Zoological Journal of the Linnean Society, 2004, **142**, 83–90. With 5 figures

Oldest shrimp and associated phyllocarid from the Lower Devonian of northern Russia

JERZY DZIK[1]*, ANDREY Yu. IVANTSOV[2] and YURIY V. DEULIN[3]

[1]*Instytut Palaeobiologii PAN, Twarda 51/55, 00–818 Warszawa, Poland*
[2]*Palaeontological Institute of the RAS, Profsojuznaja 123, Moscow 117647, Russia*
[3]*Arkhgeoldobytcha, Arkhangelsk, Troitskiy prospekt 168, Russia*

Received September 2003; accepted for publication January 2004

A mass occurrence of schooling, weakly sclerotized eocaridid shrimps in the Early Devonian pelagic environment of northern Russia suggests that the body-plan of the Eumalacostraca originated as an adaptation to swimming in the open sea. They probably replaced their ecological analogues, the archaeostracan phyllocarids *Caryocaris*, as a consequence of the rebuilding of the global marine environment during the later Ordovician. This may explain the rarity of the eumalacostracans in the Devonian and the difficulty with documenting their links with the archaeostracans. The new eocaridid shows similarities to the Carboniferous *Anthracophausia* in the general appearance and weak sclerotization of the carapace and appendages, but lacks its derived characters. The morphology of the pleural lobes, which have minute spines, is the only identified distinguishing character of the proposed new genus and species ***Archangeliphausia spinosa*** **gen.** et **sp. nov.** Its carapace was probably firmly connected dorsally with the thoracic segments. The only associated fossils of the assemblage represent a bizarre archaeostracan ***Pechoracaris aculicauda*** **gen.** et **sp. nov.,** with a weakly sclerotized carapace lacking any hinge or rostral plates but with reduced furca, an extremely long caudal spine and pleopods transformed into spines. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, **142**, 83–90.

ADDITIONAL KEYWORDS: Crustacea – early Palaeozoic – Eumalacostraca – evolution – fossils – origin.

INTRODUCTION

While there is a relatively good fossil record of eumalacostracan Crustacea from the Late Devonian, only a few poorly preserved specimens are known from the Middle Devonian. The latter represent the oldest eumalacostracans known until recently (Wells, 1957; Brooks, 1962a, 1969; Schram, 1979). It is generally accepted that archaeostracan phyllocarids are likely candidates as ancestors of the more advanced malacostracans (e.g. Rolfe, 1981; Richter & Scholtz, 2001); the main difference between them is in the organization of the posterior part of the abdomen (pleon). Although a hypothetical model of evolutionary transition from the abdominal spine-bearing archaeostracans to the uropod-bearing eumalacostracans has been available for some time (e.g. Dzik, 1980), no truly transitional forms have ever been found and the oldest known eocaridid malacostracans already show a well developed fin tail.

An explanation for the poor fossil record of the oldest eumalacostracans may be found in the recent discovery of their earliest Devonian representatives in material from a deep borehole in northern Russia, which is the subject of the present paper. These crustaceans show weak sclerotization of their carapaces and appendages and occur in low-diversity, almost monospecific assemblages interpreted as typical for schooling, pelagic animals (Schram, 1981). The only other associated fossils represent an archaeostracan with a general appearance also suggestive of the pelagic habit.

These are not the first malacostracans to be found in the Devonian of Russia. Previous records include the Late Devonian *Eopteridium striatum* Rohdendorf, 1970 from a similar horizon in a borehole drilled near Ukhta on the Timan peninsula. This is purported to

---

*Corresponding author. E-mail: dzik@twarda.pan.pl represent the tail fin of an anthracophausiid (Schram, 1980). A more complete possible eocaridacean was found in Upper Devonian borehole material at Kaluga in central Russia (Schram, 1980).

MATERIAL AND GEOLOGICAL SETTING

The fossils studied come from the Medynskoye 1 borehole located on the Medynskiy Zavorot peninsula about 200 km east of the mouth of the Pechora River in the Timan-Pechora region of polar Russia. The specimens were collected from between 4255.0 and 4262.7 m. Crustacean carapaces are abundant on the bedding surfaces of the dark grey calcareous laminated claystone. Fossil crustaceans have been found also in a similar, somewhat brownish shale at between 4262.7 and 4267.6 m and rarely even deeper (4267.6–4274.3 m), where the rock changes basally into mudstone with sandstone intercalations. They are absent from the overlying more calcareous shale (4189.4–4196.9 m) and marl (4187.6–4189.4 m), although rare fragmentary specimens have been recovered between 4144.0 and 4148.0 m.

The crustacean-bearing strata are bracketed from both below and above by index fossils. From 4267.6 to 4274.3 m, dermal scales of the thelodont agnathan fish *Katoporodus* have been extracted, which indicates a date of late Pridolian to earliest Lochkovian (Märss, 1986; Märss *et al*., 1995). Frasnian conodonts (including *Polygnathus decorosus*) have been found between 3089.8 and 3092.3 m, *c*. 200 m above the crustacean strata. In other boreholes of the region, Lochkovian (including, *inter alia, Ozarkodina remscheidensis*) and Eifelian (including, *inter alia*, *Eognathodus bipennatus*) conodont assemblages occur between the documented Frasnian and the base of the Devonian. This suggests that the crustacean fauna is of early Devonian, possibly Lochkovian, age.

Specimens are preserved as flattened in shale but with some relief. In most cases they are crowded on the bedding plane surfaces, suggesting either a catastrophic origin of the assemblage or, more likely, bottom conditions inhospitable to scavengers due to the presence of hydrogen sulphide. Most specimens are whole animals, although isolated carapaces and abdomens possibly representing exuvia are also common. The specimens vary in size, although no distinct size classes interpretable as moulting stages are recognizable, because of variable deformation of carapaces during compaction of the clay. Calcified skeletons are well preserved, especially in larger specimens, showing minute punctation on the surface.

The material is stored in the Museum of the Palaeontological Institute of the Russian Academy of Sciences in Moscow (abbreviation: PIN, collection number 4983).

SYSTEMATICS

SUBCLASS MALACOSTRACA LATREILLE, 1806
ORDER PHYLLOCARIDA PACKARD, 1879
SUBORDER HOPLOSTRACA SCHRAM, 1973
FAMILY UNDETERMINED
***PECHORACARIS* GEN. NOV.**

Type species: A. aculicauda sp. nov.

Diagnosis: Hoplostracan with very long spine-like telson without furca, elongated carapace reaching fifth pleomere; pleopods transformed into spines.

Etymology: Derived from the Pechora River region, where the fossils were found, and Latin *caris* (shrimp).

Affinities: The most striking aspect of this arthropod is its single caudal spine (Figs 3, 5). In this respect it somewhat resembles the enigmatic 'trilobitomorph' *Burgessia bella* Walcott, 1912 from the famous Middle Cambrian Burgess Shale of British Columbia (Hughes, 1975). Such affinity is unlikely, however, as the new Russian arthropod shows strongly sclerotized mandibles, which indicates its advanced crustacean affinities.

Probably the closest relative of *Pechoracaris aculicauda* is '*Elymocaris*' *urvantsevi* Dunlop, 2002 from roughly coeval strata of the Severnaya Zemla archipelago. Although the presence of a medial dorsal plate and rostral plate is claimed in the original description (Dunlop, 2002), the evidence for this seems rather weak. '*E.*' *urvantsevi* shows a similar shape of the carapace to the new archaeostracan, covering all but the last three segments of the abdomen. Its spinose furca is normally developed, but is significantly shorter than the telson spine.

Among the archaeostracans, an elongated caudal spine and reduced furca are known in the Early Devonian *Heroldina* and *Aristozoe*, and in the Early Carboniferous *Sairocaris*. The giant *Heroldina rhenana* (Broili, 1928) from the Hunsrück Slate of Germany, reaching up to 60 cm in length, is different from the Russian crustacean in the presence of a large rostral plate and dorsal hinge of the carapace (Bergström *et al*., 1989; Bartels *et al*., 1998). In its strongly elongated last abdominal segment, *Heroldina* resembles *Aristozoe regina* Barrande, 1972 from the Koněprusy Limestone of Bohemia (Chlupač, 1963) and *A. virga* Chlupač, 1970 from the earliest Devonian Lochkov Limestone. Another Bohemian aristozoid, *Pygocaris schuberti* Perner 1916 from the Lochkov Limestone, had a thin cuticle (Chlupač, 1963) but still does not show even a remote similarity to the Russian form. Archaeostracans with somewhat reduced furca, elongated medial spine and possibly lacking separate rostral plate are known from as far back in the geological past as the Middle Ordovician (Hannibal & Feldmann, 1997).

The hoplostracan *Sairocaris elongata* (Peach, 1882), that notably co-occurs with *Anthracophausia* in the Early Carboniferous Glencartholm Volcanic Beds of Scotland, has a very short carapace, exposing posterior thoracic segments (Schram, 1979). If the Russian form is truly related to *Sairocaris*, a carapace reduction took place in the evolution of the lineage.

PECHORACARIS ACULICAUDA SP. NOV.
(FIGS 1, 5 A)

Holotype: PIN 4983/21b (Fig. 1D)

Type horizon and locality: Dark-grey claystone from between 4255.0 and 4262.7 m, Early Devonian (Lochkovian?). Borehole Medynskoye 1 in the Timan-Pechora region of polar Russia.

Material: Thirty relatively complete specimens and many more fragments.

Diagnosis: As for the genus.

Etymology: Derived from Latin *acus* (needle) and *cauda* (tail), referring to the form of the telson.

Material: Sixty relatively well preserved specimens, mostly with abdomen.

Description: The carapace lacks any hinge or separate dorsal plates, as visible in slightly obliquely compressed specimens. The lower margin frequently shows a narrow strengthening belt, probably a little thicker than the rest of the cuticle, perhaps representing a doublure. In specimens PIN 4983/20 and 4983/7, minute sparsely distributed denticles are recognizable near the posterior end of the carapace at its margin. Two somewhat more prominent spines arm the ventro-posterior lobe of the carapace in PIN 4983/1d. The anterior end of the carapace narrows parabolically and is a little pointed, as shown by PIN 4983/8a. The carapace length in the studied material ranges from 2.5 mm to 4.7 mm (Fig. 1B). In most specimens dark crushed mandibles are visible

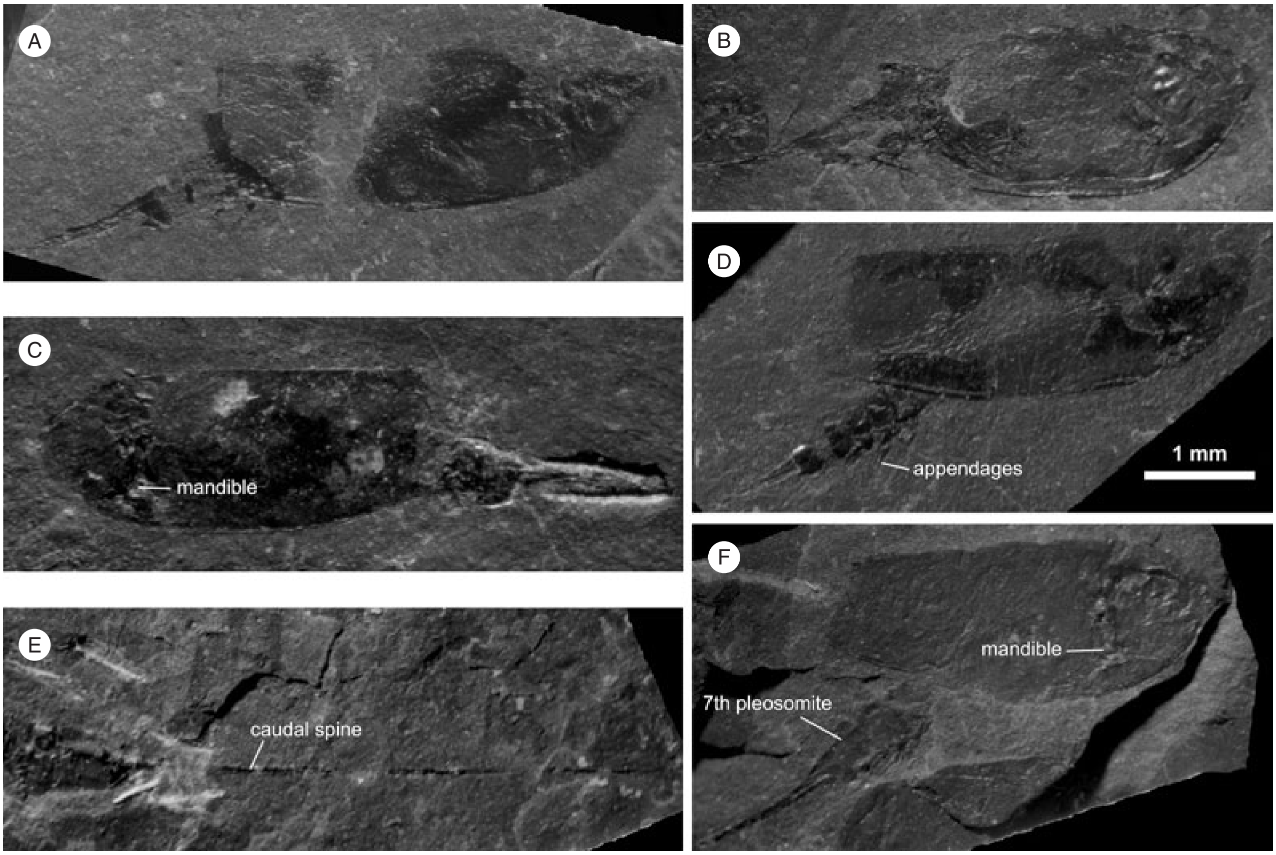

Figure 1. ***Pechoracaris aculicauda* sp. nov.** from the Medynskoye 1 borehole, Timan-Pechora region, polar Russia, depth 4255.0–4262.7 m, Lower Devonian (Lochkovian?); flattened specimens in laminated claystone. A, carapace with abdomen and partially preserved spine (PIN 4983/21a). B, slightly obliquely compressed specimen (PIN 4983/31a). C, specimen with well preserved dorsal margin of the carapace (PIN 4983/10). D, holotype showing spinose appearance of abdominal appendages (PIN 4983/21b). E, partially preserved specimen with complete abdominal spine (PIN 4983/7). F, specimen with clearly visible crushed mandibles (PIN 4983/31b).

across the compressed carapace near its anterior end (Fig. 1F). Appendages of the abdomen are transformed into paired sharp spines (Fig. 1D), somewhat longer than their segments. The caudal spine is definitely much longer than the carapace (Fig. 1E) but its exact length is difficult to trace in the fossils, the spine being either exfoliated or hidden in the sediment.

ORDER EOCARIDACEA BROOKS, 1962
FAMILY ANTHRACOPHAUSIIDAE BROOKS, 1962 (OR EOCARIDIDAE BROOKS, 1962)
***ARCHANGELIPHAUSIA* GEN. NOV.**

Type species: A. spinosa sp. nov.

Diagnosis: A generalized anthracophausiid with abdominal pleura bearing a single small spine on their ventral margin.

Etymology: Derived from the latinized name of Arkhangelsk and *phausis* (Greek = shine).

Affinities: Brooks (1962) indicated a recessed 'eye socket' of the proximal segment of peduncle of antennules as the diagnostic character of his Anthracophausiidae. This feature is not represented in the new genus, which is quite generalized in this respect and may have been anatomically close to the Devonian eocaridids, as indicated also by the long abdominal pleura. However, the more general aspects of *Anthracophausia* listed by Brooks (1962) – weak sclerotization of generally smooth carapace, margins reinforced with an unusually narrow band, a short rostrum, and lateral flattening of the body due to compression – fit well the Russian material.

The Carboniferous species of *Anthracophausia* reveal dramatically different outlines of abdominal pleura from those in the Russian species. In *A. strongi* Brooks, 1962, from the Late Carboniferous Mazon Creek fauna of Illinois, the pleural lobes of the abdominal tergites are broadly rounded. In *A. dunsiana* from the Early Carboniferous Glencartholm Volcanic Beds of Scotland they narrow to form a sharp apex (Schram, 1979). In the new species, rounded lobes are armed with short spines, which seems to be enough to substantiate its taxonomic distinction. Another possible difference between the Russian form and the Carboniferous species of *Anthracophausia* is the increasingly posterior orientation of the abdominal pleural lobes towards the telson (although not easily discernible because of strong flattening of the specimens). In fact, the faint parabolic lines visible on the paratype of *A. strongi* (Brooks, 1962; pl. 48: 3) may also indicate a similar shape of the posterior pleural lobes in that species. Some gradient in the shape of pleural lobes is also observable in *A. dunsiana*.

All these distinguishing characters are probably primitive (plesiomorphic) and the new genus is probably transitional between the benthic Eocarididae and typical Carboniferous Anthracophausiidae. It may represent the beginning of the lineage of *Anthracophausia*. Because of the significant time and morphological distance it seems practical, however, to separate them at the generic level.

The Anthracophausiidae probably gave rise to the Recent euphausiaceans, closest to the ancestry of Eumalacostraca among the extant orders (Jarman *et al.,* 2000). The identified distinction of the anthracophausiids in respect to the euphausiaceans is invariably connected with their basal position in the evolutionary tree: the wide telson, lack of hinge-like connection between the first pleotergite and the carapace, and ventrally extended lobes of the carapace.

The Late Carboniferous anthracophausiids are considered near-shore marine filter feeders (Schram, 1981). Offshore eumalacostracan communities are inadequately known, with the available evidence restricted to the British late Early Carboniferous, the low diversity community being represented there by schooling species preserved in great numbers of individuals probably as an effect of mass killing (Schram, 1981).

***ARCHANGELIPHAUSIA SPINOSA* SP. NOV.**
(FIGS 2–4, 5B)

Holotype: Specimen PIN 4983/1a (Figs 2A, 4B).

Type horizon and locality: Dark-grey claystone from a depth of 4255.0–4262.7 m, Lower Devonian (Lochkovian?). Borehole Medynskoye 1, Timan-Pechora region of polar Russia.

Material: Sixty more or less complete compressions.

Diagnosis: As for the genus.

Description: The largest specimen, PIN 4983/35, probably belongs to this species (Fig. 2B). It measures 12.5 mm in length from the carapace rostrum to the end of the telson. The smallest reasonably complete specimen is PIN 4983/37 (Fig. 2C) with an estimated length of *c.* 6.5 mm. The size of most specimens is close to the mean between these values. As the specimens are mostly complete skeletons, not exuvia, the dominance of larger individuals may reflect the structure of the original population at its repeated catastrophic extinctions.

Three basal segments of the 1st antenna are preserved in specimens PIN 4983/18 and 25. The proximal segment is approximately three times longer than the third one, while the second segment is intermediate in length (Fig. 5B). Of the 2nd antenna only the scaphocerite is preserved in a few specimens, the most

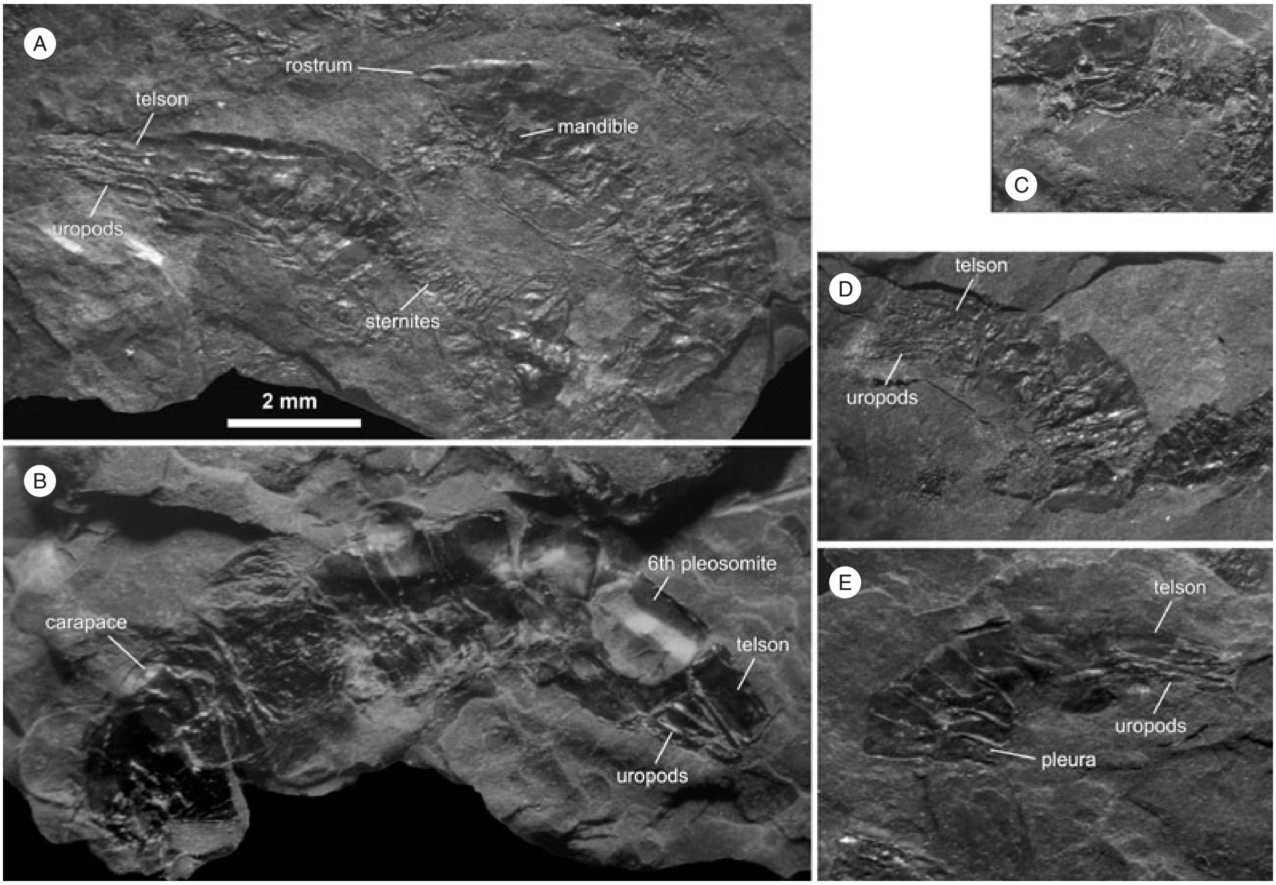

Figure 2. ***Archangeliphausia spinosa* sp. nov.** A, holotype (PIN 4983/1a: right) and associated specimen (PIN 4983/1b). B, largest specimen found (PIN 4983/35), with relatively thick cuticle. C, juvenile specimen (PIN 4983/37). E, specimen with dorsoventrally compressed telson and uropods (PIN 4983/28; see also Fig. 4C). D, posterior part of abdomen with well preserved 6th pleosomite and telson (PIN 4983/8).

complete being those of PIN 4983/2, 18, and 24 (Fig. 3A). The scaphocerite is oval, represented only by an organic film on the rock surface and its margins are not easy to trace.

The carapace has a sharp, relatively short rostrum, the ocular sinus being clearly visible in specimens PIN 4983/24A and B. The lower margin of the carapace, well preserved in holotype specimen PIN 4983/1a, has a very narrow band (Figs 2A, 4A). Being thicker, this band would have strengthened the cuticle. It is calcified and shows openings of pore canals; the posterior margin is hardly discernible except in the isolated dorsoventrally compressed carapace of specimen PIN 4983/43.

Laterally compressed sternites of thoracic segments are preserved in many specimens. The boundaries between the segments are discernible some distance dorsally of the sternites. All segments except for the first are recognizable in the specimen associated with the holotype (Figs 2A, 4B). They disappear at approximately half the height of the body, which probably corresponds to the limit of connection of the body with the carapace.

No remnants of the apparently weakly calcified thoracopods are preserved. Some faint marks may correspond to pleopods, but they are completely undefined morphologically.

The pleosomites increase gradually in length posteriorly, the 6th pleomere being very much longer than the preceding ones. Their pleura are somewhat expanded posteriorly to form oval lobes. The lobe of the 5th pleuron appears to extend almost to the midlength of the 6th pleosomite. All pleura bear sharp spines at their ventral tips, best preserved in specimens PIN 4983/31 and 24b (Fig. 3G).

The 6th pleosomite has almost parallel sides when, as in PIN 4983/36, compressed dorsoventrally (Fig. 3F). There is a kind of hinge connection with the basal segment of the uropods.

The telson is best preserved in PIN 4983/28 (Figs 2E, 4C), although its parts are recognizable in several other specimens. Its sides are gently convex

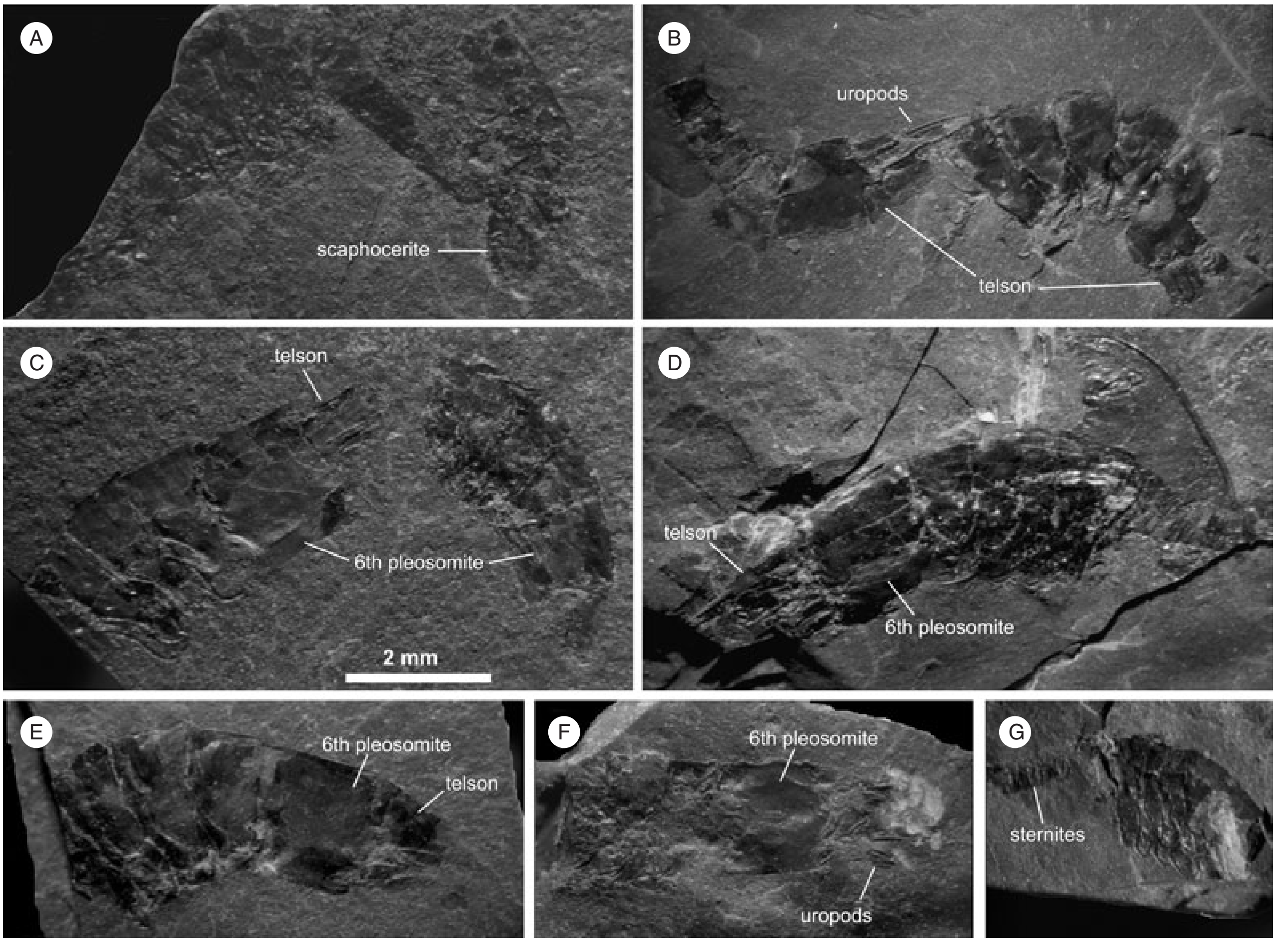

Figure 3. ***Archangeliphausia spinosa*** **sp. nov.** A, specimen with oblique dorsoventrally compressed carapace and well preserved scaphocerite of 2nd antenna (PIN 4983/2). B, specimens with partially preserved telson and uropods (PIN 4983/32a, b). C, specimens with partially preserved telson and uropods (PIN 4983/12a, b). D, posterior part of abdomen with well preserved 6th pleosomite (PIN 4983/4a). E, posterior part of abdomen with well preserved pleura (PIN 4983/39). F, dorsoventrally compressed 6th pleosomite and partial uropods (PIN 4983/36). G, specimen with well preserved spinose pleura (PIN 4983/31).

but almost parallel to each other. The posterior margin bears about eight indistinct indentations probably corresponding to bristle bases. The surface, as preserved in some stronger sclerotized fragmentary specimens (e.g. PIN 4983/32; Fig. 3B), is externally smooth. The rami of the uropods were strongly sclerotized only along their external margins. This prevents delineation of their shapes, but they were probably rather wide.

EVOLUTIONARY IMPLICATIONS

The new findings extend the eumalacostracan fossil record by at least 20 Myr. Their most surprising aspect is that the shrimps appear to have been pelagic, with weakly sclerotized appendages and carapace. It thus appears that the most anatomically generalized and geologically oldest eumalacostracans were living in an open-sea pelagic environment which could be their environment of evolutionary origin. This may have some bearing on interpretation of the origins of the uropod-bearing malacostracans.

There is little doubt that the phyllocarids were ancestral to the higher malacostracans (Rolfe, 1981) even if the exact course of the evolutionary transformation remains undocumented. The poor record of this transition is puzzling, as the fossil record of the crustaceans is relatively good and has been improving rather rapidly of late, assisted by the introduction of chemical methods to the extraction of phosphatized fossils. The north Russian early Devonian shrimp fauna may offer an explanation for this discrepancy between palaeontological expectation and reality: the entire transition could have taken place in an open-

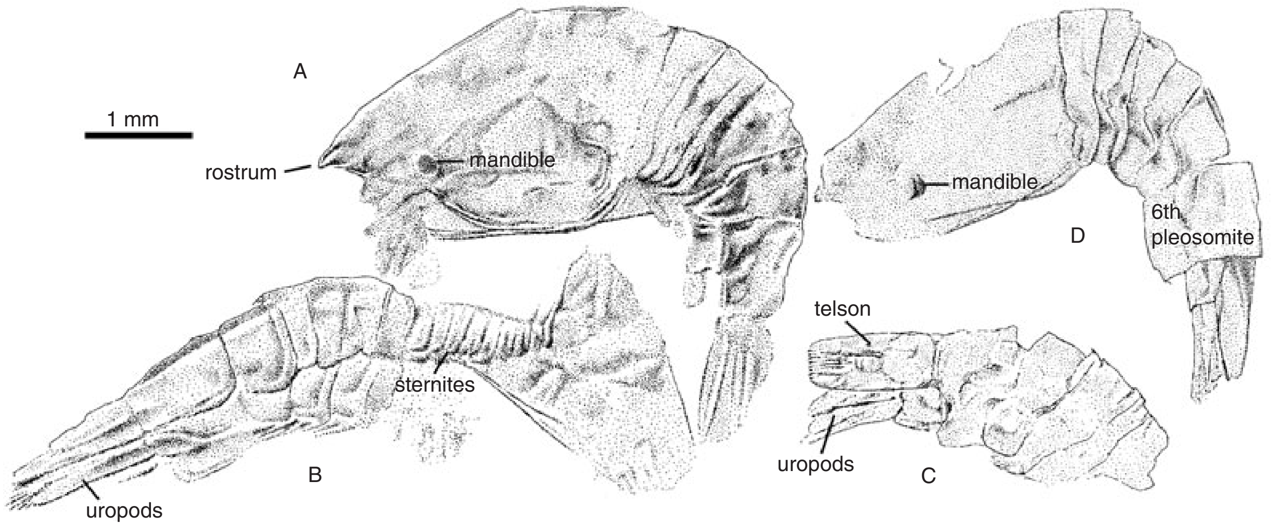

Figure 4. ***Archangeliphausia spinosa* sp. nov.** A, holotype (PIN 3993/1a). B, specimen PIN 4983/1b. C, specimen with dorsoventrally compressed telson and uropods (PIN 4983/28). D, specimen PIN 4983/1c.

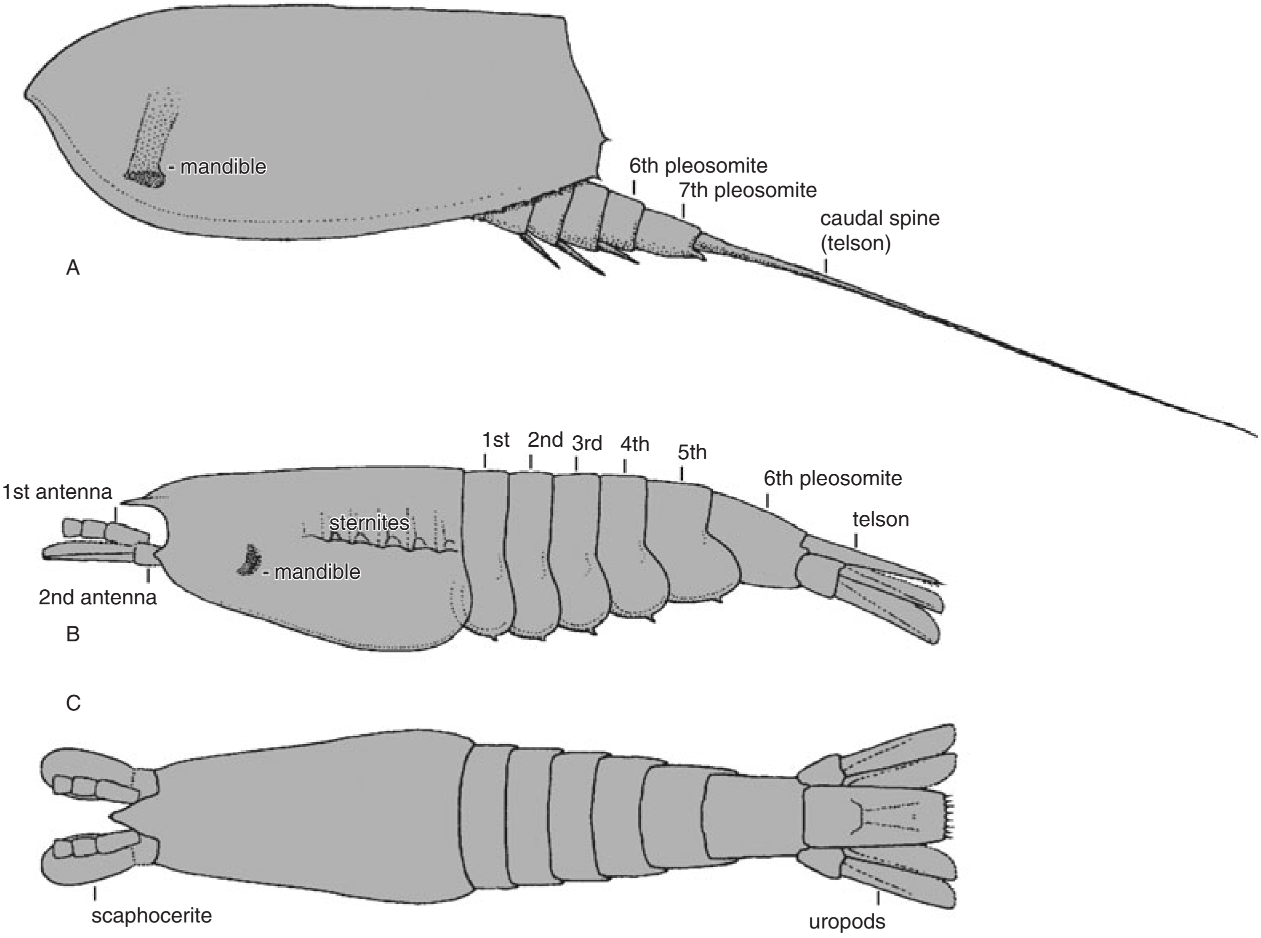

Figure 5. Restoration of (A) ***Pechoracaris aculicauda* sp. nov.** and (B) ***Archangeliphausia spinosa* sp. nov.**

sea pelagic environment. The oceanic environments of the Palaeozoic are poorly represented in the geological record; when sediments from this period are examined, fossils are rare and of poor quality.

The crucial anatomical transformation from the archaeostracan phyllocarids to the least derived eumalacostracans concerns the tail fan. In the archaeostracans, the telson and furca take the form of more of less elongated spines. They may be widened in some pelagic forms (*Caryocaris*), apparently to assist with swimming (Vannier *et al.,* 2003). Nevertheless, the tail fin of the eumalacostracans did not originate from archaeocarid flapping appendages of this kind. The swimming function is served in shrimps by the modified appendages of the 6th abdominal segment together with the widened body of the 7th segment (eumalacostracan telson). There is no homology between the eumalacostracan 7th segment and the phyllocarid telson (Schminke, 1976). The furca-bearing 8th abdominal segment (telson) of the phyllocarids was apparently lost in the course of evolution to the Eumalacostraca.

Some Carboniferous shrimps may have preserved remnants of the ancestral archaeostracan furca and the telson on the tip of the 7th segment, in a form of three minute spines (Brooks, 1962). A spinose tip of the telson occurs also in Carboniferous stomatopods, although there the median spine is unified with it (Jenner, Hof & Schram, 1998). It can be hypothesized that the spinose furca and telson underwent reduction at the origin of the eumalacostracans (Dzik & Jażdżewski, 1978; Dzik, 1980). The abdominal adaptation to swimming thus developed at the origin of the eumalacostracan clade from the defensive spines of an archaeostracan ancestor different from *Caryocaris*.

If the eumalacostracans displayed their typical body-plan around the time of the Silurian–Devonian boundary, it is possible that their ancestry is located deep in the Silurian. This places it close to the fundamental transformation of the pelagic environments influenced by the latest Ordovician glaciation. The first eumalacostracans may have replaced the superficially similar pelagic archaeostracan *Caryocaris* as a consequence of that ecological event.

REFERENCES

Bartels C, Briggs DEG, Brassel G. 1998. *The fossils of the Hunsrück slate*. Cambridge: Cambridge University Press.

Bergström J, Briggs DEG, Dahl E, Rolfe WDI, Stürmer W. 1989. Rare phyllocarid crustaceans from the Devonian Hunsrück slate. *Paläontologische Zeitschrift* **63:** 319–333.

Brooks HK. 1962a. Devonian Eumalacostraca. *Arkiv för Zoologi* **2** **(**15**):** 307–317.

Brooks HK. 1962b. The Paleozoic Eumalacostraca of North America. *Bulletin of American Paleontology* **44:** 163–338.

Brooks HK. 1969. Eocarida. In: Moore RC, ed. *Treatise on invertebrate paleontology, part R, Arthropoda 4*, Vol. 1. Boulder, CO: Geological Society of America, 332–345.

Chlupač I. 1963. Phyllocarid crustaceans from the Silurian and Devonian of Czechoslovakia. *Palaeontology* **6:** 97–118.

Chlupač I. 1970. New phyllocarid crustaceans from the lowest Devonian of the Barrandian. *Časopis pro Mineralogii a Geologii* 15: 327–334.

Dunlop J. 2002. Arthropods from the Lower Devonian Severnaya Zemlya Formation of October Revolution Island (Russia). *Geodiversitas* **24:** 349–379.

Dzik J. 1980. Isolated mandibles of early Palaeozoic phyllocarid Crustacea. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1980:** 87–106.

Dzik J, Jażdżewski K. 1978. The euphausiid species of the Antarctic region. *Polskie Archiwum Hydrobiologii* **25:** 589–605.

Hannibal JT, Feldmann RM. 1997. Phyllocarid crustaceans from a Middle Ordovician black shale within the Ames Structure, northwest Oklahoma. *Oklahoma Geological Survey Circular* **100:** 370–373.

Hughes CR. 1975. Redescription of *Burgessia bella* from the Middle Cambrian Burgess Shale, British Columbia. *Fossils and Strata* **4:** 415–435.

Jarman SN, Nicol S, Elliott NG, McMinn A. 2000. 28S rDNA evolution in the Eumalacostraca and the phylogenetic position of krill. *Molecular Phylogenetics and Evolution* **17:** 26–36.

Jenner RA, Hof CHJ, Schram FR. 1998. Palaeo- and archaeostomatopods (Hoplocarida, Crustacea) from the Bear Gulch Limestone, Mississsippian (Namurian), of central Montana. *Contributions to Zoology* **67:** 155–185.

Märss T. 1986. Pozvonochnyie silura Estonii i zapadnoy Latvii. *Fossilia Baltica* **1:** 1–103.

Märss T, Fredholm D, Talimaa V, Turner S, Jeppson L, Nowlan G. 1995. Silurian vertebrate biozonal scheme. In: Lelièvre H, Wenz S, Blieck A, Cloutier R, eds. Premiers vertébrés et vertébrés inférieurs (VIII Congr. Intern, Paris, 4–9 septembre 1995).*Geobios Mémoire Spécial* 19, 369–372.

Richter S, Scholtz G. 2001. Phylogenetic analysis of the Malacostraca (Crustacea). *Journal of Zoological Systematics and Evolutionary Research* **39:** 113–136.

Rolfe WDI. 1981. Phyllocarida and the origin of the Malacostraca. *Geobios* **14:** 17–27.

Schminke HK. 1976. The ubiquitous telson and the deceptive furca. *Crustaceana* **16:** 243–250.

Schram FR. 1979. British Carboniferous Malacostraca. *Fieldiana Geology* **40:** 1–129.

Schram FR. 1980. Miscellaneous Late Paleozoic Malacostraca of the Soviet Union. *Journal of Paleontology* **54:** 542–547.

Schram FR. 1981. Late Paleozoic crustacean communities. *Journal of Paleontology* **55:** 126–137.

Vannier J, Racheboeuf PR, Brussa ED, Williams M, Rushton AWA, Servais T, Siveter DJ. 2003. Cosmopolitan arthropod zooplankton in the Ordovician seas. *Palaeogeography, Palaeoclimatology, Palaeoecology* **195:** 173–191.

Wells JW. 1957. An anaspid crustacean from the Middle Devonian of New York. *Journal of Paleontology* **31:** 983–984.