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INDICE

GARBARI F., SENATORI E. - Il genere <i>Allium</i> L. in Italia. VI. Contributo alla citosistemica di alcune specie	Pag. 1
DERI P. - B-cromosomi in popolazioni polisomiche di <i>Dugesia benazzii</i> (Tricladida paludicola) della Corsica	» 25
MAZZA M. - Accrescimento larvale negli scorpioni d'acqua (Heteroptera Nepidae)	» 39
BORGOGNINI TARLI S.M. - Studio antropologico di resti scheletrici etruschi rinvenuti nella necropoli di Sovana M. Rosello (Grosseto)	» 45
FORMICOLA V. - I dermatoglifi digitali e palmari di 200 Lunigianesi (100 maschi e 100 femmine)	» 97
SIMONETTA A.M. - Remarks on the origin of the Arthropoda	» 112
<i>Elenco dei Soci per l'anno 1975</i>	» 135

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REMARKS ON THE ORIGIN OF THE ARTHROPODA

Riassunto — L'A. esamina il significato degli Artropodi del Cambrico medio nel quadro del problema generale dell'origine degli Artropodi. Anche il significato di *Aysheaia*, un genere prossimo agli Onicofori ed ai Tardigradi, viene preso in considerazione con particolare riguardo all'ipotesi di un'origine monofiletica di Onicofori, Miriapodi ed Insetti. L'A. conclude che gli elementi disponibili indicano che gli Artropodi costituiscono un insieme naturale, contrariamente alle ipotesi di una loro origine polifiletica, che hanno riscosso crescenti consensi in questi ultimi anni, e che il loro piano di organizzazione fondamentale deve essersi realizzato nel tardo Precambriano. E', d'altra parte, probabile che, dato il differenziamento che gli Artropodi avevano già riassunto nel Cambriano medio, alcune « classi » di questo *phylum*, ed in particolare i Crostacei, siano polifiletiche.

Summary — The problem of the origin of the Arthropoda is discussed, especially in the light of the evidence provided by the Middle Cambrian faunas. It is concluded, contrary to the theory advocating the division of the *phylum* into « Arthropoda » and « Uniramia », that the Arthropoda are basically monophyletic and that they do not include the Onycophora. It also appears that some Arthropod « classes » (notably the Crustacea) may be poliphyletic.

The reconstruction of the possible common ancestor of a whole Phylum, despite being a game whrought with pitfalls and almost hopeless, as there is practically no chance ever to find the fossil of such an animal and as the evidence which comparative morphology and embryology can provide is usually such as to be liable to various alternative interpretations, is, nevertheless, almost a necessity if we are to frame the higher taxinomic categories, such as classes, in a reasonable order.

After a rather long period during which a broad consensus obtained on the arrangement of the higher categories of the Ar-

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thropoda, the current revival of research in comparative anatomy has gradually built up sufficient new evidence as to induce such qualified scholars as MANTON [1950, 1952, 1958a, 1958b, 1969a, 1969b, 1973] for instance, to suggest to explode the Arthropod phylum and to split it into two: the Arthropoda proper, which are considered to include the Crustacea, the Chelicerata and the related or supposedly related groups, and the « Uniramia », to include the Insecta, the Myriapoda « sensu lato » and the Onycophora.

Such views, based on some amongst the best morphologic work done on the Arthropods, have been thence further supported by ANDERSON's [1973] interpretation of the comparative embryology of Annelids and Arthropods.

They have been gaining an increasing acceptance, so that it can be safely said that the taxonomy of this phylum or groups of phyla is now in a state of flux such as it never was in the minds of zoologists for over sixty years.

A basic requirement of any satisfactory theory is that it accounts for *all* known facts. If apparently it does not, then either it is the interpretation of the apparently conflicting evidence that is at fault, or it is the theory itself that requires revision. I must thence forestate that also the hypotheses proposed further on do not seem to meet this requirement, so that the following remarks, partly based on original researches on relevant Cambrian fossils (SIMONETTA [1961, 1962, 1963, 1964, 1970] and SIMONETTA & DELLE CAVE [1975a, 1975b]) are hence proposed for consideration, and I must stress that they are submitted as tentative ideas in search for criticism. The original evidence and the discussion of the reconstructions proposed for the relevant fossils, as well as the analysis of the possible relationship of the various taxa with later groups, can not be summarized here and the reader is referred to SIMONETTA & DELLE CAVE [1975a] to decide whether to accept the reconstructions figured in this paper.

As mentioned, MANTON and others (ex. MANTON & TIEGS [1959]; MANTON [1973]) have accumulated considerable evidence mainly on the possible evolution of mouthparts, but quite significant also on that of the locomotive apparatus, this is such as to induce the proposal to consider: 1st) that if the Arthropoda are considered as one phylum, then the Onycophora should be included into it, and 2nd) that the Onycophora might be more closely related to the Myriapod-Insect assemblage than to the other Arthropods and

hence that, as the more typical Arthropod features, such as the articulated leg and the metameric body covered by distinct sclerites, may well be acquired by convergent evolution, the whole assemblage may be conveniently split in two phyla.

MANTON [1972], ANDERSON [1973] and others therefore hold that it is preferable to split the Arthropoda into at least two phyla, the one including the Onychophora, Myriapoda and Insecta being called Uniramia.

To the relevant proposition, in spite of the whole well arranged argument supporting close relation of the Insect-Myriapod group, to the Onychophora, there is a very critical piece of evidence which does not fit into the picture: that is the fossil species known as *Aysheaia pedunculata* Walcott.

This was originally described by WALCOTT as a Polichete Annelid, but since HUTCHINSON [1930] it has been considered as an Onychophoran.

Four reconstructions have been proposed, by HUTCHINSON [1938], by SNODGRASS [1958], SHAROV [1965] and by SIMONETTA & DELLE CAVE [1975b] (fig. 1), this last based on additional specimens with respect to those used by HUTCHINSON and by SNODGRASS. This last reconstruction, if accepted, poses, apparently, considerable difficulties to the hypothesis of a close relationship between the Onychophora and the Arthropoda, as *Aysheaia* appears as an almost perfect intermediate between an Onychophoran and a Tardigrade.

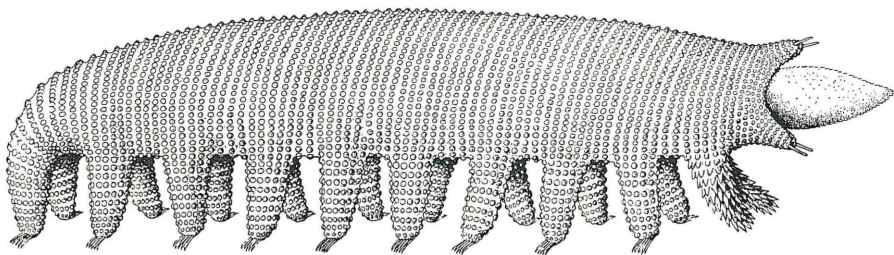


Fig. 1 - *Aysheaia pedunculata* Walcott (Middle Cambrian).

Indeed the fossils are so preserved that, had there been present some sort of jaw it would most probably be visible, moreover the « head » does not have tentacles and thus its morphology ap-

proaches much to that of a Tardigrade. The highly reflecting pin-like structures which protrude from the circum-oral papillae in one specimen, can be either some sort of secrete squeezed off during burial and thence bear evidence of glands analogous with the slime glands of the Onychophora, or be stylets of a sort, corresponding with the buccal apparatus of the Tardigrada. The number of legs of *Aysheaia* (10) is low for an Onychophoran, but quite plausible, as an increase in length with evolution is possible, and is high for a Tardigrade, but the fact that the last pair of legs are placed at the very end of the body is a Tardigrade feature, not to be found in the Onychophora, and the multiple hooks which terminate the legs are equally a Tardigradan character⁽¹⁾. In some specimens there is visible a structure which may be an extended pharynx.

Not so, instead the modified first pair of leg. However, unless we assume that the first pair of legs, clearly post-oral, are homologous with the antennae of the Onychophora, an idea that probably no zoologist will be prepared to accept, as it runs contrary to embryological evidence, this must be considered a peculiar specialization of *Aysheaia*. Nevertheless also this feature could be interpreted as pointing to a relationship between *Aysheaia* and the Tardigrada, as one might well consider it as an « attempt » to develop specialized sensory appendages in a group primitively devoid of specialized sensory appendages (be either cirri, tentacles etc.), as it is probably the case in the Tardigrada.

Obviously enough the fact that *Aysheaia* has features intermediate between the Onychophora and the Tardigrada does bring into the picture the Tardigrada, rather than rule out the Onychophora from the Arthropoda, though, it makes the problem more complicated, mainly as it would require a reappraisal of the embryological evidence: for instance great significance is generally attributed to the mode of formation of the mouth, anus and mesoderm and there the Tardigrada would stand alone, among the Articulata in being enterocelic and deuterostomous!

We shall then turn to a different line of evidence to see whether the evidence for a distinct origin for the Insecta and the Myriapoda from the other Arthropods runs into other difficulties.

We know in some detail the walking appendages of two or three scores of Cambrian and Ordovician Arthropods, about one

(1) Not all of Tardigrada, however, have multiple hooks.

third of them being Trilobites and the others belonging to a considerable range of ordes, most of them from the middle Cambrian Burgess shale of British Columbia. Now in all instances, in spite of considerable variations in detail, all these appendages conform with the same basic plan viz. a multisegmented walking leg, the actual number of articles being somewhat variable, with an outer branch attached to its basal article; this outer branch is quite variable in morphology, but appears to be primarily a respiratory appendage, though it is clear that at least in some instances it had an important function also as a swimming organ (Figs. 2, 3, 4, 6, 7, 8, 9, 10). In all known instances the middle Cambrian Arthropods, except *Sydneyia*, have no trace of ventral or pleural sclerites and it is obvious that hydrostatic pressure, as maintained by MANTON (1969 b) afforded the rigidity at the junction with the body which was needed for operating the leg. In *Sydneyia* there obtained a sternal plate of a sort (fig. 2: C-E), apparently extending also to the pleural region. BRUTON (pers. comm.) thinks that actually the coxa of *Sidneyia* extended in the pleural region in the same way as that of the living Xiphosurans. I have seen his evidence and I agree that he is probably right; there is however one specimen which shows clearly the existance of a continuos sclerite bridging both the pleural and the sternal areas. If the coxa had the structure maintained by BRUTON, it apparently articulated in front of the sterno-pleural plate. See also SIMONETTA (1963), SIMONETTA & DELLE CAVE [1975a], BRUTON (in press), HUGUES (in press).

It can be shown that *Sidneyia* fed on very hard animals like trilobites, and was equipped, the only instance in the whole Burgess shale fauna, with powerfull crushing gnathobases at each of its walking legs.

It seems therefore that at least in some instances sternal sclerites arose as an adaptation to give better leverage to the masticatory apparatus, while in other their appearance must have been an adaptation to give leverage either for bulky aquatic animals or for terrestrial ones, to keep the body off the ground.

As sternal and pleural sclerites must have been developed independently in a number of taxa, there is little doubt that they were both conditioned by the possible movements of the legs in the animals in which they were developing and at the same time were themselves directing the possible evolution of the gait and of the morphology of the legs. Thus it may be expected that the basic

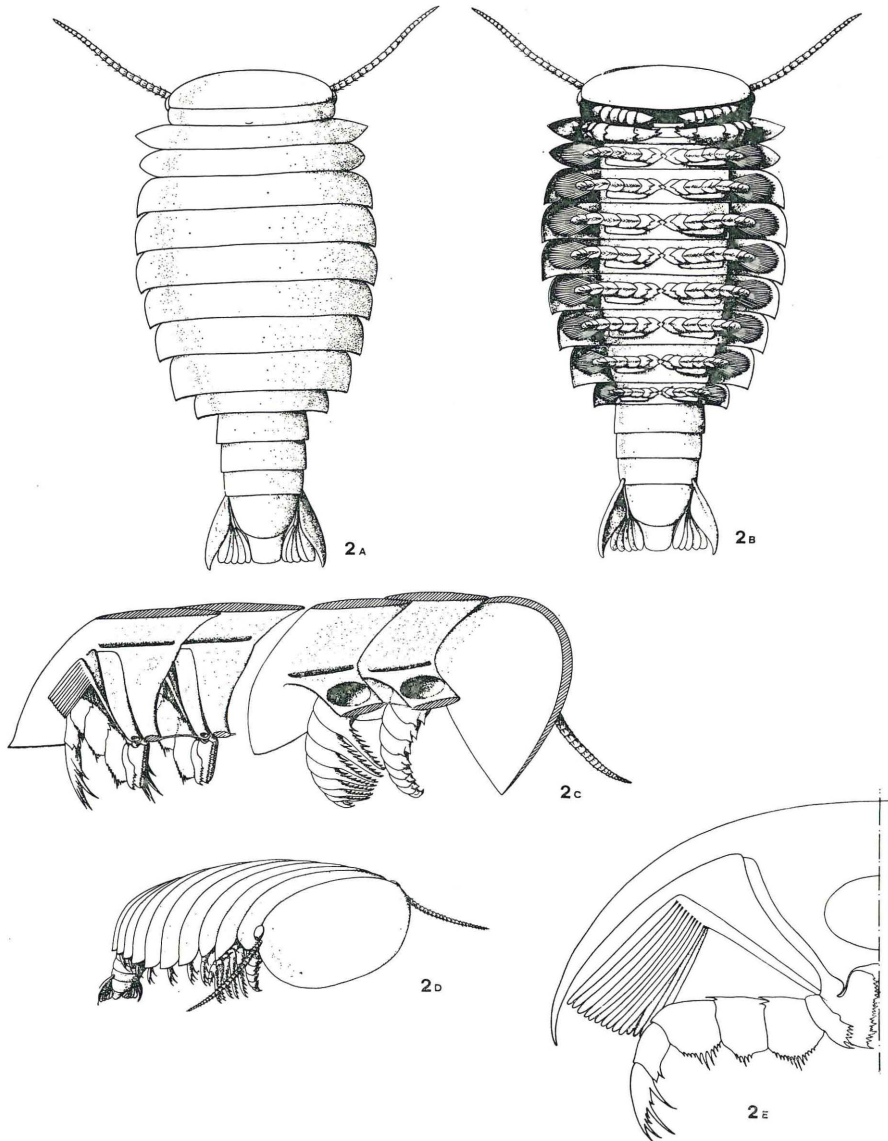


Fig. 2 A-E - *Sidneyia inexpectans* Walcott (Middle Cambrian).

features which differentiate the living classes are specialized ones arising probably in Ordovician or Silurian times. Were all these types of walking legs derived from a single type of legs or not? Indeed if there is a strong case for deriving all the types of Arthropod legs from a single basic type, then it would follow that the

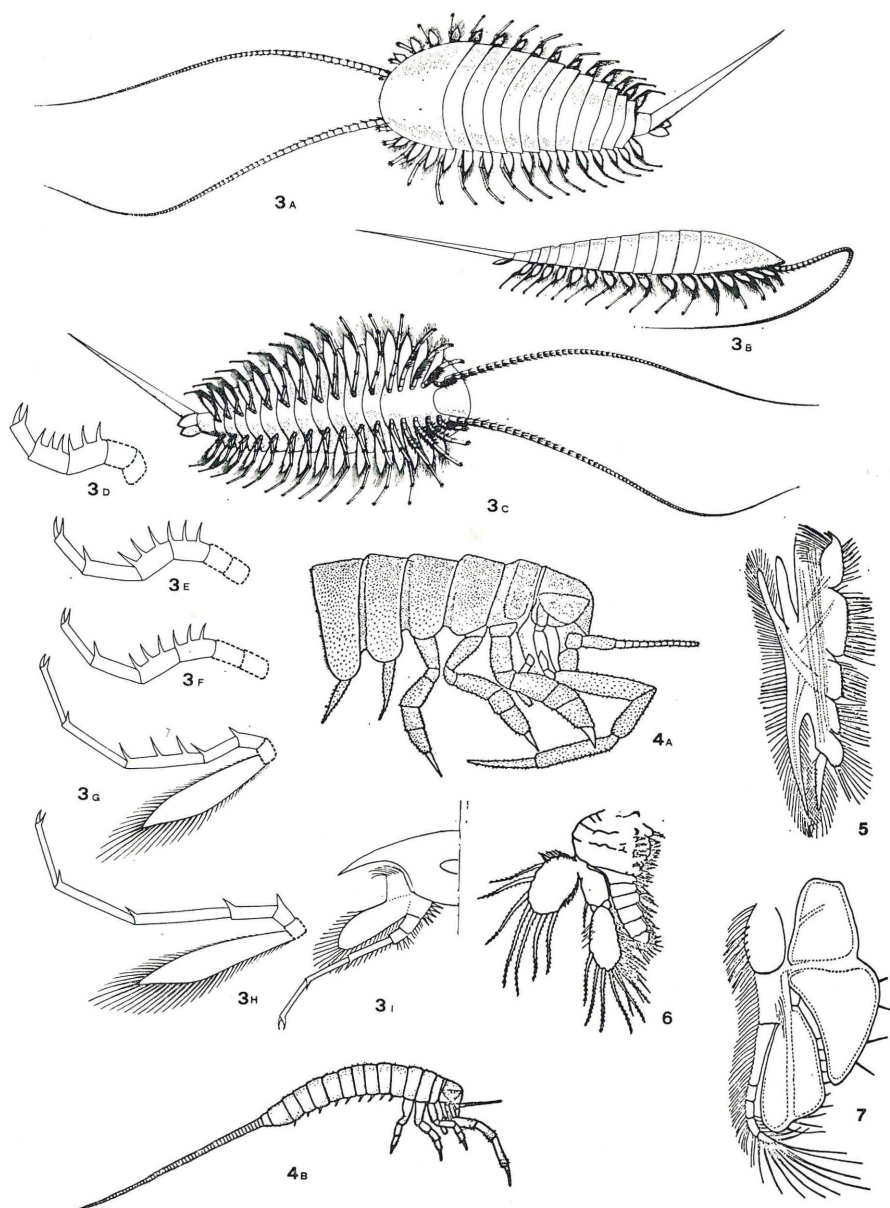


Fig. 3 - 3A-I - *Emeraldella brocki* Walcott (Middle Cambrian); 4 A-B - *Dasyleptus brogniarti* Sharov (Lower Carboniferous); 5 - *Estheria* sp. thoracic appendage (living); 6 - *Hutchinsonella macracantha* Sanders, thoracic appendage (living); 7 - *Nebalia* sp. thoracic appendage (living).

case for the Arthropods being a monophyletic group would be strengthened, albeit the living classes being very distantly related.

We must concede that none of the known Cambrian and Ordovician species appears to be close to the Insecta and Myriapoda; while some appear to stand rather close to the Xiphosura and Crustacea and point to a polyphyletic origin of the Crustacea (figs. 3, 4, 5, 6, 7, 8, 9, 10), on the other side the mere exiguity of the number of species of Arthropods other than Trilobites known from this period make highly improbable that among them there are the ancestors of all later groups and, anyway the species known in some detail are separated from the Devonian, when the colonisation of lands may have occurred such a long span of time, that a wide morphologic gap is to be expected. Thence it would not be surprising if, were we to have come across a Cambrian ancestor of the Antenno-tracheate, we would not recognize it.

We have, however figured among the species illustrated for purpose of comparison also the Monuran *Dasyleptus brognarti* in order to call attention to its at least superficial similiarity with some of the Emeraldellida. Other comparisons which the reader may do by himself are between the modern Anostraca and the Devonian *Lepidocaris* and the Cambrian genera *Leancoilia*, *Alalcomeneus*, *Actaeus* and *Yohoia*. Likewise the recent genera *Synagoga*, *Ascothorax*, *Cyzicus*, *Leptodora* and *Nebalia* have been figured for comparison with the Cambrian *Odaraia*, *Eurysaces*, *Protocaris*, *Waptia* and *Canadaspis*, the better known of the many Cambrian genera provided with a carapace. Finally several Palaeozoic Chelicerata have been figured for the sake of comparison with the Middle Cambrian Emeraldellida.

Anyway it appears to be significant that all the walking legs known from pre-Silurian time conform to a single basic type, whichever the other differences among the animals, and these were great. Few as the actually known appendages are, until we get positive evidence to the contrary, we must, I think, assume that this type was universal among all Arthropods of the age. This the more so that the so called « trilobite-type » of leg is such as not to preclude the possibility to evolve from it a leg such as that of Insecta⁽¹⁾ or of any Myriapod⁽²⁾.

(1) The term is used as covering both the Ento-and the Ectognatha and without taking issue as to taxonomic position of the various Entognathous orders.

(2) I am not here taking any definite position as to the relationships of the Progoneate and Opisthgoneate orders.

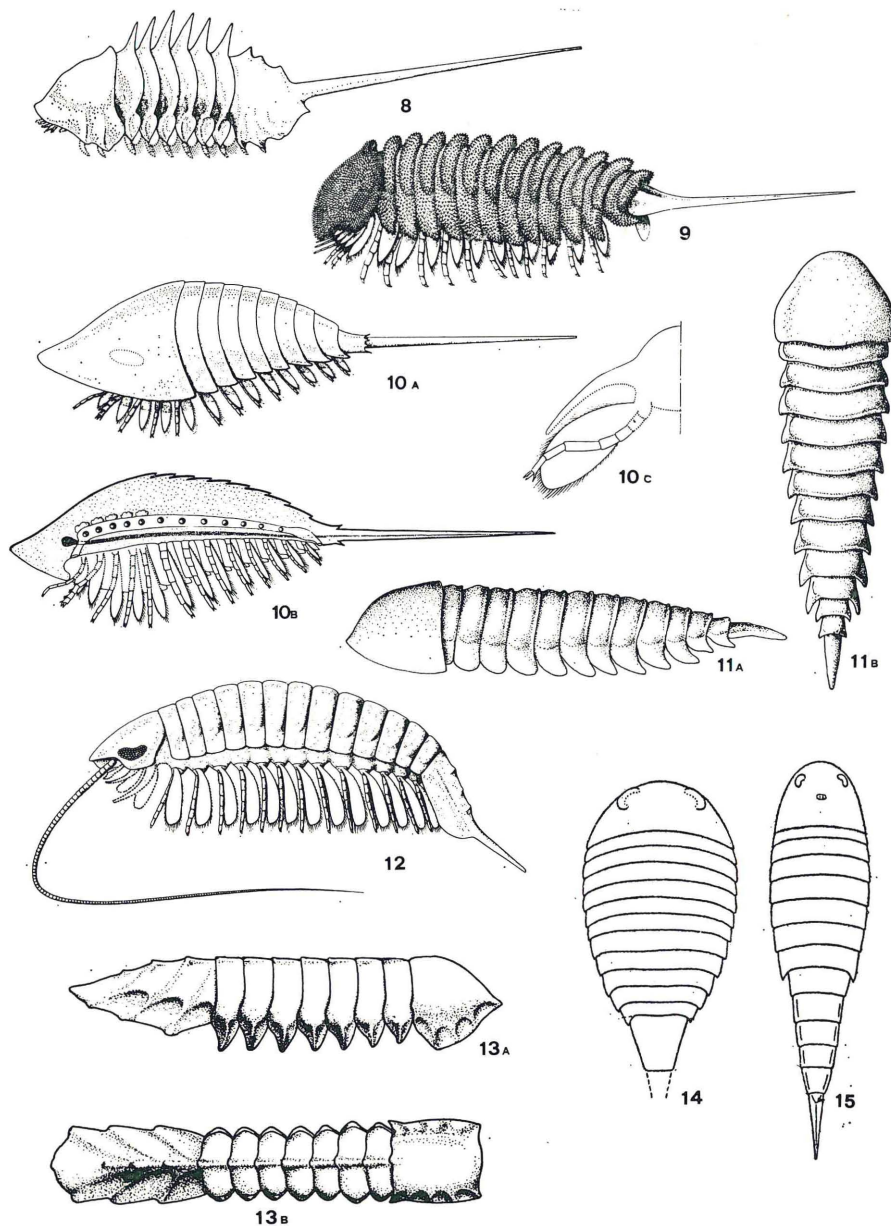


Fig. 4 - 8 - *Thelxiope palaeothalassia* Simonetta-Delle Cave (Middle Cambrian); 9 - *Habelia optata* Walcott (Middle Cambrian); 10 A-C - *Molaria spinifera* Walcott (Middle Cambrian); 11 A-B - *Habelia brevicauda* Simonetta (Middle Cambrian); 12 - *Emeraldoides problematicus* Simonetta (Middle Cambrian); 13 A-B - *Mollinsonia symmetrica* Walcott (Middle Cambrian); 14 - *Palaeomerus hamiltoni* Størmer (Lower Cambrian); 15 - *Hughmilleria norvegica* (Klaer) (Upper Silurian).

The loss of the outer branch, considering its primary function as a gill, is to be expected as a result of the colonisation of Land. True: at least many of the Carboniferous Insects known appear to have had aquatic larvae, but orders such as the Dictyoptera and the Orthoptera had an entirely terrestrial development and the fact that Carboniferous insects come almost all from layers deposited in swamps has good chances to have biased the record. Thus, if we must consider that:

A) the Onycophorans were apparently evolving from a stock close to the Tardigrada in marine environment during the middle Cambrian and that in a biocenosis that, so far as it can be judged, was established on open mud-flats or rather, as maintained by WHITTINGTON [1971 a], on a muddy slope. This does not support the contention by MANTON [1950, 1969 a, b] that the Onycophora evolved their cuticle devoid of sclerites and their unarticulated legs as an adaptation to squeeze through narrow passages. It seems rather that having basically reached the Onycophoran size and type of organisation in the sea, the Onycophora found themselves pre-adapted for their present mode of life on dry lands. The peculiar Gondwanian distribution of the Onycophora might even be considered as evidence of very late colonisation of land, strange as it may seem, as many modern Onycophorans stand quite temperate climates and it is somewhat strange that none ranges North of the ancient Thetis Sea.

B) that in view of the direct palaeontological evidence showing that one basic type of leg was present in quite diverse Cambrian Arthropods, we should assume, for the time being, a monophyletic origin for the Arthropoda and henceforth that the evidence provided to support the thesis of the separate origin of the « Uniramia » should be revised to see whether it is not liable to an alternative interpretation in terms of adaptation to a terrestrial biotope⁽¹⁾.

(1) The « Uniramia » can not possibly have occupied a terrestrial biotope before the Silurian as until that age there was not a terrestrial flora to feed terrestrial animals. Thus we must envisage the ancestor of the « Uniramia » as being marine or fresh-water animals, presumably, unless they were exceedingly small, with some sort of branchial apparatus.

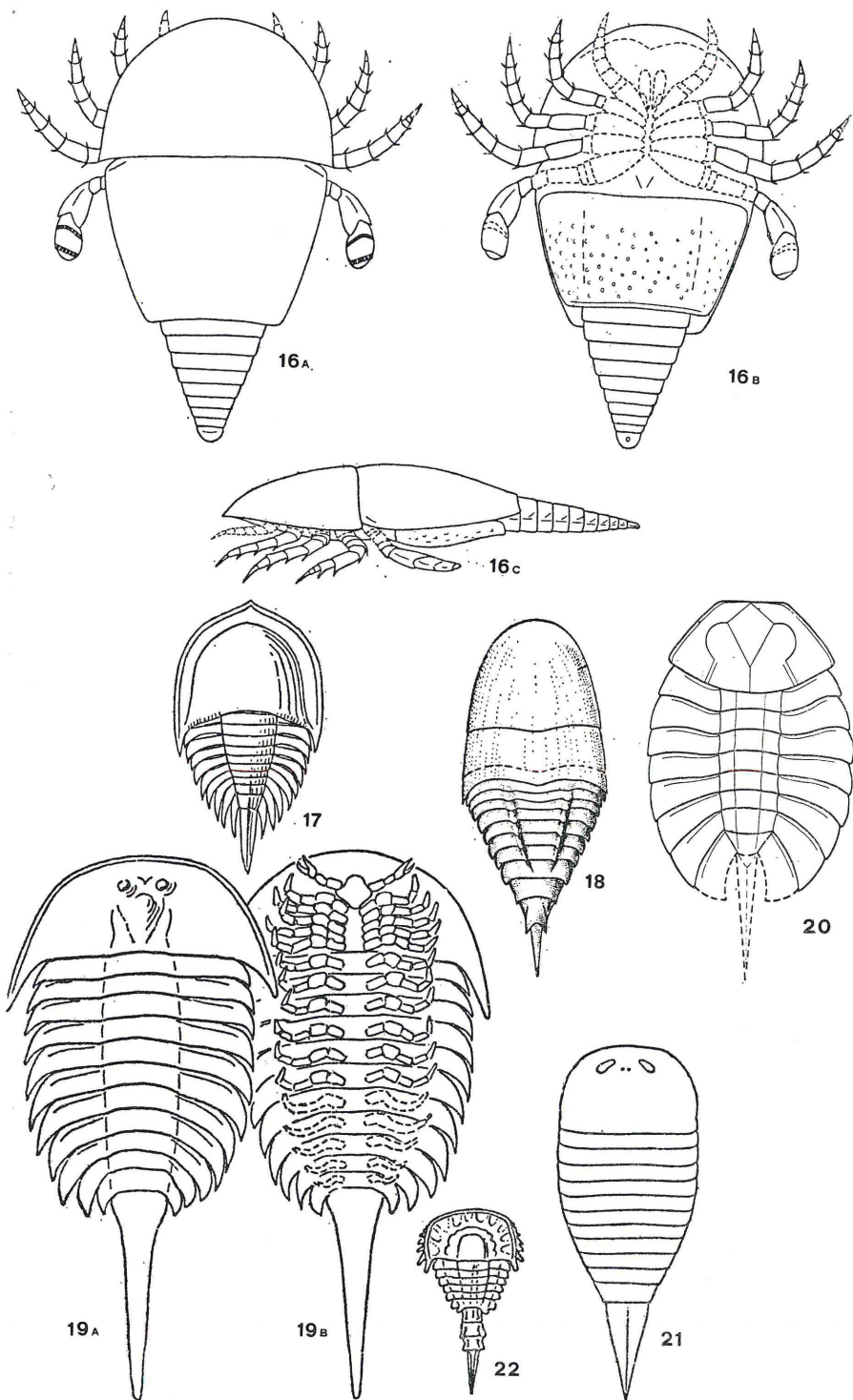


Fig. 5 - 16 A-B - *Diploaspis casteri* Størmer (Lower Devonian); 17 - *Pseudoniscus roosevelti* Clarke (Silurian); 18 - *Borchgrevinkium taimyrensis* Novojilov (Upper Lower Devonian); 19 A-B - *Aglaspis spinifer* Raasch (Upper Cambrian); 20 - *Triopus draboviensis* Barrande (Middle Ordovician); 21 - *Strabops thacheri* Beecher (Upper Cambrian); 22 - *Hemiaspis limuloides* Woodward (Silurian).

These assumptions, curiously enough, do not seem to challenge MANTON's theories on the evolution of mouth-parts, as these are quite varied in the middle Cambrian fossils, and, though differentiated, they are so primitive that one or the other could evolve in any of the patterns shown by MANTON⁽¹⁾. It is indeed the embryological evidence which is more difficult to line up with the hypothesis that the Arthropoda are monophyletic. On the other side while the embryological evidence, as interpreted by ANDERSON [1973], appears to support a polyphyletic origin for the Arthropoda and even a closer relationship between the Onycophora, Insecta and Myriapoda with the Oligochaeta, than between the « Uniramia » and the Crustacea, this seems to be flatly contradicted by the biochemical evidence that, while the main supporting protein in the Annelida is collagen, which makes up also the cuticle; collagen is remarkably scarce in the Arthropoda and the Arthropod cuticle is always made up of chitin and arthropodin! The cuticle of the Onycophora is fairly well known, and it appears to be a remarkably simple and primitive chitinous structure.

The cuticle of the Tardigrada has been recently studied by Baccetti, whose finds support our contention, as it is basically a chitinous structure, quite comparable with that of the Onycophora, but not with that of the Annelida.

Is it possible to envisage the structure or the Ancestral or « Ur-Arthropod »? Obviously this is highly speculative, but it may be attempted, taking as a starting point two considerations.

The first is that by the early Cambrian there existed a fair number of typical Trilobites (whether the famous Ediacara fauna, which lacks the Trilobites, belongs to the uppermost pre-Cambrian, as it is generally agreed or to the lowermost Cambrian does not make any great difference) and that recent advances in the knowledge of the Non-Trilobite Cambrian Arthropods show clearly (cfr. SIMONETTA & DELLE CAVE [1975a]) that the Trilobita can not have been themselves the ancestors of the Non-Trilobite taxa, than the hypothetic Ur-Arthropod must have been living at the close of the Precambrian era.

(¹) It is especially notable that some middle Cambrian Arthropods had either the whole of some cephalic appendages or only the tip of them specialized for dealing with food and especially large preys. Some, as *Sidneyia* had both a gnathobasic crushing apparatus in their thoracic appendages, just as in the Xiphosura, and whole-leg jaws.

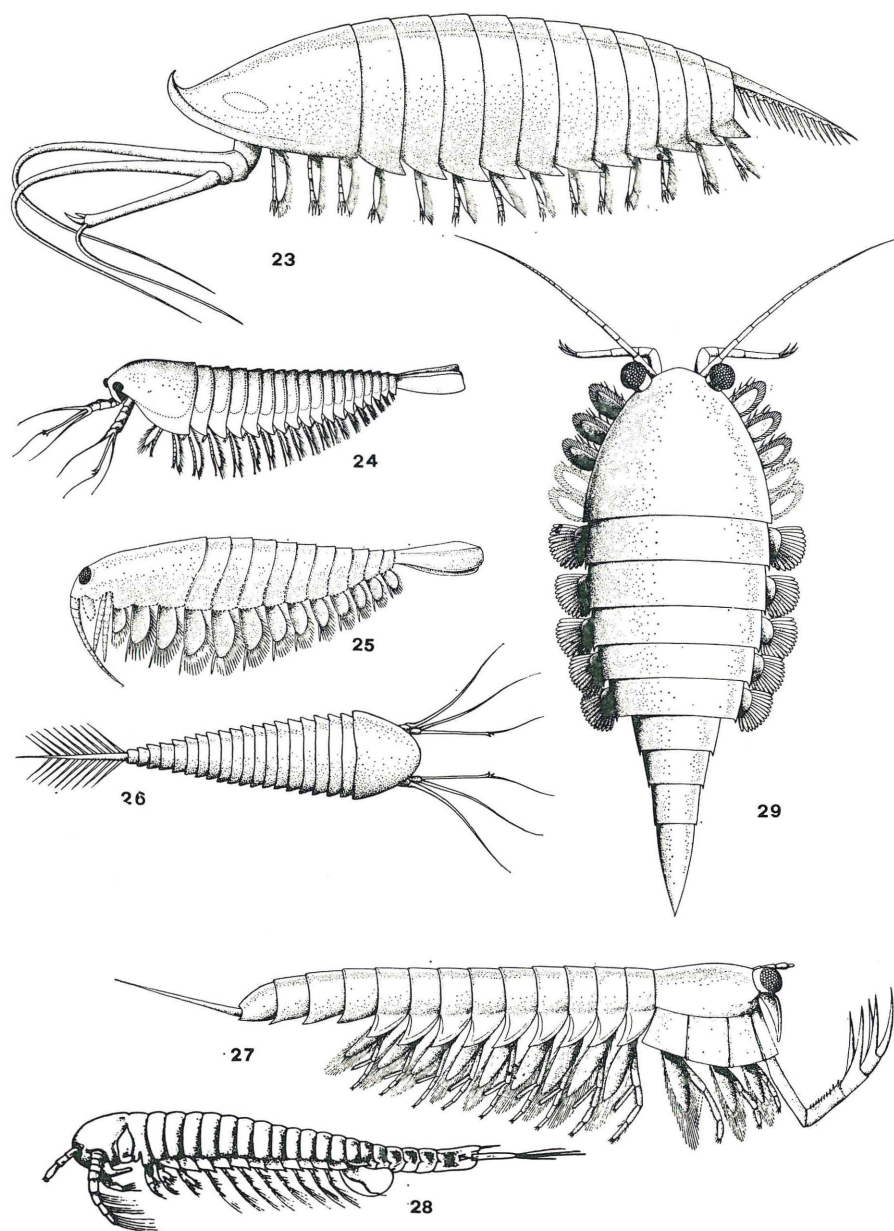


Fig. - 6 - 23 - *Leancoilia superlata* Walcott (Middle Cambrian); 24 - *Leancoilia amphiction* Simonetta (Middle Cambrian); 25 - *Alalcomeneus cambricus* Simonetta (Middle Cambrian); 26 - *Leancoilia protogonia* Simonetta (Middle Cambrian); 27 - *Yohioia tenuis* Walcott (Middle Cambrian); 28 - *Lepidocaris rhyniensis* (Devonian); 29 - *Actaeus armatus* Simonetta (Middle Cambrian).

The second consideration, which we shall see combines with the first one is that at the beginning of the Cambrian the free oxygen in the atmosphere must have been just somewhere between 1 and 2% of the whole make up of the troposphere. What was the content in free oxygen in the sea water is not precisely known, but it can not possibly have exceeded the oxygen content of the atmosphere. TOWE [1970] has pointed that the biosynthesis of collagen requires the availability of molecular oxygen and that, this being still at premium at the close of the Precambrian, very little, if any, was available for the synthesis of collagen. TOWE has, therefore, concluded that untill the end of the Precambrian the Metazoa could not have evolved except as minute and very simple structured animals⁽¹⁾.

Whilst we can assume that TOWE's argument is essentially correct, still it might be considered that the Metazoa could have evolved to a reasonable degree of complexity, even if under rather minute forms, if either of the following conditions obtained: 1) the development of a cuticle basically of non collagen structure may represent a sufficient support to the epidermis, so that support by collagen rich connective tissue may be notably reduced⁽²⁾. If this holds true, then the difficulty to produce a sizable amount of collagen may have been a cause to the development of the external skeletal structures of the Arthropods. 2) that there was no free larval stage or that growth was by quiescent stages. Protozoa can and actually do store nutrients. If the ontogeny of the early Metazoa developed entirely within the egg, then the need for free oxygen for activities other than organogenesis could have been curtailed. While active feeding and swimming in such a medium poor in oxygen as the Precambrian sea was, would have been highly competitive with the availability of oxygen for tissue building purposes, as pointed by TOWE, if development obtained in an entirely quiescent condition, then enough oxygen might still be made available for the make up of the minimum collagen needed

(1) More precisely: the hydroxylation of prolin and of lisin that causes the formation of hydroxyprolin and hydroxylisin, which are essential constituents of collagen, requires the availability of molecular oxygen and is operated by an oxygenase. Oxydations by oxygenases and peroxidases are involved also in the synthesis of resilin, which is a structural protein peculiar to the Arthropods.

(2) Collagen would still be required for support of internal structures and for muscle attachments, however in very small quantities.

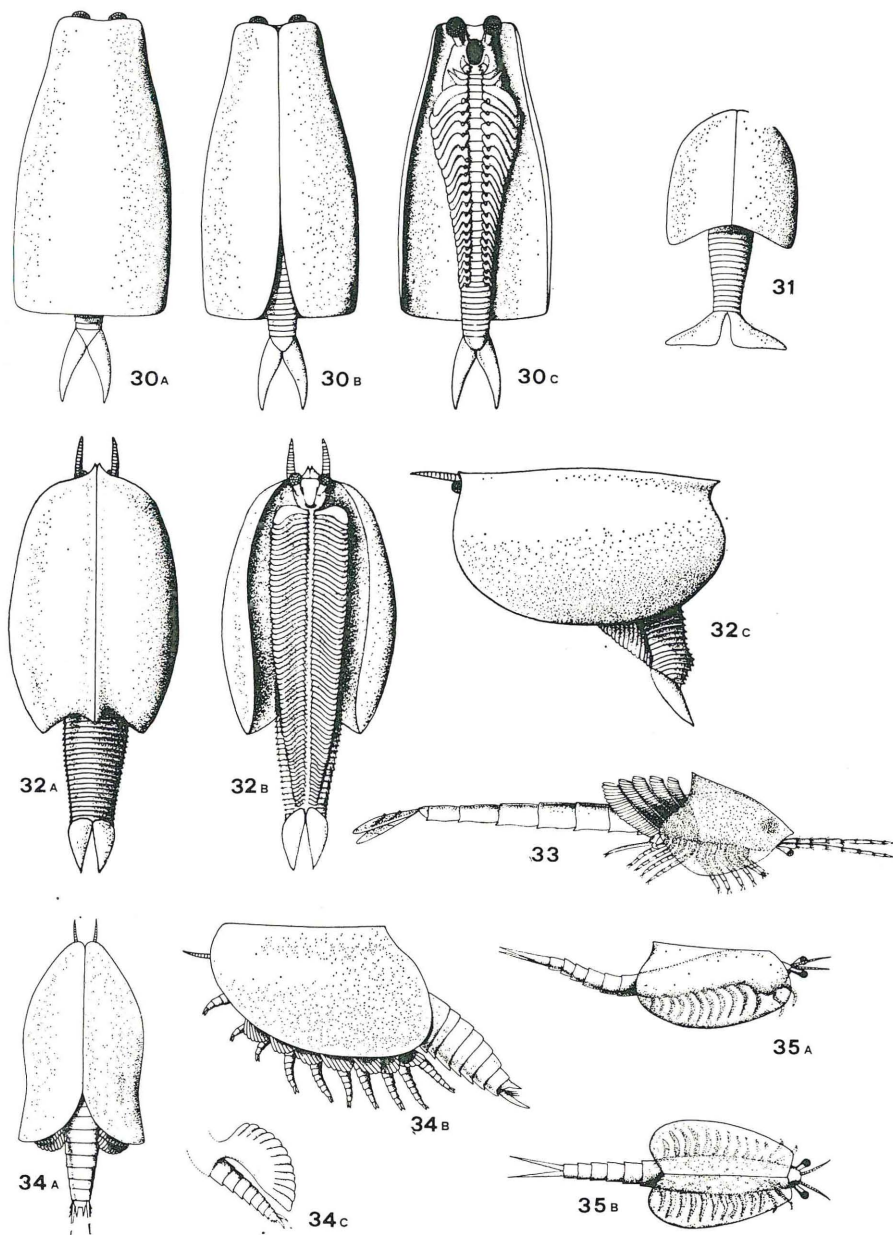


Fig. 7 - 30 A-C - *O daraia alata* Walcott (Middle Cambrian); 31 - *Eurysaces pielus* Simonetta-Delle Cave (Middle Cambrian); 32 A-B-C - *Protocaris pretiosa* Resser (Middle Cambrian); 33 - *Waptia fieldensis* Walcott (Middle Cambrian); 34 A-C - *Canadaspis perfecta* (Walcott) (Middle Cambrian); 35 A-B - *Canadaspis ovalis* (Walcott) (Middle Cambrian).

for the development of a minute and simple Pro-Arthropod. 3) the presence of an active oxygen exchanger, if available, might have helped to compensate for the biotope deficiency in free oxygen, particularly when coupled with minute size, which makes the bulk: surface ratio particularly favorable. The fact that all the respiratory pigments of living animals show considerable affinities in their basic chemical structure might be taken as an indication that they were all evolved from a type of oxygen exchanger present in the ancestral Metazoa. 4) that photosynthetic bacteria or unicellular plants were symbionts within the early Metazoan tissues, like the zoochlorellae and zooxantellae, which are so common even nowadays in aquatic animals from Protozoa to Annelida. If such conditions existed, provided the body was sufficiently transparent, the oxygen available to tissues could have been out of proportion to the oxygen content of the surrounding water. I am rather favourable to this last hypothesis to meet both TOWE's argument for the difficulty of evolving complex animals in the Precambrian and the fact of the abrupt appearance in the fossil record of large and comparatively complex animals, as obviously animals so delicate as to be transparent, be either planctonic or benthonic, stand practically no chance to be preserved as fossils.

If the above premises are granted, than a first consequence as to the structure of the ancestral Arthropod will follow, and this is significant in connection to the problem of the affinities of the Arthropods with the Annelida.

CLARCK R. B. [1969, 1972] has convincingly argued that « If it is correct to regard the coelomate organisation as serving primarily a mechanical function, it is most likely to have made its first appearance in large animals » and that indeed the secondary or true coelom is basically and hydrostatic and plastic skeleton.

It positively requires, to exist at all, not only size but a strong connective, bound by collagen, which TOWE has maintained that could not exist in the Precambrian (however fairly large Annelids occur in the Ediacaria fauna, which has been variously assigned to the very end of the Precambrian or tho the earliest Cambrian). The occurrence of a syncoelom in the Arthropods may well be primitive and the well developed coelom in the Annelida may be a comparatively late acquisition evolved on a basically metameric mesoderm, which developing cavities needed not disintegrate their walls once abundant collagen was available.

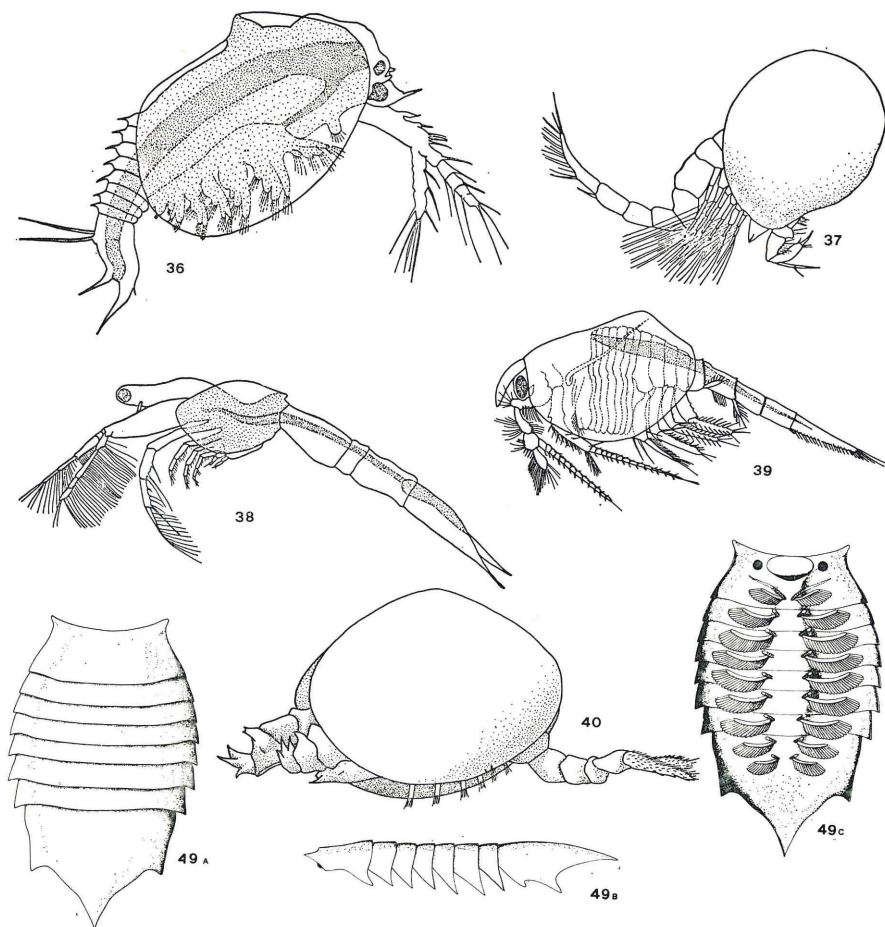


Fig. 8 - 37 - *Synagoga* sp. (living); 38 - *Leptodora* sp., the carapace is displaced and arranged in a position comparable with that of the other species illustrated (living); 39 - *Nebalia* sp. (living); 40 - *Ascothorax* sp. (living); 49 A-C - *Helmetia expansa* Walcott (Middle Cambrian).

If that is so, and it appears quite plausible, then many age honoured arguments on the comparative morphology of Annelids and Arthropods fade into obsolescence, as comparison must be done between small, simple, probably uncompletely segmented « protoanellids » and a « protoarthropod » which structure may therefore be summarized as follows: It must have included very few metameres: though the Nauplii, with but two postoral segments, may be somewhat specialized and be larvae which have

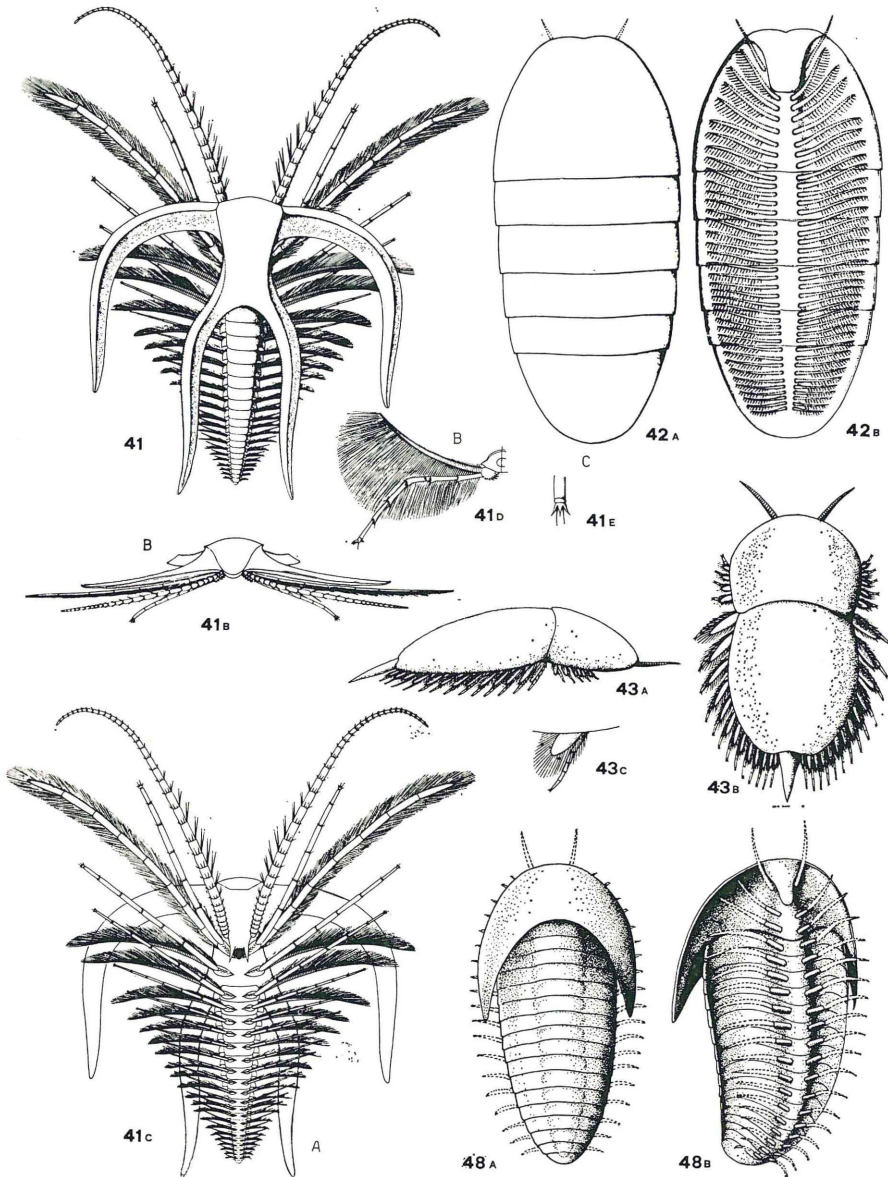


Fig. 9 - 41 A-E - *Marrella splendens* Walcott (Middle Cambrian); 42 - *Tegopelte gigas* Simonetta-Delle Cave (Middle Cambrian); 43 A-C - *Naraoia compacta* Walcott (Middle Cambrian); 48 A-B - *Nathorstia transitans* Walcott (Middle Cambrian).

evolved the ability to hatch and feed at a degree of development somewhat earlier than that of their pre-cambrian ancestor, the Protaspis of the Trilobita had but three postoral segments (CISNE, in press, BERGSTROM and STURMER [1973]) and since they retained the feature, which we shall see to be probably primitive, to have an unjointed dorsal tergum, they may have been closer to the true primitive condition. A well segmented, articulated body is most unlikely at such a primitive stage of evolution, as the bending of a very small animal enclosed in a cuticle, involves the operation of comparatively strong longitudinal muscles to overcome the resistance due to the turgescence (hydrostatic pressure within the animal) and that implies, apparently, a fair development of connective tissue, which could scarcely have been available. Instead I suggest to envisage as a possibility a rather flat, more or less oval animal which cuticle was dorsally strengthened by one or few sclerites hardly movable with respect to one-another. The hypothesis that the dorsal skeleton was not articulated suggests the possibility that the metamerisation of the anatomical structures may have been incomplete. This seems to offer a better basis to develop the typical intersegmental articulation of the terga than the usual assumption that the ancestor of the Arthropoda was a fully segmented animal.

A dorsal shield made of one or a few unhinged sclerites, somehow like that of some Heterotardigrada (however the best armoured Heterotardigrads are terrestrial), could have provided the necessary basis to operate, albeit at a slow gait, some sort of flap like ventral appendages. Appendages must have begun as unsegmented structures, as they are in most very minute living Arthropods (the Urd-Arthropod which I am suggesting, may well have been about half a millimeter long). These appendages, if my guess is correct, must have been entirely ventral and may well have left a free « pleural lobe » lateral to their insertion. A structure somewhat similar may have obtained in the puzzling *Parvancorina* from the Ediacara fauna and in the probably related middle Cambrian *Skania fragilis*, both animals, however, which may well have nothing to do with the ancestry of the Arthropods, (though WALCOTT claimed *Skania* to be an Arthropod).

A sort of ventral groove must have been present, along which a stream of particles may have been moved towards the mouth

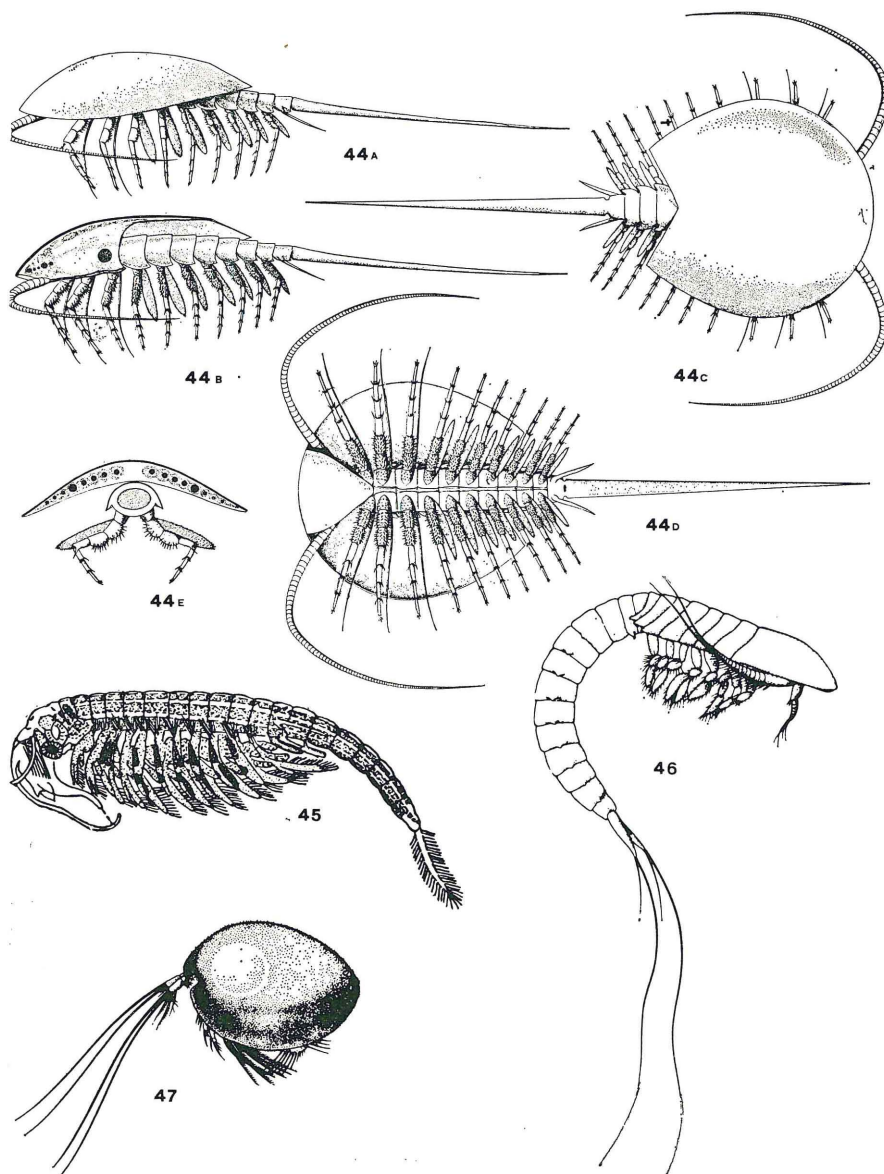


Fig. 10 - 44 A-C - *Burgessia bella* Walcott (Middle Cambrian); 45 - *Chirocephalus* sp. (living); 46 - *Hutchinsoniella macracantha* Sanders (living); 47 - *Macrocypridina castanea* (living).

by some fringes of hairs⁽¹⁾. It may well be that at such a stage of evolution a strip of ciliated epithelium still lined the alimentary groove, like in the *Gasterotricha*, where the cuticle leaves room for some strip of ciliary epithelium. In such case the appendages were used solely for locomotion. Musculature must have been entirely smooth. Indeed striated muscle is a specialisation for active, rapid and well coordinated activity, especially when coordination in the movement of various segments is concerned; but as it involves a very high oxygen consumption, striated musculature is most unlikely to have been present at the beginning of Arthropod evolution.

An epistomium must have been present: not only is certainly a primitive feature in the Arthropods, but it was necessary to have the mouth opening backwards, so as to allow the feeding by micro-particles moving cranially in a ventral groove.

Light sensitive receptors were most probably present and, if the animal was a comparatively flat creeping one, they must have faced upwards, a situation which appears to be primitive in the Arthropods.

Very close to the mouth there must obviously have been glands of some sort, other glands were probably present along the ventral groove, opening at the base of the appendages.

Such a structure must be postulated to account for the development of segmental excretory organs.

BEKLEMISHEW [1969] has summarized and developed the evidence purporting to the significance and development of metamorphism as an adaptive type of symmetry, and therefore it is not necessary to discuss the point here.

ADDENDUM

When the typescript of this paper had been already completed CISNE (Science, vol. 186; no. 4158: 13-18) has published a paper on the morphology and phylogenetic significance of Trilobites. Though his evidence does not run in any way against

(1) It might be argued that the activity of such an apparatus may have been relevant in determining the caudo-cranial flow in the dorsal vessel of the Arthropoda, however this would lead us off the main subject of this paper; anyway the direction of flow is the same in the Annelida, where it can be explained by various adaptive hypotheses, so that the point does not seem of great relevance for a phylogenetic discussion.

the main arguments of this paper, it has no direct bearing on its chief purpose. CISNE rightly underlines the peculiar fact that the «Uniramia» except *Aysheaia* are a strictly terrestrial assemblage.

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