The oldest arthropods of the East European Platform

JERZY DZIK AND KAZIMIERA LENDZION

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Cassubia Lendzion 1977 and *Liwia* new name (for *Livia* Lendzion 1975 preoccupied) found in the subsurface Żawiszany formation of the basal Cambrian in NE Poland are identified as an anomalocarid and a 'soft-bodied' trilobite, respectively, each being the oldest representative of its group. The presence of four free thoracic tergites in *Liwia*, the relatively strong sclerotization, and the apparent segmentation of the pygidial shield (expressed in the metameric distribution of marginal spines) indicate that the 'soft-bodied' trilobites achieved their organization by secondary softening of the dorsal exoskeleton and suppression of the development of thoracic tergites in ontogeny. □ *Cambrian, trilobites, anomalocarids, phylogeny, Poland.*

Jerzy Dzik, Zakład Paleobiologii PAN, Aleja Żwirki i Wigury 93, PL–02–089 Warszawa, Poland; Kazimiera Lendzion, Instytut Geologiczny, Rakowiecka 4, PL–00–579 Warszawa, Poland; 9th March, 1987.

Present knowledge of earliest arthropods with unmineralized cuticle is based on a few Lagerstätten, most of them being Middle (Conway Morris 1986) or even Late Cambrian (Müller & Wallosek 1985) in age. Recently, new Early Cambrian localities preserving soft-bodied arthropods with appendages have been found in China (Zhang & Hou 1985) and Greenland (Conway Morris *et al.* 1987). There is also evidence that even older strata of the basal Cambrian, discovered in the marginal parts of the East European Platform in the subsurface of NE Poland, provided appropriate conditions for preservation of organic arthropod skeletons. Unfortunately, they are covered by almost five kilometers of younger sediments. Deep drilling done by the Instytut Geologiczny (Geological Survey of Poland) along the SW margin of the Platform resulted in discoveries of diverse assemblages of Early Cambrian fossils (Lendzion 1983), the most remarkable of them being arthropods with preserved appendages (Lendzion 1975).

The purpose of the present paper is to discuss the phylogenetic implications of these arthropods based on additional morphologic studies, including some preparation of the specimens.

Age of the fauna

The holotypes of '*Livia*' *plana* Lendzion 1975 and *Cassubia infercambriensis* (Lendzion 1977) were found in the core of the Kościerzyna IG 1 borehole in proximity, at depths of 4920.2 m and 4920.7 m, respectively. Specimens of *Mobergella radiolata* Bengtson 1968 occur throughout this part of the core, being abundant to about 20 m above. Undeterminable fragments of mineralized trilobite carapaces occur not closer than 300 m above this level. The holotype of '*Livia*' *convexa* Lendzion 1975 was found in the core of the Wyszków IG 1 borehole (Fig. 1) at 2240.3 m associated with poorly preserved fossils probably representing *Mobergella* sp. Trilobites are known from this core beginning at about 100 m higher. A hypostome of *Schmidtiellus* sp. (Areń & Lendzion 1978: Pl. III:2) was found at 2115.2 m. The association of both these occurrences with mobergellids of the *M. radiolata* group suggests that they are approximately coeval and that they correspond in age to the strata containing numerous specimens of *Mobergella* already known from Scandinavia. In Scandinavia *Mobergella* occurs in rocks of the *Schmidtiellus mickwitzi* Zone (Martinsson 1974; Bergström & Gee 1985; Ahlberg *et al.* 1986). The presence of *Schmidtiellus* sp. and *Holmia* sp. much higher in the core of borehole Wyszków IG 1 suggests that the Polish assemblage with '*Livia*' is slightly older than the *S. mickwitzi* Zone, if its base is defined on the first occurrence of the nominal species.

According to Jankauskas (in Areń & Lendzion 1978) acritarchs occurring in borehole Kościerzyna IG 1 together with '*Livia*' *plana* and *Cas-*

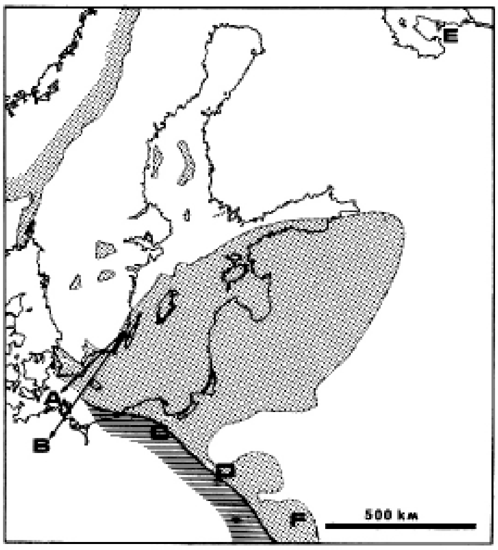


Fig. 1. Localities of the oldest articulate Metazoa of the East European Platform and the distribution of lithofacies of the Early Cambrian. Boundary of the area with preserved Cambrian rocks indicated by stippled line; domination of fine and coarse clastics shown as hachured and stippled areas, respectively. ☐ A. Hiddensee Island, where an erratic boulder with *Xenusion* sp. has been found (Krumbiegel *et al.* 1980). ☐ B. Sewekow, type locality of *Xenusion auerswaldae* Pompeckj 1927 (Jaeger & Martinsson 1967), probable source area of erratics indicated by arrows. ☐ C. Kościerzyna IG 1 borehole with *Cassubia infercambriensis* (Lendzion 1975) and *Liwia plana* (Lendzion 1975). ☐ D. Wyszków IG 1 borehole with *L. convexa* (Lendzion 1975). ☐ E. Onega peninsula, type locality of *Spriggina borealis* Fedonkin 1979 and other Ediacarian articulates (Fedonkin 1985). ☐ F. Dominopol 44 borehole with *Wolynaspis unica* Tchernysheva 1967 (Kirjanov & Tchernysheva 1967).

subia infercambriensis form an assemblage intermediate in composition between those typical for the East Baltic Lontova and Lükati beds, which is consistent with the above considerations.

Even if the strata containing the soft-bodied arthropods are older than the oldest mineralized trilobites of the Baltic area, it does not necessarily mean that they represent the Tommotian, the presumed pre-trilobite epoch of the Cambrian.

It is generally accepted that *Holmia* and *Schmidtiellus*, co-occurring with *Mobergella radiolata* in Scandinavia, are successors of *Archaeaspis* (see Ahlberg *et al.* 1986), which occurs in Siberia as high as in the third trilobite zone of the Atdabanian, together with *Nevadella* and above the *Profallotaspis* and *Fallotaspis* Zones (Repina 1983). The *Schmidtiellus mickwitzi* Zone seems thus to be not older than the *Pagetiellus anabarus* Zone of Siberia, although the *M. radiolata* group is known in Siberia as low as in the uppermost Tommotian (Missarzhevsky & Rozanov 1969).

Further evidence of the relatively late age of the strata with the oldest trilobites in the Baltic region is given by the morphology of *Wolynaspis unica* Tchernysheva 1967, the oldest trilobite in the Ukrainian part of the East European Platform (Kirjanov & Tchernysheva 1967). It was found in borehole Dominopol 44 in Volhynia at a depth of 268.8–274.0 m, together with *Volborthella*. With its oval cephalon lacking genal spines *Wolynaspis* seems to be an ancestor of *Choubertella*, a daguinaspid used to define a zone in Morocco where it occurs with an evolutionarily advanced assemblage of trilobites (Hupé 1953). *W. unica*, in its widely disposed eyes, closely resembles *Profallotaspis*, which may be an indication of its ancestry. In any case, it is a morphologically advanced form which can hardly be compared with the oldest trilobites of Siberia.

In conclusion, we estimate the age of the part of the subsurface Zawiszyn formation containing these soft-bodied arthropods as the *Fallotaspis* Zone of the Atdabanian.

The anomalocarid *Cassubia* (Lendzion 1977)

The only specimen was found in the core of borehole Kościerzyna IG 1 at the depth 4920.7 m and is represented by both part and counterpart (Fig. 2) preserved as a thin carbon(?) film on a bedding plane of dark grey claystone. Initially it was interpreted as part of the body with eleven segments and a single chelicera-like appendage at the anterior end (Lendzion 1975). Additional preparation of the specimen and the results of photography under alcohol have prompted a reassessment.

New interpretation. – It seems noteworthy that particular segments of the appendage in its well-preserved distal part show conspicuous gradient in their width (Fig. 2). When extrapolated proximally, it fits proportions of the remaining part of the specimen, previously thought to be a thorax (Lendzion 1975). Moreover, remnants of metamerically arranged structures, which may correspond to the processes preserved completely in the distal part, occur along the supposed

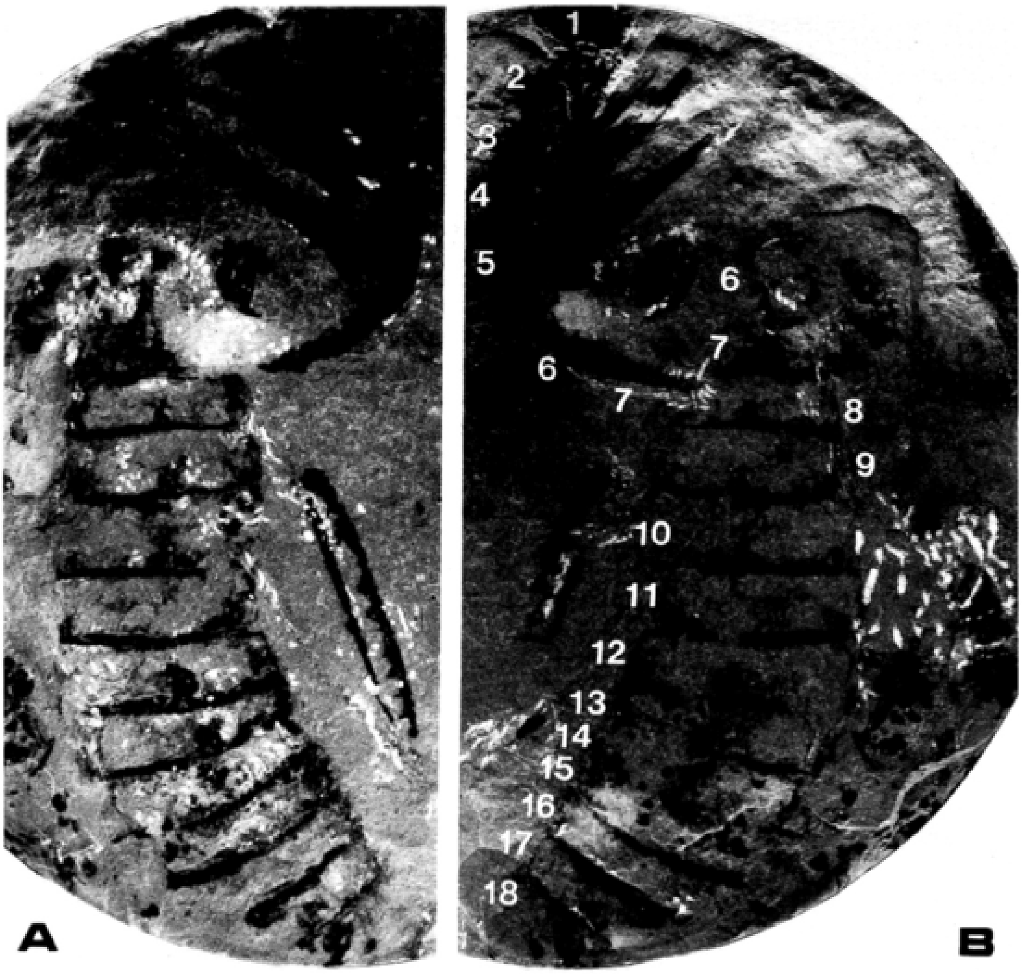


Fig. 2. ☐ A–B. Holotype of *Cassubia infercambriensis* (Lendzion 1975), IG 1432 II 22 (part and counterpart), Kościerzyna borehole, depth 4920.2 m, subsurface Zawiszyn formation; submerged in alcohol, ×2.

thorax. The appearance of the distal part of the specimen clearly indicates its anomalocarid nature. It thus seems rational to consider the whole fossil as representing a single, broken appendage of an anomalocarid. A reconstruction of the appendage is therefore proposed (Fig. 3A) with at least 18 short segments, each armed with flat, ventral processes (blades), smoothly tapering distally. Whether these blades were paired or not cannot be determined. However, the parallel arrangement of two elongated structures lying alongside the main part of the appendage (Fig. 2A), which may represent displaced blades, suggests that they were really paired and equal in size in each segment. The margins of the blades facing distally, at least in the most distal part of the appendage, are densely serrated (Fig. 2B). The serration is reminiscent of the bases of setae, with tips pointed somewhat ventrally. No direct evidence of the presence of such setae has been found, however.

Whether the blades of the appendage had setae or not, their general appearance in *Cassubia infercambriensis* indicates a filtratory function. They could have been used to sieve water and sediment in search of small benthic animals.

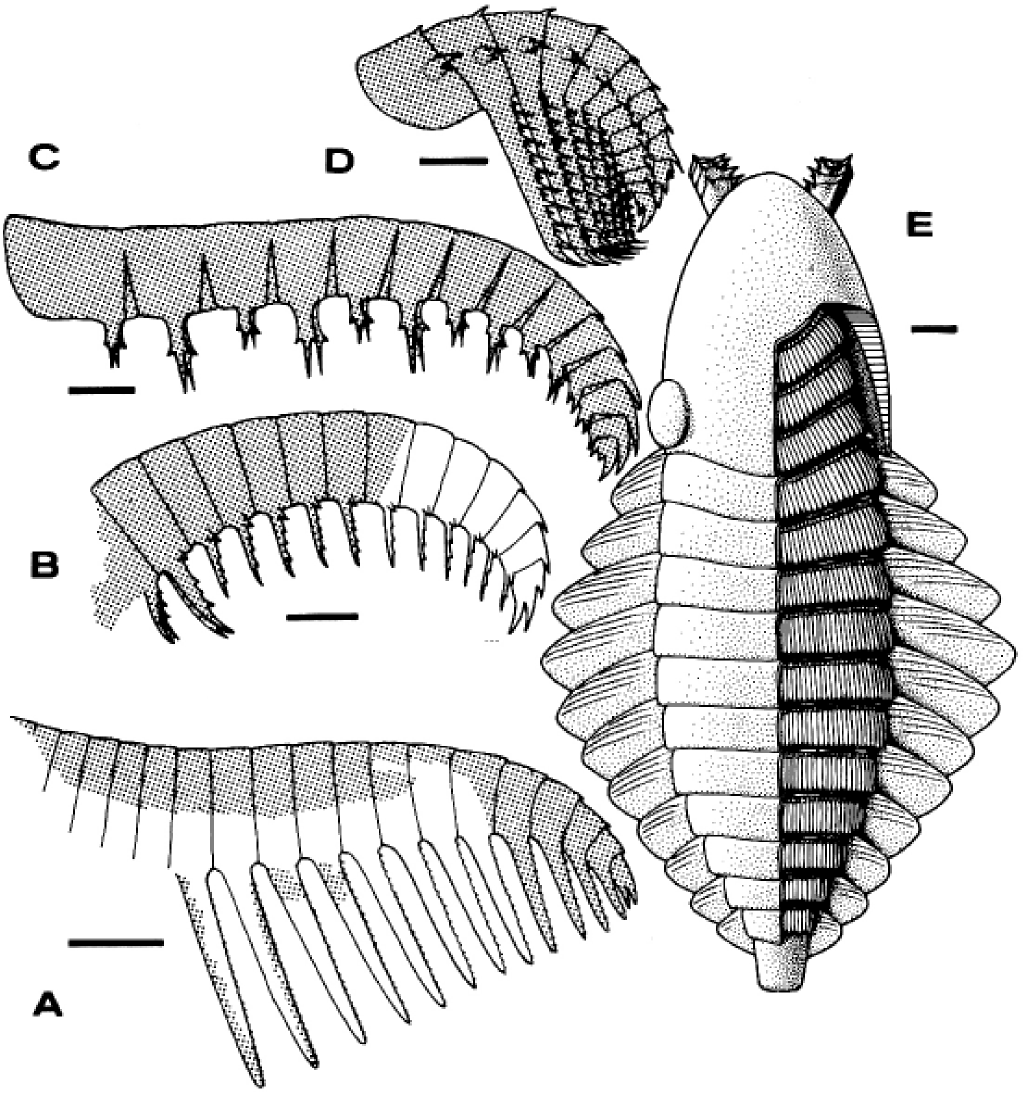


Fig. 3. Tentative reconstruction of the appendage of *Cassubia infercambriensis* (Lendzion 1975) (□ A) compared with appendages of other known species of the Anomalocarididae (□ B–D; based on Briggs 1979). □ B. *Anomalocaris* cf. *pennsylvanica* (Resser 1929), Kinzers Formation, Pennsylvania, Early Cambrian; distal part based on specimens of *A. pennsylvanica* from the same locality. □ C. *A. canadensis* Whiteaves 1892, Burgess Shale, British Columbia, Middle Cambrian. □ D. *A. nathorsti* (Walcott 1911), same locality. □ E. Reconstruction of the body of *A. nathorsti* in dorsal view (after Whittington & Briggs 1985 with modifications proposed by Bergström 1986; see also Briggs & Whittington 1987 and Bergström 1987). Bar scale = 1 cm.

The above interpretation of the holotype of *Cassubia infercambriensis* cannot be considered unequivocal. It is possible that the 'thorax' and 'chelicerae' represent both appendages of the pair, transversely superimposed on each other. Even the possibility that the more extensive part represents the trunk cannot be ruled out, although the proportions of the body of better known anomalocarids (Fig. 3E) make it unlikely. These uncertainties in interpretation of the fossil do not preclude the classification of *Cassubia* in the family Anomalocarididae Raymond 1935, although they may have bearing on estimated number of segments, which is unusually high in the interpretation followed here.

Relationships of CASSUBIA. – *Cassubia infercambriensis* is the oldest known anomalocarid. The oldest representative previously was *Anomalocaris pennsylvanica* (Resser 1929) from the Kinzers Formation of Pennsylvania (Briggs 1979). It represented the *Olenellus* Zone and was thus significantly younger than *Cassubia*, but still Early Cambrian in age. The type specimens of this species are rather poorly preserved and do not allow reconstruction of the detailed morphology of the ventral processes. From the same formation, however, Briggs (1979) described specimens, identified by him as *A.* cf. *pennsylvanica*, which show paired narrow processes with sparse denticulation only along their distally facing margins (Fig. 3B), as in *Cassubia*. This suggests a relationship between these forms.

Another species, *A. canadensis* Whiteaves 1892, known from both late Early and Middle Cambrian strata (Briggs 1979; Briggs & Mount 1982; Whittington & Briggs 1985), differs from *A.* cf. *pennsylvanica* in having spine-like processes equipped with accessory single denticles on both distal and proximal sides. Quite a different organization is characteristic for appendages of *A. nathorsti* (Walcott 1911), the best known anomalocarid, occurring in the Middle Cambrian (Briggs & Robison 1984; Whittington & Briggs 1985). Its appendages were armed with a single row of comb-like blades and another row of short spines, possibly homologues of respective rows of paired spines on appendages of *A. canadensis*. One may propose an evolutionary derivation of *A. nathorsti* from a form like *C. infercambriensis* or *A.* cf. *pennsylvanica* by a differential evolution of each of the two rows of blades.

Taxonomic nomenclature. – Although both *A. nathorsti* and *A. canadensis* had a *Peytoia*-type oral apparatus and similar body form (Whittington & Briggs 1985), they differ significantly in the organization of their anterior appendages, with *A. canadensis* bearing long appendages with paired spines while *A. nathorsti* shows an unpaired elaborated armament of filtratory combs and spines. The filtratory function of the appendages seems to us rather self-evident, showing many analogies with filtratory appendages of Recent crustaceans (for instance pelagic euphausiaceans; e.g. Dzik & Jażdżewski 1978) although Whittington & Briggs (1985:602) prefer to see all anomalocarids as predators. Both of these species contrast with *C. infercambriensis* and *A.* cf. *pennsylvanica*, both probably having paired serrate blades. We believe that these differences warrant separation of *C. infercambriensis*, *A. canadensis*, and *A. nathorsti* within different genera (*Peytoia* Walcott 1911 and *Laggania* Walcott 1911 are available names for *A. nathorsti*).

Affinities of anomalocarids. – With their highly unusual body organization the Anomalocarididae cannot be directly compared with any other known articulates (Whittington & Briggs 1985) and similarities to a remipedian crustacean *Tesnusocaris* (see Schram *et al.* 1986) are quite superficial and probably related to a similar mode of life.

Probably more significant are similarities in the body plans between *Anomalocaris* and *Opabinia*, pointed out by Bergström (1986). He stressed potential value for comparative anatomic studies of the peculiar modes of imbrication of appendages in these animals. Namely, the body appendages of *Anomalocaris* and the uropods of *Opabinia* overlap in such a way that each distal lamellar appendage covers the posterior part of its preceding neighbour. Quite the opposite arrangement is typical of tergites of *Anomalocaris* and lateral projections of the body in *Opabinia*. In both cases these flat structures have 'gills' sandwiched in between, which supports their homology. To reach complete homologization of the body plan of these creatures one needs the proboscis of *Opabinia* to have been the result of an evolutionary transformation of an ancestral pair of grasping appendages of the *Anomalocaris*-type (Bergström 1986, 1987). Families Anomalocarididae Raymond 1935 and Opabiniidae Walcott 1912 can thus provisionally be connected to form the order Opabiniida Størmer 1944. A class rank name Dicephalosomita Sharov 1966 (setting aside its semantic reliability) is also available for them.

The above hypothesis of relationships (opposed by Briggs & Whittington 1987) implies that organization of the ambulatory appendages of the common ancestor of *Opabinia* and *Anomalocaris* should be of the *Anomalocaris* or rather *Cassubia* type. The time distribution of known anomalocarids suggests that the presence of the processes (blades) on the ventral surface of their

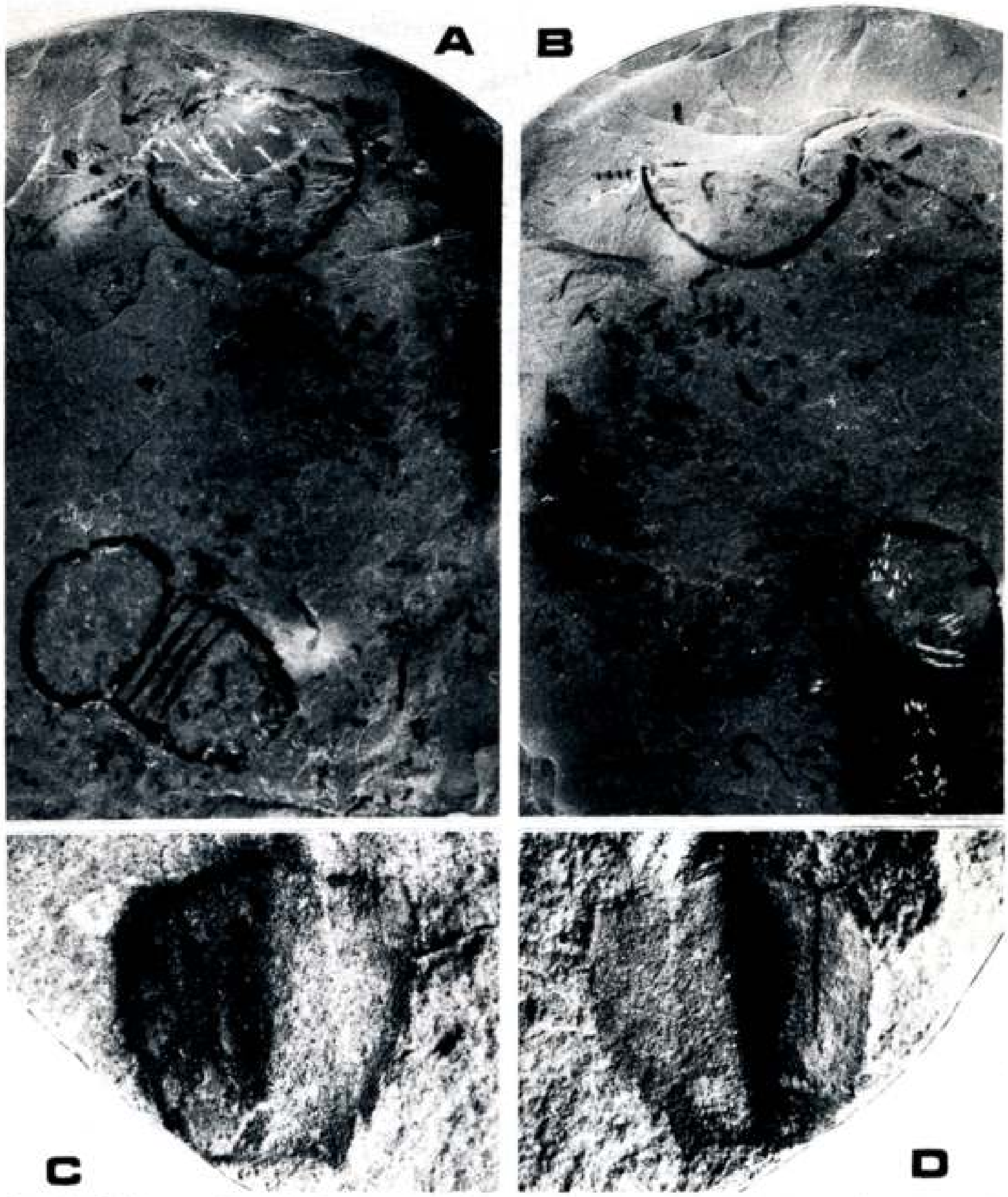


Fig. 4. ☐ A–B. Holotype of *Liwia plana* (Lendzion 1975), IG 1432 II 22 (part and counterpart), Kościerzyna IG 1 borehole, depth 4920.9 m, subsurface Zawiszyn formation. ☐ C–D. Holotype of *L. convexa* (Lendzion 1975), IG 1432 II 20 (part and counterpart), borehole Wyszków IG 1, depth 2240.3 (specimens except for D submerged in alcohol). × 2.

appendages is an ancestral feature. It is noteworthy that such processes arm also appendages of *Xenusion auerswaldae* Pompeckj 1927, an onychophoran approximately coeval to *Cassubia* (Jaeger & Martinsson 1967; Dzik & Krumbiegel in preparation), and its possible successor *Aysheaia* from the Middle Cambrian Burgess Shale (Whittington 1978). On the other hand, dorsally located filamentous gills were identified also in Ediacarian *Spriggina* (Birket-Smith 1981). Although little more than enumeration of these similarities is now possible on the basis of sparse empirical evidence, these earliest known articulates may not be as phylogenetically distant as it is usually claimed.

A soft-bodied trilobite *Liwia*

The generic name *Livia* was proposed for two species of trilobite-like arthropods from the basal Cambrian of NE Poland (Lendzion 1975). Unfortunately, this name is preoccupied by *Livia* Latreille 1802 (a homopteran insect) and we therefore replace it here with *Liwia*, new name, a spelling closer to that of the river Liwiec, from which it was derived.

The type species *L. convexa* (Lendzion 1975) is known from an isolated pygidium with fragments of two thoracic segments attached (Fig. 4C–D) found in a fine-grained sandstone in borehole Wyszków IG 1 (see Fig. 1) at the depth 2240.3 m. The specimen is preserved in full relief. Another specific name, *L. plana* (Lendzion 1975) was proposed for a complete though flattened specimen, less than half the size, found on a bedding plane of dark grey claystone in borehole Kościerzyna IG 1 (see Fig. 1) at the depth 4920.9 m. More detailed examination of the core slab revealed an isolated cephalon with antennae still in place located in the proximity of the holotype (Fig. 4A–B). The second specimen is somewhat larger, but a significant size difference remains between the specimens from Wyszków and Kościerzyna. Whether it vindicates their separation into different species is debatable, but an authoritative decision cannot be taken with the available material.

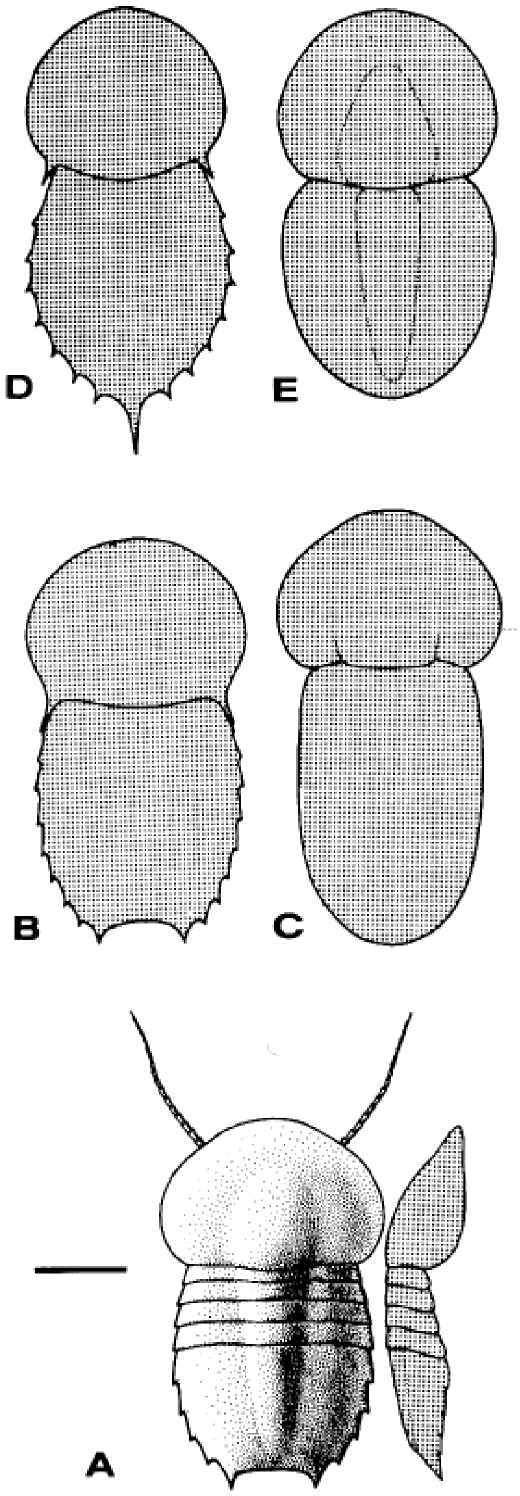
Although the outline of the body and appearance of segments and antennae are clearly visible on the core slab from Kościerzyna (Fig. 4A–B), the central parts of the cephala and the pygidium lack any preserved cuticle on either part or counterpart. Presumably, the cuticle was very thin in these areas. There is no evidence of eyes or cephalic sutures in these specimens. Rather, it seems that their cephala were uniformly and gently convex, very probably with a somewhat elevated axial part as indicated by relief of the three-dimensionally preserved pygidium from Wyszków (Fig. 5A).

Relationships of L*IWIA*. – *Liwia* is similar to recently described species of the soft-bodied trilobite *Naraoia* from the Early Cambrian Chiungchussu Formation of China (Fig. 5B–C); (Zhang & Hou 1985). Although *N. spinosa* Zhang & Hou 1985, like other species of the genus occurring in the Early and Middle Cambrian (Whittington 1977; Robison 1984), completely lacks thoracic segments, its pygidium is exactly the shape of that of *Liwia*, except that additional segments seem to be incorporated into it, as indicated by the presence of additional pairs of marginal spines (Fig. 5B). Taking into consideration the oval shape of the cephalon, the lack of eyes, the large pygidium, the unmineralized dorsal exoskeleton, and the presence of long antennae, it seems clear that *Liwia* is a soft-bodied trilobite, a representative of the Naraoida Størmer 1944. The presence of four free segments and the apparent segmentation of the pygidium expressed in a metameric distribution of marginal spines, indicate an ancestral position for *Liwia* among naraoids. With free thoracic segments still present, *Liwia* would not fit the diagnosis of the family Naraoidae Walcott 1912, as emended by Whittington (1977), therefore a new family Liwiidae is here proposed.

The high level of tagmosis clearly shown by the morphology of the pygidium of *Liwia* cannot be an archaic feature. The soft-bodied trilobites evidently derived from typical trilobites having a small pygidium and well segmented thorax. What remains to be explained is whether the lack of facial sutures is an original inherited feature (in which case they could be related to the Olenellida) or whether these sutures disappeared in connection with an evolutionary decalcification of the skeleton and disappearance of eyes.

Little can be found in the fossil record to support an olenellid ancestry for the Liwiidae. The cephalon of *Wolynaspis unica*, the oldest trilobite found in the southern part of the East European Platform (Kirjanov & Tchernysheva 1967), shows, with its oval outline and lack of genal spines, a superficial similarity to that of *Liwia*. Nevertheless, a daguinaspid affinity of *Wolynaspis* seems rather well established and it is quite unlikely that its pygidium was different from that of *Daguinaspis*. Rather, it was very small, as in other Olenellida.

Somewhat more persuasive arguments can be assembled to support a common ancestry of the Naraoida and Agnostida. An eodiscid *Pagetiellus*



appeared in Siberia in strata approximately coeval to these with *Liwia* (Khomentovsky & Repina 1965), showing a large oval pygidium with convex, smooth dorsal surface, as in the naraoids. The tendency to reduction and loss of eyes is typical of the miomeran trilobites and could have been completed in the lineage leading to the naraoids even earlier. Such a derivation would require a fundamental reorganization of the physiology (mechanisms of cuticle formation and moulting) and *Liwia* does not fill the gap between the orders. Similarities between the miomeran and soft-bodied trilobites may be related to similar mechanisms of evolutionary development of tagmatization, as suggested by another similar example of reduction of free thoracic tergite number in the corynexochid trilobites (Robison & Campbell 1974). In all these cases a retardation of the ontogenies may be involved.

It thus appears that the exact position of the Naraoida in the class Trilobita remains to be elucidated. No unequivocal evidence for the presence of naraoids in younger than Middle Cambrian strata has yet been published. Whittington (1977:416) accepted the view of Repina & Okunieva (1969) that their species *Maritimella rara* Repina & Okunieva 1969 from undated Early Palaeozoic strata of the Pacific coast of Asia belongs to the Naraoidae. One of us (JD) had an opportunity to examine original specimens of arthropods from these beds housed at the Institute of Geology and Geophysics of the Siberian Branch of the Academy of Sciences of the U.S.S.R. in Novosibirsk. They show a quite peculiar mode of preservation, with rather thick (phosphatic?) coatings covering carapaces. It seems highly probable that the peculiar tagmatization of this and associated forms is a result of an artificial fusion of originally free thoracic segments as a result of post-mortem diagenetic processes. It is even possible that the supposed taxonomic diversity of the assemblage from these strata is a result of differential preservation of

Fig. 5. Composite reconstruction of the carapace and antennae of *Liwia*, with the pygidium of *L. convexa* combined with the whole body contour of *L. plana* (□ A), compared with silhouettes of known species of *Naraoia* (B–E). □ B. *N. spinosa* Zhang & Hou 1985, Chiungchussu Formation, Yunnan, Early Cambrian (based on Zhang & Hou 1985). □ C. *N. longicaudata* Zhang & Hou 1985, same locality and source of data. □ D. *N. spinifera* Walcott 1931, Burgess Shale, British Columbia, Middle Cambrian (based on Whittington 1977). □ E. *N. compacta* Walcott 1912, same locality and source of data. Bar scale = 1 cm.

remains of a single species of chelicerate-like arthropod.

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