

A TRIASSIC GIANT AMPHIPOD FROM NEVADA, USA

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ABSTRACT

A giant fossil amphipod *Rosagammarus minichiellus* n. gen., n. sp. occurs in a Triassic limestone (Luning Formation, west-central Nevada) in association with ichthyosaurs (*Shonisaurus* sp.) and the deep-water trace fossil *Protopaleodictyon* ichnosp. Fossil pereion and pereopod morphology suggest affinities with Acanthogammaridae, a freshwater amphipod family largely endemic to Lake Baikal. The large size (17 cm) of the Triassic amphipod shows that supergiant, deep marine amphipods comparable to modern *Alicella gigantea* Chevreux, 1899 were extant during the early Mesozoic. By analogy with *A. gigantea*, *R. minichiellus* was likely a necrophagous, benthopelagic scavenger that fed on ichthyosaur and other sea floor carcasses. *Rosagammarus minichiellus* appears to be the oldest known fossil amphipod, extending the known geological range of Amphipoda by at least 170 million years.

KEY WORDS: Acanthogammaridae, Amphipoda, giant amphipods, Nevada, Triassic

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INTRODUCTION

Fossil amphipods are astonishingly rare considering their diversity and abundance in the modern biota. This may be the case because amphipods decay rapidly after death in comparison to isopods and other better sclerotized and mineralized crustaceans (Hurley, 1958). Also, amphipods typically inhabit groundwater environments or marine habitats below the Calcium Carbonate Compensation Depth (CCD), where preservational conditions are not favorable (Holsinger and Longley, 1980).

Although amphipods are thought to have a Carboniferous origin (Bousfield, 1982a, b; Bousfield and Poinar, 1994), until now their fossils are unknown before the late Eocene. Woodward (1870) interpreted the Silurian fossil *Necrogammarus* as an amphipod, but Selden (1986) showed that this fossil is an incomplete specimen of a pterygotid eurypterid. Bate (1859) interpreted the Permian crustacean *Palaeocranion* as an amphipod, but Glaessner (1957) showed that it is in fact an isopod. Cretaceous amphipods were reported by Alonso et al. (2000), but Vonk and Schram (2007) demonstrated that these specimens are in fact fragmentary tanaids.

True amphipods *Niphargus*, *Palaeogammarus*, *Synurella*, plus members of Cragonyctidae occur in Eocene-Oligocene Baltic amber (Zaddach, 1864; Stebbing, 1888; Lucks, 1928; Hurley, 1973; Just, 1974; Jazdzewski and Kulicka, 2000a, b, 2002; Coleman and Myers, 2001; Coleman and Ruffo, 2002; Weitschat et al., 2002; Coleman, 2004, 2006; Jazdzewski and Kupryjanowicz, 2010). Miocene amber has produced *Andrussovia*, *Gammarus*, *Hellenis*, and *Praegmelina* and other taxa (Hurley, 1973; Mukai and Takeda, 1987; Karasawa, 1997).

Coleman (2004: 122) notes that it is a mystery how these "aquatic animals could have been preserved in amber." Some

appear to have been desiccated before preservation and were windblown into the amber-forming resin (Coleman, 2004). Terrestrial amphipods (Talitridae) in amber have been reported from Chiapas, Mexico (Bousfield and Poinar, 1994) and the Dominican Republic (Bousfield and Poinar, 1995). Modern talitrids frequently dry out and die when they are washed up in the strandline.

Many extant families and genera of amphipods may have lived during the Mesozoic (Myers and Lowry, 2003). Karaman (1984) established new genera for several fossil groups, and at present some 13 genera and 26 species of fossil amphipods are known.

MATERIAL AND METHODS

A Mount Holyoke College expedition to the Shoshone Mountains, Nevada during May 2013 produced a Triassic fossil specimen that appears to be the oldest known amphipod, the largest fossil amphipod, and the first amphipod confirmed from pre-Cenozoic strata. The new specimen was collected in Union Canyon to the east of the eastern boundary of Berlin-Ichthyosaur State Park (Fig. 1). The fossil is associated with specimens of the graphoglyptid trace fossil *Protopaleodictyon* ichnosp. (Fig. 2). In turn, *Protopaleodictyon* is associated with the *Nereites* ichnofacies (Seilacher, 1967; Frey and Pemberton, 1984), thus confirming the inference of Holger (1992) of a deep-water environment for the Upper Shaly Limestone Member of the Luning Formation.

The fossil preserves portions of two leg types that are characteristic for Amphipoda. It consists of a partial dorsal pereion with portions of three pereopods, two with large coxal plates and one with a smaller coxa (Figs. 3-10). The taxonomically significant coxa 5 is preserved in its entirety, still in its proper orientation with respect to the basis of pereopod 5 (Fig. 7). Fine details of cuticular structure are preserved on the fossil surface (Figs. 6, 9). The anterior or posterior regions of the animal are not preserved, but the specimen is nevertheless sufficiently complete to permit establishment of the new taxon, *Rosagammarus minichiellus* n. gen., n. sp.

We estimate that *R. minichiellus* had a total length of 17 cm. Although this is only one half the length of the largest specimens of *Alicella gigantea* Chevreux, 1899, *R. minichiellus* is nevertheless a giant amphipod comparable to modern supergiant deep-water amphipods.

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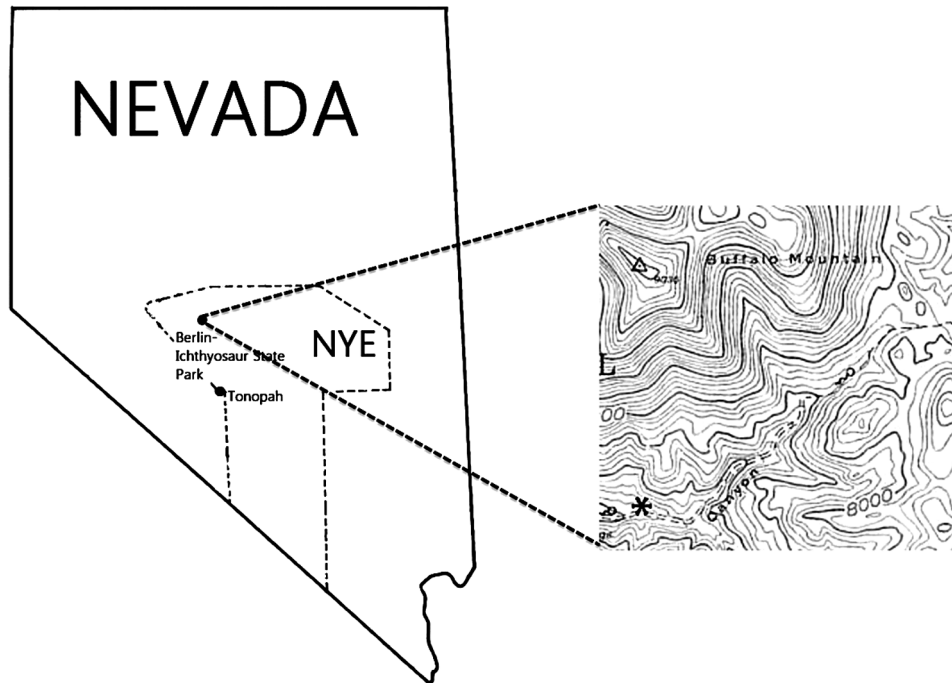


Fig. 1. Field locality map, West Union Canyon, Shoshone Range, showing the the fossil locality (asterisk) in Nye County, Nevada. Map from Silberling (1959). The fossil site occurs in the Shaly Limestone Member of the Luning Formation in an eastward extension of its main outcrop area (Holger, 1992, her Fig. 2).

SYSTEMATICS

Class Malacostraca Latreille, 1802
 Superorder Peracarida Calman, 1904
 Order Amphipoda Latreille, 1816
 Gammaroidea Latreille, 1802
 ?Acanthogammaridae Garyaev, 1901
Rosagammarus n. gen.
 (Figs. 3-10)

Description.—The specimen consists of the anterior-central portion of the pereion, including portions of pereionites, coxal plates and pereiopods 3-5. The animal is preserved lying on its side (as would be expected for the laterally flattened amphipod body) in a somewhat compressed lateral-



Fig. 2. *Protopaleodictyon* ichnosp. Shaly Limestone Member of the Luning Formation, Late Triassic (Norian), Union Canyon, Shoshone Range, Nye County, Nevada. Field sample 1 of 5/16/13. Scale bar in centimeters.

dorsal view. The various parts of the pereion have been compressed and displaced by sediment compaction. Pereiopod 4 has been rotated approximately 135° counterclockwise (as viewed from a dorsal vantage) during compaction.

Coxal plates 3 and 4 are well developed and elongate, not fused with pereionites. Coxal plate 3 with widely-spaced setal spurs on its posterior margin (Fig. 5), with broad ridge on its dorsolateral surface (Fig. 3). Coxa 5 short and wide, greatest dimension 8 mm (Fig. 7), with an acutely narrowing anterior end and an oblique notch along its distal edge that nests with a comparable notch on the proximal end of the pereiopod 5 basis (Figs. 7-8). Pereiopod 3 with a slightly conical ischium, relatively short merus that expands rapidly at its distal end, and a cylindrical to distally gradually tapering carpus (Fig. 3). Pereiopod 4 with narrow, cylindrical basis, a short, roughly cylindrical ischium and a very elongate (15 mm), curved merus (Fig. 3). Only the proximal part of the Pereiopod 4 carpus known (Fig. 3). Pereiopod 5 known from the coxa and a robust, elongate basis bearing a proximal notch as noted above (Figs. 7-8). Gnathopod 2 known only from a short fragment that may represent part of its basis (Fig. 3). A pereion dorsal plate (from the mid-pereion) bears a broad spine on its lateral edge (Fig. 8). A second pereion dorsal plate (from a more anterior section of the pereion, inferred here to be pereion dorsal plate 2) apparently lacks a spine (Fig. 9). It has rotated about 140° clockwise with respect to the other parts of the animal as viewed from the amphipod's left side. Recessed setal pores are evenly distributed over the surface of the heavily mineralized exoskeleton (Figs. 9-10). Setal pores on the proximal part of coxal plate 3 are surrounded by smaller satellite pores or pore-like structures (Fig. 6).

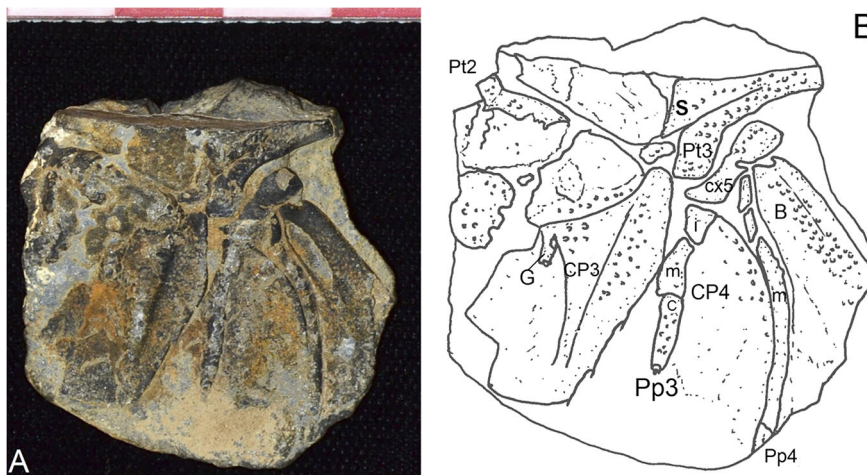


Fig. 3. *Rosagammarus minichiellus* n. gen., n. sp. Luning Formation, Nevada, Triassic. A, Photograph of fossil specimen; scale bar in centimeters; B, diagrammatic sketch of Fig. 3A identifying key parts of exoskeleton. Abbreviations are as follows: B, basis; c, carpus; cx, coxa; CP, coxal plate; G, gnathopod; i, ischium; m, merus; Pp, pereiopod; Pt, pereionite; S, spine.

Rosagammarus minichiellus n. sp.

Material collected.—One specimen found in float derived from the Shaly Limestone Member of the Luning Formation (Late Triassic, Norian (*Tropites welleri*-*Mojsisovicsites kerri* zones; Silberling, 1959)) in a dry stream bed north of the Union Canyon jeep trail (National Forest District Road 024; Fig. 1). The fossil is probably derived from the middle part of the Shaly Limestone Member of the Luning Formation, where interbedded limestones are brownish-gray with “irregular orange-brown, red, or lavender patches” (Silberling, 1959, p. 16) as visible on the specimen. The site is located outside of the boundary of the state park. Rangers at Berlin-Ichthyosaur State Park routinely direct visitors to this site for recreational fossil collecting.

Body Length.—Estimated total body length 17 cm.

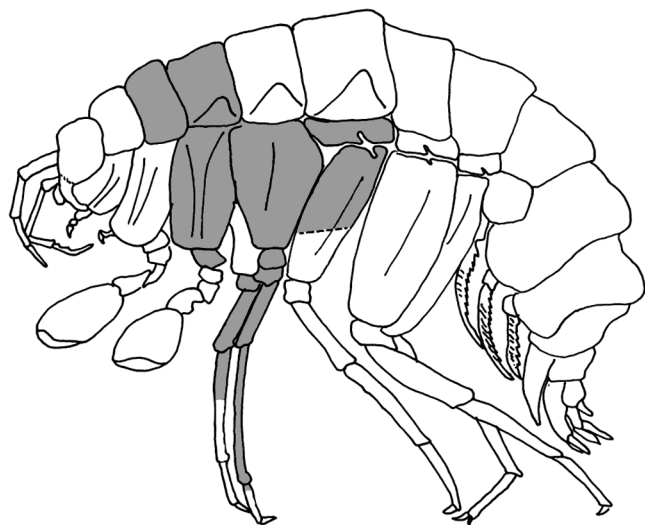


Fig. 4. *Rosagammarus minichiellus* n. gen., n. sp. Reconstruction of entire amphipod, using a sketch of a generalized acanthogammarid as template. Fossil material recovered is shown in gray. Head and tail regions are conjectural. Estimated total length 17 cm.

Types.—Deposited in the North Carolina Museum of Natural Sciences. Holotype: adult, NCSM 11756. Collected 15 May, 2013 (field sample 2 of 5/15/13; Lat 38.884340; Long -117.568915).

Description.—As for the genus.

Etymology.—Named for Rose Minichiello, who discovered the fossil.

DISCUSSION

Superfamily Gammaroidea includes a large number of families and subfamilies. Phylogenetic relationships among the Gammaroidea remain controversial even after Bousfield’s reorganization of Gammaridae (Bousfield, 1973, 1977; Holsinger, 1974, 1977; Karaman and Barnard, 1979; Barnard and Karaman, 1980). Interfamilial taxonomic relationships are so uncertain that Ah Yong et al. (2011) list 190 amphipod families in alphabetical order rather than recognize superfamilies.

Rosagammarus may belong to an extinct family that included giant, deep-sea early Mesozoic amphipods with elongate pereiopods, deep coxal plates 1-4, and the posterior lobe of the coxa deeper in coxa 5. *Rosagammarus* shows pronounced morphological similarities to the Acanthogammaridae, a freshwater family largely endemic to Lake Baikal. We suggest this could indicate a phylogenetic affinity between *Rosagammarus* and Acanthogammaridae. Our rendition of *R. minichiellus* (Fig. 4) maps the fossil material onto a generalized outline of an acanthogammarid.

Acanthogammarids are characterized by being mainly “large, carinate and/or processiferous... [pereiopods] often very elongate... coxal plates 1-4 deep, coxae 5-7, anterior lobe usually deeper” (Bousfield, 1977: 294). Regarding the latter feature (anterior lobe of the coxa deeper), most acanthogammarids are unlike *Rosagammarus*.

There are some similarities in leg structure between *Rosagammarus* and members of the Eusiridae; however, overall pereionite and coxal plate structure in *Rosagammarus* would seem to be more similar to that of the acan-

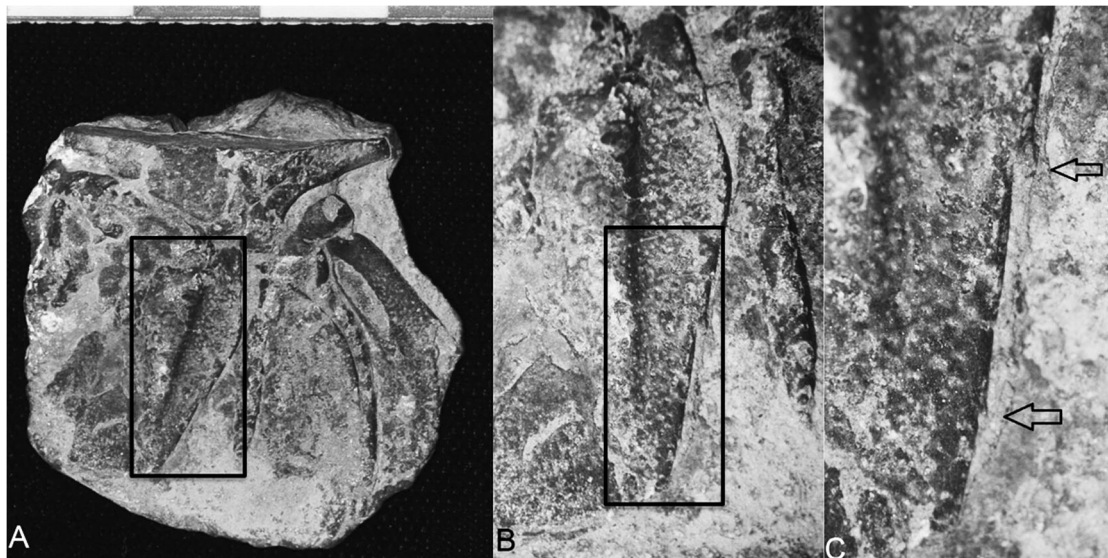


Fig. 5. *Rosagammarus minichiellus* n. gen., n. sp. Setal spurs on the posterior margin of coxal plate 3. A, entire specimen with position of coxal plate 3 indicated, scale bar in centimeters; B, coxal plate 3, showing setal spurs, inset box shows position of Fig. 5C; C, posterior edge of coxal plate 3 with arrows indicating setal spurs.

thogammarids. Furthermore, large spines in eusirid amphipods occur on the pereion in a sagittal position, not in a lateral position as seen in both *Rosagammarus* and the acanthogammarids. In eusirids, coxa 5 tends to taper more sharply in a posterior direction instead of tapering more sharply in an anterior direction, as is the case for *Rosagammarus*.

Confident family-level assignment of *R. minichiellus* must await either more complete fossil material, clarification of family-level relationships among Gammaroidea, or both. Incidentally, the supergiant modern deep sea amphipod *A. gigantea* Chevreux (Lysianassoidea: Alicellidae) lacks spines, has subquadrate coxal plates that become deeper in an anterior direction, relatively short pereopods, and is quite distinct from *R. minichiellus* at the superfamily level.

The large, elongate basis of pereopod 5 is comparable to the elongate, robust basis of *Propachygammarus maxi-*

mus (Garyaev, 1901) from Lake Baikal, a freshwater acanthogammarid that reaches 7 cm in length. The juxtaposition of a robust basis in pereopod 5 and elongate merus and carpus in pereopod 4 with an oblique distal end of its merus are also features shared with *Propachygammarus maximus* (Garyaev, 1901). A broad spine occurs on one of the pereion dorsal plates in *R. minichiellus*.

Takhteev (2000) identified three different ecomorphs among nectobenthic amphipods. Both *Rosagammarus* and *Propachygammarus* belong to Takhteev's type 2 ecomorph, whose main morphological characteristics are "large body size, strong cuticle and widely outstretched extremities" (Takhteev, 2000: 204). Takhteev (2000) emphasized the large number of morphological convergences known between marine and freshwater amphipod genera.

The setal pore arrangement on the exoskeleton in *Rosagammarus* is very similar to that seen on *Brandtia* sp.,

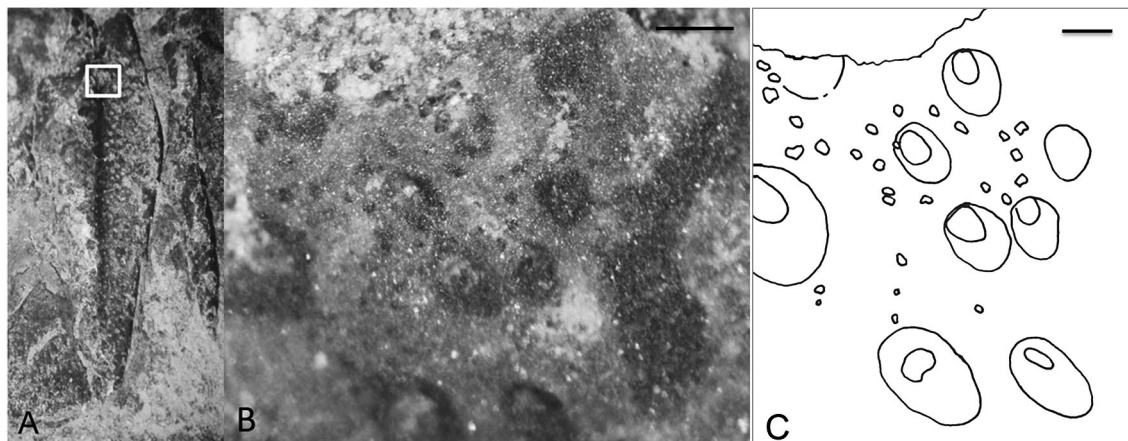


Fig. 6. *Rosagammarus minichiellus* n. gen., n. sp. Satellite pore structures surrounding setal pores on the proximal part of coxal plate 3. A, coxal plate 3, with inset box showing position of Fig. 6B; B, satellite pore structures surrounding larger setal pores, scale bar = 0.5 mm; C, sketch from photograph showing relationship between satellite pore structures and setal pores, scale bar = 0.25 mm.

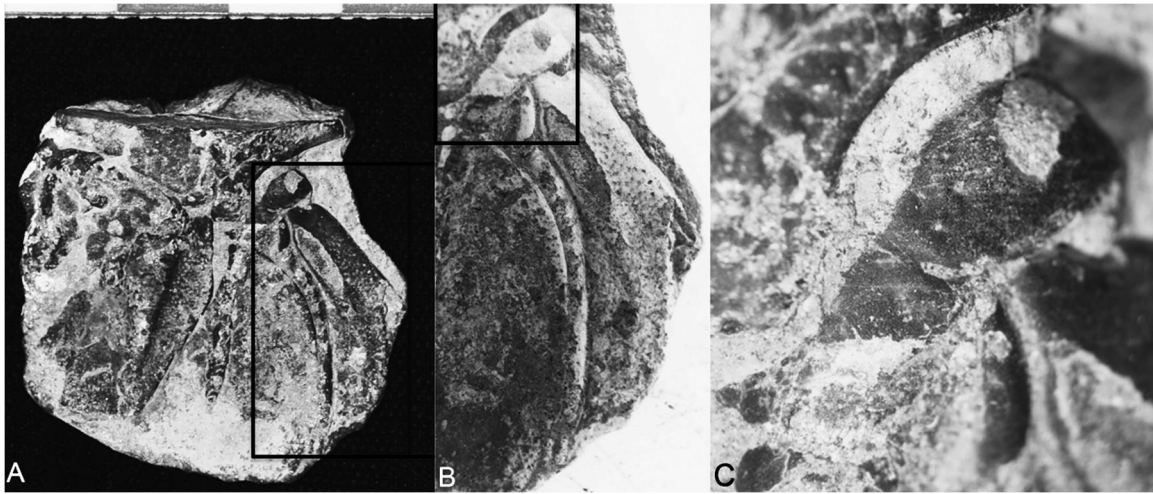


Fig. 7. *Rosagammarus minichiellus* n. gen., n. sp. Coxa 5 and pereiopod 5 basis. A, entire specimen with coxa 5 and pereiopod 5 basis in box, scale bar in centimeters; B, coxa 5 and pereiopod 5 basis, with box showing position of Fig. 7C, negative image; C, coxa 5 showing acutely narrowing anterior end and an oblique notch along its distal edge that nests with a comparable notch on the proximal end of the pereiopod 5 basis.

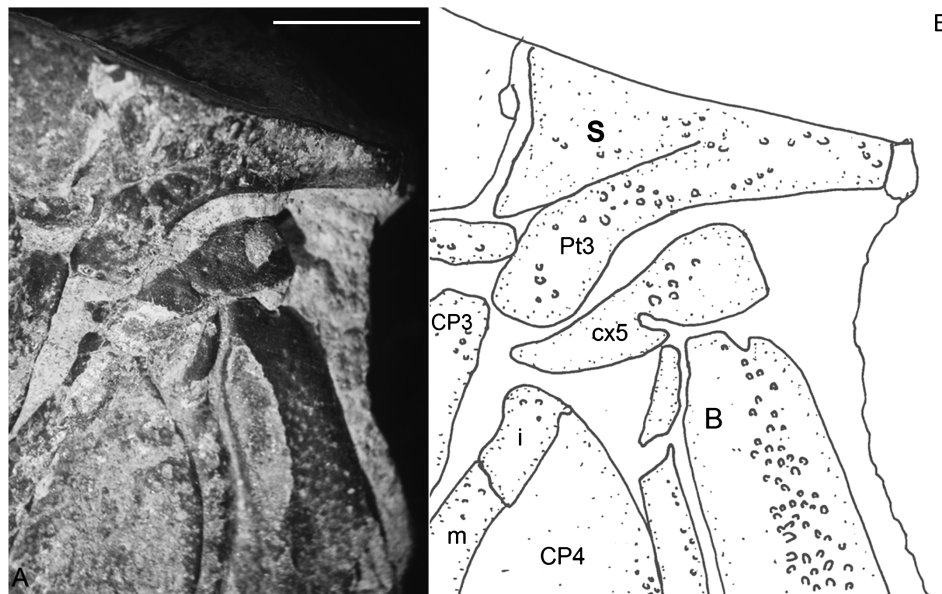


Fig. 8. *Rosagammarus minichiellus* n. gen., n. sp. Pereiopod 5 region. A, enlargement of the pereiopod 5 region, scale bar = 7 mm; B, sketch from photograph showing relative positions of: B, basis; cx5, coxa 5; CP, coxal plate; i, ischium; m, merus; Pt, pereionite; S, pereionite spine.

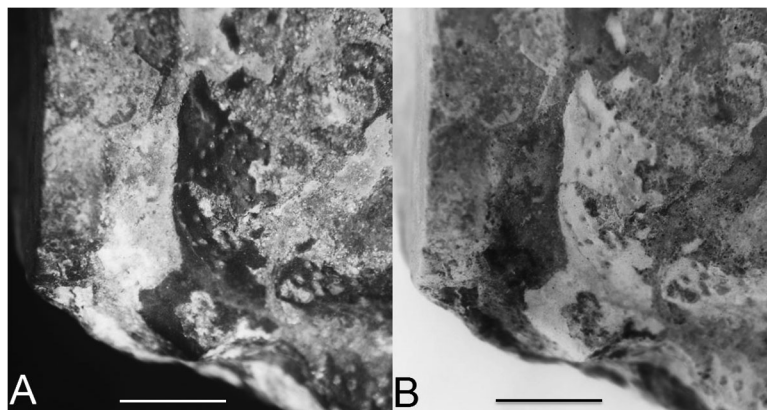


Fig. 9. *Rosagammarus minichiellus* n. gen., n. sp. Anterior pereionite, probably pereion dorsal plate 2 (indicated as Pt2 in Fig. 3B). A, reflected light, scale bar = 2 mm; B, negative image of same view; scale bar = 2 mm.

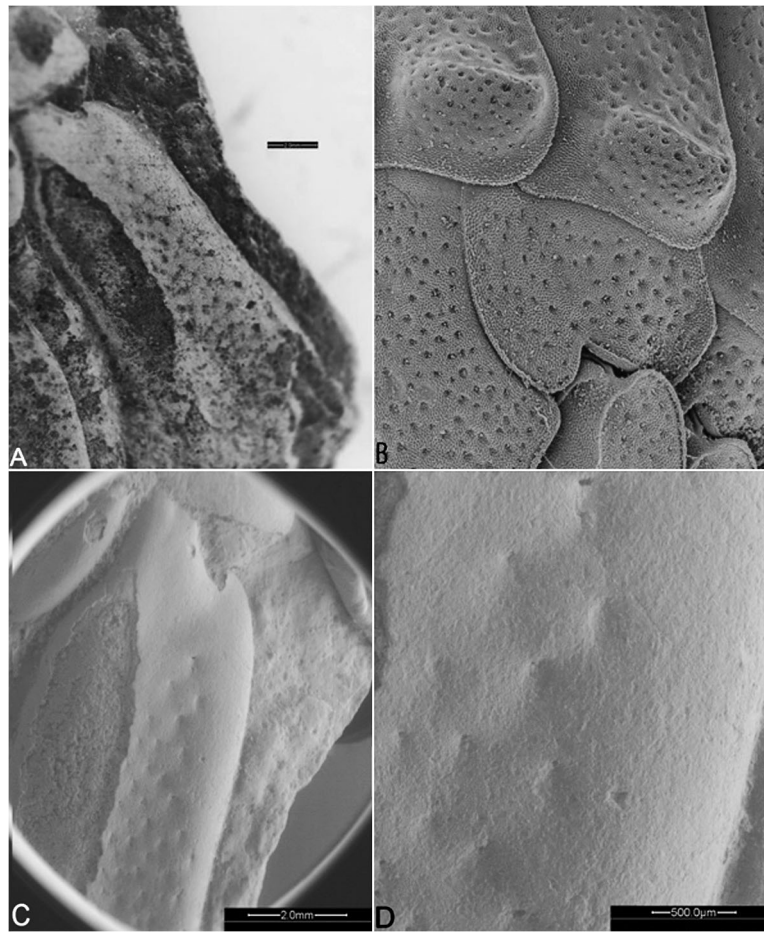


Fig. 10. *Rosagammarus minichiellus* n. gen., n. sp. and acanthogammarid *Brandtia* sp. Comparisons of cuticular structure. A, pereopod 5 basis, negative image to show setal pore details, scale bar = 1.5 mm; B, cuticle ornamentation of *Brandtia* sp., an acanthogammarid amphipod from Lake Baikal. Scanning electron micrograph showing plate arrangement and setal pore pattern, width of view approximately 2.0 mm, courtesy Petr Jan Juračka; C, low vacuum scanning electron micrograph showing setal pores on pereopod 5 basis, scale bar 2 mm; D, low vacuum scanning electron micrograph showing setal pores on pereopod 5 basis, scale bar 500 μm .

an acanthogammarid amphipod (Fig. 10). Coxa 5 has an oblique notch along its posterior edge that nests with a comparable notch on the pereopod 5 basis, a feature that occurs in the same region in *Brandtia* (Fig. 10). This coxal notch is comparable to the notch visible on the ventral edge of coxa 5 in *Valettioopsis ruffoi* Serejo and Wakabara, 2003 as shown in Fig. 2A of Serejo and Wakabara (2003). The shape of coxa 5 in *R. minichiellus* with its acutely narrowing anterior end is quite comparable to that of *Eulimnogammarus* (*Eulimnogammarus*) *czerskii* (Dybowski, 1874). This is in contrast to *Acanthogammarus* (*Brachyropus*) *nassonowi* Dorogostaiskii, 1922 and *Garjajewia dogieli* Bazikalova, 1945 where coxa 5 becomes conspicuously wider at its anterior edge. Coxal plates 3 and 4 in *R. minichiellus* are of comparable relative size to those of *Hyaellopsis* (*Dorogammarus*) *castanea* (Dorogostaiskii, 1930), where the coxal plates 1-4 are broad and shield-like.

Setal spurs similar to those on the posterior edge of coxal plate 3 in *Rosagammarus minichiellus* n. gen., n. sp. are seen in *Micruropus galasii* Bazikalova, 1962, *Acanthogammarus* (*Acanthogammarus*) *subbrevispinus* Bazikalova, 1945 and other Baikalian species.

Paleoecology

Capture of supergiant amphipods in deep marine traps has focused interest on these colossal crustaceans, whose maximum length may exceed 34 cm (Lowry and De Broyer, 2008; Jamieson et al., 2013). Abyssal gigantism in isopods has been linked to increased oxygen availability in cold bottom waters (Chapelle and Peck, 1999, 2004). Giant isopods belonging to the genus *Bathynomus*, however, inhabit deep, low oxygen waters in the Gulf of Mexico (Pless et al., 2003).

Rosagammarus minichiellus was probably a deep marine, necrophagous, benthopelagic scavenger ecologically comparable to members of Alicellidae and other deep marine amphipods (Lowry and De Broyer, 2008; Duffy et al., 2012). If *Rosagammarus* was as patchily or sparsely distributed on the deep-sea floor as is *Alicella*, then this fossil represents an exceptionally rare and fortunate discovery. This may in fact represent a case of exceptional fossil preservation. It appears that a Stow Sequence fine-grained turbidite, consisting of carbonate mud emplaced in deep water (Stow, 2006), led to a local cessation of carbonate dissolution (as would ordinarily occur below the CCD), and hence preservation of the

calcareous amphipod fossil in a micritic (lithified lime mud) matrix.

Timofeev (2001) interpreted deep-water gigantism in marine crustaceans as a temperature-dependent phenomenon associated with Bergmann's Principle. However, Jamieson et al. (2013: 111) note that this concept "does not adequately explain deep sea gigantism where little or no variation has been recorded in temperature vertically through the water column." Jamieson et al. (2013) instead favor the hypothesis that gigantism in *A. gigantea* renders the animal somewhat immune to predation from abyssal predators due to its size.

Another factor that may influence abyssal gigantism in necrophagous, benthopelagic scavengers is the quantity of large detritus that falls to the sea floor. The ichthyosaur *Shonisaurus* is comparable in size (Holger, 1992) to a modern sperm whale (*Physeter*). The appearance of very large sea floor carcasses (Dahl, 1979; Thurston et al., 2002) on the Triassic sea floor could have provided the trophic resources needed for the appearance of giant deep marine amphipods such as *Rosagammarus*.

Paleobiogeography

Alicella gigantea, the largest known amphipod (Chevreux, 1899; De Broyer and Thurston, 1987; Lowry and De Broyer, 2008; Jamieson et al., 2013), inhabits deep abyssal and hadal plains (Barnard and Ingram, 1986, 1990). *Alicella* occurs at great depth in both the Atlantic and the Pacific. Its rarity in spite of wide biogeographic distribution is puzzling (Barnard and Ingram, 1986; De Boyer and Thurston, 1987). Jamieson et al. (2013: 112) attribute the "extremely disjunct geographical distribution... of this most enigmatic species" to *A. gigantea* being either very patchily distributed, or very sparsely distributed.

Large (but not supergiant) deep-sea amphipods belonging to the genus *Eurythenes* have extremely wide geographic distribution in the modern seas. For example, *Eurythenes gryllus* (Lichtenstein in Mandt, 1822) has been reported from all major marine bodies of water with the interesting exception of the Mediterranean (Stoddart and Lowry, 2004).

Due to limitations of the fossil record, amphipod paleohistory is largely inferred from modern geographic distributions (Myers, 1991; Conlan, 1995). Vonk and Schram (2003) utilized cladistics to reveal some of these biogeographic patterns for ingolfiellidean amphipods. Biogeographic analysis indicates that amphipods had to be widespread in Pangea, Gondwana, and Laurentia (Vonk and Schram, 2003; Myers and Lowry, 2009; Väinölä et al., 2008). For example, the global distribution of *Bactrurus* has been linked to the formation and breakup of Pangea (Holsinger, 1986).

Considerable uncertainty has been expressed regarding whether or not the highly diverse, endemic Lake Baikal amphipod fauna (72 genera and 363 species) represents an *in situ* freshwater diversification (Danileya et al., 2011), or whether the diversity was inherited from an earlier marine phase (Bazikalova, 1945; Väinölä et al., 2008). These freshwater forms are not entirely restricted to Lake Baikal. For example, a "Baikaloid" deep-water amphipod occurs in Fuxian Hu, a karst lake in Yunnan, China (Sket, 2000).

Hou et al. (2011) used phylogenetic analysis to show that the modern amphipod *Gammarus* originated in salt water of the Tethyan region and subsequently (by the Middle Eocene)

colonized freshwater habitats. The gammaridean stygobiont amphipods of Metacragonyctidae, formerly thought to be an exclusively New World taxon, were recently found in the Mediterranean (Jaume and Christenson, 2001), who attribute this biogeographic pattern to a wide Tethyan distribution for the ancestors of *Metacragonyx*.

If pereion, pereopod, setal spur, and cuticular surface texture similarities between *R. minichiellus* and acanthogammarids indicate shared descent, the result has important implications for our understanding of the paleobiogeography of the ancient Pacific Ocean and the dispersal patterns of organisms of the Tethyan region (Newton, 1988; Smith et al., 1990) during the Norian Stage (Late Triassic). Norian species of the plicate, thin-shelled clam *Monotis* occur abundantly both in Nevada-California (*M. subcircularis*) and in eastern Siberia (*M. zabaikalica*). The biogeographic range of *Monotis* is thought to have expanded dramatically during the Late Norian (Westermann, 1973).

The occurrence of a fossil amphipod with acanthogammarid affinities in Cordilleran North America suggests that acanthogammarids were once widespread in Tethyan marine environments. Marine acanthogammarids appear to be extinct, but we should not exclude the possibility that some still occur in an unsurveyed deep marine habitat.

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