specimen 8259, TLM external view; B – detail, anterior view from A (note the bulbous shape of the radial marginal canals); C – female RV, specimen 8260, TLM external view; D – male LV, specimen 8261, TLM external view; E – female RV, specimen 8260, SEM internal view; F–G – posterior and anterior details of hinge teeth from E; H – male LV, specimen 8261, SEM internal view, detail of central ventral area. Scale bars: A, C, D, E – 0.2 mm; B – 0.1 mm; F–H – 0.05 mm.

anterior side. The anterior tooth slightly divided into 2–3 cusps which decrease in height and increase in elongation (Fig. 3G). The inter-cardinal bar smooth (Fig. 3E).

Left valves with open cardinal sockets connected by a cardinal furrow. The lower wall of the hinge in the left valve has well developed anterior and posterior teeth and a smooth anti-slip bar (Fig. 4A–E). At its anterior side a dimorphic tooth separated by a diastema is visible, namely in the female the anterior tooth is shorter and more rounded (Fig. 4A–B), while in the male it is more elongated (Fig. 4D–E).

The surface of valves is well ornamented with fossae delineated by poorly developed muri (Fig. 4F). On the antero-dorsal side an ocular tubercle appears and on the postero-ventral side in the case of the male a well developed carina develops which continues further ventrally. The flange is well developed on the anterior and posterior sides. The postero-ventral carina is less visible in the female valve.

The valves of the juvenile stage A-1 (L = 541 μm, H = 298 μm, *N* = 1) resemble the shape of the female adult valve (Fig. 7B), however, these are slightly more elongated and less high in the posterior portion (Hmax/h_{75} = 75%).

Measurements: mean ± *SD* (min-max) in μm:
♂ carapace (*N* = 4): L = 623 ± 11.5 (606–629), H = 320 ± 9.0 (308–328),
♀ carapace (*N* = 22 for L, *N* = 10 for H): L = 625 ± 13.1 (599–650), H = 322 ± 13.6 (294–333).
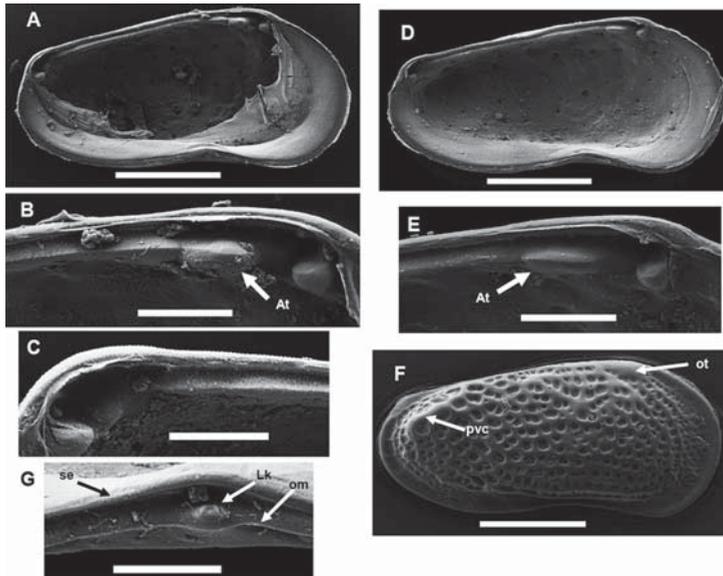Valve coloration: transparent on the margins and light yellowish in the central area.

Figure 4. A–F – *Leptocythere karamani* KLIE, Recent, Lake Ohrid, adult valves viewed in SEM; A – female LV, specimen 8259, general internal view; B-C – anterior and posterior hinge details from A; D – male LV, specimen 8261, internal view; E – anterior hinge detail from D; F – male LV, specimen 8262, external view; G – female RV, specimen 8260, internal detail of central ventral area. For the explanations of the abbreviations see Material and Methods section. Scale bars: A, D, F – 0.2 mm; B, C, E, G – 0.05 mm.

Male appendages

A1 (Fig. 5A–C) relatively short and stout, consisting of five functional movable podomeres, 2-segmented base and 3-segmented ramus. First podomere dorso-distally with a row of thin setulae (pseudochaetae), without any true seta. Second podomere set dorsally with two groups of brushes consisting of long setulae and with one long chelate ventro-distal seta reaching with an accompanying seta half of the length of terminal podomere. Third podomere (the first podomere of the ramus) with one dorso-distal clawlike seta nearly reaching the distal end of terminal podomere. Fourth podomere bears two groups of setae. The first is at the middle of the dorsal margin where the podomere narrows and consists of short and long clawlike setae as well as a single flexible short seta arising from the median side. The points of insertion of the three setae most probably mark the boundary between two former podomeres. The second setae group at the distal margin consists of two long setae (one set dorso-distally and one apically) and one long and one short clawlike setae at the dorso-distal corner between the two flexible setae. The fifth elongated terminal podomere distally with two setae (one short and one long), one clawlike seta and one aesthetasc as long as the podomere. The point of insertion of the aesthetasc is located medially compared to the remaining setae and claw. All clawlike setae or claws on A1 from ca. first third of their length are gutter-shaped and each bear an accompanying fine and flexible hairlike seta arising from the gutter at around distal third of the claw and extending slightly beyond the distal end of the claw.

A2 (Fig. 5D–E) composed of an elongated basal protopod without setae, 3-segmented endopod and long exopod (spinneret seta) extending almost to the tips of the terminal claws and divided at about two thirds of its length. First endopodal podomere sub-quadrangular
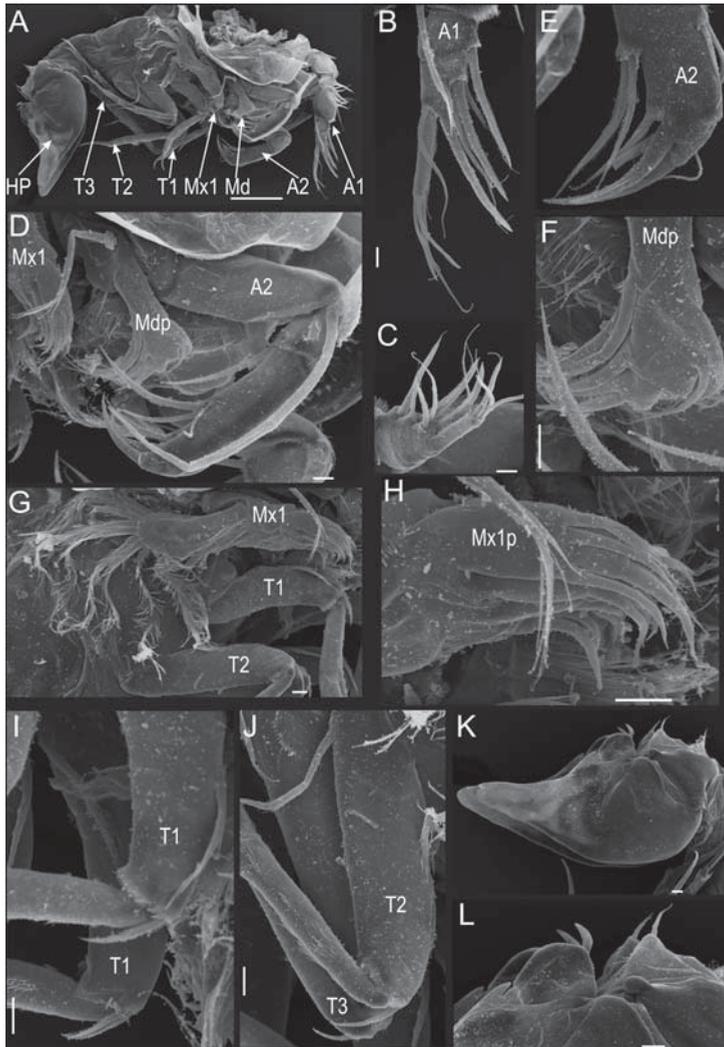
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Figure 5.   *Leptocythere karamani* Klie, male, Recent, Lake Ohrid: A – critical-point-dried entire body without valves viewed from the right side; B – ramus of left A1 in medial view; C – detail of apical chaetotaxy of right A1; D – right A2 and Md in lateral view; E – detail of apical chaetotaxy of left A2 in medial view; F – right Mdp in lateral view; G – right Mx1 in lateral view; H – detail of right Mx1 palp and endites in lateral view; I – T1 articulated joint between protopod and first endopod podomere with knee-setae; J – T2 and T3 knee-setae; K – right HP in lateral view; L – detail of copulatory complex of HP. Scale bars: A – 0,1 mm, B–L – 0,01 mm.

bearing long ventro-distal seta not reaching the end of penultimate podomere. Second endopodal podomere long and narrow, with two unequal setae inserted at two-thirds of the length of dorsal margin, ventro-medially with two unequal setae and one aesthetasc not reaching the distal end of the podomere, as well as with one ventro-distal seta. Terminal podomere set with two strong claws, one subapical and one apical.

Md (Fig. 5D, F) consisting of coxa and 3-segmented palp. Coxa stout, heavily sclerotized and bearing ventrally strong endite armed with six or seven blunt teeth. First palp podomere (protopodal basis) with two unequal, internally directed setae and a greatly reduced exopodal vibratory plate bearing one main very long ray and one short secondary ray. Undivided second palp podomere (first endopodal segment) elongated and bearing in the dorsal two-thirds three externally directed setae (extending beyond the distal end of the terminal podomere), medio-ventrally with four setae (two shorter arising on the medial surface) projected internally as well as ventro-distally with two unequal setae and dorso-distally with one seta. Terminal palp podomere carries three sub-equal clawlike setae and one seta (not seen in all studied specimens).

Mx1 (Fig. 5G–H) composed of a single-podomere protopod bearing three endites, endopod constituting a palp with two podomeres and exopod forming a well-developed branchial plate carrying about 14 normal long and short plumous rays. First palp podomere with three sub-equal dorso-distal setae and dorso-ventrally with one long seta and one very short seta not reaching the distal end of the terminal podomere. Second palp podomere with about three distal clawlike setae. Endites with unknown number of distal setae which are closely packed together and lying on top of one another.

T1 (Fig. 5A, I) slender and 4-segmented. Setal formula of first podomere: 1 + 1 : 2 : 1 (proximal of the two dorsal setae very short). Second podomere elongate, bearing one ante-
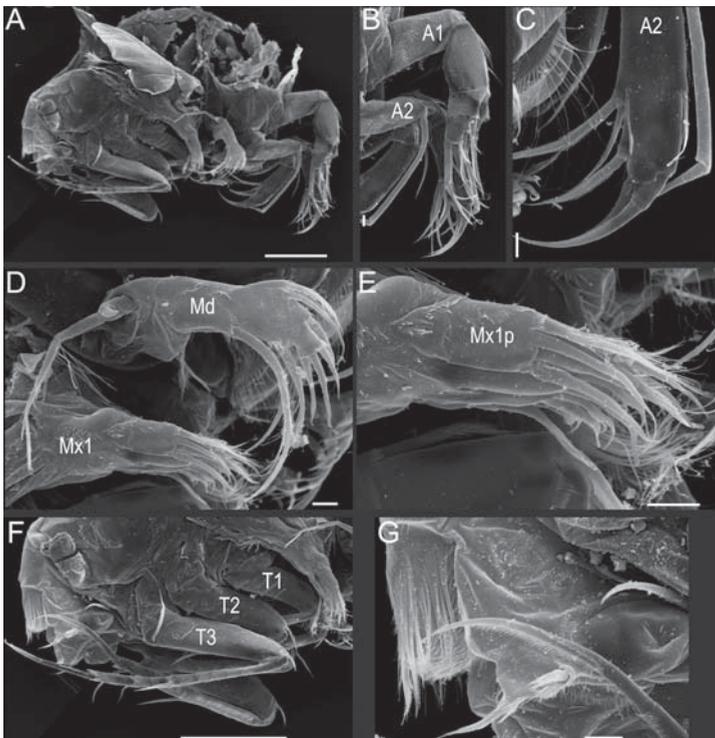

Figure 6. *Leptocythere karamani* KLIE, female, Recent, Lake Ohrid: A – critical-point-dried entire body without valves viewed from the right side; B – right A1 in lateral view; C – detail of apical chaetotaxy of right A2 in lateral view; D – right Md and Mx1 in lateral view; E – detail of right Mx1 palp and endites in lateral view; F – thoracopods and rear end of the body; G – detail of CR and rear end of the body. Scale bars: A, F – 0,1 mm, B–E, G – 0,01 mm.

ro-distal seta not reaching the distal end of the third (penultimate) podomere, which has not any seta. Terminal podomere with a regularly curved claw which is slightly shorter than two last podomeres combined (80–90 : 100).

T2 (Fig. 5A, J) with the chaetotaxial armament of first segment as 1 + 1 : 1 : 1 (proximal of the two dorsal setae very short and not seen in all studied specimens), with antero-distal seta of second podomere reaching slightly beyond the distal end of penultimate after penultimate podomere, and apical claw larger than two last podomeres combined (120–130 : 100).

T3 (Fig. 5A, J) with the larger podomeres and apical claw than those of the preceding walking legs T1–T2. Setal formula of first podomere: 1 : 1 : 1. Antero-distal seta of second podomere as in T2. Apical claw larger than two last podomeres combined (125–136 : 100).

HP (Fig. 5A, K–L) large, occupying c. 1/4 of the male body cavity. Distal lobe of the peniferum elongated and bluntly rounded. Lateral lobe greatly reduced. Proximal lobe pronounced. Ejaculatory duct coiled, with the end enclosed in the copulatory process which forms a short and wide channel terminated by a tooth-like part. Typical for Leptocytheridae curved and finger-like clasping organ reduced or absent (difficult to locate). A small blister-like structure interpreted here as the cup-shaped organ is situated near the base of the caudal extremity with seta.

Nauplius eye with fused cups and black pigmented.

Female appendages (Fig. 6A–G)

Podomere arrangement and chaetotaxial armament similar to those in male. Ratio of the length of the terminal claw to the length of the last two podomeres of T1, T2 and T3 as: 75 : 100, 100 : 100 and 132 : 100, respectively.

CR with two setae. Abdominal extremity conical with obtuse end and with a brush of caudal setulae (Fig. 6F–G).

3.3. Comparative Data

As a first step we compared the shape of our specimens identified as *L. karamani* with the original drawings by Klie (1939, Figs. 19 and 21) and SEM pictures by Petkovski and Keyser (1992, Plate 2, Figs. 19 and 21). Using the standardised for surface morphometic algorithm of *Morphomatica* one can see (Figs. 2B, 5A, 7C) that the valve-shape of our specimens fits remarkably well the outlines published by the above mentioned authors. This means that the general shape of *L. karamani* is very stable. The ornamentation of our specimens also largely conforms to those published by the mentioned authors, respectively, we recognised the same large fossae and the postero-ventral carina (Fig. 4F). However, we noted that in Petkovski and Keyser's (1992) figures (Plate 2, Figs. 19 and 21) there is a difference in the surface ornamentation between the female and the male, that is the female displays fossae of only one order while the male has fossae of two orders. As compared to our observations (Fig. 4F), one sees in the above Petkovski and Keyser's (1992) figures well developed small conuli on the anterior area of the right valves.

In the next step we compared the shape of *L. karamani* with that of other endemic Ohrid species of the genus, *L. proboscidea* and *L. angulata*, as figured by Klie (1939). Figure 5D–E documents slight differences, respectively the outline of the *L. proboscidea* male is more elongate than that of *L. karamani*, while *L. angulata* differs from our material only minimally. The ornamentation of *L. karamani* differs strongly from that of *L. proboscidea* and minimally from that of *L. angulata* as figured by Petkovski and Keyser (1992: Plate 1, Figs. 9 and 11, Plate 2, Figs. 13 and 15).

It is interesting to see that the outline of the valves of *L. karamani* (Fig. 7F) is similar to that of *Amnicythere nodosa* (*sensu* Sokač) from late Miocene at Hennersdorf in the Vienna Basin and with that of *A. fallax* (*cf.* Devoto 1965: Fig. 53A–D). Also the anterior marginal area with its radial pore canals and the anti-slip bar of *A. nodosa* from Hen-
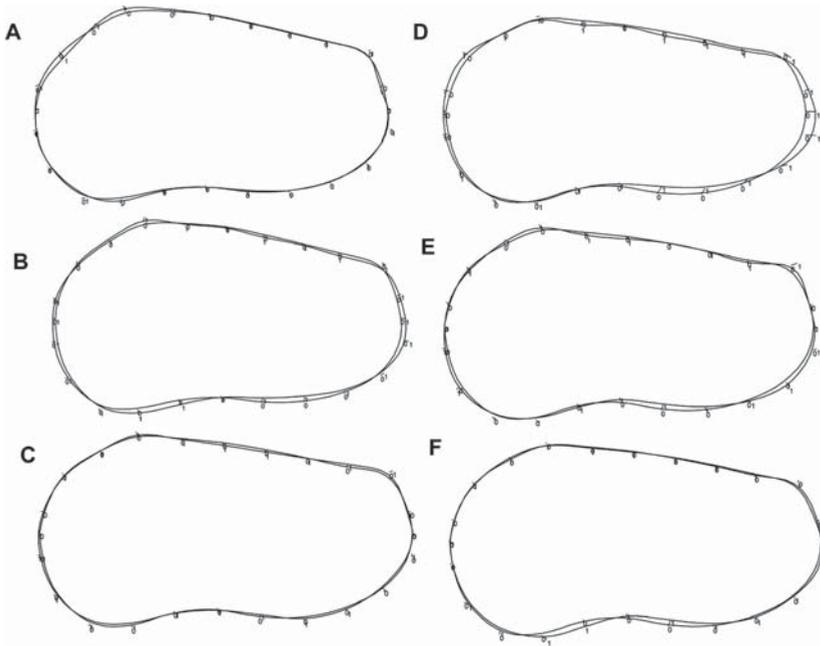
Figure 7. Comparative analysis of the shape of the *Leptocythere* valves using the standardized algorithm for surface of *Morphomatica* programme ver. 1.6 by the superposition of one valve (1) on the reference one (0); A – *Leptocythere karamani* KLIE, female LVs: (0) specimen 8259 and (1) *L. karamani* from KLIE (1939: Fig. 19); B – (0) same as in A and (1) juv. A-1 *L. karamani*, Recent Lake Ohrid; C – *L. karamani*, male LVs: (0) specimen 8261 and (1) *L. karamani* from KLIE (1939: Fig. 21); D – (0) same as in C and (1) male LV of *Leptocythere proboscidea* from KLIE (1939: Fig. 16); E – (0) same as in C and (1) male LV of *Leptocythere angulata* from KLIE (1939: Fig. 27); F – (0) same as in C and (1) male LV of *Amnicythere nodosa* (*sensu* SOKAČ, 1972), fossil, Late Miocene (Pannonian E), Hennersdorf section, specimen 8228.

nersdorf (Fig. 8C–F) are similar. Only the surface ornamentation of the fossil *Amnicythere* (Fig. 8B) differs from that of *L. karamani*, as it displays also the secondary reticulation (*sensu* HORNE *et al*. 2002) besides areas with the primary reticulation.

Finally, it is interesting to note that *L. prespensis* has valves of reduced size, and the shape is only minimally paedomorphic (Figs. 1A and 2E–F). It resembles in this aspect the fossil species *Amnicythere tenuis* (Fig. 2D) from Hennersdorf.

Considering limbs, comparisons of *L. karamani* with other species belonging to the family Leptocytheridae were carried out using our own material of *L. lacertosa* from the Baltic Sea and descriptions provided in the literature. We analysed: a) the other Ohrid-Prespa species (*L. angulata*, *L. proboscidea* and *L. prespensis*) based on descriptions of KLIE (1939), PETKOVSKI (1959) and PETKOVSKI and KEYSER (1992); b) several marine-brackish water *Leptocythere* species from the Atlantic coast of Europe and the Baltic Sea using mainly descriptions by SARS (1925) and ATHERSUCH *et al*. (1989); and c) a number of leptocytherid species assigned to *Leptocythere* and *Amnicythere* from the Black and Caspian seas based on descriptions of SCHORNIKOV (1964; 1966; 1969).

Leptocythere karamani and *L. prespensis* have long ventro-distal seta on the 2nd podomere of A1, extending beyond the distal end of the penultimate podomere (Fig. 5A–B). In the marine and brackish water European *Leptocythere* species as well as in the species
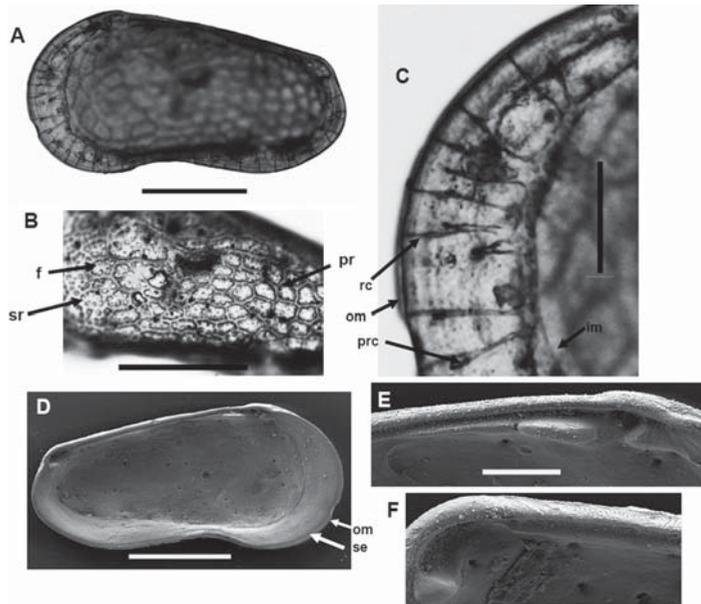
Figure 8. *Amnicythere nodosa* (*sensu* Sokač, 1972), fossil, Late Miocene (Pannonian E), Hennersdorf, male LV, specimen 8228; A – TLM general external view; B – detail of central area (surface ornamentation) from A; C – anterior part with marginal canals from A; D – SEM general internal view; E–F – details of the anterior and posterior parts of the hinge (note the elongated anterior tooth of the "anti-slip bar") from D. Scale bars: A, B, D – 0.2 mm, C – 0.1 mm, E–F – 0.05 mm.

from the Black and Caspian seas assigned to this genus this seta is usually short, just reaching the distal end of the penultimate podomere or shorter, see *e.g.*, Plate 80 in Sars (1925) for *L. castanea* (Sars) and Figs. 5, 7 and 8 in Schornikov (1966) for *L. devexa* Schornikov, *L. nitida* Schornikov and *L. macallana* (Brady and Robertson), respectively. On the contrary, this seta in all examined Caspian and Black Sea species assigned to *Amnicythere* is very long, extending even beyond the distal end of the terminal podomere, see *e.g.* Figs. 6, 9 and 10 in Schornikov (1964) for *A. stratiocostata* (Schweyer), *A. longa* (Negadaev) and *A. gracilloides* (Schornikov), respectively (all these species in this paper as belonging to *Leptocythere* were transferred to *Amnicythere* by Schornikov (1973)).

   Also the morphology of hemipenis of the Ohrid leptocytherids (Fig. 5K–L here and Figs. 18, 23, 24 and 29 in Klie (1939)) differs from that of most *Leptocythere* species. In the Ohrid species a) lateral lobe is totally absent, merged with the copulatory process or reduced (exception *L. prespensis*) *versus* this lobe well developed, usually pointed and orientated posteriorly in the *Leptocythere* species; b) clasping organ reduced or absent (difficult to locate) *versus* this organ well-developed as an elongated posteriorly and curved rod-like process in the *Leptocythere* species; c) copulatory process either elongated tube-like and curved apically in a hook (as in *L. proboscidea* and *L. prespensis*) or less elongated, wider channel terminated by a tooth-like part (as in *L. angulata* and *L. karamani*) *versus* this process relatively simple tube-like in the *Leptocythere* species. Compare *e.g.*, Figs. 33–40 for the British *Leptocythere* species in Athersuch *et al.* (1989) and Figs. 5–7 for the Black sea *Leptocythere* species in Schornikov (1966). In contrast, the Ohrid leptocytherids bear a closer resemblance to the *Amnicythere* species from the Black and Caspian seas in a) the substantial reduction or the absence of an elongated, curved and finger-like clasping organ,

as well as b) underdevelopment of the lateral lobe of the peniferum. Compare *e.g.* Figs. 8–9 and 1–2 in Schornikov (1964 and 1966, respectively) for the *Amnicythere* species from the Black and Caspian seas.

4. Discussion

4.1. The characteristics of the Ohrid leptocytherids and arguments for their taxonomic reassignment

From the information of Klie (1939), Petkovski and Keyser (1992) and our data (see above), it appears that all the species from Lake Ohrid discussed above, viz. *L. karamani*, *L. proboscidea*, *L. angulata* and *L. aff. prespensis*, have an anterior vestibulum predominantly with uni-ramified pore canals, and only antero-ventrally are there a few bi- or tri-ramified ones. In contrast, the *Leptocythere* species are characterised by the comb-like polyfurcate radial pore canals (*cf.* Bonaduce *et al.* 1975; Athersuch *et al.* 1989 and our data above).

The present contribution describes for the first time the hinge structure of an Ohrid leptocytherid, namely that of *L. karamani*. It is of entomodont type with a strong anterior anti-slip tooth and smooth posterior anti-slip bar on the left valve. Such type of hinge structure characterises the genus *Amnicythere*, as defined by Devoto (1965), Stancheva (1968) and reviewed by Gliozzi *et al.* (2005). It differs from the *Leptocythere* type which displays a crenulated anti-slip bar and anterior tooth (*cf.* Hanai, 1961; Athersuch *et al.*, 1989).

The shape of the valves for the three Ohrid leptocytherids (*L. angulata*, *L. karamani* and *L. proboscidea*) is elongate with an oblique dorsal margin, pointing to a neotenous origin. It resembles the shape of fossil species of Lake Pannon (*e.g.*, *A. nodosa* in Sokač, 1972) and of the Pleistocene species from Central Italy, *A. fallax* (Devoto, 1965).

The valve morphology of the *Leptocythere prespensis* resembles that of *Amnicythere tenuis*, a species widely distributed in the Parathetys domain during the Middle and Late Miocene (Danielopol *et al.*, 2011b; authors' data).

Finally, the results from the comparative morphological studies on limbs appeared in agreement with those on the valves. The Ohrid leptocytherid species bear a closer resemblance in the chaetotaxy of A1 and the hemipenis morphology to the living representatives of the genus *Amnicythere* rather than to those of the genus *Leptocythere*. Furthermore, differences between the Balkan non-marine leptocytherids in the hemipenis morphology indicate that *L. karamani* may represent a more derived clade, whereas *L. prespensis* and *L. ostrovskensis* Petkovski and Keyser seem to be more ancestral, as suggested by Namiotko *et al.* (2011a). As regards the genus *Amnicythere*, most of the c. 70 species assigned to it (Kempf, 1980; 1997) are known from fossils without information on the morphology of soft parts. We were able to compare our material from Lake Ohrid with only about half of c. 11 living representatives of *Amnicythere* known at present, all inhabiting fresh to oligo-(meso-)haline waters of the basins of Black-Azov, Caspian and Aral seas (Schornikov, 1972; 2011b). Unfortunately, there is still a lack of consensus in the literature on the generic assignment of several extant leptocytherid species and specific relationships within *Amnicythere* remain ambiguous (Schornikov, 2011a), although some authors have already attempted to improve the diagnosis of this genus based on the limb morphology criteria (Schornikov, 1973). To disentangle this taxonomic problem detailed morphological studies and complete descriptions of all living species are a prerequisite.

Considering the above comparative data we conclude that the leptocytherid species of Lake Ohrid should be assigned to the genus *Amnicythere* Devoto, 1975.

4.2. On the Biogeographic Origin of the Ohrid Leptocytherids

As mentioned in the introduction, most Leptocytheridae species are distributed in marine habitats. However, the Ohrid leptocytherids belong to a genus which mainly has lake-dwelling species. The most ancient *Amnicythere* species, *A. tenuis* (REUSS) is known from Miocene (Sarmatian, respectively Late Serravallian) marine facies in the Central and Eastern Paratethys domain (*e.g.*, CERNAJSEK, 1974; RADU and STOICA, 2005; TOTH, 2008). This species or possibly closely related species of this phylogenetic lineage occurred also in Lake Pannon (*cf.* SOKAČ, 1972; KRSTIĆ, 1973; DANIELOPOL *et al.*, 2011b). Other fossil *Amnicythere* species were inhabitants of low saline non-marine habitats (Late Miocene-Pliocene) in Eastern Europe (STANCHEVA, 1968; OLTEANU, 1995). Some *Amnicythere* species still exist in the Aral, the Caspian and the Black seas, living in fresh to brackish waters (SCHORNIKOV, 1972; 1973; 2011a; 2011b). They were also found in Italy and Spain in Late Messinian deposits belonging to the so-called *Lago-Mare* (GLIOZZI *et al.*, 2005). The type species of the genus, *Amnicythere fallax* (DEVOTO), is a fossil (Pleistocene) species sampled in a shallow freshwater lacustrine facies with influx of running water in the Liri Valley, Central Italy (DEVOTO, 1965).

ALBRECHT and WILKE (2008) reviewed the main hypotheses on the origin of Lake Ohrid and its fauna. One of them, the "Lake Pannon derivate hypothesis", is relevant to our topic, namely that some of the Lake Ohrid species derived from faunistic elements which originally existed in Lake Pannon and which spread through temporary stepping-stone lacustrine connections during the Miocene and/or Pliocene. The morphological similarity between the studied specimens of *Amnicythere nodosa* (*sensu* SOKAČ, 1972) from Lake Pannon in the Vienna Basin at Hennersdorf (Pannonian E stage) and *Amnicythere karamani* (KLIE) allows us to advance the hypothesis that the Ohrid leptocytherids could be related to species which pre-existed in Lake Pannon. We consider that some of these latter taxa were able to colonise lakes in southern Europe including the Balkans after they adapted to a freshwater environment.

The evidence for this assertion is the existence of *A. fallax* in Pleistocene in Italy, south of Rome, and the fossil and Recent distribution of freshwater leptocytherids in the Balkans, including the Late Pliocene record of *A. karamani* from the Megalópolis Basin in Greece, the Early Pleistocene records of two leptocytherid species in Prevlaka, Croatia as well as all leptocytherids living today in the Dessaretes lake-system, that is Lake Ohrid, Lake Prespa, Lake Vegoritis and Lake Pamvotis (GRIFFITHS and FROGLEY, 2004). Therefore, it is very plausible that the Ohrid *Amnicythere* fauna is derived from lineages which originally existed in Lake Pannon and from which by stepping-stones spread to southern European freshwater systems like the Dessaretes lake area. Note that PETKOVSKI and KEYSER (1992) reported *Leptocythere prespensis* (known previously only from Lake Prespa) or a closely related species to occur also in Lake Ohrid. The colonisation of Lake Ohrid by leptocytherids from the other Dessaretes lakes could occur directly by various hydrological connections, like the karstic connection with Lake Prespa (*cf.* ALBRECHT and WILKE, 2008; ALBRECHT *et al.*, 2008; BELMECHERI *et al.*, 2009) or by inter-lake long-range passive dispersion. SYWULA (1990) described such a long-range passive dispersion for *Cytherissa lacustris* (SARS), and one should note that DEVOTO (1965) in the lacustrine facies of the Liri Valley found *Amnicythere fallax* together with *Cytherissa lacustris* as well as with several typical shallow-water dwelling species. Therefore, we favour for the biogeographic origin of the leptocytherids of Lake Ohrid colonisation from one of the surrounding former Dessaretes lakes. When exactly the colonisation of Lake Ohrid by leptocytherids happened and if there was one or several invasions can not be resolved at present.

5. Concluding Remarks

The biodiversity of Lake Ohrid fascinated many generations of naturalists. Two questions were repeatedly asked: (1) from where the various animal groups colonised Lake Ohrid, and (2) how the huge endemic diversity we nowadays observe has developed during the time.

The Ohrid Leptocytheridae offer an example of colonisation by non-marine ostracods. Because of their relationship with leptocytherid taxa from Tertiary lakes in Central and Eastern Europe and with those still presently existing in the Caspian and the Black seas, it offers a unique chance to continue a comparative investigation of their evolutionary pathways, respectively their genetic relationships, physiological adaptations and morphological polymorphism. We need to better understand their ecological distribution, especially their salinity tolerance. It is strange that in the last stage of Lake Pannon (the so-called Paludina-lake) which existed in Serbia during the Late Pliocene and at the beginning of the Pleistocene (KRSTIĆ, 1995) the leptocytherid group became extinct.

To fulfil the above mentioned programme of research one should combine the modern perspective traced by CRISTESCU *et al.* (2010) with the more classical actuo-palaeontological approach, as proposed in DANIELOPOL *et al.* (2008). We recall here that during the 6th European Ostracodologists' Meeting in Frankfurt/Main in 2007 (EOM-6) these latter authors proposed a programme of cooperative projects dealing with a renewal of ostracod investigations of the Parathetys Sea and Lake Pannon. *Inter alia*, two topics were especially underlined as important tasks: (1) the update of the systematics of the various ostracod groups in order to closely match the fossil system with that of the living fauna, and (2) the reciprocal transfer of ostracodological information derived from research on recent and fossil taxa. The present study on the *Amnicythere* of Lake Ohrid combined with information from the palaeo-Lake Pannon and those of the Caspian and the Black seas fulfil the aims proposed during the EOM-6. We would like to see other colleagues following this way of research which is intellectually stimulating.

The endemic fauna of Lake Ohrid has a cultural value. It is the material on which generations of dedicated scientists will be able to work in the future, using their scientific creativity. In this sense the remarkable fauna and the whole environment of Lake Ohrid have to be protected because they represent humanity's values.

6. Acknowledgements

7. Postscript

After we completed this MS we received the publication of I. SCHÖN and K. MARTENS, "Molecular analyses of ostracod flocks from Lake Baikal and Lake Tanganyika", Hydrobiologia **682**: 91–110. The authors propose for the dispersal of a cytheroid ostracod a scenario similar to our *Amnicythere* model, namely from the ancient Lake Baikal, where most of the fauna is supposed to be ecologically specialised, one of its representatives, *Cytherissa lacustris* (SARS), spread outside the lake and colonised other lacustrine systems at a regional scale.

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