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A new phytal limnic ostracod *Rosacythere carpathica* sp. nov. from the Upper Cretaceous of the Western Carpathians: implications for evolution of the Timiriaseviinae

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ABSTRACT

Rosacythere first appeared in the Bajocian and for a long time was only a minor genus that flourished during the Early Cretaceous in freshwater lakes of humid and hot tropical climate and characterized by a dominance of charophytes. An apparent decline of morphologically diversified *Rosacythere* with the beginning of the Late Cretaceous could be related to marine transgression and expansion and domination of angiosperms in freshwater macrophytic communities. *Rosacythere* reappeared in Santonian–Campanian organodetrinitic limestone with the dasyclad alga *Munieria*, adapted to limnic conditions. *Rosacythere carpathica* sp. nov., *Neuquenocypris (Alleniella) colloti*, and two unidentified ostracod taxa colonised this environment, which offered ostracods similar living condition to the Early Cretaceous charophyte meadows.

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1. Introduction

Nonmarine Mesozoic ostracods diversified mainly during the Late Jurassic–Early Cretaceous and their associations are well known from many parts in the world (Colin and Carbonel, 1996). The events at the Cretaceous–Tertiary boundary did not affect the nonmarine ostracods; a sharp diversity decrease of the typical Mesozoic genera *Timiriasevia* and *Cypridea* is evident from the Albian onwards (Babinot et al., 1996) although they persisted in Paleogene intracontinental basins of Asia and India (Guan, 1988; Bhandari, 1998). The extinction of most of the Timiriaseviinae could be related to their narrow ecological tolerance limits, poor dispersion abilities, and paleogeographical and paleoclimatological disturbances (Colin and Danielopol, 1979). The earliest individuals having generic diagnostic features of *Rosacythere* Colin, 1980 (carapace about 0.5 mm, rosette ornamentation, inverse hingement with positive elements on the left valve, no or one to two vertical sulci, marked sexual dimorphism) were discovered in Middle Jurassic deposits (Colin and Carbonel, 1996). This limnic genus had

a main period of speciation from Aptian to Cenomanian (Colin and Carbonel, 1996) with 11 known species. Later, only the phylogenetically related *Frambocythere* and *Kovalevskiella* evolved from the same *Kovalevskiella* group with a period of maximum development in the late Maastrichtian–early Eocene (*Frambocythere*), and Oligocene–Recent (*Kovalevskiella*), the latter restricted to stygobitic environments (Colin and Carbonel, 1996; Gidó et al., 2007). A discovery of freshwater ostracods in the Upper Cretaceous *Munieria* limestone of the western Carpathians has enlarged the stratigraphical range of *Rosacythere*. We describe the morphology and relations of this new *Rosacythere* to other taxa and we analyse its water habitat. We also discuss the paleobiogeographical distribution of *Rosacythere* taxa and possible causes of an apparent decrease in the diversity of the genus following changes in the composition of aquatic macrophytes during the Cretaceous.

2. Material and methods

The limestone was dissolved in a 10% solution of acetic acid for 24 hours. After this chemical procedure, the material was washed on sieve mesh 0.08 mm, dried in a drying machine and successively observed by binocular and scanning electron microscope. Thin sections were made at the Faculty of Natural Sciences in Bratislava.

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All the ostracod and alga specimens are deposited in the Slovak National Museum (SNM) in Bratislava (Slovakia) under catalogue number No. RPxx-yy.

3. Geological and stratigraphical setting

The outcrop No. 336/98 Ostrá skala is situated approximately 1 km SW from hill Ostrá skala on southern margin of Slovenský raj National park in central Slovakia, northwest of the town Dobšiná (Fig. 1; 48° 51' 57,7" N; 20° 16' 53,3" E). The outcrop is a part of the

terrigenous and carbonate succession preserved as a denudation relict on the Triassic carbonates of the Silica Nape and Meliata Unit. Mello et al. (2000) compared the sedimentary succession with Gossau Group and Havrila in Mello et al. (2000) divide it into two groups with an intermediate marine member between them (Fig. 2). The lower, freshwater –?brackish group is composed of two contemporaneous and alternate facies. (A) Dark, grey and brown carbonate claystone and marl with coal seam, and (B) grey and brown detritic limestone with the alga *Munieria grambasti sarda* Cherchi et al., 1981, and ostracod *Neuquenocypris (Alleniella) colleti*

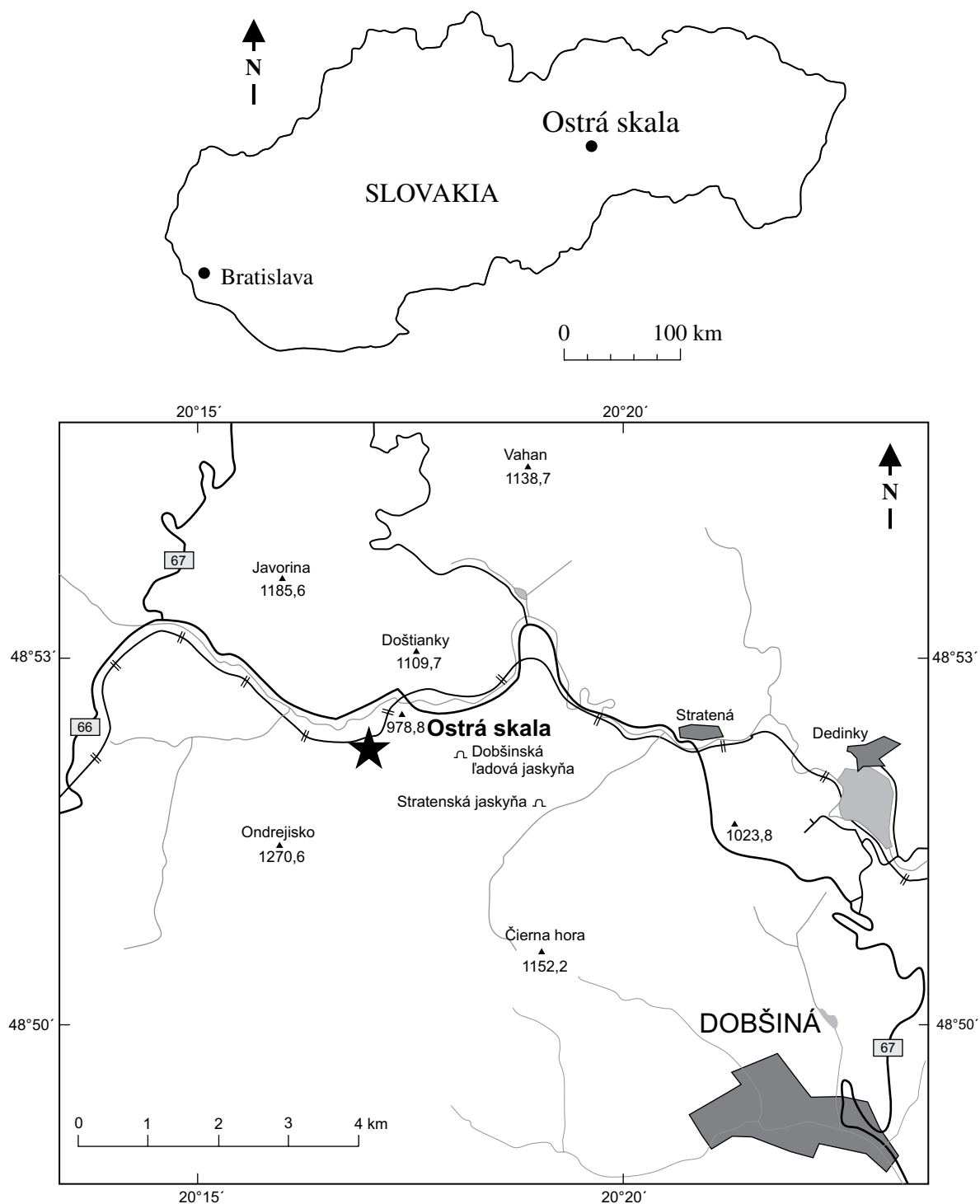


Fig. 1. Map showing the geographical position (black star) of the outcrop No. 336/98 Ostrá skala.

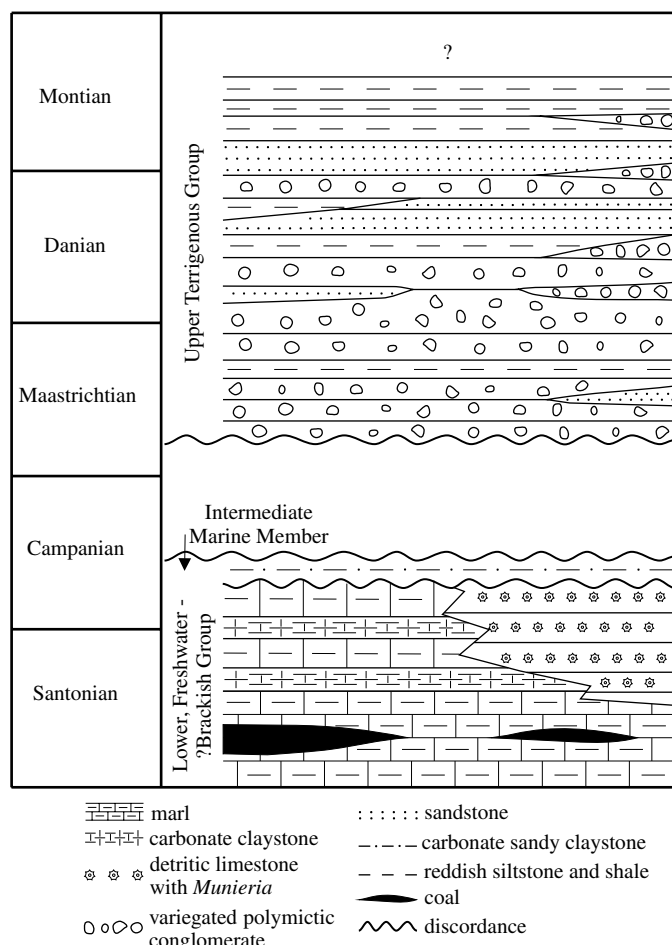


Fig. 2. Lithostratigraphic column of the Upper Cretaceous and Paleogene terrigenous and limnic carbonate succession in the environs of Slovenský raj National park (Slovakia) (after Mello et al., 2000, modified).

(Babinot, 1975) known from the Campanian and Maastrichtian deposits of southern France (Babinot et al., 1996).

A dark grey marl and sandy carbonate claystone (Fig. 2) is an intermediate member between the lower and upper group. Andrusov and Snopková (1976) discovered in these deposits a rich Santonian and Campanian palynomorph association of the Normapolles group: *Oculopolis orbicularis*, *O. parvoculus*, *O. zaklinskaiae*, *Papilopolis minimalis*, *Semiculopolis praedicatus*, *S. lapillus*, *Pseudooculopolis principalis*, *Trudopolis capsula*, *T. conector*, and *T. rusticus*. The planktonic foraminifers *Globotruncana arca* and *G. fornicata plummerae* and the benthic one *Stensioeina pommerana* recorded in the same deposits occurred in the early Campanian. The other planktonic foraminifers *Globotruncana linneiana linneiana*, *G. linneiana marginata*, *G. fornicata fornicata*, *G. cretacea*, and *G. aff. tricarinata* may reflect marine incursions of a freshwater sedimentary basin (Samuel, 1977; Mello et al., 2000). Thus, the lower group has a stratigraphic range of Santonian–Campanian and a limestone of the profile No. 336/98 that is a part of lower group is of the same age. The upper group is composed of variegated polymictic conglomerate, sandstone and reddish siltstone and shale. Discordance is supposed between the lower and upper groups but a discordance surface is not observable on the existing outcrops. This discordance is proved by the presence of *Munieria* limestone pebbles in the upper group. Only rare and badly preserved foraminifers *Globorotalia* and *Globigerina* of the Upper Cretaceous and Paleogene were found (Scheibnerová, 1960). Mello et al. (2000) estimated a Maastrichtian–Paleocene age for this group.

4. Lithology and paleoenvironment of the lower, freshwater –?brackish group

4.1. Carbonate claystone and marl facies

The carbonate claystone, marl, and carbonate clayey schist of the lower facies are only sporadically visible on the surface. A clayey carbonate matrix of this weakly bioturbated claystone and marl with parallel lamination is also composed of framboidal pyrite and the grains of the clastic quartz, muscovite, chlorite, and Cr spinels. Carbonaceous plant detritus, sporomorphs, and ostracods are present only occasionally. Noth (1874) and Illés (1904) noted a presence of 50 to 150 mm thick coal lenses and small gastropod and bivalve shells in these deposits.

4.2. Detritic limestone facies

The outcrop No. 336/98 Ostrá skala (Fig. 1) is composed of light grey and brown organodetritic limestone with alga *Munieria* (Fig. 3). A length/diameter ratio of thali segments of *Munieria* from Ostrá skala shows a close relation to *Munieria grambasti sarda* from Cenomanian lacustrine algal limestone of Sardinia (Cherchi et al., 1981), Coniacian (?)–Santonian Ajka Coal Formation of Hungary (Gellai and Tóth, 1982; Haas, 1999), upper Santonian–lower Campanian Gosau Group of Austria (Schlagintweit and Wagneich, 1992) and differs in this ratio from *Munieria grambasti grambasti* Bystrický, 1976 (Fig. 4). The limestone is classified as grainstone, packstone, and wackestone with laterally and vertically variable organic detritus content. The limestone is fine grained with frequent parallel and sporadically lenticular cross lamination and graded bedding with a variable bed thickness from 30 to 210 mm. *M. grambasti sarda* is a permanent and the most abundant rock forming component. The algal peloids originating from the destruction of bluegreen algae mats are also abundant and they become the dominant particles, together with almost complete *Munieria* thali, in the grainstone layers (Fig. 3). Previous studies (Martín-Closas, 2000; Schudack, 1989) consider *Munieria* to belong to the Charophyta, indicative of freshwater environments. A new morphological study of the Cretaceous *M. baconica* attributes this alga to the Dasycladales living mainly under marine conditions, but dasyclad genera can live in brackish waters or even in freshwater (Feist et al., 2003).

Upper Cretaceous *Munieria* are known from the Bitumenmergel Member in the eastern Alps (Schlagintweit and Wagneich, 1992), where they occur in the deposits of a freshwater, well-aerated, locally anoxic marl lake in the vicinity of an open marine basin (Russeger et al., 1998). They are associated mainly with gastropods and bivalves, less commonly with Characeae and the sclerosponge *Didemnoidea moreti* (Durand Delga, 1957) (Bodrogi et al., 1994). This alga was found together with *Atopochara* in Ajka Coal Formation (Hungary) (Gellai and Tóth, 1982; Feist et al., 2003) formed in a freshwater basin in transition to brackish conditions (Haas, 1995). This led us to conclude, in accordance with Feist et al. (2003), that *Munieria* lived in a limnic environment and a resemblance of *Munieria* to Charophyta may then be regarded as convergence in relation to the habitat. The carapaces and valves of *Rosacythere carpathica* sp. nov. are frequent and relatively abundant. This genus is known from purely freshwater and mixed freshwater/brackish Cretaceous taphocenoses (see section 6). *Neuquenocypris* is a non-marine Cretaceous pandemic genus. Numerous species were described from the characean zone of *Tolypella grambasti* of Maastrichtian age in Patagonia (Musacchio and Simeoni, 1989). *Neuquenocypris* (*Alleniella*) *colloti* and two other non-specified ostracod taxa (Fig. 5K,L) are persistent but rare components of the sedimentary sequence at the outcrop No. 336/98 Ostrá skala. Characeans (*Chara* sp.), sclerosponges (*Didemnoidea moreti*), the

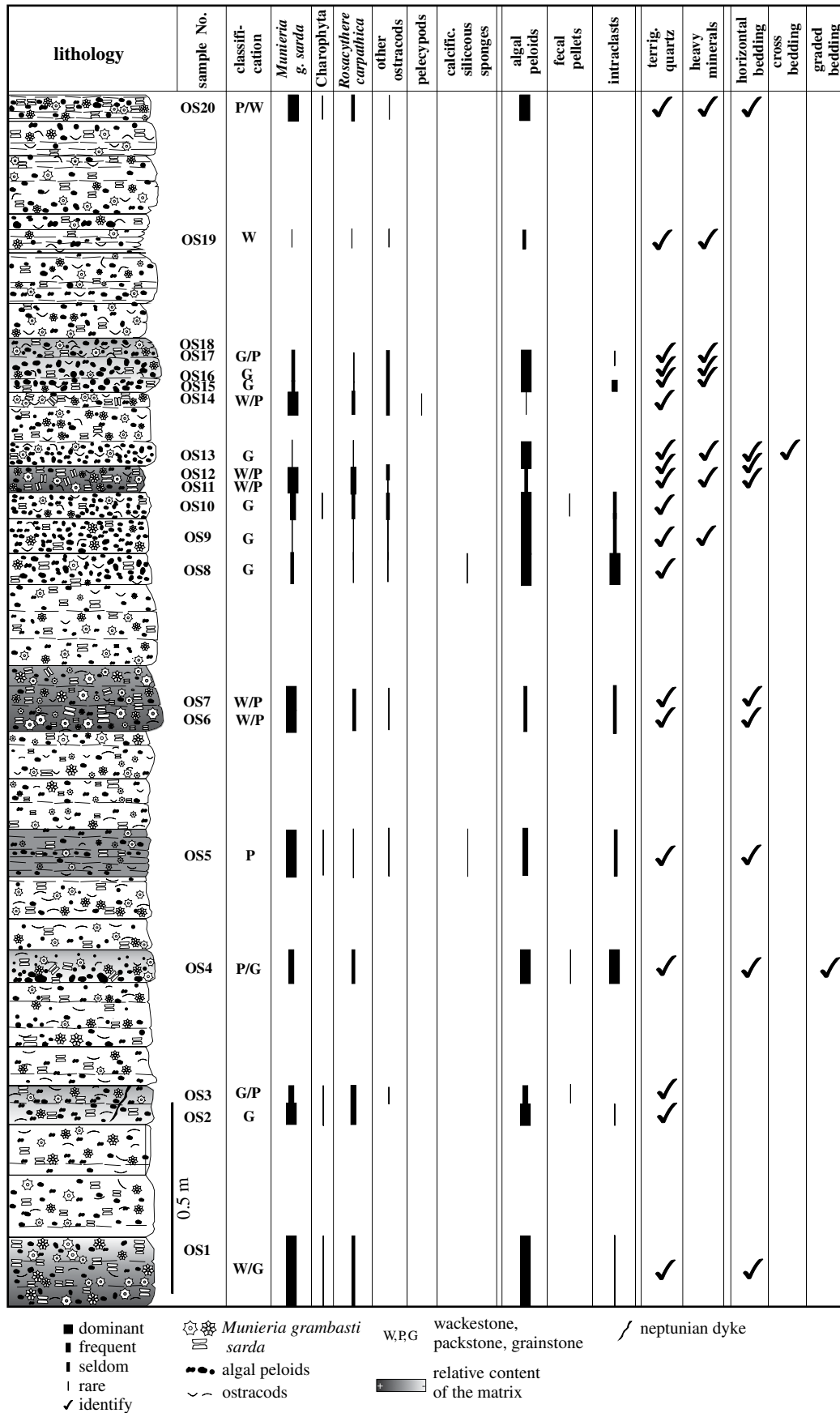


Fig. 3. Lithological column of organodetritic *Munieria* limestone and distribution of the rock forming components in the outcrop No. 336/98 Ostrá skala.

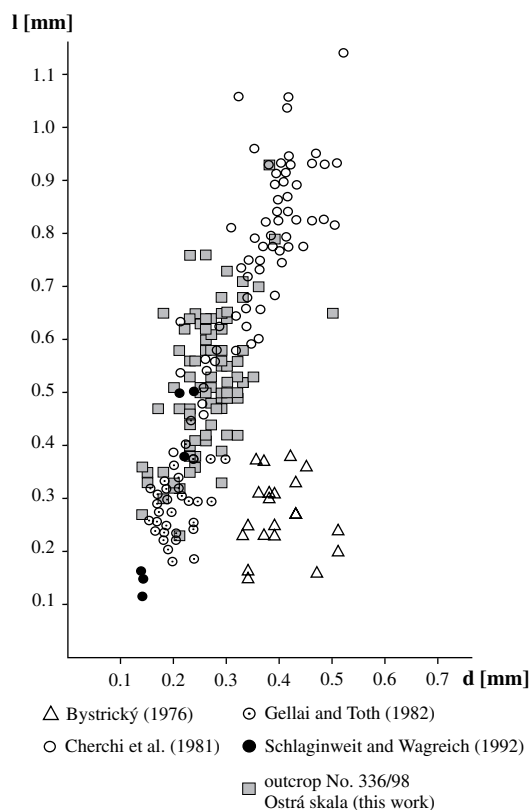


Fig. 4. Length (h) / diameter (d) ratio of the *Munieria* thalus segments. Measured thali fall into the field of *Munieria grambasti sarda* Cherchi, Gušič, Schmidt, and Schroeder, 1981.

coprolite *Helicerina kainachensis* Fenninger and Hubmann, 1994, hexactinellid spicules, rhaxes and *Gemeridella minuta* Borza and Mišík, 1975 all occur rarely (Fig. 3). *Gemeridella minuta* is rarely present in layers 4, 8, 10 of the outcrop No. 336/98. Mišík and Borza (1978) suppose its algal origin. This algal problematicum was identified in marine, mainly basinal deposits of the western Carpathians ranging from Carnian to early Albian age.

Didemnoidea moreti was identified in layers 4, 5, and 9 of the studied outcrop. This microfossil is known as spicula ascidians (Bonet and Benveniste-Velasquez, 1971). Bodrogi et al. (1994) attribute *D. moreti* to coralline sponges. *D. moreti* is known from the western Carpathians in marine pelagic and shallow limestones of the Carnian to lower Albian, and elsewhere from the Upper Cretaceous lacustrine Bitumenmergel Member in Austria (Bodrogi et al., 1994). *Gemeridella minuta* and *D. moreti* are here identified for the first time in the Upper Cretaceous deposits of the western Carpathians and their association with freshwater fauna and flora is exceptional. Crustacean coprolites identified as *Helicerina kainachensis* were occasionally found in layers 3, 4, and 5 and are also recorded from the western Carpathians deposits for the first time. The diameter of the coprolites ranges from 0.29 to 0.44 mm. They contain four lateral, two basal, one dorsal, and one median canals (Fig. 5P). These coprolites are also known from the freshwater upper Santonian–lower Campanian limestone of the Kainach Gosau Group in which the diameter of coprolites attains a maximum of 0.39 mm (Fenninger and Hubmann, 1994). Clastic mineral grain of the quartz, Cr spinels, and zircon in the range from 0.0 to 0.2 mm, or 0.5 mm are rare and their content is below 1%. The fossil components of the studied organodetrinitic limestone are of both marine (*Didemnoidea moreti* and *Gemeridella minuta*) and nonmarine (*M. grambasti sarda*, *Rosacythere*, *Neuquenocypris* (*Alleniella*) *colloti*, *Helicerina kainachensis*, *Chara* sp.) origin. The nonmarine

components prevail in their frequency and abundance over the marine components, which are rare (in fact, *Didemnoidea moreti* is also known from lacustrine formations, see above) and thus the grey and brown detritic limestone with *Munieria* are considered to be of nonmarine, freshwater origin.

5. Systematic paleontology

Other abbreviations—ACM, antero-central margin; ADM, antero-dorsal margin; AM, anterior margin; C, carapace; DM, dorsal margin; h, height of the valve in mm; h/l, height/length ratio; l, length of the valve in mm; LV, left valve; N, number of measured specimens; PDM, postero-dorsal margin; PM, posterior margin; PVM, postero-ventral margin; RV, right valve; VM, ventral margin; w, width of the carapace in mm; ϕ , average; ♀, female valve; ♂, male valve.

Class: OSTRACODA Latreille, 1802
 Subclass: Podocopa Sars, 1866
 Order: Podocopida Sars, 1866
 Suborder: Cypridocopina Jones, 1901
 Superfamily: Cypridoidea Baird, 1845
 Family: Ilyocyprididae Kaufmann, 1900
 Genus *Neuquenocypris* Musacchio, 1973
 Subgenus *Alleniella* Musacchio and Simeoni, 1991

Type species. *Neuquenocypris* (*Alleniella*) *tenuipunctata* Musacchio and Simeoni, 1991, p. 370–371, fig. 6; fig. 10 (1–2, 5–7).

Neuquenocypris (*Alleniella*) *colloti* (Babinot, 1975) Fig. 5A–J

1975 *Ilyocypris colloti* n.sp. Babinot, p. 7–8, pl. 1, figs. 7–14.

1980 *Ilyocypris colloti* Babinot, 1975; Babinot, p. 246–247, pl. 51, figs. 1–3.

1980 *Ilyocypris* cf. *colloti* Babinot, 1975; Bessière, Tambareau, Villatte, p. 291, pl. 1; fig. 12.

1985 *Ilyocypris colloti* Babinot, 1975; Babinot, Colin, Damotte, pl. 69, figs. 4–6.

1987 *Ilyocypris colloti* Babinot, 1975; Babinot, p. 198, pl. 2, fig. 18.

1996 *Neuquenocypris* (*Alleniella*) *colloti* (Babinot, 1975); Babinot, Colin, Tambareau, p. 167.

Material. Several dozen carapaces. The open valves are rare. Remarks. *N. (Alleniella) colloti* is known from the lower Campanian continental Fuvélien deposits of Provence and upper Maastrichtian Auzas Marls of Petites-Pyrénées (both in France).

Suborder: Cytherocopina Gründel, 1967
 Superfamily: Cytheroidea Baird, 1950
 Family: Limnocytheridae Klie, 1938
 Subfamily: Timiriaseviinae Mandelstam, 1960 emended Colin and Danielopol, 1978
 Genus *Rosacythere* Colin and Danielopol, 1980 emended Colin and Carbonel, 1996

Type species. *Theriosynoecum grekoffi* Colin, 1974, p. 185–187, pl. 1, figs. 1–7, text-fig. 1.

Rosacythere carpathica sp. nov.
 Fig. 6A–N

Derivation of name. After Carpathians, central European mountain range.

Type material. Holotype: SNM RP34-18, a complete LV♀ and 13 paratypes: SNM RP34-11, C; SNM RP34-12, C; SNM RP34-13, C;

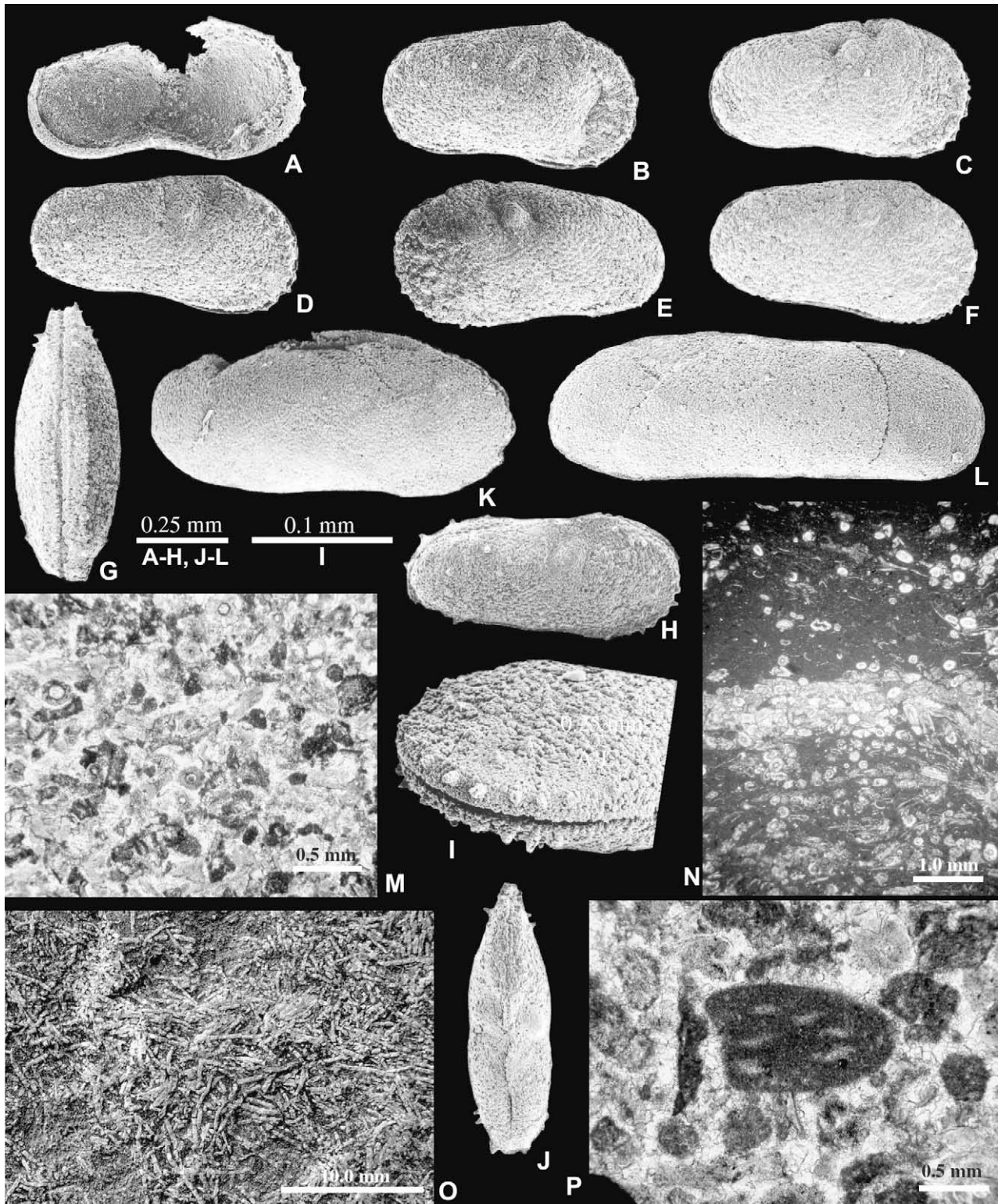


Fig. 5. *Neuquenocypris (Alleniella) colloti* (Babinot, 1975), Ostrá skala, sample OS19 73. A, LV, No. RP34-1, internal lateral view. B, Carapace from the right side, SNM RP34-2, external lateral view. C, Carapace from the right side, SNM RP34-3, external lateral view. D, Carapace from the right side, SNM RP34-4, external lateral view. E, Carapace from the left side, SNM RP34-5, external lateral view. F, Carapace from the right side, SNM RP34-7, dorsal view. G, Carapace, SNM RP34-8, ventral view. H, Carapace from the right side, SNM RP34-6, external oblique lateral view. I, Detail of the anterior margin, SNM RP34-6, external oblique lateral view. J, Carapace, SNM RP34-6, dorsal view. K, Ostracod gen. et spec. indet 2, carapace, SNM RP34-10, Ostrá skala, sample OS19, 750 external lateral view. L, Ostracod gen. et spec. indet 1, carapace, SNM RP34-9, Ostrá skala, sample OS19, external 753 lateral view. M, Bioclast association composed of *Munieria grambasti sarda*, *Rosacythere carpathica* sp. nov. and peloids in grainstone, layer No. 16. N, *Munieria grambasti sarda* and valves and carapaces of *Rosacythere carpathica* sp. nov. in laminated limestone, layer No. 12. O, Thali of *Munieria grambasti sarda* visible on weathering surface of the limestone. P, Crustacean coprolite *Helicserina kainachensis* Fenninger and Hubmann, 1994 in grainstone, layer No.17.

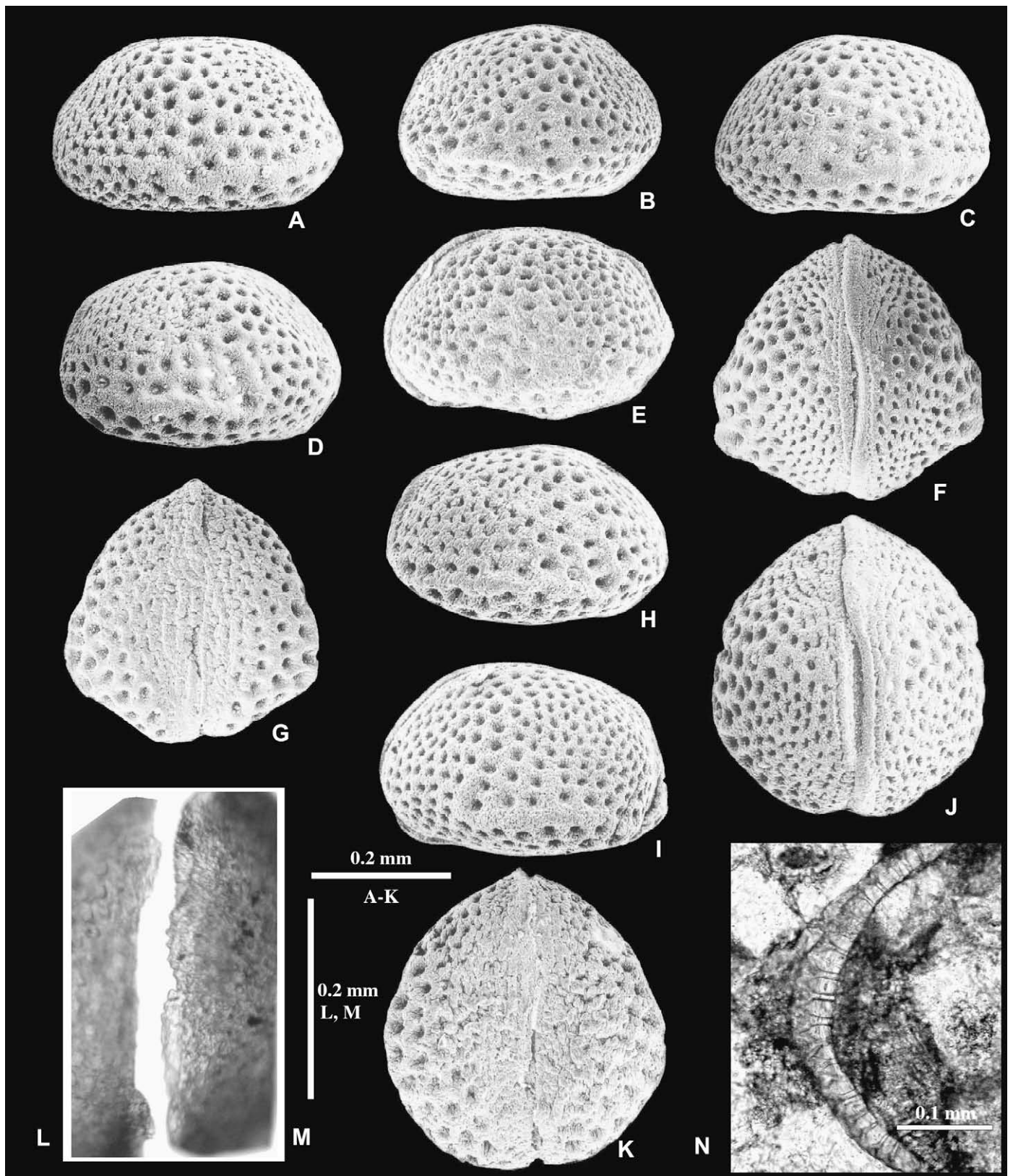


Fig. 6. *Rosacythere carpathica* sp. nov., Ostrá skala, sample OS19. A, LV♀, holotype, SNM RP34-18, external lateral view. B, C ♂ from the right side, paratype, SNM RP34-22, external lateral view. C, LV♂, paratype, SNM RP34-15, external lateral view. D, RV♀, paratype, SNM RP34-17, external lateral view. E, C ♀ from the left side, paratype, SNM RP34-23, external lateral view. F, C ♂, paratype, SNM RP34-11, dorsal view. G, C ♂, paratype, SNM RP34-13, ventral view. H, C ♀ from the right side, paratype, SNM RP34-25, external lateral view. I, C ♀ from the left side, paratype, SNM RP34-24, external lateral view. J, C ♀, paratype SNM RP34-12, dorsal view. K, C ♀, paratype, SNM RP34-14, ventral view. L-M, Hingement in transmitted light in dorsal view. M, LV♀, paratype SNM RP43-3; L, RV♂ paratype SNM RP43-4. N, Thin section of outer lamella of *Rosacythere carpathica* sp. nov. The conical pits terminate in pore canals, sample OS11, SNM RP26700.

SNM RP34-14, C; SNM RP34-15, LV; SNM RP34-17, RV; SNM RP34-22, C; SNM RP34-23, C; SNM RP34-24, C; SNM RP34-25, C; SNM RP43-3, LV; SNM RP43-4, RV; thin section SNM RP26700.

Type locality. Outcrop No. 336/98 Ostrá skala (Fig. 1); coordinates–48° 51' 57,7" N; 20° 16' 53,3" E.

Stratigraphic horizon: *Munieria* limestone of Santonian–Campanian, Upper Cretaceous.

Diagnosis. *Rosacythere carpathica* sp. nov. has large circular and conical fossae, centro-ventral and longitude carina, broad carapace in dorsal view, and inverse lophodont hinge. The width of the carapace approaches or is equal to the length of the carapace.

Description. LV♀ (holotype) anterior curved; DM straight to slightly curved; anterior and posterior angles well rounded; DM passes to long, oblique, and curved PDM, PM strongly rounded; VM straight to slightly concave; outline elongated, sub-elliptical; ventral part large and flat; maximum height at middle length. RV♀ -ACM rounded; ADM long and slightly curved; DM curved and sloping toward posterior; anterior angle not visible; posterior angle tapered; PM behind the posterior angle straight and oblique, then curved; VM rounded, concave; outline elongated, sub-elliptical; ventral part large and flat; maximum height at anterior.

Sexual dimorphism: obvious on adult carapaces and valves, indistinct on juvenile carapaces of A-1 stage; males are slimmer in the postero-dorsal area, without brood pouch; centro-ventral carina of the male more prominent and looking like ears in dorsal view (Fig. 6F).

Overlap: evident; RV overlaps the LV along entire contact of the valves.

Muscle scars: not visible.

Hinge: inverse lophodont (Fig. 6L, M).

The hinge of the LV is composed of a large, elongate anterior tooth; median groove and robust, elongated posterior tooth. The hinge of the RV has an elongated socket, median bar, and elongated posterior socket.

Ornamentation: prominent; surface covered with circular and conical fossae (Fig. 6N), which terminate in normal pore canals on the interior surface; the largest fossae are in the central area and their diameter becomes smaller toward the outer margin; a longitude carina is developed on centro-ventral area; sulci absent.

Marginal zone: inner lamella 0.065 mm wide at AM and of the same size at PM; it is slightly larger on VM; inner margin at PVM inwardly situated; this inward position is more expressed on the LV than on the RV; other characters not clearly visible.

Other material and Dimensions. Several hundred complete and damaged carapaces and disarticulated valves.

Remarks. *Rosacythere carpathica* sp. nov. is attributed to the group *Kovalevskiella* on the basis of the inverse lophodont hinge, the most significant character, which clearly distinguishes this group from all other groups in the subfamily Timiriaseviinae (Gidó et al., 2007). It differs from *Frambocythere* and *Kovalevskiella* of the same group by having the ventro-posterior margin displaced inwardly. The other genera have one or two deep sulci (Colin and Carbonel, 1996; Gidó et al., 2007) which are apparently missing on *Rosacythere carpathica* sp. nov. The ornamentation of *Frambocythere* is composed of small circular fossettes (Colin and Carbonel, 1996), but the surface of *Rosacythere carpathica* sp. nov. is covered with circular fossae. *Rosacythere carpathica* sp. nov. differs from other *Rosacythere* by having the large and conical fossae, and by lacking a conspicuous anterior angle on the antero-dorsal margin. It differs from *R. lacobrigensis* Cabral and Colin, 1998 in that its valves are rounded in external lateral view and it lacks a sulcus. The

posterior surface of *R. grekoffi* is covered by tubercles (Colin and Danielopol, 1980). *R. ? consobrina* from the late Cenomanian of Utah (Tibert et al., in press) seems very similar with regard to absence of the sulcus, but the maximum width of *R. carpathica* sp. nov. is situated at middle length. No other described *Rosacythere* species has as broad a carapace as *R. carpathica* sp. nov., in which the width reaches the length of the carapace.

6. *Rosacythere* in evolving Mesozoic lacustrine ecosystems

6.1. Jurassic and Early Cretaceous *Rosacythere*

The oldest *Rosacythere* appeared in the Bajocian of France (Fig. 7) in association with *Timiriasevia* sp., *Cypridea ? postelongata* (Cypridoidea, Cyprideinae) and charophytes. Timiriaseviinae competed in nonmarine habitats with Cyprideinae which were better at dispersal (Colin and Danielopol, 1979) which could be the reason why *Rosacythere* species were still a minor and neglected group in mid-Mesozoic lakes. *Rosacythere* reappeared in the Berriasian–Barremian faunas composed of nonmarine *Cypridea*, *Darwinula* and

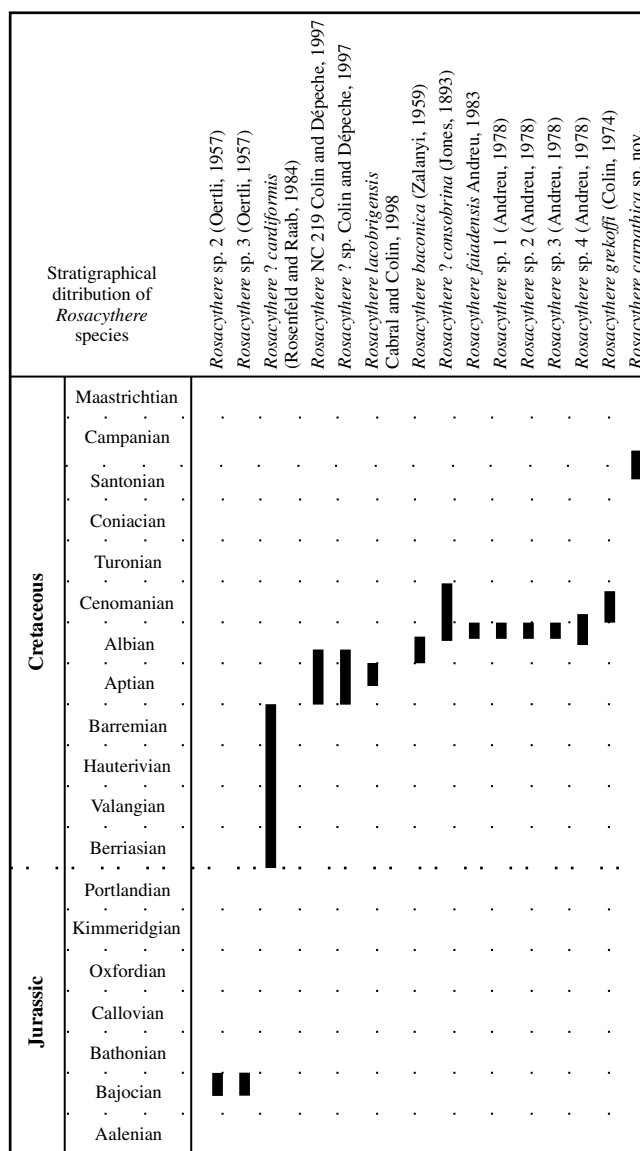


Fig. 7. Stratigraphical distribution of *Rosacythere* species (after Colin and Carbonel, 1996; Colin and Dépêche, 1997; Swain, 1999; Császár, 2002; Tibert et al., in press).

Vecticypris together with marine *Antepaijenborchella*, *Metacytheropteron* and *Veeniacythereis* (Honigstein et al., 1985; Rosenfeld et al., 1988). *Rosacythere* became more diversified in the tropical and humid Tethyan domain (Figs. 7,8) (Cabral and Colin, 1998; Fluteau et al., 2007), when the Aptian transgression accelerated the disappearance of true *Theriosynoecum* (Colin and Danielopol, 1979). *Rosacythere lacobrigensis* from Portugal is confirmed from a freshwater-oligohaline milieu covered by charophytes (Cabral and Colin, 1998). *Rosacythere* ? sp. Colin and Dépêche, 1997 and *R. NC 219* Colin and Dépêche, 1997 settled the intra-cratonic moderately alkaline lakes of West Africa, in a hot climate with alternating humid and arid seasons, but the genus was not found up to now in the South American freshwater basins with strong faunal similarities to the African ones (Colin and Dépêche, 1997; Fluteau et al., 2007). Apart from *R. laconbrigensis*, two other species lived until the early Albian. The late Albian seems the most favourable period in the diversification of *Rosacythere* (Fig. 7). The genus also spread to the North American continent (*R. ? consobrina* (Jones, 1893)) (Swain, 1999; Tibert et al., in press) with a high morphological similarity to the Berriasian–Barremian *R. ? cardiformis* (Rosenfeld and Raab, 1984), but the nonmarine environment of southwestern Europe was the main centre of its diversification (Fig. 8). Five described species were found as allochthonous assemblage components in association with marine *Cytherelloidea*, *Bairdia*, *Neocythere*, *Rehacythereis*, *Limburgina*, *Pterygocythereis*, *Dolococytheridea*, euryhaline *Neocyprideis*, *Risaltina*, and freshwater *Cetacella* ? and *Vecticypris*? (Andreu, 1978, 1983). *R. baconica* (Zalányi, 1959) seems a key species for next evolution of the genus. It absolutely prevails in the mixed marine (*Paracypris*, *Cytheridea*, *Cytherella*) and freshwater (*Candona*, *Darwinula*, *Metacypris*) associations from the lower and middle Aptian Tés Clay Formation in Hungary deposited under nonagitated shallow-water conditions (Zalányi, 1959; Császár, 1986, 2002). Its mass occurrence was observed in gray clay, but Zalányi (1959) notes a slight increase in individual abundance of *R. baconica* in a limestone with *Munieria baconica* what appears the earliest discovery for co-existence of *Rosacythere* with dasyclad alga. The Albian *Rosacythere* ? *consobrina* and *R. sp. 4* (Andreu, 1978)

survived until the Cenomanian, and new *R. grekoffi* appeared at this time in association with freshwater *Vecticypris* (Colin, 1974) and charophytes (Babinot et al., 1996). Cenomanian *Rosacythere* ? cf. *consobrina* was found with other freshwater ostracods in estuarine/lagoonal biofacies of humid to semi-humid tropical climate and dominated by brackish *Fossocytheridea*, *Asciocythere* and *Hourcqia* (Tibert et al., in press; Fluteau et al., 2007).

6.1.1. Variability in outline

The outline of *Rosacythere* from the left lateral view is variable and with a well pronounced antero-dorsal angle (Fig. 9B–E). This variability is remarkable from a dorsal view. The male carapaces have an elliptical (Fig. 9H), drop-like outline, slim at anterior (Fig. 9I), or elliptical, large at anterior and posterior (Fig. 9J). This morphological variability in outline signifies a high rate of speciation just as found in other Mesozoic Timiriaseviinae (Colin and Danielopol, 1979).

6.1.2. *Rosacythere* and charophyte habitat

The Jurassic and Early Cretaceous *Rosacythere* were associated with the charophytes, which dominated freshwater macrophytes between the Permian and Early Cretaceous (Martín-Closas, 2003) and their high diversification during the Late Jurassic and Early Cretaceous in the Tethyan realm was connected with global extension of freshwater environments (Martín-Closas, 2003; Martín-Closas et al., 2007). The charophytes colonised shallow, well illuminated areas affected by oscillating water tables (Martín-Closas and Gomez, 2007). As laboratory experience shows, *Chara* offers a suitable microhabitat for protection of ostracods against predation and provides more food than other water plants (Mbahinzireki et al., 1991). If *Rosacythere* species were phytophilous taxa living on charophytes, their high diversification in the Early Cretaceous times is not surprising. Moreover, *Rosacythere baconica* co-existed with the freshwater dasyclad *Munieria baconica* in the Early Cretaceous (Zalányi, 1959). It is worth mentioning the same ecological preferences and habitat of early Miocene *Kovalevskiella* (Carbonel et al., 1986) and an extant timiriaseviine, *Metacypris cordata*, living in

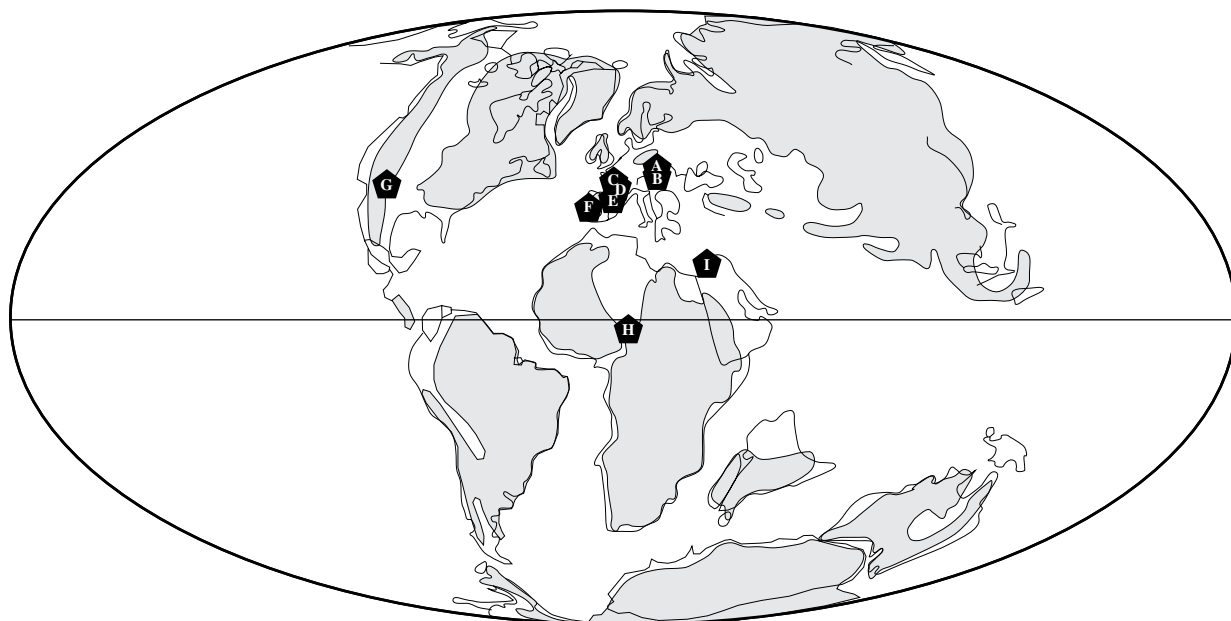


Fig. 8. Late Cretaceous (94 Ma) paleogeographical situation (Scotese, 2001) and distribution of *Rosacythere* A. *R. carpathica* sp. nov.; B. *R. baconica* (Zalányi, 1959); C. *R. sp. 2* (Oertli, 1957), *R. sp. 3* (Oertli, 1957); D. *R. grekoffi* (Colin, 1974); E. *R. sp. 1* (Andreu, 1978), *R. sp. 2* (Andreu, 1978), *R. sp. 3* (Andreu, 1978), *R. sp. 4* (Andreu, 1978), *R. faiadensis* (Andreu, 1983); F. *R. lacobrigensis* Cabral and Colin, 1998; G. *R. ? consobrina* (Jones, 1893); H. *R. NC 219* Colin and Dépêche, 1997 and *Rosacythere* ? sp. Colin and Dépêche, 1997; I. *R. ? cardiformis* (Rosenfeld and Raab, 1984) (after Rosenfeld et al., 1988; Colin and Carbonel, 1996; Colin and Dépêche, 1997; Tibert et al., in press).

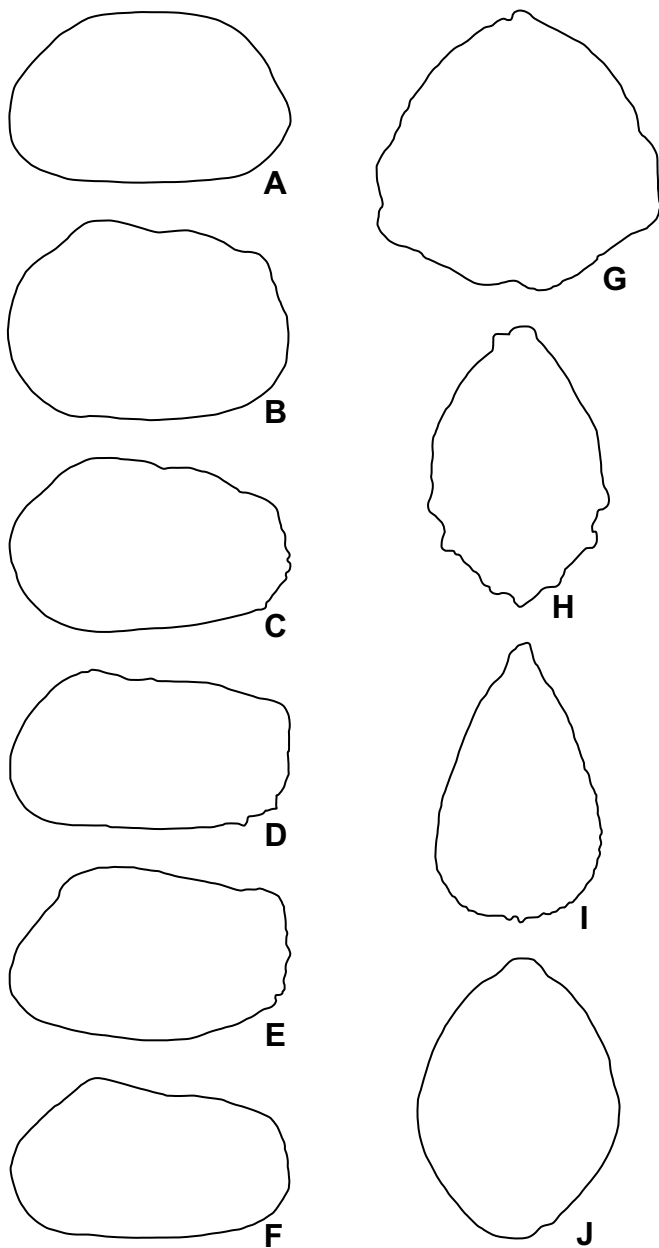


Fig. 9. LV in external lateral view and carapaces in dorsal view of *Rosacythere* species. The outline displays a high morphological variability similar to other Mesozoic Timiriaseviinae. A, G. *R. carpathica* sp. nov., A. ♀; C. ♂; B, H. *R. grekoffi* (Colin, 1974), B. ♀; H. ♂; C, I. *R. baconica* (Zalányi, 1959), C. ♀; I. ♂; D, J. *R. lacobrigensis* Cabral and Colin, 1998, ♂; E. *R. NC 219* Colin and Dépêche, 1997, ?♂; F. *R. sp. 2* (Oertli, 1957), ??, Not to scale.

shallow water habitats formed by roots of macrophytes and organogenic sediments (Danielopol et al., 1996). An allochthonous occurrence is the second feature of the Jurassic and Early Cretaceous *Rosacythere*. They occur in taphocoenoses composed of marine and brackish taxa indicating a position of the freshwater habitats close to the sea under a humid and hot tropical climate.

6.2. Biotic and abiotic changes during the Late Cretaceous

In the Late Cretaceous, marine transgression flooded large continental areas (Fluteau et al., 2007) which certainly strongly influenced the limnic habitats close to the sea. The composition of aquatic macrophytes changed and angiosperms expanded and

Table 1

Dimensions in mm of *Rosacythere carpathica* sp. nov. from the outcrop No. 336/98 Ostrá skala

	N	l	φ	H	h/l	w	φ
LV♀ holotype	1	0.421	–	0.253	0.60	–	–
LV♂ paratype	1	0.395	–	0.258	0.65	–	–
RV♀ paratype	1	0.414	–	0.273	0.66	–	–
C♀	29	0.399–0.453	0.428	–	–	0.367–0.44	0.403
C♂	21	0.382–0.434	0.409	–	–	0.364–0.427	0.387
C A-1	15	0.322–0.35	0.336	–	–	0.276–0.324	0.298
C A-2	2	0.263–0.281	–	–	–	0.218–0.237	–

dominated almost all freshwater macrophytic communities worldwide (Martín-Closas, 2003; Cohen, 2003). These biotic changes in the mid–late Mesozoic also affected insect diversification, prey–predator relationships and geochemical recycling in lakes (Cohen, 2003). During the Cenomanian–Coniacian, the diversity of European limnic ostracods decreased and numerous taxa disappeared (Babinot et al., 1996). Species diversification and emergence of new genera in Europe, some of them extant, started in the Santonian (Babinot et al., 1996; Khand, 2000), and at the end of the Cretaceous a European ostracod fauna expressed an affinity to Argentinean and Indian ones (Babinot et al., 1996; Bajpai and Whatley, 2001). 3

6.3. Late Cretaceous

Rosacythere reappeared in limnic faunas at the end of the Cretaceous in the *Normapolles* province broadly centered on eastern North America and Western Europe in a paleolatitude from approximately 20 to 45°N (Sims et al., 1999) and characterised by a temperature higher than at present (Amiot et al., 2004). This reappearance is linked to the occurrence of the freshwater dasyclad *Munieria* (Fig. 3) with its similar external morphological organization to that of the charophytes. This environment (Fig. 5O) could offer the same conditions for the life of *Rosacythere carpathica* sp. nov. as did the Early Cretaceous charophyte meadows, with regard to refuge and food sources. The phytal zone covered by *Munieria* and rarely by *Chara* also hosted *Neuquenocypris*, a pandemic non-marine ostracod genus occurring with charophytes (Musacchio and Simeoni, 1989). An external lateral view of the valves of *R. carpathica* does not show a prominent antero-dorsal angle (Fig. 9A) and the width of the carapace became very large and almost equal to its length (Fig. 9G, Table 1). This extension enlarged the capacity of the female brood pouch in which the fertilized eggs hatched and juveniles lived. A female of *Metacypris cordata* with a similar outline in dorsal view to *Rosacythere carpathica* sp. nov. is capable of retaining about 12 eggs and juveniles inside the carapace, which moult two or three times before leaving the brood pouch (Danielopol and Horne, 1996; Meisch, 2000), but slimmer *Kovalevskiella* sp. retains only the eggs and juveniles of the first stage (Meisch, 2000). It seems that a larger brood pouch could increase the number of the surviving juveniles, because Timiriaseviinae show slow post-embryonic development (Meisch, 2000). Thus, an adaptation to life on dasyclad algae and enlargement of the carapace helped *Rosacythere* to survive in newly evolved lacustrine ecosystems.

7. Conclusions

The discovery of *Rosacythere* in an Upper Cretaceous limestone shows that the genus did not become extinct in the Cenomanian, as previously thought. A co-occurrence with dasyclad alga *Munieria* in the early and middle Aptian helped this phytal genus to survive the major Cretaceous paleogeographical and paleobiological changes.

The presence of *Rosacythere carpathica* sp. nov. in a freshwater limestone confirms its strictly lacustrine nature and habitat within freshwater macrophytes (Babinot et al., 1996). *Rosacythere* enlarged its carapace and fully adapted to an environment with the *Munieria*.

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