

Arthropods from the Lower Devonian Severnaya Zemlya Formation of October Revolution Island (Russia)

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Dunlop J. A. 2002. — Arthropods from the Lower Devonian Severnaya Zemlya Formation of October Revolution Island (Russia). *Geodiversitas* 24 (2) : 349-379.

ABSTRACT

New arthropods from the Lower Devonian (lower Lochkovian) Severnaya Zemlya Formation, October Revolution Island, Russia, are described. Three groups of non-ostracode arthropods are present. Cheloniellids (Arachnata, Cheloniellida) are represented by *Paraduslia talimaae* n. gen., n. sp., Chasmataspids (Chelicerata, Chasmataspida) by *Octoberaspis ushakovi* n. gen., n. sp., and phyllocarids (Crustacea, Malacostraca, Phyllocarida) by *Elymocarid urvantsevi* n. sp. This fauna is significant as both cheloniellids and chasmataspids are extremely rare groups, while phyllocarids remain uncommon. Furthermore, this new chasmataspid material reveals two important morphological characters for the group: a genital appendage and metastoma. Both were previously considered autapomorphic for eurypterids; their presence in chasmataspids strongly suggests that Chasmataspida and Eurypterida are sister groups.

KEY WORDS

Arthropoda,
Chasmataspida,
Cheloniellida,
Phyllocarida,
Eurypterida,
Devonian,
Severnaya Zemlya,
Russia,
phylogeny,
genital appendage,
metastoma,
new genera,
new species.

RÉSUMÉ

Arthropodes du Dévonien inférieur de la Formation Severnaya Zemlya, Île de la Révolution d'Octobre (Russie).

De nouveaux arthropodes du Dévonien inférieur (Lochkovian inférieur) de la Formation Severnaya Zemlya, Île de la Révolution d'Octobre, Russie, sont décrits. Trois groupes d'arthropodes non-ostracodes sont présentés. Les cheloniellides (Arachnata, Cheloniellida) sont représentés par *Paraduslia talimaae* n. gen., n. sp., les chasmataspides (Chelicerata, Chasmataspida) par *Octoberaspis ushakovi* n. gen., n. sp. et les phyllocarides (Crustacea, Malacostraca, Phyllocarida) par *Elymocarid urvantsevi* n. sp. Cette faune est remarquable par la présence de cheloniellides et chasmataspides qui sont des groupes extrêmement rares de même par celle des phyllocarides. En outre, ce nouveau matériel de chasmataspides révèle deux caractères morphologiques importants pour le groupe : un appendice génital et un metastoma, qui ont été considérés précédemment comme autapomorphies des eurypterides. Leur présence chez les chasmataspides suggère fortement que ces derniers et les Eurypterida sont des groupes-frères.

MOTS CLÉS

Arthropoda,
Chasmataspida,
Cheloniellida,
Phyllocarida,
Eurypterida,
Dévonien,
Severnaya Zemlya,
Russie,
phylogénie,
appendice génital,
metastoma,
nouveaux genres,
nouvelles espèces.

INTRODUCTION

In 1978 an expedition led by Dr Vladimír Menner investigated the geology of the Severnaya Zemlya Archipelago off the Tajmyr peninsular, Russia (see Männik *et al.* 2002: fig. 1, for locality maps). A large number of Silurian and Devonian fossils were collected, mostly comprising vertebrate material. However, from one of the islands, October Revolution Island, over 200 arthropod fossils were recovered from the Lower Devonian Severnaya Zemlya Formation (Karatajūtė-Talimaa *et al.* 1986). Though previously figured in the literature (Novilskaya *et al.* 1983), these fossils have not been studied in detail. This paper describes the three groups of arthropod (excluding ostracodes) recorded from this locality: cheloniellids, chasmataspids and phyllocarid crustaceans.

MATERIALS AND METHODS

All specimens are held in the Geological Institute of Lithuania (GIL), T. Sevcenkos 13, LT 2600, Vilnius, collection number 35. The majority of specimens are provided with an outcrop number (oc) and a bed number (bd) indi-

cating where in the sequence they were collected (see geological setting). Material derived from other localities is noted in the text. Unless noted otherwise, descriptions are of the appearance of the animal in life with respect to ridges, tubercles, etc. Specimens were studied under a binocular microscope and, where necessary, were carefully prepared using a large needle. Interpretative drawings were made from the specimens and photographs. Specimens of fossil eurypterids and extant xiphosurans were studied for comparative anatomy. All the measurements of the description parts are in mm.

GEOLOGICAL SETTING AND PRESERVATION

The material described here comes from the October Revolution Island which is part of the Severnaya Zemlya Archipelago (see Männik *et al.* 2002 for details). The material was collected from loose nodules exposed at the surface, not *in situ* from the rock. The arthropods come primarily from three outcrops: outcrop 1 on the Matusевич River, bed 21 (Männik *et al.* 2002: figs 2, 7); outcrop 41 on the Spokojnaya River, bed 12 (Männik *et al.* 2002: fig. 6); out-

crop 67 on the Pod'emnaya River, bed 12 (Männik *et al.* 2002: fig. 1). The detailed stratigraphy and age ranges of the exposures at each of these localities are given in Männik *et al.* (2002) and the arthropods all come from the Severnaya Zemlya Formation, of Lower Devonian (lower Lochkovian) age. The fossils of the Severnaya Zemlya Formation comprise abundant vertebrates, mostly jawless heterostracans, osteostracans and anaspids, but also small to large predatory acanthodians. The arthropods comprise ostracodes as well as the phyllocarids, cheloniellids and chasmataspids described here. Articulated plant fossils are also recorded (Novilskaya *et al.* 1983). The occurrence of the plant remains and non-ostracode arthropods only in the Severnaya Zemlya Formation indicates a unique depositional environment in the early Lochkovian time in the Severnaya Zemlya region.

The arthropod fossils are preserved in flattened nodules originally from a finely laminated argyrolitic limestone. The nodules range in colour from dark grey to light brown, though this brown colour is a weathering effect and the natural matrix colour is grey. The nodules from the Pod'emnaya River tend to be darker in colour than those from the Matusевич and Spokoinaya rivers. Counterparts were not recovered with any of this material. The specimens themselves are generally darker than the surrounding matrix, typically dark brown or grey in colour. Most specimens retain some three-dimensional relief and details of cuticle ornamentation. Some specimens are better preserved than others, and most have been at least partially deformed due to compression. The best specimens are typically those preserved as external moulds and in general these show the most morphological detail. A number of the chasmataspid and crustacean specimens are preserved as internal moulds, some through replacement by a crystalline mineral, possibly calcium phosphate. These retain their original three-dimensional shape better than some non-crystalline specimens but lack details of morphology.

SYSTEMATICS

CHELONIELLIDA Broili, 1932

REMARKS

Seven specimens can be referred to the taxon Cheloniellida Broili, 1932, recognised as a distinct arthropod clade by Dunlop & Selden (1997) (see also below). The four most complete specimens (GIL 35/700-703, Figs 1-4) are described and figured here. A number of additional but incomplete specimens (35/704-706) may also represent cheloniellids. The identity of these fossils as cheloniellids, compared to previous records of this group (e.g., Stürmer & Bergström 1978; Selden & White 1984; Chlupáč 1988) is based on their broadly oval shape with a series of tergites bearing a distinct median axis, ending posteriorly in a terminal furca, clearly visible in 35/700 and 35/702 (Figs 1; 2). In addition to this, 35/702 (Figs 1B; 2B) and 35/703 (Figs 3B; 4B) preserve a number of mostly dissociated, filamentous fragments throughout the length of their bodies. These are similar to the stout lamellar spines described in *Cheloniellon calmani* Broili, 1932 by Stürmer & Bergström (1978) where they were believed to be associated with the outer branch of a series of biramous appendages (see also below).

Paraduslia n. gen.

TYPE SPECIES. — *Paraduslia talimaae* n. gen., n. sp., by monotypy.

ETYMOLOGY. — From its similarity to the Ordovician form *Duslia insignis* Jahn, 1893.

DIAGNOSIS. — Small, narrow cheloniellid, approximately twice as long as broad, with at least 12 trunk segments. Terminal furca short and eyes apparently absent. Marginal fringe of spines (seen in *Duslia insignis*) absent.

REMARKS

In overall appearance these fossils resemble the Upper Ordovician cheloniellid *Duslia* Jahn, 1893. Both have a narrow median axial region which extends onto the prosomal dorsal shield

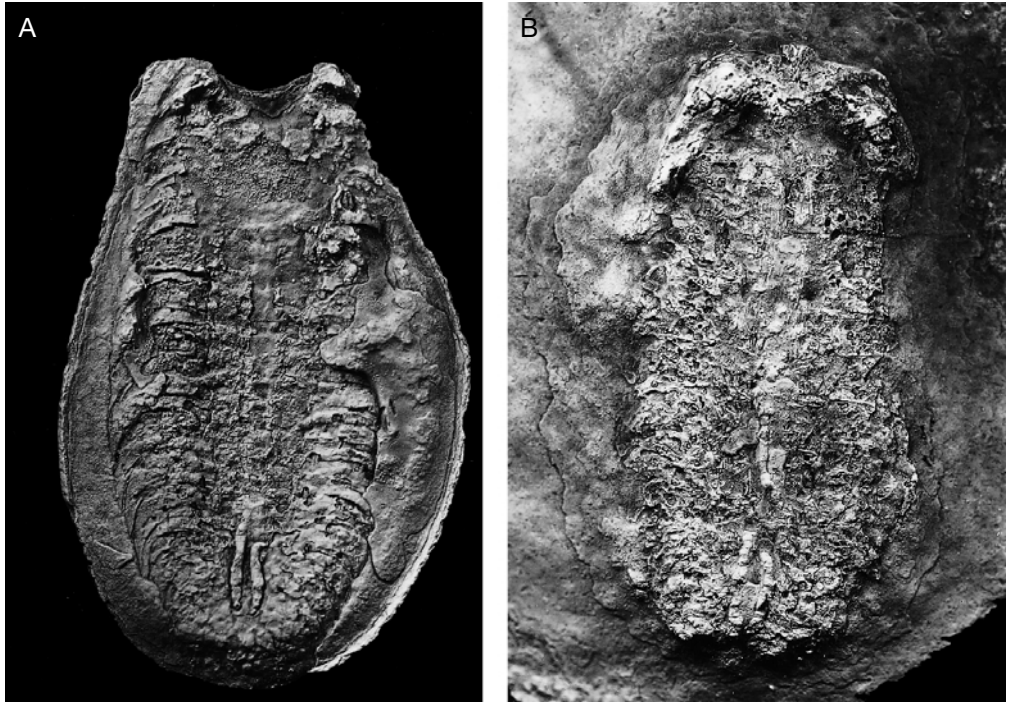


Fig. 1. — *Paraduslia talimaae* n. gen., n. sp.; **A**, No. 35/700 (holotype), 29 × 16 mm; **B**, No. 35/702, 33 × 15 mm.

(or carapace). Both appear to lack eyes and both have a relatively small pair of terminal furcae, as compared to the very long furcae of *Cheloniellon* Broili, 1932. Because of this similarity to *Duslia* the new generic name *Paraduslia* n. gen. is proposed for this material. The proportions of the body, the larger number of trunk segments and the lack of marginal tergal spines in the new fossils distinguish them from *Duslia*.

Paraduslia talimaae n. sp.
(Figs 1-5)

HOLOTYPE. — GIL No. 35/700 (oc 41/bd 12).

ETYMOLOGY. — In honour of Dr Valentina Talimaa (GIL) for her permission to work on this material and her hospitality in Vilnius.

OTHER MATERIAL EXAMINED. — GIL Nos. 35/701 (oc 1/bd 21), 35/702 (oc 41/bd 12), 35/703 (oc 41/bd 12), 35/704 (right bank of upper part of Spokoinaya river) (not figured), 35/705 (oc 41/bd 12) (not figured), 35/706 (oc 1/bd 21) (not figured).

GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTION. — All material is from the Severnaya Zemlya Formation (Lower Devonian [lower Lochkovian]), October Revolution Island.

DIAGNOSIS. — As for the genus.

REMARKS

Though it is possible that this material represents more than one species there are no reliable characters to separate the specimens other than size. On these grounds all material is referred to a single species.

DESCRIPTION

No. 35/700 (holotype)

Specimen in dorsal view and quite well preserved (Figs 1A; 2A). Maximum preserved length 29, maximum width 16. Carapace shape and carapace margins indistinct. Median axis of opisthosoma narrow and distinct, width 2. Tergite margins quite clear on left side where

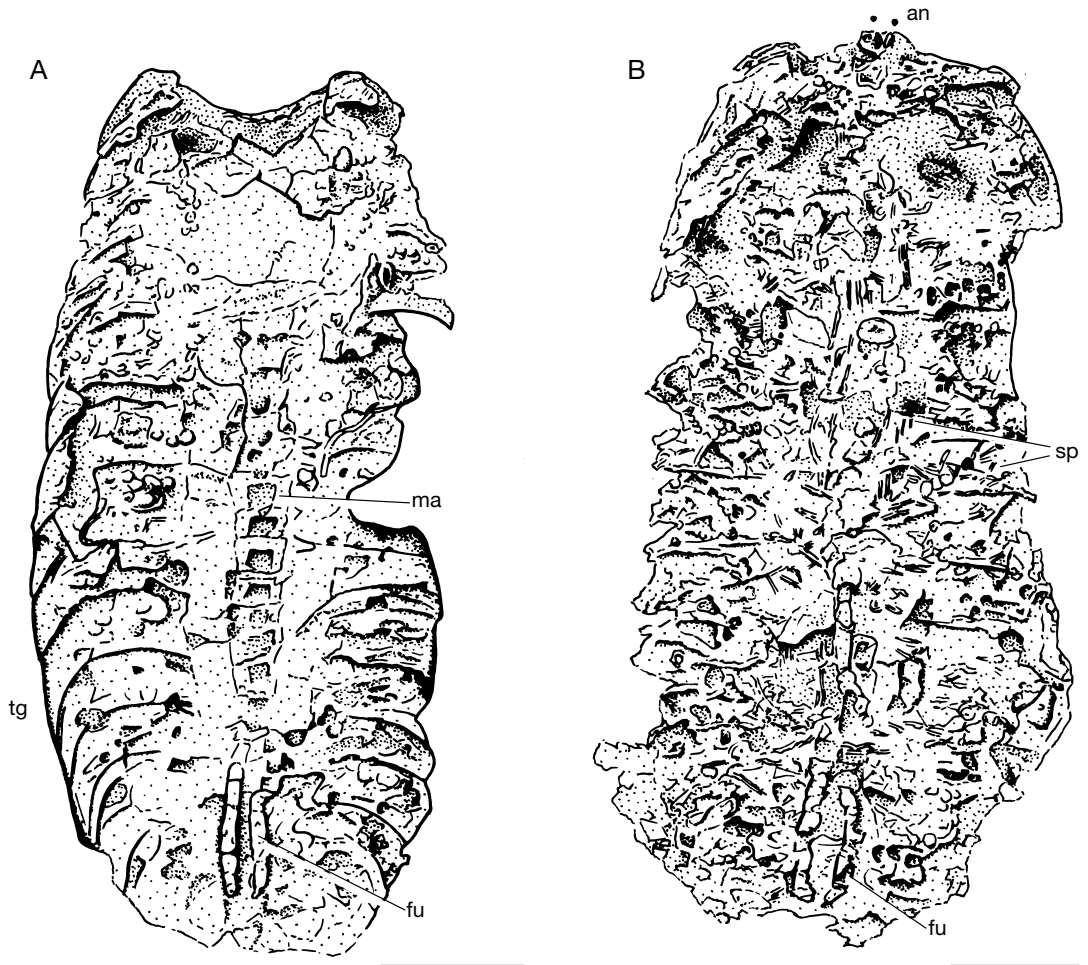


FIG. 2. — *Paraduslia talimaae* n. gen., n. sp., interpretative drawings of the specimens shown in Fig. 1; **A**, No. 35/700 (holotype); **B**, No. 35/702. Abbreviations: **an**, bases of antennae; **fu**, furca; **ma**, median axis of opisthosoma; **sp**, spines, probably lamellar spines; **tg**, tergite. Scale bars: 5 mm.

four tergites show shape and curvature very clearly. Lateral margins of up to eight tergites distinct with median axis suggesting at least 12 trunk segments were present in life. Furca distinct, each ramus composed of three pieces, a very short proximal section, a longer median section which widens distally, and a shorter, tapering distal section.

No. 35/701

Specimen preserved in dorsal view though details lacking and whole animal slightly

skewed about its median axis (Figs 3A; 4A). Maximum length 18, width 9. Carapace reasonably well preserved with a broadly rounded anterior margin. Posterior margin of carapace curved. Median axis evident along length of specimen and extends onto posterior region of carapace to form a raised diamond-shaped area with a slight anterior projection. Additional furrows faintly visible more laterally on the carapace. Eye tubercles absent. Axial region clearly preserved on trunk with up to 13 tergites present. Pleural region of tergites

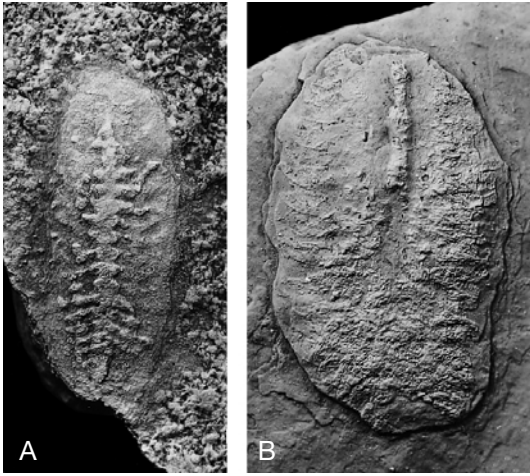


FIG. 3. — *Paraduslia talimaae* n. gen., n. sp.; **A**, No. 35/701, 18 × 9 mm; **B**, No. 35/703, 20 × 16 mm.

poorly preserved and tergite boundaries indistinct here. Furca not preserved.

No. 35/702

Specimen probably in ventral view. Outline and segmentation of body very indistinct but medial axis visible along part of its length (Figs 1B; 2B). Maximum length 33, width 15. Pair of tiny (length 0.5) white structures orientated parallel with the long axis of the body clearly preserved. Interpreted here as antennae. Much of body with covering of short (length typically 2), filamentous structures, slightly paler than the surrounding fossil. Some filaments orientated along long axis of body, especially close to median axis, but most with no particular pattern of orientation. Most filaments grouped into associations of about five to ten elements. Filaments interpreted here as part of appendages, though appendages themselves absent. Furca well preserved.

No. 35/703

Poor specimen, antero-posterior and dorso-ventral orientation difficult to distinguish. Segmentation very indistinct, though part of median axis preserved (Figs 3B; 4B). Maximum length 20, width 12. Specimen with numerous filamentous structures, often associated into

groups and slightly paler than the surrounding fossil. Some filaments orientated along the long axis of the body (as in 702). Other filaments longer and more regular in their distribution, approximately perpendicular to the long axis of the body. Furca and appendages not preserved.

MORPHOLOGICAL RECONSTRUCTION

The new material ranges in length from two to four cm. Compared to other cheloniellids these examples are relatively elongate, being approximately twice as long as broad. Eyes appear to be absent. One specimen (35/701, Figs 3A; 4A) preserves an area of the median axis on the prosomal dorsal shield (or carapace), but shows no evidence for raised lateral eye tubercles on this carapace comparable with those of, for example, *Cheloniellon*. None of the specimens clearly show the total number of trunk segments though counting segments in the axial regions of both 35/700 and 35/701 (Figs 1A; 2A; 3A; 4A) suggests there were at least 12 in total. By comparison *Cheloniellon* has nine, *Duslia* has 10 and the other cheloniellids are incomplete making their segment count uncertain. Specimen 35/700 clearly shows that the tergites bend posteriorly at their lateral margins (Figs 1A; 2A) and have a shallow groove running close to the posterior margin of the tergite. This specimen also suggests that the tergites have a shallow depression across the median axis (Figs 1A; 2A).

Unfortunately appendages are mostly absent in this new material. A small pair of white structures at the front of 35/702 (Figs 1B; 2B) are interpreted as the bases of the antennae as just in front of them are two small white circles suggesting a narrow pair of antennae continuing deeper into the matrix. Long antennae are present in *Cheloniellon*. The rest of the appendages are absent in the present material although by comparison with *Cheloniellon* a series of gnathobasic head appendages and biramous trunk appendages would be expected. The lamellar spines of the outer ramus of the opisthosomal appendages are seen in 35/702 and 35/703 as described above. Stürmer & Bergström (1978) noted that these spines were

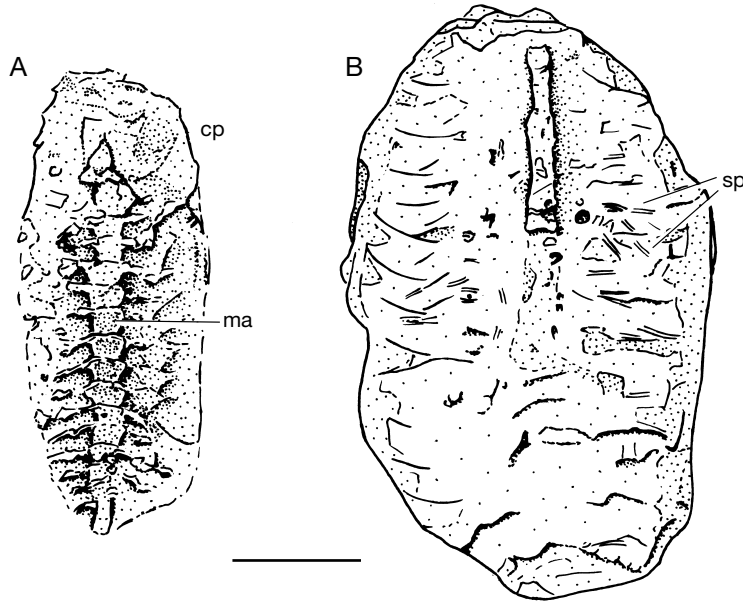


FIG. 4. — *Paraduslia talimaae* n. gen., n. sp., interpretative drawings of the specimens shown in Fig. 3; **A**, No. 35/701; **B**, No. 35/703. Abbreviations: **cp**, carapace (note raised, diamond-shaped central area); **ma**, median axis of opisthosoma; **sp**, spines, probably lamellar spines from appendages. Scale bar: 5 mm.

so stiff in *Cheloniellon* that at times the cuticle of the rest of the body would be bent around them during compression. Likewise, these spines are unusually well preserved in the Severnaya Zemlya material, especially 35/702, suggesting that their cuticle was very resilient. Their distribution is somewhat random in 35/702 where the spines are mostly short and fragmentary. However in 35/703 there is more of a pattern with groups of slightly longer spines projecting laterally from the midline, as though associated with an appendage series. A reconstruction of the dorsal surface of this new cheloniellid is presented in Fig. 5.

PHYLOGENY

The affinities of the cheloniellids as a group remain problematic and this new material adds little to the debate, except to confirm the presence of the stout lamellar spines in an additional taxon to *Cheloniellon*. Originally *Cheloniellon* was believed to be similar to trilobites (Broili 1932), though subsequent authors have sug-

gested that it is related to trilobites and Cambrian “merostomoids” (Størmer 1944), that it is a late representative of a trilobitiform group giving rise to Chelicerata (Størmer & Bergström 1978), that it is related to “loricate” crustaceans (Delle Cave & Simonetta 1991) or that it is the sister group to Chelicerata (Wills *et al.* 1995; Dunlop & Selden 1997).

The clade Arachnata (alternatively Arachnomorpha) has been erected for chelicerates, trilobites, and a number of related arthropods comprising many of the problematic Burgess Shale-type animals (e.g., Wills *et al.* 1995), although clear apomorphies defining Arachnata and relationships within the clade remain unresolved. Dunlop & Selden (1997) proposed that a number of Palaeozoic arachnate genera, *Duslia*, *Cheloniellon*, *Triopus* Barrande, 1872, *Neostrabops* Caster & Macke, 1952 and *Pseudarthron* Selden & White, 1984 could be grouped together into a clade for which Broili’s (1932) name *Cheloniellida* was available. The new taxon, *Paraduslia* n. gen., can be added to

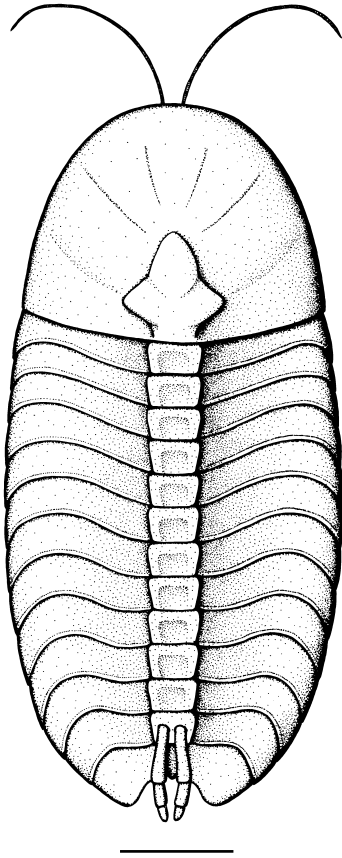


FIG. 5. — Reconstruction of the dorsal surface of *Paroduslia tallimae* n. gen., n. sp. Scale bar: 5 mm.

this list and as such represents only the sixth genus of this group. Cheloniellids range from the Ordovician to the Lower Devonian (Dunlop & Selden 1997) making *Paroduslia* n. gen. one of the youngest records of this group. *Paroduslia* n. gen. could be interpreted as a sister taxon to *Duslia* based on the synapomorphies of a reduced furca and loss of eyes. However this interpretation must be treated with caution as the number of trunk segments is greater in *Paroduslia* n. gen., while the terminal end of the body and the morphology of the furca, and hence the plesiomorphic furcal condition, is not known for all cheloniellid taxa. Likewise, the absence of eyes is based only on a single *Paroduslia* n. gen. specimen in which the preservation is not ideal.

MODE OF LIFE

Stürmer & Bergström (1978) believed *Cheloniellon* had the overall body plan of a benthic animal (though not a burrower) and that it was a predator, since they identified xiphosuran-like gnathobases for masticating food. Chlupác (1988) regarded the eyeless *Duslia* as a probable shallow burrower in a low energy environment. *Paroduslia* n. gen. also appears to lack eyes which might favour a burrowing mode of life. The function of the lamellate spines in both *Paroduslia* n. gen. and *Cheloniellon* remains unresolved. Broili's (1932) original suggestion that they aided swimming seems unlikely, though Stürmer & Bergström (1978) regarded the spines as very stiff compared to known respiratory lamellae, e.g., xiphosuran book gills. In the absence of any other known respiratory organs in cheloniellids a respiratory function for the lamellar spines seems the most plausible. Perhaps if these animals were living in close association with the substrate the stiffness of the spines prevented mechanical damage by the substrate. Overall, *Paroduslia* n. gen. may have had a mode of life analogous to living xiphosurans, acting as a predator and/or scavenger either on, or just within, the substrate.

CHELICERATA Heymons, 1901

CHASMATASPIDA Caster & Brooks, 1956

REMARKS

In an early report on the Severnaya Zemlya Formation, Novil'skaya *et al.* (1983) figured three specimens which they provisionally interpreted as eurypterids. In fact these fossils do not show the typical eurypterid pattern of opisthosomal tagmosis, i.e. a preabdomen of seven segments and a postabdomen of five segments. Instead, they have a broad preabdomen of three large segments and a postabdomen of nine segments (Figs 6-10). This pattern of tagmosis is consistent with another, rare chelicerate taxon, Chasmataspida. Originally thought to be xiphosurans, only four chasmataspid genera have been described (Caster & Brooks 1956; Stürmer 1972;

Dunlop *et al.* 1999) with Chasmataspida being recognised as a separate clade within Chelicerata by Dunlop & Selden (1997) and Dunlop *et al.* (1999). In total there are about 70 chasmataspid specimens from Severnaya Zemlya, ranging in size from about 1 to 4 cm long, with the better preserved examples (GIL 35/324, 35/336-337, 35/339, 35/707, 35/711-714, 35/719, 35/735) described and figured here (Figs 6-9).

Family DIPLOASPIDIDAE Størmer, 1972

DIAGNOSIS. — Small chasmataspids with semicircular or subrectangular carapace and with a distinctly tapering postabdomen and a short telson; postabdomen in Chasmataspididae elongate and not strongly tapering. No division of preabdominal tergites into medial and lateral plates (after Anderson *et al.* 2000).

REMARKS

Heteroaspis is now regarded as a junior synonym of *Diploaspis* following the revision of Dunlop *et al.* 2001: 253-269.

There are clear differences between *Chasmataspis* Caster & Brooks, 1956, in its monotypic family Chasmataspididae, and the known Devonian examples, *Diploaspis* Størmer, 1972, *Heteroaspis* Størmer, 1972 and *Forfarella* Dunlop, Anderson & Braddy, 1999, which can probably all be referred to a single family Diploaspididae (see Dunlop *et al.* 1999 for a discussion). Additionally, the one known appendage in *Chasmataspis* is chelate (Caster & Brooks 1956) while the Devonian fossils, as far as we know, have pediform appendages (Størmer 1972). The Devonian examples may all have had paddles, but so far these have only been found in *Diploaspis* Størmer, 1972 and now in this Severnaya Zemlya material (see below). These Russian fossils, with their undivided preabdomen, tapering postabdomen and short telson, can be referred to Diploaspididae with some confidence.

Octoberaspis n. gen.

TYPE SPECIES. — *Octoberaspis ushakovi* n. gen., n. sp., by monotypy.

ETYMOLOGY. — From October Revolution Island, where this material was discovered, and the typical chasmataspid suffix, *aspis*.

DIAGNOSIS. — Diploaspid with a pair of short, styli-form epimera on the terminal opisthosomal segment which lie adjacent to the telson. Preabdomen rounded and sculptured with tubercles.

REMARKS

The single pair of epimera on the pretelson, adjacent to the telson of the Siberian specimens is not seen in *Diploaspis* and *Heteroaspis* although broader postabdominal epimera are present in the new taxon from Scotland (Anderson *et al.* 2000). Tuberculation is absent in *Diploaspis* and *Heteroaspis*, although new, undescribed chasmataspid material from Germany is also tuberculate (Markus Poschmann pers. comm.). *Forfarella* is poorly preserved, but has a trapezoidal, posteriorly tapering preabdomen which differs from the more rounded preabdomen seen in the Severnaya Zemlya material. Based on these differences, a new genus, *Octoberaspis* n. gen., is proposed.

Octoberaspis ushakovi n. sp.

(Figs 6-10)

Eurypteridae – Novilskaya *et al.* 1983: 94, fig. 5.

HOLOTYPE. — GIL No. 35/336 (oc 67/bd 12).

ETYMOLOGY. — In honour of G. A. Ushakov, an Arctic explorer and the leader of the first expedition to Severnaya Zemlya in 1930-1932.

ADDITIONAL MATERIAL. — GIL Nos. 35/324, 35/337, 35/338 (the latter two on the same block as the holotype), 35/339, 35/379, 35/707 (all oc 67/bd 12), 35/711, 35/712 (both oc 1/bd 21), 35/713, 35/714 (both oc 67/bd 12), 35/719 (oc 1/bd 21), 35/735 (oc 67/bd 12).

ADDITIONAL MATERIAL (NOT FIGURED). — GIL Nos. 35/708-710, 35/715-717 (all oc 67/bd 12); 35/718, 35/720 (both oc 41/bd 12), 35/721-734, 35/736-749 (all oc 67/bd 12), 35/750-768 (all oc 1/bd 21); 35/769-777 (all oc 41/bd 12); 35/778 (oc 40/bd 6).

GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTION. — All material is from the Severnaya Zemlya Formation (Lower Devonian [lower Lochkovian]), October Revolution Island.

DIAGNOSIS. — As for the genus.

DESCRIPTION

No. 35/336 (holotype)

Specimen Nos. 35/336 and 35/337 are preserved together in one nodule (Figs 6B; 7B) along with a poorer specimen, 35/338, not described here. No. 35/336 very well preserved as external mould showing dorsal surface. Total length 25, carapace length 7, preabdomen length 8, postabdomen length 10, including telson. Maximum width 14. Carapace subquadrate with approximately straight posterior margin merging into a genal spine on the right side. Middle of carapace somewhat deformed, but with evidence for at least one median eye in the centre of the carapace. Reniform lateral eye tubercles present. All 13 opisthosomal segments preserved. Fragments of three appendages preserved beyond margin of left side of carapace. Opisthosomal tergite 1 short, tuberculate and occupying full width of carapace. Preabdominal tergites 2-4 large with curving posterior margins and distinct ornament of tubercles. Postabdominal segments taper smoothly towards telson. Segment 5 longest, but successive tergites strongly telescoped together. Postabdominal segments with slight posterior curvature; ornamentation absent. Pretelson with pair of short, styliform epimera. Telson short and styliform.

No. 35/324

Excellent specimen preserved as external mould in dorsal view (Figs 6A; 7A). Total length 34, carapace length 9, preabdomen length 7, postabdomen length 18. Maximum width 13. Carapace well preserved, rounded anteriorly and showing both median and lateral eyes. Median eyes small and located in slight triangular depressions on posteriorly tapering tubercle in centre of carapace. Broad depressions present either side of median eyes. Lateral eye tubercles reniform, each located at the posterior end of what appears to be an ophthalmic ridge. Slight ridge preserved close to anterior margin of the carapace where it follows the carapace curvature. Small prosomal limb fragment preserved on left side of specimen beyond carapace margin. All 13 opisthosomal segments preserved. Tergite 1

short, but lateral tuberculation evident. Tergites 2-4 large, forming the preabdomen, with tergite 4 longest. Preabdomen with strong sculpture of tubercles, with most tubercles concentrated at the lateral margins. Postabdomen elongate with all segments approximately the same length and narrowing gradually posteriorly. Postabdominal segments lack ornamentation. Terminal segment with poorly preserved pair of epimera surrounding a short telson. Telson with slight median depression.

No. 35/337

Specimen preserved in dorsal view as an internal mould (Figs 6B; 7B). Total preserved length 18, carapace length 8, preabdomen length 5, postabdomen length 5, though terminal end of postabdomen missing. Maximum width 12. Carapace rounded anteriorly, highest in the centre where the median eyes would be expected, but morphological details lacking. Preabdomen distorted and lacks detail, though tuberculation at the lateral margins well preserved. Postabdomen telescoped with short segments tapering posteriorly. Terminal end of postabdomen and telson absent.

No. 35/339

Specimen preserved as internal mould in dorsal view (Figs 8C; 9C). Total length 20, carapace length 8, preabdomen length 7, postabdomen length 5. Maximum width 12. Carapace rounded anteriorly and with straight posterior margin, but shows few morphological details. Two appendages, possibly prosomal limbs 3 or 4, preserved beyond carapace margin. Limbs slender with evidence for division into short podomeres. All 13 opisthosomal segments preserved. Tergite 1 distinct and short. Preabdomen poorly preserved with much of tergites 2-4 missing to reveal the featureless ventral plate beneath them. Postabdomen highly telescoped and bends down towards the matrix at the distal end such that posterior tip is absent. First postabdominal segment (segment 5) broken to reveal full length of next segment tucked under it.

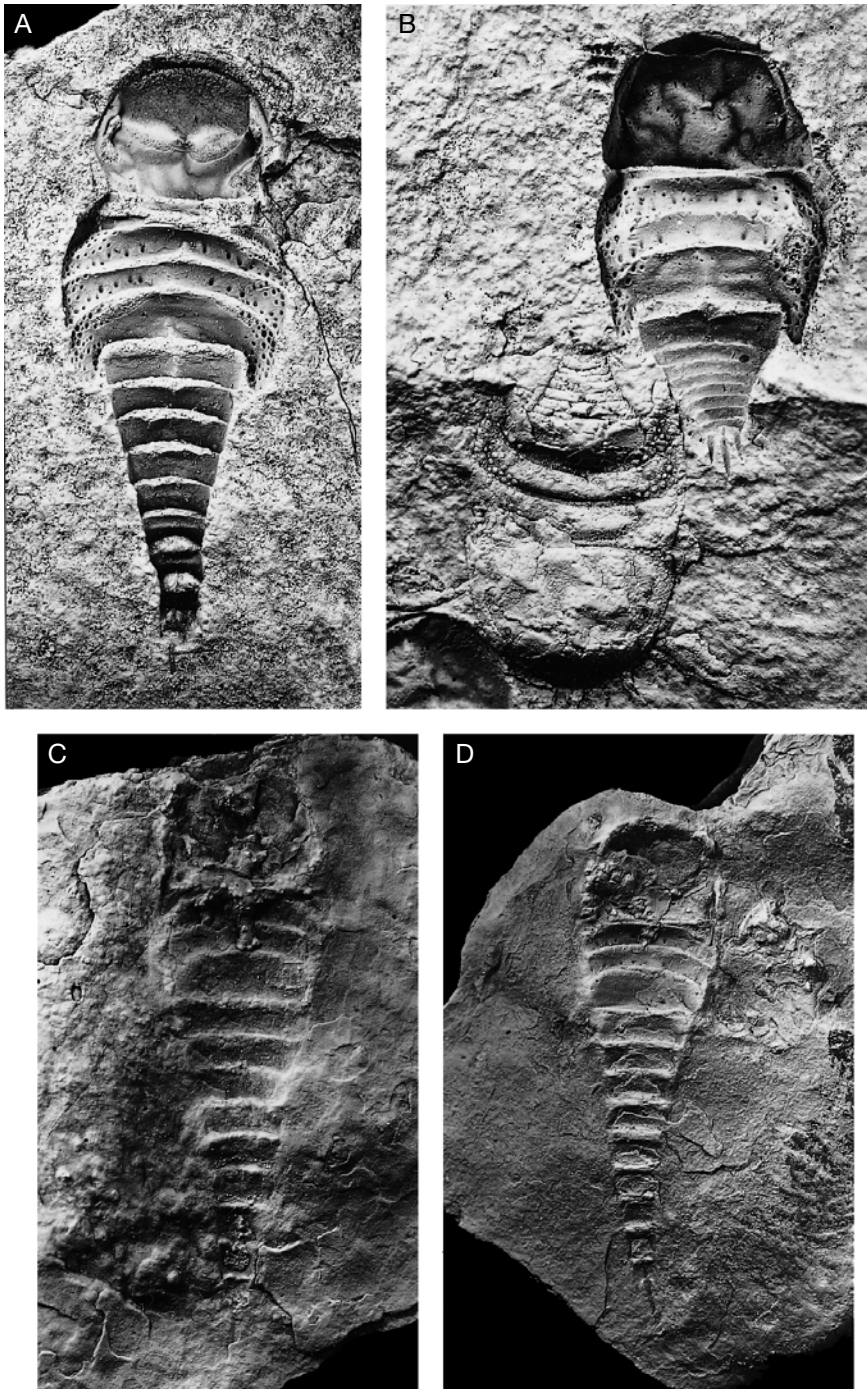


FIG. 6. — *Octoberaspis ushakovi* n. gen., n. sp.; **A**, No. 35/324, 34 × 13 mm; **B**, Nos. 35/336 (holotype) (above), 24 × 14 mm, and 35/337 (below), 18 × 12 mm; **C**, No. 35/711, 33 × 9 mm; **D**, No. 35/712, total length 30 mm.

No. 35/379

Specimen probably in ventral view, but with prosoma missing (Figs 8E; 9E). Total preserved length 27, preabdomen length 9, postabdomen length 18. Maximum width 12. Preabdomen composed of broad, mostly featureless, but slightly folded area (the ventral plate) overlying tuberculated tergites visible on right margin of preabdomen. Postabdomen well preserved, though segments have become slightly disarticulated and separated by thin areas of matrix. Postabdomen tapers posteriorly with all segments approximately the same length. Postabdominal segments lack ornamentation. Thirteenth segment with clear pair of short, styliform epimera. Short, styliform telson lies between these epimera.

No. 35/707

Specimen preserved in dorsal view (Figs 8B; 9B). Total length 26, carapace length 9, preabdomen length 7, postabdomen length 11. Maximum width 12. Carapace rounded anteriorly with distinct ridge close to carapace margin and median eyes clearly visible as a pair of tiny circles in the centre of the carapace set into slight triangular depressions. Lateral eyes not preserved. Appendage fragments preserved on right side of specimen, including a poorly preserved paddle. Tergite 1 not preserved. Preabdomen poorly preserved with much of the segmentation missing to reveal the ventral plate underneath. Postabdomen quite well preserved, though segmentation indistinct. Postabdomen tapers towards the fragmentary pretelson segment and telson.

No. 35/711

Specimen preserved in ventral view, mostly as an external mould, but with some structures in positive relief (Figs 6C; 7C). Total length 33, prosoma length 7, opisthosoma length 26, tagmosis into preabdomen and postabdomen not clearly demarcated. Maximum width 9. Prosoma poorly preserved, but may show areas corresponding to coxae of prosomal appendages. Prosomal appendages not pre-

served. Opisthosoma without characteristic broad preabdomen visible in dorsal view. Segment 1 (the metastoma) not clearly preserved. Segments 2-4 expressed as sclerites (probably operculae). Distinct genital appendage preserved on the midline in positive relief, length 4, originating from segment 2 and extending down to posterior margin of segment 3. Genital appendage relatively squat, apparently consisting of a single section, widening posteriorly with a distinctly trilobed terminal end. Postabdomen tapers posteriorly with all segments approximately same length. Epimera on segment 13 poorly preserved, but short, styliform telson present.

No. 35/712

Specimen preserved in ventral view (Figs 6D; 7D). Total length 30, prosoma length 6, preabdomen length 5, postabdomen length 19. Prosoma fairly poorly preserved, but with distinct shield-shaped metastoma representing opisthosomal segment 1. Opisthosomal segments 2-4 expressed as sclerites (probably opercula). Anterior two sclerites strongly curved posteriorly and sculptured with a small number of tubercles. Sclerites 2 and 3 approximately same length, sclerite 4 longer. Sclerite 2 with indeterminate, squat median structure reaching entire length of plate. Median structure apparently composed of rectangular basal section and triangular distal section, again interpreted as a genital appendage. Postabdomen tapers posteriorly, curving slightly to the right, with all segments approximately the same length. Segment 13 with poorly preserved pair of short, styliform epimera. Telson short and styliform.

No. 35/713

Small, probably juvenile specimen in dorsal view (Figs 8F; 9F). Length 11, carapace length 4, opisthosoma length 7. Differentiation into preabdomen and postabdomen not so distinct as in adults. Maximum width 4. Carapace rounded with proportionally large median and lateral eye tubercles. Opisthosoma apparently with full complement of 13 segments, postab-

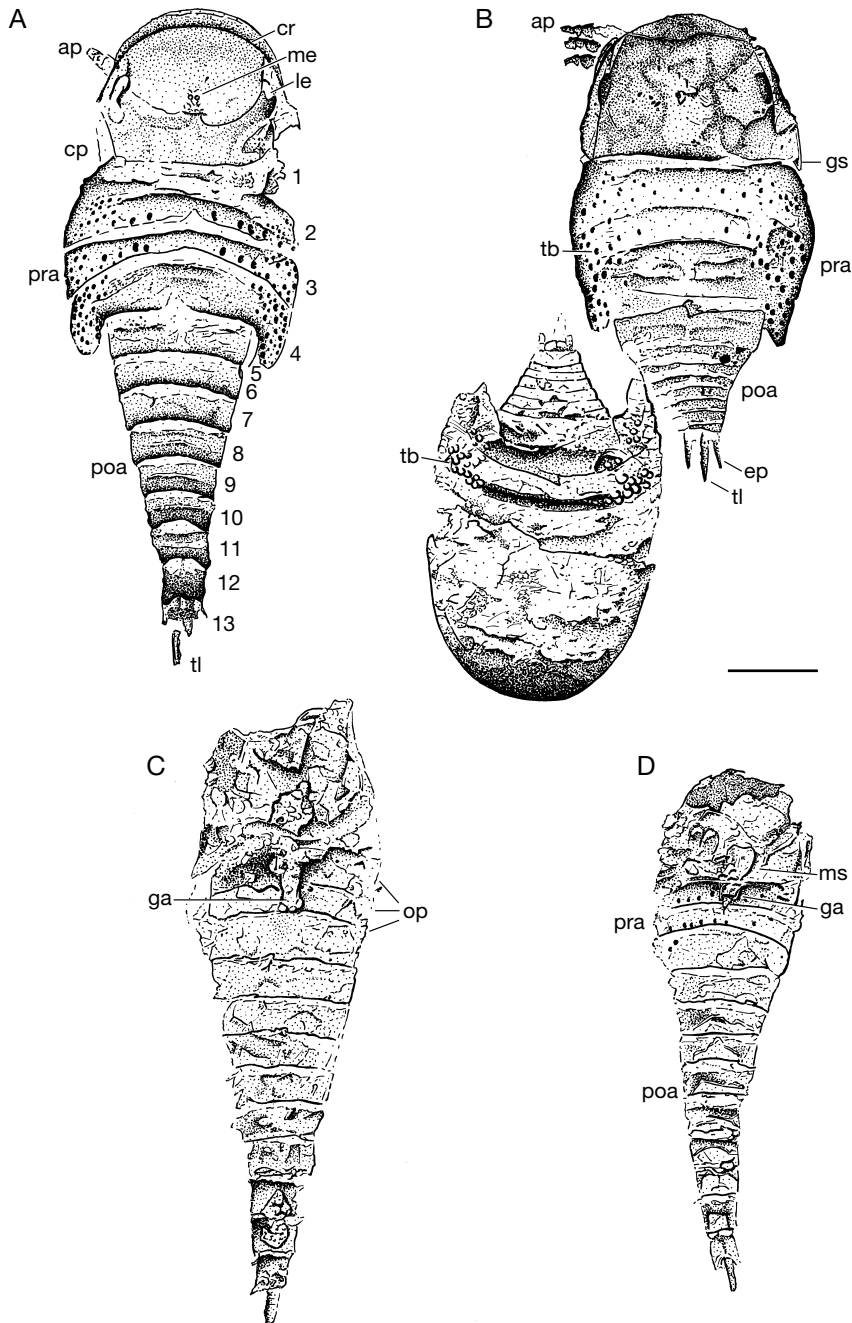


FIG. 7. — *Octoberaspis ushakovi* n. gen., n. sp., interpretative drawings of the specimens shown in Fig. 6; **A**, No. 35/324; **B**, Nos. 35/336 (holotype) (above) and 35/337 (below); **C**, No. 35/711; **D**, No. 35/712. Abbreviations: **ap**, prosomal appendage; **cp**, carapace; **cr**, marginal carapace rim; **ep**, epimera of pretelsonic segment; **ga**, genital appendage; **gs**, genal spine; **le**, lateral eye tubercle; **me**, median eye tubercle; **ms**, metastoma; **op**, opisthosomal operculae; **pra**, preabdomen; **poa**, postabdomen; **tb**, preabdominal tuberculation; **tl**, telson, opisthosomal segments numbered. Scale bar: 5 mm.

domen tapering posteriorly, though posterior-most segments difficult to distinguish. Telson slender and proportionally longer than in adults.

No. 35/719

Small, probably juvenile, specimen preserved mostly in outline and in dorsal view (Figs 8G; 9G). Total length 8, carapace length 3, preabdomen length 3, postabdomen length 3. Maximum width 3.5. Carapace rounded anteriorly but lacks detail. Eyes and appendages not preserved. Preabdomen rectangular and segmentation not evident. Postabdomen tapers distally where segment boundaries are faintly visible. Telson not preserved.

No. 35/735

Relatively poor specimen in dorsal view in centre of nodule surrounded by a number of additional fragments (Figs 8A; 9A). Total preserved length 27, carapace length 8, preabdomen length 8, postabdomen length 11, though terminal end missing. Maximum width 12. Carapace broadly rounded anteriorly with genal spine on right side, but details lacking. Small paddle clearly preserved on left side at the posterior left corner of the carapace. Terminal three podomeres of paddle preserved, a broad proximal segment, length 3, widening distally and an oval distal segment, length 3. Small diamond-shaped podomere articulates between them. Preabdomen with somewhat indistinct segmentation. Tergites on left side removed during preparation to reveal ventral plate underlying the tergites. Scratches on ventral plate are preparation artefacts. Left side of ventral plate itself further removed to reveal ventral surface of preabdomen at its lateral margins where it forms a double tucking under to form ventro-lateral region of opisthosoma. This ventral surface matches outline of dorsal surface and has marginal, ventral tuberculation similar to the marginal dorsal tuberculation. Ventral opercula not revealed during preparation. Postabdomen telescoped, but poorly preserved and segmentation indistinct. Telson faintly preserved.

Chasmataspida incertae sedis

No. 35/714

Poor specimen lacking details, but appears to show different proportions of the postabdomen in comparison to the other material (Figs 8D; 9D). Total preserved length 29, carapace length 8, preabdomen length 7, postabdomen length 14, though not all postabdominal segments preserved. Maximum width 12. Carapace rounded anteriorly, but lacking detail. Appendages absent. Preabdomen appears broader than long but segmentation and ornamentation not preserved. At least seven postabdominal segments preserved, all very narrow compared to preabdomen, average width 3. These segments do not clearly taper posteriorly.

MORPHOLOGICAL RECONSTRUCTION

Carapace

The carapace is broadly rounded anteriorly with a distinct ridge, or rim, close to the anterior margin (No. 35/324, Figs 6A; 7A). The posterior margin of the carapace is approximately straight, though in the more complete carapaces small genal spines are present at the postero-lateral corners of the carapace (e.g., No. 35/336, Figs 6B; 7B). Genal spines are also known from *Chasmataspis* and though not explicitly described from *Diploaspis* and *Heteroaspis*, appear to be present based on Størmer's (1972) plates and figures of the Alken an der Mosel fossils. The carapace lacks any obvious ornament, like that seen on the preabdomen. The detailed shape of the carapace in life is difficult to reconstruct since there is evident compression of the material, though there appears to be slight lobes on the carapace between the median and lateral eyes. This, however, would be difficult to interpret as a xiphosuran-like cardiac lobe. There are lateral depressions of the carapace delineated by curving lines posterior to the lateral eyes (No. 35/324, Figs 6A; 7A, No. 35/713, Figs 8F; 9F; 11). A similar morphology has been reconstructed for some eurypterid carapaces (e.g., Størmer 1955: fig. 17).

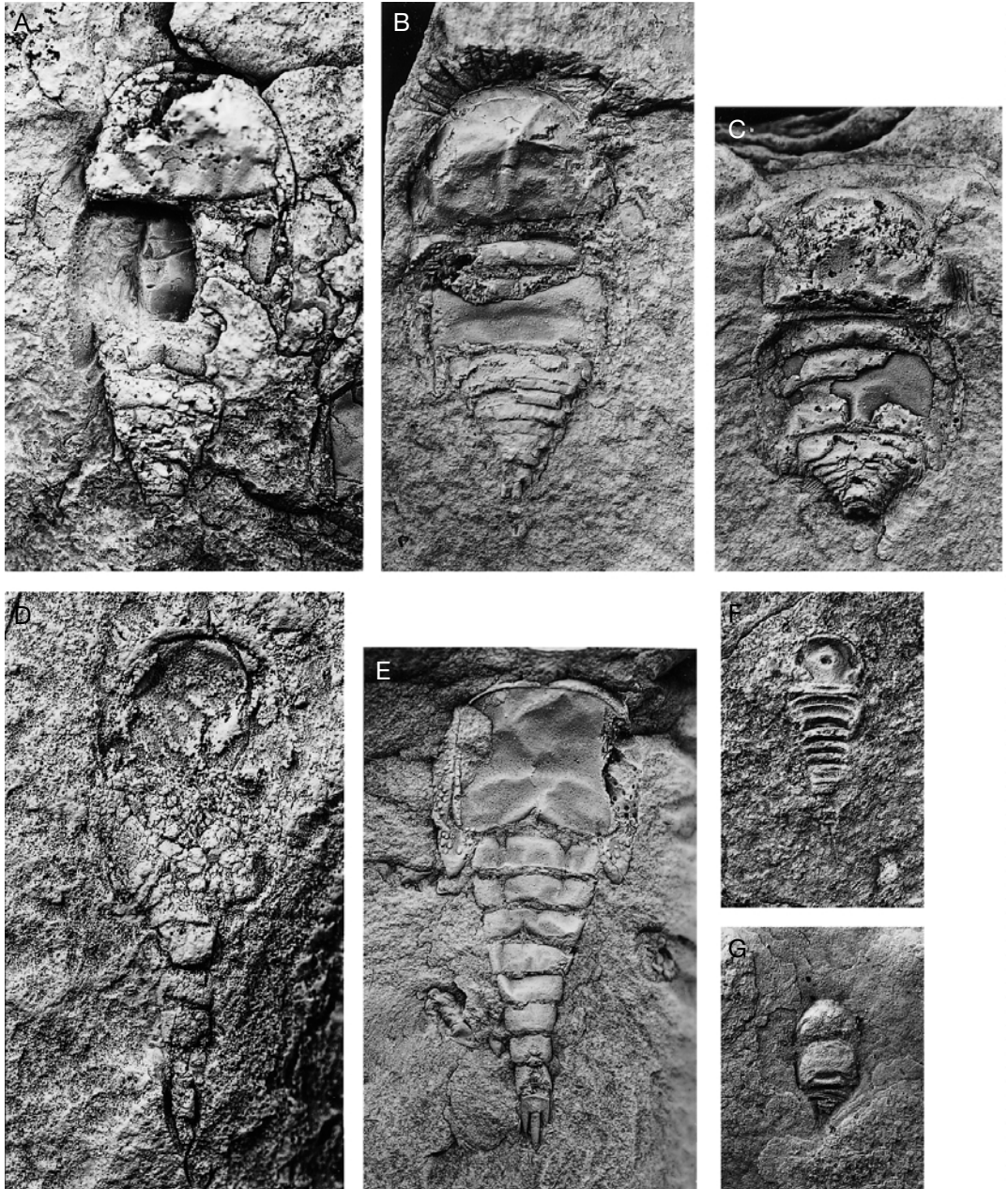


FIG. 8. — **A-C, E-G**, *Octoberaspis ushakovi* n. gen., n. sp.; **A**, No. 35/735, 27 × 12 mm; **B**, No. 35/707, 26 × 12 mm; **C**, No. 35/339, 20 × 12 mm; **E**, No. 35/379, 27 × 12 mm; **F**, No. 35/713 (juvenile), 11 × 4 mm; **G**, No. 35/719 (juvenile), 8 × 3.5 mm; **D**, *Chasmataspida incertae sedis*, No. 35/174, 29 × 12 mm.

Eyes

The median eyes, or ocelli, are tiny structures located in V-shaped depressions on a small,

posteriorly tapering tubercle in the centre of the carapace (Nos. 35/324, 35/707, Figs 6A, B; 7A, B). Lateral eye tubercles can be clearly

seen in 35/324 as well (Figs 6A; 7A). The lateral eyes are fairly small, kidney-shaped and located close to the lateral margins of the carapace at about the same level as the median eyes. The lateral eyes appear to be situated on slight ridges, at least anterior to the eye tubercle itself, where a short ridge curves laterally towards the anterior carapace rim (No. 35/324, Figs 6A; 7A). These are similar to the ophthalmic ridges of xiphosurans, though the presence of this character should be treated with caution as it has been considered an autapomorphy of the latter group (Anderson & Selden 1997) and is not obvious in *Chasmataspis*, *Diploaspis* or *Heteroaspis*.

Prosomal appendages

The prosomal appendages are poorly preserved. Apart from the metastoma (see below), the morphology of the coxal region and chelicerae (if present) are unknown. However, a number of specimens (e.g., Nos. 35/324, 35/336, 35/707, 35/339, Figs 6A, B; 7A, B; 8B, C; 9B, C) show fragments of narrow, pediform appendages projecting beyond the carapace. Similar, though dissociated, appendages were described in *Diploaspis* by Størmer (1972). The present material, with the legs *in situ*, suggests they were somewhat eurypterid-like, since in xiphosurans the appendages are held entirely beneath the carapace. Unfortunately the detailed morphology of these pediform chasmataspid appendages remains unknown and the fossils do not show the number of podomeres, whether or not they bore spines and whether or not they were chelate (like at least one leg described by Caster & Brooks [1956] from *Chasmataspis*).

In addition to these pediform appendages, this new material includes two examples of paddles (Nos. 35/735, 35/707, Figs 8A, B; 19A, B) similar in size and position to those figured by Størmer (1972) in *Diploaspis*. These paddles probably represent the modified sixth prosomal appendage, though with an incomplete coxal region this cannot be proven here. Three podomeres of the paddle can be seen in this material, two larger podomeres with a smaller, diamond-shaped

podomere in between them (No. 35/735, Figs 8A; 9A) which appears to act as some sort of articulation between the “blades” of the paddle. Though strongly resembling the paddles of many eurypterids, and Recent portunid crabs, this morphology differs slightly to the eurypterid paddle (e.g., Størmer 1955), which does not have a diamond-shaped podomere in this somewhat lateral position. Furthermore there is no obvious distal “claw” in the chasmataspid paddle, something that is seen in eurypterids.

Opisthosomal segmentation

This new material, along with an ongoing revision of the *Chasmataspis* type material, indicates that chasmataspids had 13 opisthosomal segments (e.g., Anderson & Selden 1997), not 12 as reported by Caster & Brooks (1956) and most subsequent authors. The extra-segment comes from the recognition of a short tergite between the carapace and the preabdomen which can be seen in Nos. 35/324 and 35/336 (Figs 6A, B; 7A, B). This is a genuine sclerite, and not just a space where the prosoma and opisthosoma have disarticulated, because in both specimens there are traces of tuberculation on this first tergite. Following this, tergites 2-4 are broad sclerites that form the dorsal surface of the preabdomen (e.g., No. 35/324, Figs 6A; 7A), or “buckler” to use Caster & Brooks’ (1956) term. These preabdominal tergites are associated with three ventral opercula (see below). Following the preabdomen, segments 5-13 are interpreted as ring-like segments with fused tergites and sternites, and form the nine-segmented postabdomen (e.g., Nos. 35/324, 35/379, Figs 6A; 7A; 8E; 9E). The short telson is not considered a true body segment.

Preabdomen

Dorsally the preabdomen is slightly wider than long, somewhat rounded in appearance and is divided into three tergites (tergites 2-4) with slightly curved posterior margins (e.g., Nos. 35/324, 35/336, Figs 6A, B; 7A, B). Tergite 4 is the longest and has a pair of broad projections forming the postero-lateral corners. In *Chasmataspis* the “buckler” of tergites appears to be a fully

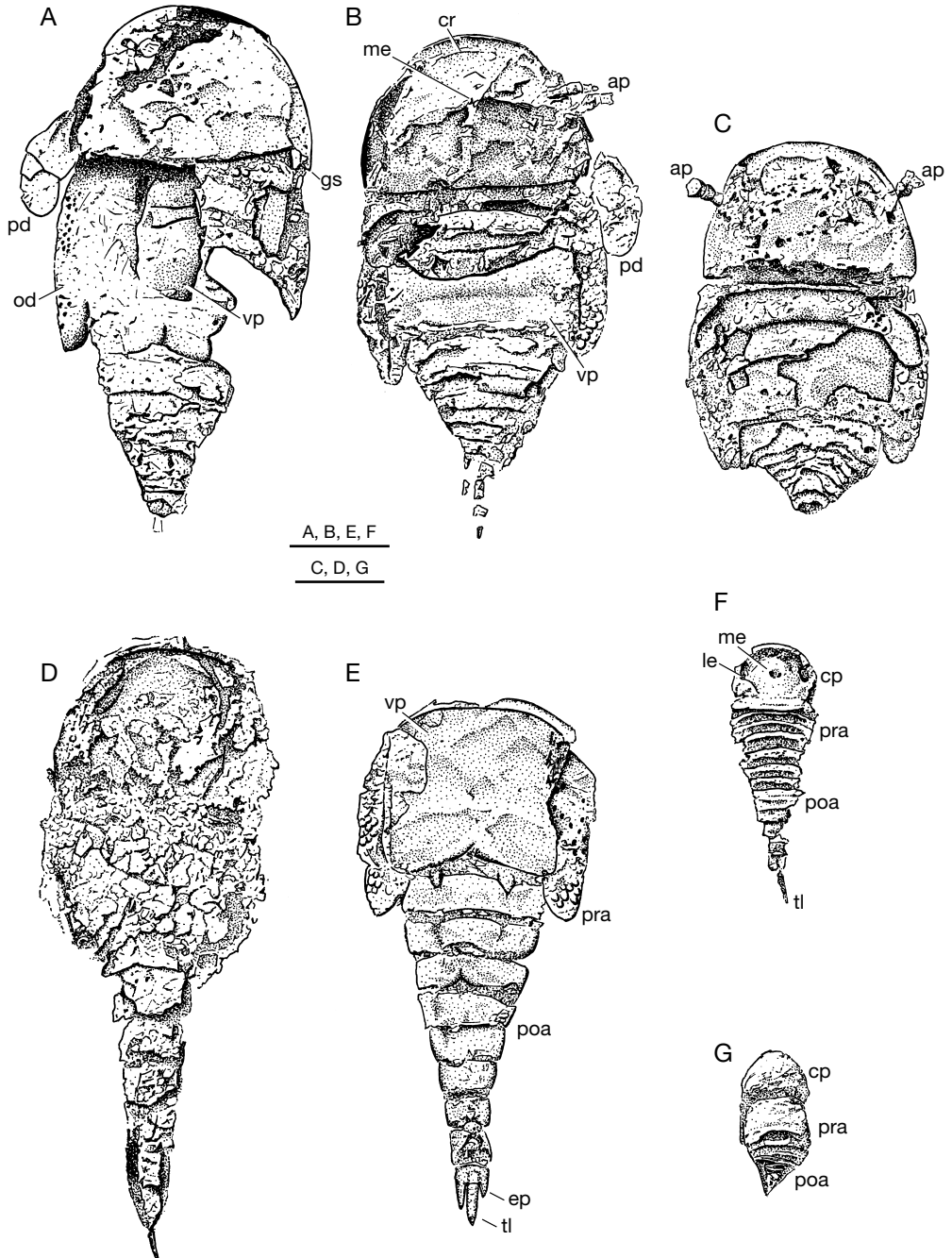


FIG. 9. — Interpretative drawings of the specimens shown in Fig. 8; **A-C, E-G**, *Octoberaspis ushakovi* n. gen., n. sp., **A**, No. 35/735; **B**, No. 35/707; **C**, No. 35/339; **E**, No. 35/379; **F**, No. 35/713 (juvenile); **D**, *Chasmataspida incertae sedis*, No. 35/714. Abbreviations: **ap**, prosomal appendage; **cp**, carapace; **cr**, marginal carapace rim; **ep**, epimera of pretelsonic segment; **gs**, genal spine; **le**, lateral eyes; **me**, median eyes; **od**, opisthosomal doublure where tergites tuck round onto ventral surface; **pd**, paddle (prosomal appendage VI?); **pra**, preabdomen; **poa**, postabdomen; **tl**, telson; **vp**, ventral plate underlying tergites. Scale bars: 5 mm.

fused structure similar to the xiphosurid thoracetrone, but fusion appears less likely in this new material as there is a distinct overlap between the tergites. The preabdomen has a distinct ornamentation of tubercles (see also Systematics) with rows of larger, oval median tubules merging into a higher concentration of smaller tubules at the lateral margins of the tergites.

Ventrally, there are three preabdominal plates (Nos. 35/711, 35/712, Figs 6C, D; 7C, D), presumably corresponding to tergites 2-4 (see also below). This is a significant observation. Both Caster & Brooks (1956) and Størmer (1972) described their chasmataspids as having a preabdomen with a single, fused ventral plate and interpreted this as having a pair of long, posterior slits opening respectively into a pair of pouches containing the gills. This would be very different to what is known from other aquatic chelicerates, i.e. xiphosurans and eurypterids, where there are a series of ventral, plate-like operculae derived from the opisthosomal appendages. Simonetta & Delle Cave (1981) noted the obvious problems of functional morphology in getting water through narrow slits without some sort of pumping mechanism. Their suggestions about how the chasmataspid gills were oxygenated were ingenious, though not entirely convincing, while both they and Størmer (1972) further speculated that the large ventral plate might protect the gills from drying and imply that chasmataspids were at least partially terrestrial.

The new Severnaya Zemlya material suggests that chasmataspids were in fact more typical chelicerates and did have a series of plate-like opercula on the ventral surface of the opisthosoma. Furthermore, unpublished studies by the author in collaboration with Simon Braddy and Lyall Anderson have interpreted some late Cambrian material from Texas as ventral impressions of a *Chasmataspis*-like animal which also appears to have had a series of preabdominal operculae (see also Dunlop *et al.* 1999). Unfortunately chasmataspid respiratory organs, and which segments they belonged to, are unknown. Meanwhile, two questions remain

from the preabdomen of the fossils described here. Firstly, the ventral operculae are not as broad as the corresponding tergites. This implies a similar situation to Recent xiphosurans in which the tergites (here fused into a thoracetrone) continue round onto the ventral surface as a broad doublure (e.g., Størmer 1955), while the gill operculae occupy a trapezoidal space set into this doublure. This interpretation is supported by No. 35/735 (Figs 8A; 9A), which shows essentially a dorsal view but where successive layers of the preabdomen have been removed by preparation. This specimen reveals the ventral surface of the preabdomen at its lateral margins which retains the outline of the dorsal surface, and was likewise tuberculated. This interpretation is made with some reservations as no single specimen shows the entire ventral preabdomen, but the latter feature is shown in the reconstruction (Fig. 10).

Secondly, this specimen, along with Nos. 35/707, 35/339 and 35/379 (Figs 8B, C, E; 9B, C, E) preserves a broad, featureless area within the postabdomen that lacks obvious segmentation. Preparing down through a specimen, removing first the tergites and then this ventral plate, indicated that the plate is sandwiched between the dorsal tergites and the ventral preabdomen (see No. 35/735, Figs 8A; 9A). This plate is unusual for chelicerates and furthermore it is probably the same structure as the single ventral plate described by both Caster & Brooks (1956) and Størmer (1972) in their chasmataspids. Its presence is confirmed in this new material, but its interpretation remains difficult. The simplest explanation is that it is the ventral wall of the preabdomen from which the operculae hang. Nothing directly comparable is known from fossil eurypterids or xiphosurans. However examination of Recent xiphosuran material from which the gill operculae were removed showed that these operculae do overlie a single plate, essentially the fused true sternites of the opisthosoma, although unlike the chasmataspid plate observed here this has a relatively large space anteriorly where the operculae attach. Re-examination of both Caster & Brooks' (1956) and

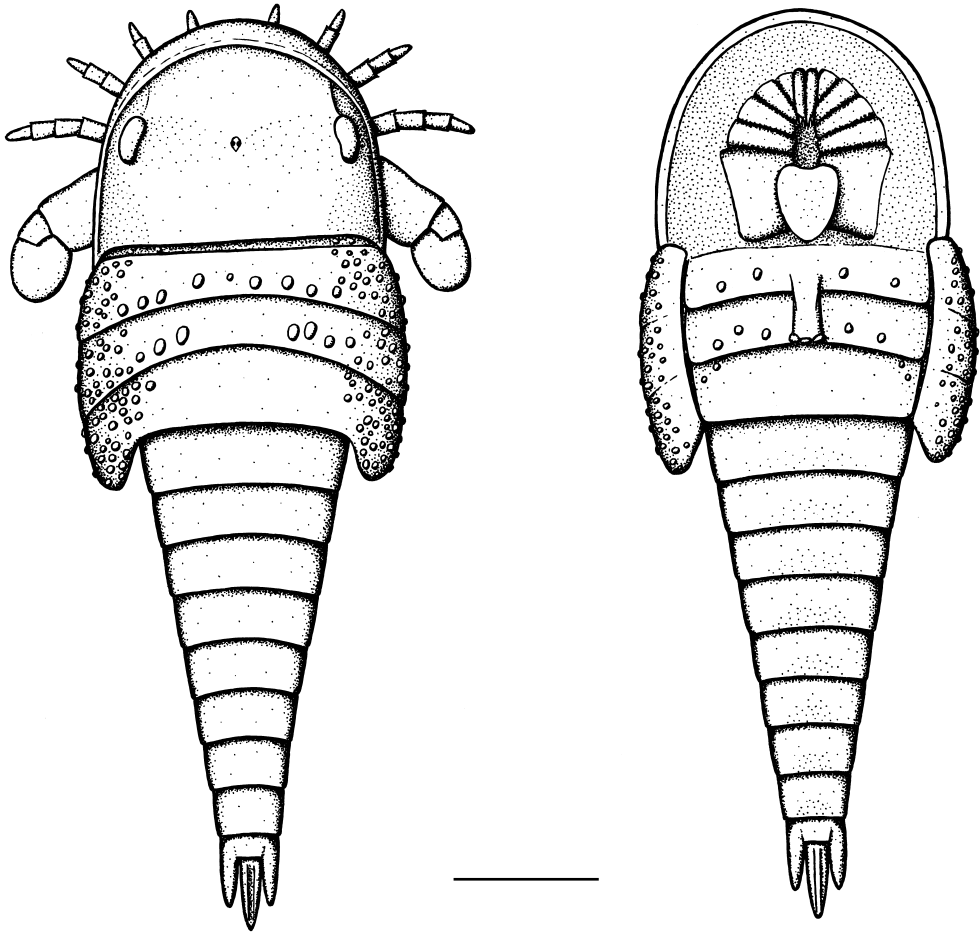


FIG. 10. — Reconstruction of *Octoberaspis ushakovi* n. gen., n. sp. in both dorsal and ventral view. Chelicerae and leg coxae hypothetical, based on comparisons with eurypterids and xiphosurans. Scale bar: 5 mm.

Størmer's (1972) material will probably be needed before this structure can be fully explained.

Genital appendage

One specimen, No. 35/711 (Figs 6C; 7C), shows a structure on the midline of the ventral preabdomen which originates on the anteriormost operculum and extends down to the posterior margin of the next sclerite. Here it widens and divides into three parts. This structure is very similar in size, shape and position to the longer, type A, genital appendage of eurypterids, a character previously thought to be unique (i.e. autapomorphic)

for this group. A second specimen, No. 35/712 (Figs 6D; 7D), shows a short, squat structure, again on the midline and located on the anteriormost preabdominal operculum. The structure here consists of a rectangular basal region and a triangular distal region pointing posteriorly. This is not unlike the shorter, type B, genital appendage in eurypterids; see Braddy & Dunlop (1997) for a recent study of eurypterid genital appendages.

A genital appendage in chasmataspids would be a significant discovery, but we must exclude the possibility that Nos. 35/711 and 35/712 are simply misidentified eurypterids. Firstly, there are

no other specimens from this locality which can unequivocally be interpreted as eurypterids. Secondly, these two specimens do not show the eurypterid body plan of a preabdomen of seven segments and a postabdomen of five segments. They are much more consistent in overall appearance with chasmatspids and their nine-segmented postabdomen plus very short telson; the telsons of most eurypterids are elongate by comparison. Finally, the genital appendage of eurypterids is associated with a large genital operculum, probably a fusion of two operculae (Braddy & Dunlop 1997). There is no large genital operculum in these Severnaya Zemlya Devonian specimens, which can therefore be regarded with some confidence as chasmatspids having a genital appendage. This structure also supports the pattern of opisthosomal segmentation presented herein. If the metastoma belongs to opisthosomal segment 1 (see below) then the next segment should be the genital segment in chelicerates (number 2), and indeed the structure interpreted as the genital appendage of chasmatspids originates on this segment.

Metastoma

As well as the genital appendage, No. 35/712 (Figs 6D; 7D) has a shield-shaped plate on the ventral prosoma. This is pointed posteriorly and has clear margins preserved on the anterior and right sides. This plate is very similar in size, position and appearance to the eurypterid metastoma, a plate covering the posterior gnathobases in these animals. Like the genital appendage, a metastoma was thought to be an eurypterid autapomorphy (e.g., Dunlop & Selden 1997), but this new material shows that it was present in chasmatspids too. The metastoma is believed by many authors (e.g., Størmer 1955) to represent the fused appendages of opisthosomal segment 1 and this interpretation would fit the pattern of chasmatspid opisthosomal segmentation presented above.

Postabdomen

The postabdomen comprises nine ring-like segments which originate beneath the preabdominal

tergites (e.g., No. 35/379, Figs 8E; 9E). The first postabdominal segment, segment 5, is usually longest, with successive segments approximately the same length. The whole postabdomen tapers posteriorly towards the telson. However, there are also a number of “short” specimens in which there is considerable telescoping of the postabdomen (e.g., Nos. 336-7, Figs 6B; 7B). Initially, it was suspected that the “short” morphotype represented sexual dimorphism, or perhaps even a different species, but careful observation of these “short” forms in which overlying segments were either removed by preparation or naturally broken revealed complete, “long” segments underneath (e.g., No. 35/339, Figs 8C; 9C). Furthermore, the degree of shortening is not consistent between specimens. This type of postabdominal telescoping is known from eurypterids (Simon Braddy pers. comm.), and is presumably taphonomic in origin.

The postabdominal segments lack the preabdominal ornamentation of large tubercles and have a slight curve to their posterior margins. Where the full length of the postabdomen is preserved there is a slight bend in some examples (e.g., No. 35/712, Figs 6D; 7D), which suggests that there was some flexibility in this structure. The thirteenth (pretelsonic) opisthosomal segment has a pair of short, tapering, posteriorly directed, epimera (No. 35/379, Figs 8E; 9E). The telson originates between these epimera and is similarly short and tapering, though a little longer than the adjacent epimera. This gives the end of the opisthosoma a trifurcate appearance. The telson itself has a slight median dorsal depression (No. 35/324, Figs 6A; 7A).

Juveniles

Specimen No. 35/719 (Figs 7G; 9G) is a very small, probably juvenile example, about 8 mm long, preserved with a truncated postabdomen. More interesting is No. 35/708 (Figs 8F; 9F), another small specimen, about 11 mm long. Its status as a juvenile is suggested by the proportionally large median and lateral eye tubercles relative to the rest of the carapace. It also shows that at least some juveniles had the full comple-

ment of 13 opisthosomal segments (it has been reported [e.g., Størmer 1955], probably erroneously, that juvenile eurypterids had less segments than adults) and that the telson was relatively long in early instars. This suggests that the short telson of the adult form is somewhat derived relative to a plesiomorphic condition still expressed in juveniles. A number of other small, but poorly preserved specimens in this material probably represent juveniles too.

Incertae sedis

One curious specimen remains among the Severnaya Zemlya material (No. 35/714, Figs 8D; 9D). Although preserved in outline, there are few morphological details. However, there are at least seven postabdominal segments preserved that appear to be rather narrower than the postabdomens of the other chasmataspid material from this locality. In fact, it is similar in overall appearance to *Chasmataspis*. Since the specimen is not well preserved I am reluctant to create a new taxon for what may be a preservational variant, but the specimen is included here for completeness.

PHYLOGENY

Four chasmataspids have been previously described: *Chasmataspis*, from the Ordovician of the USA (Caster & Brooks 1956), *Diploaspis* and *Heteroaspis*, both from the Lower Devonian of Germany (Størmer 1972), and *Forfarella* from the Lower Devonian of Scotland (Dunlop *et al.* 1999). A Middle Devonian example has also been recognised from Scotland (Anderson *et al.* 2000). Two additional taxa, *Borchgrevinkium taimyrensis* Novojilov, 1959 and “*Eurypterus*” *stoermeri* Novojilov, 1959, originally described as eurypterids, may also be chasmataspids (Størmer 1972), but this requires confirmation from the original material.

As a group, chasmataspids are undoubtedly chelicerates (Dunlop & Selden 1997), but until now their position within Chelicerata was less certain. Chasmataspids were originally interpreted as an order of the Xiphosura (Caster & Brooks

1956; Størmer 1972; Selden & Siveter 1987). Subsequently, Eldredge (1974) suggested chasmataspids were related to eurypterids based on similar appendages. Though not strictly an Eldredge character, the present study suggests that the paddles of chasmataspids and eurypterids are probably a convergent development in both groups (see also Bergström 1975). Meanwhile, Bergström (1975, 1979, 1980) questioned chasmataspid monophyly, restricting Chasmataspida to *Chasmataspis*, placing *Heteroaspis* as Chasmataspida *incertae sedis* and *Diploaspis*, with its appendages unlike those of other xiphosurans, close to the ancestry of arachnids. Simonetta & Delle Cave (1981) and Delle Cave & Simonetta (1991) regarded chasmataspids as one of the chelicerate branches radiating from among the “emeraldellids”, i.e. *Emeraldella* and similar looking “Burgess Shale” type arthropods.

Anderson & Selden (1997) excluded chasmataspids from Xiphosura due to differences in the segmentation and tagmosis of the opisthosoma, correctly recognising the presence of 13 opisthosomal segments. Dunlop & Selden (1997) recognised Chasmataspida as a monophyletic group within Chelicerata, defined by their autapomorphic opisthosomal tagmosis, i.e. a preabdomen of three segments and a postabdomen of nine. Dunlop & Selden (1997) further recognised the clade (Chasmataspida (Eurypterida + Arachnida)), with xiphosurans as the outgroup. However, this clade was based on a synapomorphy of an opisthosoma of 12 segments, a character we now know to be incorrect for chasmataspids (Anderson & Selden 1997; Dunlop *et al.* 1999; this study), and which may be incorrect for eurypterids and scorpions too (Dunlop & Webster 1999).

The new Severnaya Zemlya fossils are significant in resolving the phylogenetic position of chasmataspids. The genital appendage and metastoma seen in this material represent two strong synapomorphies for Eurypterida and Chasmataspida. These characters were previously autapomorphic for eurypterids, and their presence, and significance, in chasmataspids was

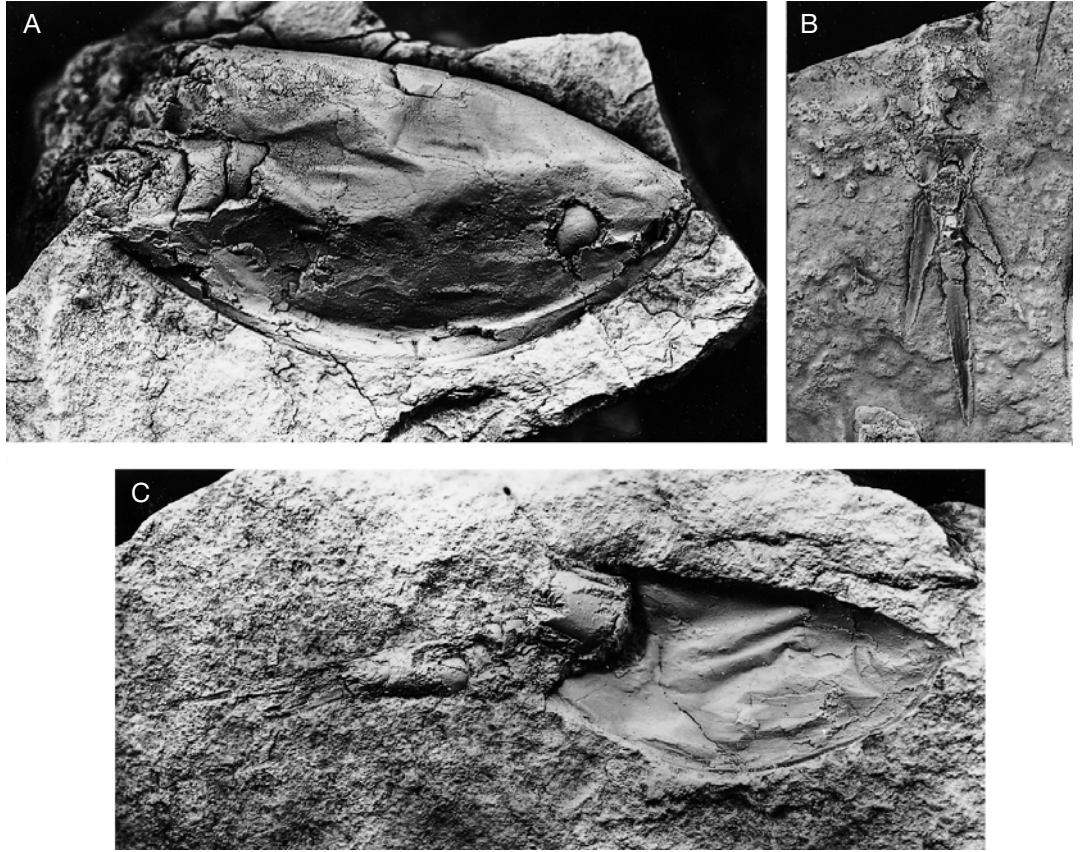


FIG. 11. — *Elymocarid urvantsevi* n. sp.; **A**, No. 35/377, 40 × 19 mm; **B**, No. 35/373, 14 × 8 mm; **C**, No. 35/372 (holotype), total length 51 mm.

noted by Dunlop (1997) and Dunlop *et al.* (1999). The genital appendage and metastoma could be seen as grounds for referring Chasmataspida to Eurypterida, although chasmataspids have genal spines and the material described here has lateral eyes associated with poorly-defined carapace ridges (both absent in eurypterids). Chasmataspids also have a different pattern of opisthosomal tagmosis. The position of the scorpions, which have been considered as the sister group of eurypterids by some authors (see Dunlop & Webster 1999), may complicate this issue. Chasmataspids share a number of characters both with xiphosurans (e.g., genal spines, opisthosomal doublure, ?ophthalmic ridges) and eurypterids (genital

appendage, metastoma, ?longer legs) and will eventually need to be placed as part of a broader revision of chelicerate phylogeny.

MODE OF LIFE

Størmer (1972) considered *Diploaspis* and *Heteroaspis* to be primarily aquatic, especially given the paddles in *Diploaspis* which suggest an animal that could swim. This interpretation seems reasonable for the Severnaya Zemlya fossils which have paddles too. Like these new Russian forms, *Diploaspis* and *Heteroaspis* are thought to have been deposited in quiet, possibly lagoonal waters. Both Størmer (1972) and Simonetta & Delle Cave (1981) speculated that chasmataspids were capable of terrestrial activity, though this proposal was

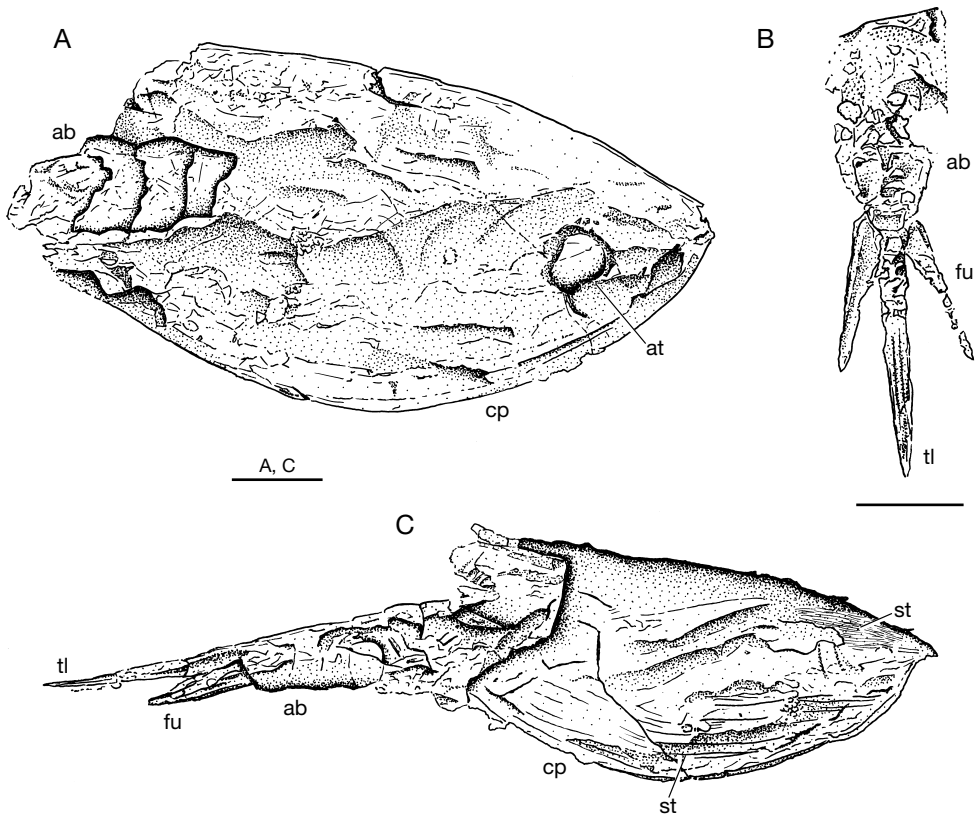


FIG. 12. — *Elymocarid urvantsevi* n. sp., interpretative drawings of the specimens shown in Fig. 11; **A**, No. 35/377; **B**, No. 35/373; **C**, No. 35/372 (holotype). Abbreviations: **ab**, abdomen; **at**, anterior tubercle; **cp**, carapace pleural fold; **fu**, furca; **st**, striae; **tl**, telson. Scale bars: 5 mm.

partly based on the belief that these animals had a ventral opisthosoma covered by a single plate which could protect the gills on land (see discussion above). There is no convincing evidence for chasmataspids having special opisthosomal structures allowing them to be habitually terrestrial; although an amphibious mode of life has been proposed for eurypterids (see Manning & Dunlop 1995 for a review) and even xiphosurans emerge onto land to breed.

With regards to feeding, most chelicerates are predators and though we have no details of the chasmataspid mouthparts it seems likely that they were essentially benthic predators with a mode of life analogous to xiphosurans. Small phyllocarids and the ostracodes recorded from the same for-

mation as the chasmataspids represent a possible source of food, although xiphosurans also dig soft-bodied prey such as worms out of the substrate. Paddles suggest these chasmataspids could swim, although whether they swam to catch prey or to avoid predators (i.e. acanthodian fish) remains speculation. Paddles might also be used to help bury themselves in the substrate.

Subclass PHYLLOCARIDA Packard, 1879

REMARKS

Approximately 70 phyllocarid crustaceans are present among this Severnaya Zemlya material and these were provisionally referred to

Ceratiocaridae by Novilskaya *et al.* (1983). Some additional arthropod fragments also probably represent crustaceans. The fossils are evidently phyllocarids, having a large, bivalved carapace comprising a cephalothoracic shield formed from two pleural folds and an anteriorly projecting rostral plate, and an abdomen projecting from this carapace ending in a telson with a pair of furcal rami. The best specimens are described and figured here (Nos. 35/372-3, 35/375, 35/377, 35/778-9, 35/781-2) (Figs 11-14).

Order ARCHAEOSTRACA Claus, 1888

REMARKS

Rolfe (1969) diagnosed this order on the presence of a hinge line on the carapace, an elongate seventh abdominal (i.e. pretelsonic) segment and a telson produced between two furcal rami, all of which are present in this new Severnaya Zemlya material.

Suborder RHINOCARINA Clarke *in* Eastman & Zittel, 1900

DIAGNOSIS. — Carapace with a median dorsal plate separating the valves behind rostral plate; last abdominal somite elongated (Rolfe 1969).

REMARKS

Although tentatively referred to Ceratiocarididae (a family of suborder Ceratiocarina) by Novilskaya *et al.* (1983), the new Severnaya Zemlya material appears to have a median dorsal plate and so can be referred to the suborder Rhinocarina *sensu* Rolfe 1969.

Family RHINOCARIDIDAE Hall & Clarke, 1888

DIAGNOSIS. — Carapace valves elongate, subovate; median dorsal plate narrow and with chevron ornament; rostral plate and median dorsal plate slightly bent along median carina (Rolfe 1969).

REMARKS

The other rhinocaridid family mentioned by Rolfe (1969), Ohioicarididae, was diagnosed by

him as having subcircular carapace valves, and as such this new Severnaya Zemlya material can be referred to Rhinocarididae with some confidence.

Genus *Elymocaris* Beecher, 1884

TYPE SPECIES. — *Elymocaris siliqua* Beecher, 1884.

ADDITIONAL SPECIES. — *Elymocaris urvantsevi* n. sp.

DIAGNOSIS. — Like *Rhinocaris* but carapace valves without posteroventral spine; no mesolateral carina, anterior tubercle present; rim with oblique, posteriorly imbricating ridges; rostral plate folded ventrally along two lateral anteriorly converging carinae; telson with broad median ridge (Rolfe 1969).

REMARKS

The Severnaya Zemlya material is referred to *Elymocaris* with some reservations. It lacks posteroventral spines on the carapace, which excludes it from *Rhinocaris* Hall & Clarke, 1888, and *Dithyrocaris* Scouler, 1835, and it has an anterior tubercle, which was reported absent by Rolfe (1969) in *Tropidocarid* Beecher, 1884, the other rhinocaridid genus lacking posteroventral spines. There is also a ridge on the telson in this new material. However, some specimens shows structures which could be interpreted as lateral carina, but could equally well be taphonomic folding of the carapace. Furthermore, the folding of the rostral plate, a diagnostic character of *Elymocaris*, is not obvious in this Severnaya Zemlya material. I am reluctant to create a new genus unnecessarily and so have referred this material to the genus which it most closely resembles, *Elymocaris*, though I note Rolfe's (1969) and Racheboeuf's (1994) comments that many supposed generic characters may only be of specific value. As such, considerable revision of the family may be required.

Elymocaris urvantsevi n. sp. (Figs 11-15)

Ceratiocaridae – Novilskaya *et al.* 1983: 94, fig. 4.

HOLOTYPE. — GIL No. 35/372 (oc 1/bd 21).

ADDITIONAL MATERIAL. — GIL Nos. 35/373 (oc 1/bd 21), 35/375 (oc 41/bd 12), 35/377-378, 35/779 (all oc 67/bd 12), 35/781 (oc 1/bd 21), 35/782.

ADDITIONAL MATERIAL (NOT FIGURED). — GIL Nos. 35/374, 35/376 (both oc 41/bd 12), 35/780 (oc 1/bd 21), 35/783-790 (all oc 67/bd 12), 35/791-817 (all oc 1/bd 21), 35/818-837 (all oc 41/bd 12).

ETYMOLOGY. — In honour of N. N. Urvantsev, a geologist who participated in the first expedition to Severnaya Zemlya in 1930-1932.

GEOGRAPHICAL AND STRATIGRAPHICAL DISTRIBUTION. — All material is from the Severnaya Zemlya Formation (Lower Devonian [lower Lochkovian]), October Revolution Island.

DIAGNOSIS. — Elymocarid with a downward-curving, hook-shaped rostral plate.

DESCRIPTION

No. 35/372 (holotype)

Almost complete specimen in lateral view (Figs 11C; 12C). Total length 51, carapace length 29, abdomen length, including telson, 22. Maximum carapace width 13. Rostral plate faint, hook-shaped. Cephalothoracic shield preserved as impression of left pleural fold, broadly oval, straighter along the dorsal surface and with a distinct, narrow margin; posterior end of shield obscured. Pleural fold with broad, oblique folds (?carina) below which is a large depression in the antero-ventral region. Pleural fold ornamented with fine antero-posterior striae, closely packed near the rostral plate, more widely spaced in the posterior ventral region of the shield. Abdomen tapers posteriorly, individual pleomeres difficult to distinguish. Styliform telson preserved along with one shorter furcal ramus. Appendages not preserved.

No. 35/373

Disarticulated carapace and abdomen (Figs 13A; 14A). Maximum carapace length 14, though posterior end of carapace not preserved. Maximum carapace width 8. Rostral plate apparently hook-shaped, but detached from rest of carapace and surrounded by other cuticle fragments. Right pleural fold of cephalothoracic shield preserved, broadly oval in outline with narrow margin, but details of morphology poor. Abdomen detached from carapace, maximum length including telson 17. Five abdominal pleomeres preserved, possibly in ventral view,

plus telson. Pleomere lengths: 3, 2, 1.5, 2, 3.5, average width 4, but narrowing posteriorly. First pleomere poorly preserved, second with faint ridge, third with large tubercle, fourth and fifth with distinct ventral ridges. Telson styliform with median groove, length 6. Both styliform furcal rami preserved, length 3. Appendages not preserved.

No. 35/375

Terminal end of abdomen in dorsal view (Figs 11B; 12B). Maximum length 23. Division of abdomen into pleomeres indistinct, but abdomen tapers posteriorly. Telson styliform, length 15, with broad median depression. Furcal rami also styliform and with median depression, but shorter than telson, length 8. Right ramus better preserved than left ramus.

No. 35/377

Large carapace preserved in positive relief (Figs 11A; 12A). Maximum preserved length 40, though posterior end of carapace absent. Maximum width 19. Rostral plate absent. Cephalothoracic shield preserved as internal mould of right pleural fold. Cephalothoracic shield broadly oval in outline though straighter along dorsal margin where a slight fold indicates a median dorsal plate was present, visible more clearly when specimen is examined from above. Pleural fold with narrow margin and oblique fold running from near where the rostral plate would be to the ventral margin about two thirds along the length of the carapace. Depression occurs below this fold, but with rounded, raised anterior tubercle nearer the rostral end of the cephalothoracic shield. Posterior margin of pleural fold broken to reveal underlying abdominal pleomeres. Rest of abdomen and appendages not preserved.

No. 35/378

Almost complete specimen in lateral view (Figs 13D; 14D). Maximum preserved length 31, carapace length 17, abdomen length, including telson, 14. Maximum carapace width 9. Rostral plate obscured. Cephalothoracic shield preserved as cast of left pleural fold, but with

the ventral half restricted to an impression of the carapace. Large area dorsal to specimen probably deformed right pleural fold and joined to left pleural fold by median dorsal plate. Pleural fold broadly oval, straighter along the dorsal surface with a distinct, narrow margin; ornamentation not preserved, but broad, slightly oblique ridge runs dorso-ventrally. Posterior margin of shield slightly broken to reveal at least three underlying pleomeres; anterior two short, posterior one longer. Abdomen tapers posteriorly. Styliform telson and one poor furcal ramus preserved. Appendages not preserved.

No. 35/779

Carapace preserved in lateral view (Figs 13E; 14E). Maximum preserved carapace length 25. Maximum carapace width 14. Rostral plate hook-shaped, curving ventrally, but slightly displaced. Cephalothoracic shield preserved as crystalline internal mould of right pleural fold, though crystalline part missing from ventral region. Pleural fold broadly oval, straighter along the dorsal surface and with a distinct, narrow margin. Part of median dorsal plate clearly preserved above the specimen. Oblique line originating close to the rostral plate creates a depression in the anterior ventral part of the cephalothoracic shield, though this effect may be exaggerated by the loss of the crystalline part in this region noted above. A second oblique line runs close to the margin of the cephalothoracic shield. Posterior part of pleural fold broken to reveal three underlying pleomeres. Remainder of abdomen and appendages not preserved. Additional, poorer specimen (not figured) preserved in same nodule.

No. 35/781

Specimen preserved in lateral view (Figs 13C; 14C). Maximum preserved length 30, carapace length 19, abdomen length 11, though not all of abdomen preserved. Maximum carapace width 9. Rostral plate well preserved, hook-shaped, curving ventrally. Cephalothoracic shield preserved as impression of left pleural fold. Pleural

fold broadly oval with distinct, narrow margin. Fine striae preserved near postero-dorsal region of the pleural fold, above where the abdomen originates. Anterior tubercle clearly preserved. Dark area below rostral plate, adjacent to margin of cephalothoracic shield, could be remains of an eye. Abdomen originates approximately a third of the way into the carapace, though individual pleomeres not discernable. Possible dark gut trace preserved within abdomen. Telson and furcal rami indistinct. Appendages not preserved.

No. 35/782

Relatively poor specimen in lateral view (Figs 13B; 14B). Maximum length 33, carapace length 20, abdomen length 13. Maximum carapace width 10. Rostral plate hook-shaped, curving ventrally. Cephalothoracic shield preserved as impression of left pleural fold with narrow margin, but details of morphology poor. Pleural fold broadly oval with oblique striae present near dorsal margin. Grey area below rostral plate adjacent to margin of cephalothoracic shield may be remains of an eye. Abdomen possibly displaced, emerging rather ventrally from the carapace and individual pleomeres not discernable. Telson styliform, apparently with shorter, styliform furcal ramus preserved dorsal to the telson. Appendages not preserved.

MORPHOLOGICAL RECONSTRUCTION

The crustaceans range in size from very large, No. 35/789 (not figured) lacks detail but is at least 11 cm long, through to small specimens of about 1 cm. Morphological terminology is based on that used by Vannier *et al.* (1997) and Rolfe (1969). Appendages are not preserved in the Severnaya Zemlya Devonian material, but in phyllocarids they comprise two pairs of large antennae, thoracic appendages typically held within the carapace, and a series of abdominal pleopods projecting beyond the carapace and used in swimming. A reconstruction of the animal in life attitude is presented in Fig. 15.

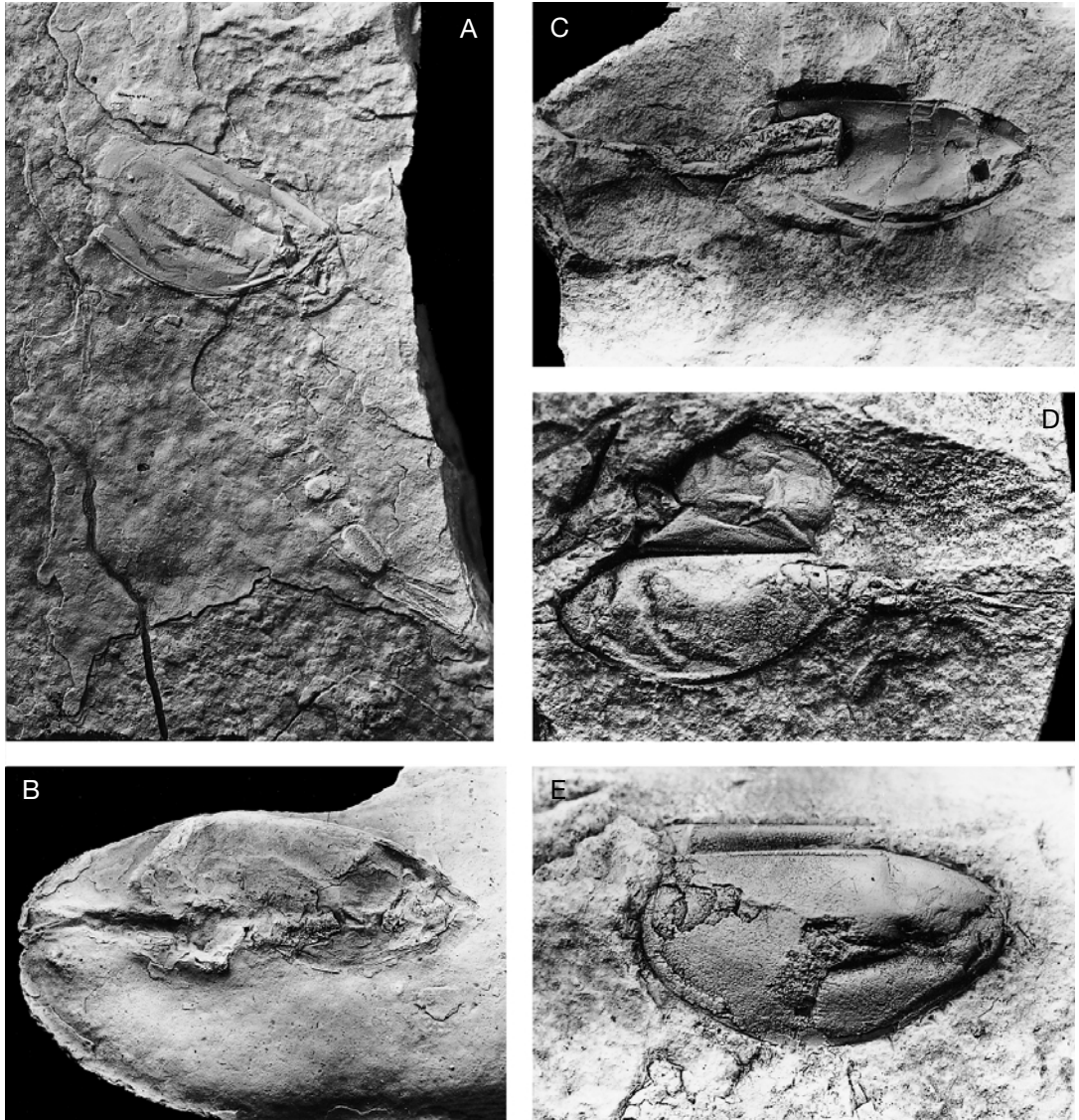


FIG. 13. — *Elymocarid urvantsevi* n. sp.: **A**, No. 35/375, maximum length 23 mm; **B**, 35/782, maximum length 33 mm; **C**, 35/781, maximum preserved length 30 mm; **D**, No. 35/378, maximum preserved length 31 mm; **E**, No. 35/779, maximum preserved carapace length 25 mm, maximum carapace width 14 mm.

Carapace

The overall morphology of the carapace is best seen in specimen Nos. 35/377, 35/372 35/781, 35/378, 35/779 (Figs 11A, C; 12A, C; 13C-E; 14C-E). The paired pleural folds are broadly elongate and are curved both dorsally and ventrally, giving the whole carapace an oval shape in

lateral view. The pleural folds have a distinct marginal rim (No. 35/781, Figs 13C; 14C) and are connected by a median dorsal plate behind the rostral plate (No. 35/779, Figs 13E; 14E). This plate appears to be strongly attached to the pleural folds; the division between the two is not well preserved in this material (Nos. 35/782,

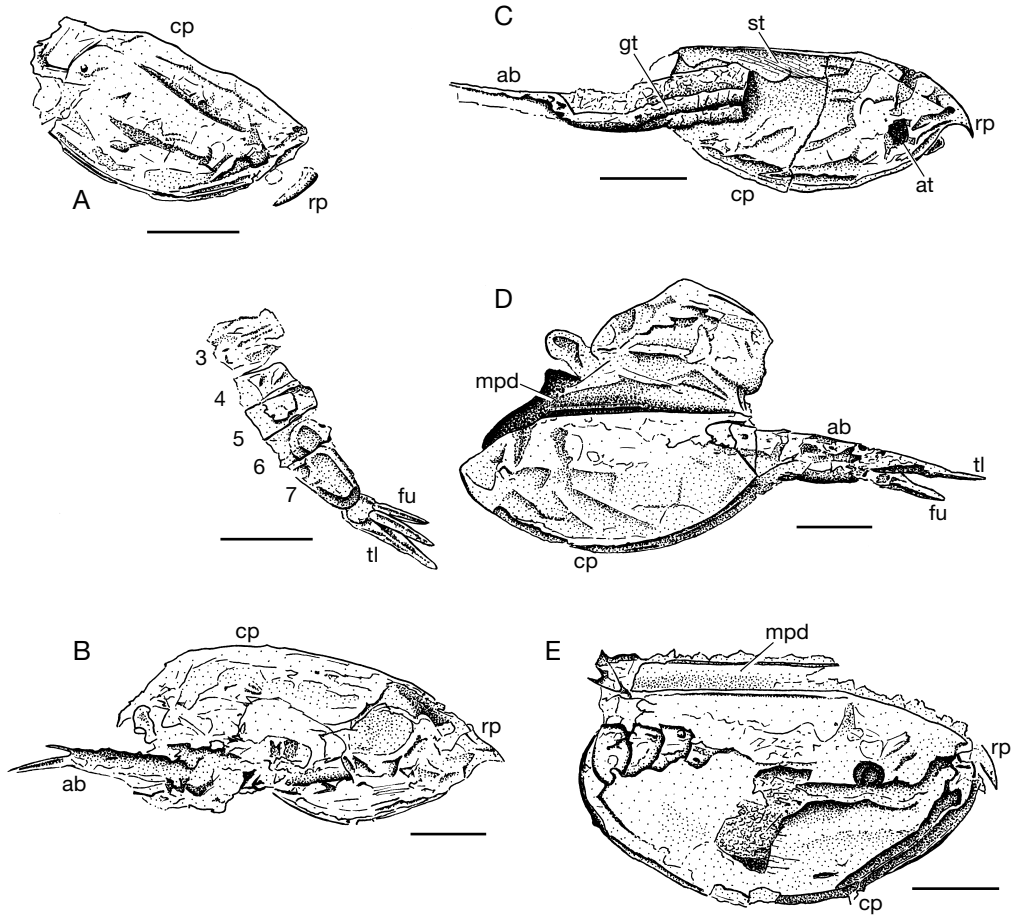


FIG. 14. — *Elymocarid urvantsevi* n. sp., interpretative drawings of the specimens shown in Fig. 13; **A**, No. 35/375; **B**, 35/782; **C**, 35/781; **D**, No. 35/778; **E**, No. 35/779. Abbreviations: **ab**, abdomen; **at**, anterior tubercle; **cp**, carapace pleural fold; **gt**, possible gut trace; **fu**, furca; **mpd**, median dorsal plate; **rp**, rostral plate; **st**, striae; **tl**, telson; abdominal segments numbered (note longer segment 7). Scale bars: 5 mm.

35/781, Figs 13B, C; 14B, C). The rostral plate has a distinct, downward-curving hook shape (see also Systematics). It is difficult to say whether or not lateral carina (i.e. strong ridges on the pleural folds) were present. Two specimens show what appear to be folds or carina on the carapace (Nos. 35/372, 35/375, Figs 11C; 12C; 13A; 14A), but these are not in the same position and could be taphonomically induced as they are not seen at all in other material. Similarly, two specimens show strong evidence for an anterior tubercle on the pleural fold (Nos. 35/377, 35/781, Figs 11A; 12A; 13C; 14C)

although it is not unequivocally present in every specimen. Some specimens also suggest that the antero-ventral region of the carapace had a slight oblique fold below which it was slightly depressed (e.g., No. 35/377, Figs 11A; 12A).

When examined in detail the carapaces of Nos. 35/372 and 35/781 (Figs 11C; 12C; 13C; 14C) clearly show a fine ornament of ridges, or striae. These striae are short, fine and closely packed near the rostral plate where they run approximately antero-dorsally (Figs 11C; 12C). Meanwhile longer, oblique striae running postero-dorsal to antero-ventral can be seen near

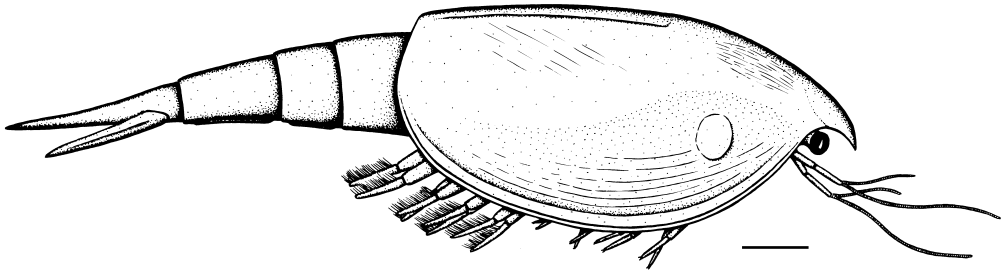


FIG. 15. — Reconstruction of *Elymocarid urvantsevi* n. sp. in lateral view. Appendages reconstructed by comparison to other phyllocarids. Scale bar: 5 mm.

the median dorsal plate (Figs 13C; 14C). Larger and more widely spaced striae are present in the ventral part of the carapace where they run longitudinally, following the ventral curvature of the pleural fold (Figs 11C; 12C). Similar striae have been reported in fossil phyllocarids by Racheboeuf (1994) and Vannier *et al.* (1997) where they have been interpreted as an aid to burrowing (see below).

Abdomen

The phyllocarid abdomen is composed of a series of seven segments, or pleomeres, the anteriormost of which originates beneath the carapace. The abdomen can be seen overlapped by the carapace, e.g., No. 35/781 (Figs 13C; 14C) where the abdomen occupies the posterior third of the space beneath the carapace. Up to five of the seven pleomeres can be seen in this material (No. 35/375, Figs 14A; 15A). No. 35/781 (Figs 13C; 14C) preserves a possible gut trace running along the length of the abdomen. The abdomen tapers posteriorly and in No. 35/375 (Figs 13A; 14A), which appears to be in ventral view judging from the position of the emerging furcal rami, there is ornamentation in the form of ridges on the posterior abdominal segments. The pretelsonic pleomere (segment 7) is longer than the preceding pleomeres (No. 35/375, Figs 13A; 14A). The telson is elongate and styliform (e.g., No. 35/373, Figs 11B; 12B) with a pair of furcal rami either side. The furcal rami are also styliform, but are shorter and originate ventrally close to the base of the telson (No. 35/378,

Figs 13D; 14D). Both the telson and furcal rami are ornamented with ridges (No. 35/373, Figs 11B; 12B).

PHYLOGENY

There are morphological differences and inconsistencies among the specimens described here. However, since these morphological differences do not divide the material neatly into two or more groups, and since there has been taphonomic distortion, all the material is referred to a single species. The systematics and phylogeny of phyllocarids remain in a somewhat unsatisfactory state (see comments by Rolfe [1969]) with no clear indication of polarity for the characters used to differentiate phyllocarid taxa. Such a revision is beyond the scope of the present work.

MODE OF LIFE

Vannier *et al.* (1997) studied living phyllocarids in an attempt to determine the palaeobiology of the Palaeozoic forms. They concluded that most Palaeozoic phyllocarids were capable of swimming, both as pelagic and nekto-benthonic forms, but that they also showed adaptations for burrowing, such as the striae on the carapace observed in the new Severnaya Zemlya material. These striae may have helped channel the sediment past the carapace during burrowing. Vannier *et al.* (1997) speculated that some Palaeozoic phyllocarids burrowed during the day to avoid predatory fish, emerging at night to feed in the water column. Considering the

predatory acanthodians present in the Severnaya Zemlya Formation, this mode of life seems appropriate for the new phyllocarid material too.

Acknowledgements

I am very grateful to Dr V. Talimaa (GIL) for the opportunity to work on this material, for her hospitality during my visit to Vilnius and for information on the geology of the original localities. I also thank Dr V. Relys for hospitality in Vilnius. Dr S. Braddy, Dr L. Anderson, Dr P. Selden and M. Poschmann are thanked for valuable discussions. I thank Dr P. Männik for advice on the geological setting of this material, E. Jantscher for proofreading the manuscript and Drs D. Siveter and F. Schram for revising the text. This work was initiated under a NERC postdoctoral fellowship at the University of Manchester.

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*Submitted on 9 November 1998;
accepted on 4 November 1999.*