Invertebrate Zoology, 2025, 22(1): 168–177

Ecdysozoa are descendants of Articulata

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ABSTRACT: A non-cladistic perspective on the origins and relationships of Annelida, Lobopoda, Arthropoda, Ecdysozoa, Crustacea, Insecta and Myriapoda. The deep similarity of jumping bristletails to syncarids show that insects originated directly from malacostracans. Myriapods are secondarily simplified descendants of early hexapods that lost the division of the body into thorax and abdomen due to the transition to a cryptic lifestyle. Entognathous hexapods model the initial stages of such 'myriapodization'. The most basal euarthropods were dinocarids with grasping antennae but without walking legs. The most primitive Articulata are Polychaeta, and the group most similar to arthropods are Aphroditoidea. By analogy with myriapods and entognaths, lobopods and non-arthropod Ecdysozoa are interpreted as side branches from the dinocarid root of Arthropoda that simplified their body plans. The most primitive annelids were spintherid-like crawlers, which evolved from Anthozoa. Metagenesis of cnidarians reappeared as metamorphosis in polychaetes. Transformations of body plans occurred through heterochronies and heterotopies.

How to cite this article: Shcherbakov D.E. 2025. Ecdysozoa are descendants of Articulata // Invert. Zool. Vol.22. No.1. P.168–177. doi: 10.15298/invertzool.22.1.11

KEY WORDS: Polychaeta, Lobopoda, Dinocarida, Arthropoda, Crustacea, Insecta, Myriapoda, evolution, heterotopies, neoteny.

Экдизозои — потомки артикулят

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РЕЗЮМЕ: Некладистический взгляд на происхождение и родственные связи Annelida, Lobopoda, Arthropoda, Ecdysozoa, Crustacea, Insecta и Myriapoda. Глубокое сходство прыгающих щетинохвосток с синкаридами показывает, что насекомые произошли непосредственно от малакострак. Многоножки являются вторично упрощенными потомками ранних гексапод, утратившими разделение тела на грудь и брюшко из-за перехода к скрытому образу жизни. Энтогнатные гексаподы моделируют начальные стадии такой «мириаподизации». Самыми базальными эуартроподами были динокариды с хватательными антеннами, но без ходильных ног. Наиболее примитивными Articulata являются Polychaeta, а наиболее схожей с членистоногими группой — Aphroditoidea. По аналогии с многоножками и энтогнатами, лобоподы и нечленистоногие Ecdysozoa интерпретируются как боковые ветви от динокаридного корня Arthropoda, развивавшиеся путем упрощения планов строения. Наиболее примитивными кольчатыми червями были подобные спинтеридам ползающие формы, которые произошли от Anthozoa. Метаморфоз полихет возник на основе чередования поколений кишечнополостных. Трансформации планов строения происходили посредством гетерохроний и гетеротопий.

Devoted to memory of Claus Nielsen.

Как цитировать эту статью: Shcherbakov D.E. 2025. Ecdysozoa are descendants of Articulata // Invert. Zool. Vol.22. No.1. P.168–177. doi: 10.15298/invertzool.22.1.11

КЛЮЧЕВЫЕ СЛОВА: многощетинковые черви, лобоподы, динокариды, членистоногие, ракообразные, насекомые, многоножки, эволюция, гетеротопии, неотения.

The old hypothesis of a close relationship between insects and malacostracans is based on skeletal morphology (Hansen, 1893) and confirmed by the fine structure of the visual system and brain and patterns of gene expression (Strausfeld, 2009, etc.; see Shcherbakov, 2023). Among malacostracans, the most similar to insects are Syncarida (Tillyard, 1930), such as mountain shrimps (Anaspidacea; Fig. 1A), which still survive in Tasmania, and Paleozoic Palaeocaridacea. The most “crustaceoid” insects are jumping bristletails (Archaeognatha, e.g., Machilidae: Fig. 1B) and extinct Monura.

Despite the fact that they live on land, Archaeognatha have retained the main features of their ancestors — aquatic Syncarida: trunk of 14 segments plus the telson; carapace not developed; rather smooth transitions between the head, thorax, and abdomen; compound eyes of the same structure; naupliar eye transformed into ocelli; huge 1st antennae with an annulate flagellum; supramandibular suture; mandibles with a separate incisor, elongated mola, and posterodorsal adductor muscle; limb-like maxillary palps; well-developed paragnaths (hypopharynx); the 2nd maxillae (fused basally to form the labium) similar to the 1st maxillae; paranotal lobes concealing limb bases; legs with long coxae converging towards the sagittal body plane; exopods (coxal and abdominal styli); free 1st thoracomere; elongate abdomen with twisted rope musculature used for jumping; complete set of abdominal limbs (freely projecting, styli-bearing coxites participating in locomotion); abdominal endopods (eversible vesicles); two pairs of abdominal limbs produced to form the male organ; male gonopores situated two segments more posterior than in females; tail fan (transformed into cerci, i.e. limbs of the 11th abdominal segment, and the paracercus); embryonic dorsal organ of the same structure and position. Such a deep similarity between archaeognathans and syncarids, in spite of their completely different lifestyles, can only be explained by their close relationship, and not by convergence (Crampton, 1922; Sharov, 1966). It means that the insects descended directly from advanced crustaceans.

The descent of one higher taxon from advanced members of another higher taxon is not a strange exception, but rather a normal mode of macroevolution, as we will try to show below. Such paradoxical transitions are made possible by heterochronies (changes in the rate or timing of developmental processes), mainly neoteny (retention of embryonic and larval features at the adult stage), as well as heterotopies (change in the spatial arrangement of embryonic development), including homeosis (transformation of one organ into another due to changes in the expression of regulatory genes). The shift of the gonopods of male syncarids from the thorax to the end of the abdomen, and their transfer to the female to form the insect’s ovipositor is an example of heterotopy including gamoheterotopy (transfer of characters from one sex to another; Meyen, 1988). In the case of insect origins, most (if not all) of these changes were associated with the colonization of land. For example, both the tail flip of shrimp (caridoid escape reaction) and the jump of Archaeognatha are powered by their muscular abdomen. When shrimp came ashore through the splash zone to become insects, their five posterior thoracic segments were homeotically transformed into abdominal segments, allowing them to make more energy-consuming leaps on land (Shcherbakov, 2017, 2023) (Fig. 2).

The cladistic paradigm reduces any phylogeny to a series of dichotomies. However, the cornerstone principle of cladistics, that each divergence event represents a symmetrical splitting of a stem lineage into two sister lineages, has never been proven. Instead, at different taxonomic levels, from speciation to the origin of higher taxa, we observe that the main, if not the only, mode of phyletic divergence is budding, when one or more daughter lineages deviate from a single mother lineage that retains its identity. Paraphyletic taxa are as natural as holophyletic taxa, and the latter generally have the potential to produce future ‘granddaughter’ taxa (see Brummit, 2006; Rasnitsyn, 2021). A new higher

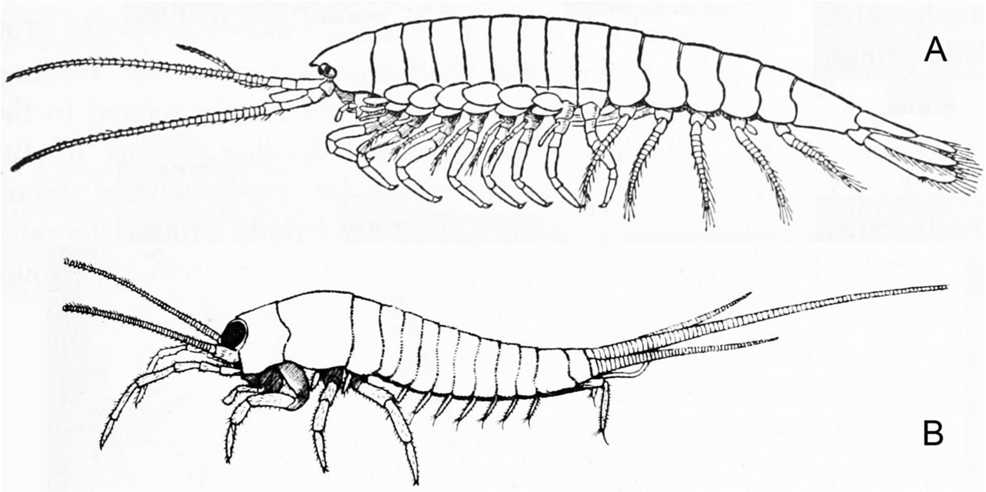

Fig. 1. A — *Anaspides tasmaniae* (Thomson, 1893) (Syncarida Anaspidacea; after Snodgrass, 1956, modified); B — *Machilis* sp. (Insecta Archaeognatha; from Snodgrass, 1930).

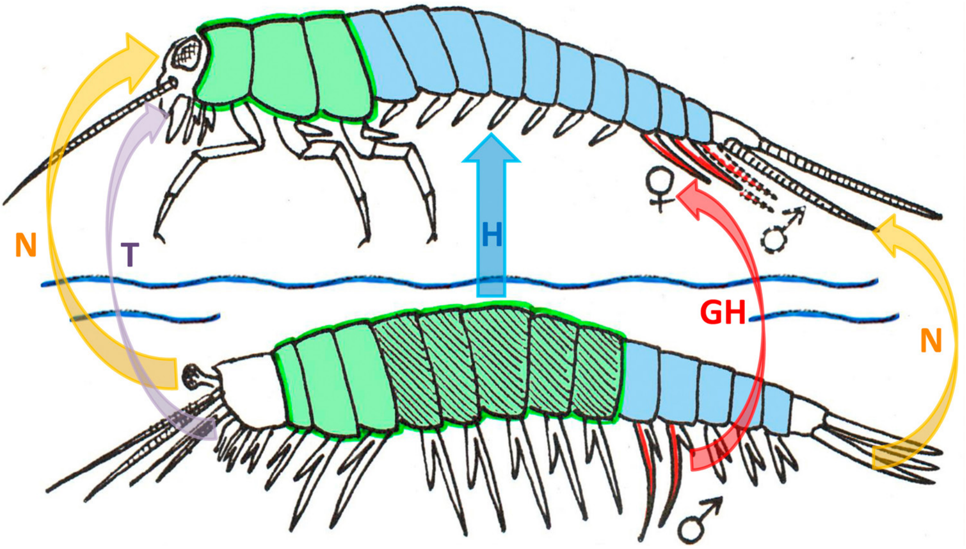

Fig. 2. Transformation of body plan of Syncarida into that of Archaeognatha (from Shcherbakov, 2017, modified). N — neoteny: retention of embryonic characters in adult (sessile eyes, uniramous 1st antennae and uropods = cerci); T — changes due to loss of nauplius (reduction of its natatory limbs — 2nd antennae and mandible endopods = palps); H — heterotopies: (1) reprograming five posterior thoracic segments into abdominal ones; (2) shift of male gonopods and gonopores in both sexes from posterior malacostracan thorax to posterior abdomen; GH — gamoheterotopy: gonopods appeared also in females to form an ovipositor.

group often arises from advanced members of an ancestral group due to expansion into a new adaptive zone. Heterotopies and heterochronies that transform the body plan generate ‘hopeful monsters’, a few of which manage to become the founders of a new group. In such transformations, some characters are suppressed, but not irreversibly lost and can be subsequently restored, since the underlying gene mechanisms are retained. The founders of a new group that colonized a new adaptive zone can subsequently evolve in opposite directions: either towards further progressive improvement of the new body plan, or towards its regressive simplification.

Evo-devo supports the old idea that myriapods evolved from insects (Haeckel, 1866). The complex system of genes controlling the thorax/abdomen division, essentially the same in all arthropods, can be easily adjusted (shifting the boundaries between tagmata) or switched off (derepressing the limb development in abdominal segments). Therefore, independent origins of secondarily homonomous forms with limbs on all trunk segments, such as Remipedia and myriapods, are suggested, rather than a parallel acquisition of similar trunk heteronomy in Crustacea and Atelocerata (Akam *et al*., 1994).

Suppression of the thorax/abdomen division is possible when the caridoid escape reaction becomes useless, e.g. in cryptic habitats. Myriapoda and Entognatha, which are usually soil-dwellers, have many ancestral (malacostracan-archaeognathan) features modified or lost: eyes reduced; ocelli suppressed; 1st antennae with true flagellar segments containing muscles; mandibles entognathous or suspended on levers, secondarily subdivided, similar to the maxillae; 2nd maxillae leg-like or lost; palps reduced; head opposed to the thorax; paranota reduced; leg bases widely separated; cerci lost. Entognathous hexapods model the initial stages of such 'myriapodization'.

Myriapods have evolved from hexapods, and the six-legged larvae of Diplopoda and Pauropoda recapitulate the ancestral state. In hexapods, the loss of trunk heteronomy was probably an easier way to restore multiple leg-bearing segments, useful in cryptic habitats, than reprogramming abdominal segments one by one. This homeotic transformation is modeled by a total deletion of the Hox genes in *Drosophila*, resulting in repatterning of the entire trunk and, moreover, both maxillary segments after the prothoracic one (Raff, Kaufmann, 1983). The change of the 2nd maxillae into a leg-like condition in Chilopoda, or their reduction to eversible vesicles (characteristic of the trunk segments) in Pauropoda, or their complete suppression in Diplopoda, are all merely by-products of the genetic mechanism governing myriapodization.

Contrary to the common opinion, Remipedia and Myriapoda are highly derived subgroups of Crustacea and Atelocerata, as are their tetrapod counterparts, snakes and legless lizards and amphibians. Both a lancelet and a snake are legless, but the snake body plan is highly derived, because its head tagma includes variously modified metameres (branchial arches), sometimes bears venom fangs, and is sharply separated from the trunk by the neck region. Likewise, a trilobite, remipede and myriapod are all multi-legged, but latter two are by no means primitive, their head tagma being sharply separated from the trunk and containing variously specialized limbs (including venomous appendages in Remipedia and Chilopoda) (Fig. 3). In a sense, myriapods are the snakes of arthropods. As in myriapods, homeotic change in snakes resulted in the trunk becoming thorax-like (Cohn, Tickle, 1999). Deriving insects from myriapods is as illogical as deriving lizards from snakes (Shcherbakov, 2017).

Insects were considered to be a sister group to either crustaceans or myriapods, and cladists interpreted this triple relationship as a controversy. However, this controversy is illusory. Insects are closely related to both crustaceans and myriapods, but the polarity of these relationships is different. Jumping bristletails, Archaeognatha, the most primitive group of insects, which descended from Syncarida, a derived group of Malacostraca, gave rise to progressively evolving winged insects on the one hand, and to regressive lineages of entognathous hexapods and myriapods on the other (Shcherbakov, 1999).

Crustacea are traced back to the Cambrian. Many of the earliest Paleozoic crustaceans and related more primitive crustaceomorphs had a thorax covered by a large bivalved carapace and a muscular abdomen ending in a tail fan or furca. Some of these bivalved forms resembled the extant Phyllocarida in their general organization, while others had antennae shaped like large grasping appendages (Aria, Caron, 2017).

In the Cambrian, two more arthropod groups with large grasping frontal appendages are known, but they did not have a bivalved carapace. The great-appendage arthropods (Megacheira) had postoral limbs with lobe-like exopods and jointed endopods. Their larvae resembled crustaceans (Liu *et al*., 2016), and Crustacea may be neotenic descendants of Megacheira.

The best-known group of ancient creatures with grasping frontal appendages are the Cambrian top predators Anomalocarididae and their kin (Radiodonta). These were very strange arthropods! First, they did not yet have jointed legs: their only pair of jointed limbs were the

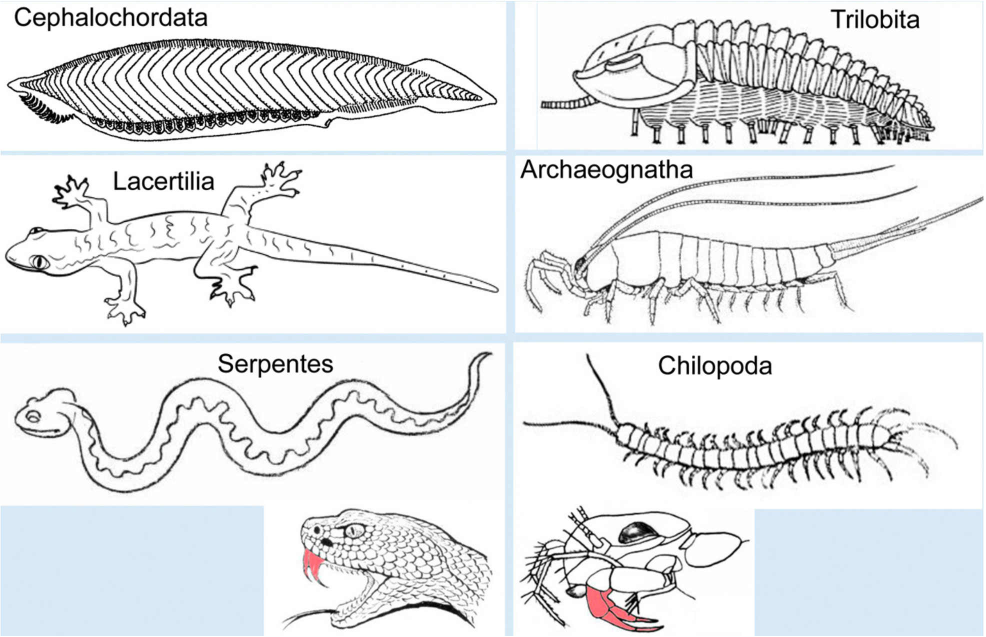

Fig. 3. Analogies between Chordata and Arthropoda.

frontal appendages, their fin-like trunk appendages lacked endopods, and their tails usually ended in two filaments or a fan (Potin, Daley, 2023). Second, their mouthparts consisting of an armed, radially symmetrical oral cone were non-appendicular and resembled the buccal ring of Onychophora and Tardigrada. Gilled lobopods (*Opabinia* etc.), united with Radiodonta in Dinocarida, had large lobopodous frontal appendages and ventral lobopodia (Budd, Daley, 2012). Radiodonts are the most primitive euarthropods, having already acquired arthropodia (as frontal appendages), but retaining the non-appendicular oral armature of their ancestors. The presence of fin-like limbs and the lack of jointed walking legs may indicate that these active swimmers originated in ancient times when the sea floor was poor in oxygen (He *et al.*, 2019).

Arthrodization in euarthropods began in Radiodonta, with their food-gathering frontal appendages, and in their descendants extended to the trunk and postoral endopods, which became the walking legs. In Megacheira, the postoral limbs were transformed: epipods immobilized as paranotal lobes, and endopods repatterned after the first antenna to acquire food-processing endites; with the transfer of grasping function to the postoral limbs, the first antenna in crustaceans became sensory (Bousfield, 1995). The primary food-gathering function was crucial for the origin of jointed arthropodia, which were later modified for walking. The appearance of benthic arthropods walking on jointed legs along the sea floor, and of arthropod legs themselves became possible when the sea floor was oxygenated and paved with nutrient-rich fecal pellets due to the Cambrian rise of filter-feeders, mainly crustaceans (Ponomarenko, 1993).

Traditionally, arthropods (together with lobopods) were considered to be descendants of Annelida, all united into Articulata (Snodgrass, 1938). Recently, an alternative Ecdysozoa hypothesis was proposed: Panarthropoda (Onychophora + Tardigrada + Arthropoda) were united with Cycloneuralia (= Nemathelminthes p.p.) and opposed to non-molting Lophotrochozoa, including Annelida (Ivanova-Kazas, 2013). Nielsen (2003) proposed a solution to the Articulata–Ecdysozoa controversy: Ecdysozoa are the sister group to Annelida within Articulata s.l., panarthropods are the sister group to cycloneuralians, and in these latter the segmentation was reduced or lost. As with the crustacean-insect-myriapod relationship, the controversy is imaginary, and the earliest panarthropods, apparently gilled lobopods, gave rise not only to other lobopods and euarthropods via Radiodonta, but also to cycloneuralians, which evolved to simplify their body plans. It is commonly accepted that Cambrian Xenusia gave rise to the gilled lobopods and radiodonts (Dzik, 2011). However, the origin of myriapodous Xenusia and Onychophora and oligopodous Tardigrada is better explained by a secondary simplification of their body plans due to life in cryptic habitats or at least by shifting from 3D to 2D environments. Zhuravlev *et al*. (2011) suggested that Xenusia gave rise to both Cycloneuralia (via Palaeoscolecida) and to Euarthropoda (via Onychophora), but it is more likely that gilled lobopods were ancestral to both euarthropod and lobopod-cycloneuralian lineages.

According to Nielsen's views on Cycloneuralia as regressive descendants of metameric ancestors, the most generalized representative of this group is Kinorhyncha, since these oligomerous animals retain the segmental organization in the ectoderm, nervous system and musculature. Traces of segmentation are still evident in the ectoderm and nervous system of nematodes: cuticular annulation, flexible segmented cephalic setae, serially arranged ganglia of motoneurons (Cobb, 1917; Vellutini, 2020). Nematoda and Nematomorpha possess most of the genes that control eye and limb development in other animals, indicating that ancestral ecdysozoans had limbs and eyes (Beregova *et al*., 2023).

If cycloneuralians evolved from lobopods, then panarthropods descended directly from polychaetes via basal dinocarids (Fig. 4). The similarities between arthropods and polychaetes are much deeper than is usually acknowledged (see Shcherbakov, 2023). The arthropod limb is homologous to the polychaete parapodium (Prpic, 2008), both being basically four-fold. It is likely that paranotal lobes of arthropods are immobilized elytra of their polychaete ancestors, while insect wings etc. are in turn remobilized paranota. The arthropod head is also comparable to the polychaete head. Arthropod first antennae, homologous to polychaete palps, differ from the following appendages in that they are mostly uniramous and lack gnathobases. The basic number of eyes, six (five when the median eyes are fused), constant from Cambrian *Opabinia* to insects (young mayfly nymphs have three ocelli and two compound eyes of nearly equal size; Ide, 1935), is essentially the same as the number of prostomial appendages (five). The similarity of eyes to prostomial appendages is confirmed by the widespread occurrence of stalked eyes in primitive arthropods.

Among polychaetes, scale worms (Aphroditoidea) are the most arthropod-like. Their palps are distinct from the other prostomial appendages. Their postoral appendages are four-fold. Their trunk is subdivided into three incipient tagmata with different arrangement of the dorsal cirri/elytra (covert tagmosis, which could be a preadaptation for development of overt tagmosis). In arthropods, tagmosis became more pronounced. The parapodial elytra, usually alternating with dorsal cirri in scale worms, became a ground-plan feature of the trunk segment through homeotic transformation of all dorsal cirri into elytra. Covert segment pairing was retained in arthropods and later sometimes restored in overt form (myriapod diplosegmentation).

Arthropods may be neotenic derivatives of aphroditoid polychaetes, which have lost the eversible pharynx and parapodial setae of adult polychaetes and retained the larval, anteroventral mouth position. Chitin, restricted to setae, pharyngeal teeth, and stomodaeal lining in polychaetes, became the main component of the arthropod cuticle. A similar homeotic expansion of morphogenetic patterns from the cephalic end to the entire body is suggested for Megacheira (see above). Joints occur in the parapodial setae (Merz, Edwards, 1998) and sometimes in the jaw apparatus of polychaetes (Shcherbakov *et al*., 2022), and the same morphogenetic pattern was employed to construct the first arthropod joints in the frontal appendages of Radiodonta. Cuticles containing α-chitin are considered a synapomorphy of the Ecdysozoa (Pentastomida, highly simplified parasitic Crustacea, also have α- rather than β-chitin; Greven *et al*., 2019), whereas annelid setae contain β-chitin. However, in insects both α- and β-chitin as well as γ-chitin (mixture of α- and β-chitins) are found (Liu *et al*., 2019).

The earliest undoubted Oligochaeta recorded from the Early Triassic was a microdrile adapted to burrowing in the bottom sediments of an ephemeral pond (Shcherbakov *et al*., 2020). The loss of larval stages and development of a cocoon-secreting clitellum were the first stages of oligochaete evolution, correlating with life in ephemeral non-marine basins. Microdriles

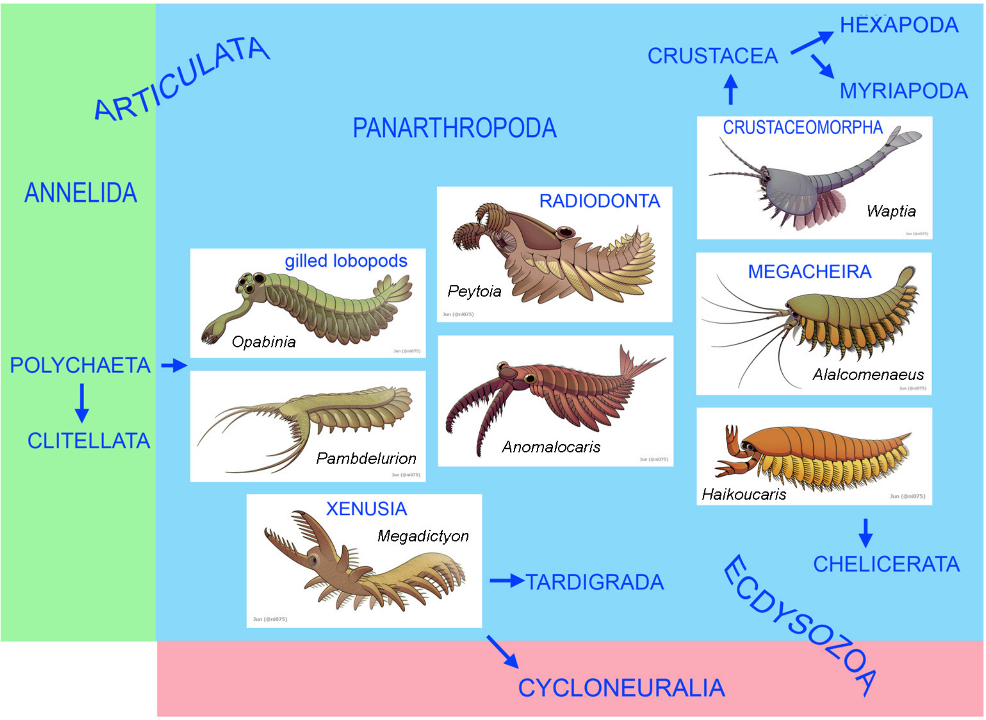

Fig. 4. Some Cambrian Panarthropoda and evolutionary lines of Articulata (reconstructions from https://commons.wikimedia.org/wiki/User:Junnn11).

gave rise to other Clitellata, such as earthworms and leeches.

The basic features of an animal's body plan primarily correlate to its Umwelt (meaningful environment; Tonnessen, 2009). Invertebrates living in the same sea bay differ dramatically in their body plan depending on whether they are: (1) active swimmers, enjoying the fully 3D space of the water column and generally possessing some kind of emergency (pursuit or escape) locomotion, or (2) crawlers on the sea floor or on corals and sponges, moving mainly along an intricately curved 2D surface, or (3) bottom sediment dwellers or endoparasites that move along a tangled 1D trajectory. The worm-like forms mostly fall into the third category and appear to be secondarily simplified due to the transition to concealed environments of reduced dimensionality.

Turning to the origin of Polychaeta, the most convincing theory seems to be that of Sedgwick (1884), who derived the metamery of Articulata from the cyclomery of Anthozoa. Beklemishev (1964) wrote, "This theory amazes with its simplicity and the far-reaching homologies that it establishes, but its paradoxical nature is striking. Its paradox arises from the attempt to derive annelids not from primitive but from highly specialized forms of coelenterates, which are anthozoans." Malakhov (2016) resolved this paradox by considering anthozoans to be the most primitive group of Cnidaria. However, as in the above cases, this paradox is imaginary, and the descent of the most primitive Polychaeta (and Annelida, and Articulata in general) from advanced Cnidaria is a normal mode of origin of new phyla and classes by transformation of the body plans.

If Sedgwick's views on the origin of annelids are true, then a good model for basal polychaetes is the genus *Spinther* Johnson, 1845 (Sharov, 1966), formerly classified in Amphinomidae, and now separated into the family of its own. Spintheridae are weird worms, ectoparasites or commensals of sponges, matching their coloration, sedentary or slowly creeping, sometimes making a cavity in the host (Pettibone, 1982; Böggemann, 2019). Adults are broadly oval,

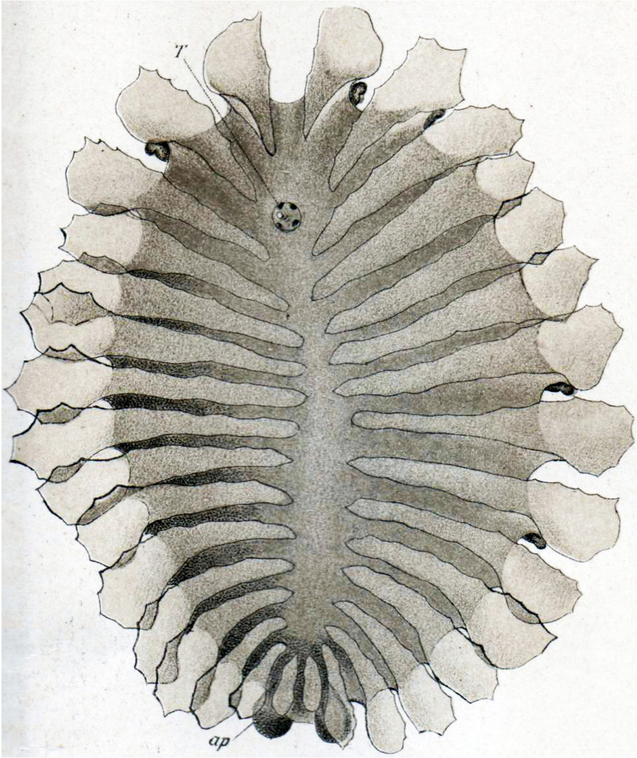

Fig. 5. *Spinther arcticus* (M. Sars, 1851), juvenile 1.8 mm long, dorsal view.
Abbreviations: ap — anal cirri; T — prostomium with a median antenna (from Graff, 1888)

and juveniles are elongate (Fig. 5). The tiny prostomium is squeezed between the anterior notopodia, which fuse medially to form a disk anterior to the prostomium. The mouth is ventral, surrounded by the anterior segments in adults; the eversible pharynx is mobile and may extend like a tongue to suck host tissues. The neuropodia are lobopodous and bear one (plus several reserve) jointed neuroseta with a hooked blade to cling the host. The notopodia form transverse lamellae that cover the dorsum, extend laterally, and are supported by numerous spiny notosetae. These notosetae are defensive; in some species of the related family Amphinomidae, or fireworms, the hollow notosetae are filled with poison and break when touched. The nervous system of Amphinomidae ('tetraneurium' with elements of independent podial and circumoral nerve cords) is primitive and closely resembles the presumed original scheme for Articulata (Sharov, 1966). Metamery in amphinomids is still imperfect: a significant proportion of individuals exhibit various aberrations, such as intercalation of half-segments or intersegmental furrows spiraling around the body (Buchanan, 1893).

Of course, spintherids are far from 'typical' polychaetes, but forms that are transitional from one phylum to another are 'atypical' by definition. We may suppose that some less specialized spintherid ancestors, living on corals or sponges, were the most basal polychaetes, neotenic descendants of Anthozoa, whose larvae ceased to settle and remained mobile throughout their lives. If this is so, then the ectoparasitic lifestyle is not necessarily an evolutionary dead end, at least as long as free larvae are retained in the life cycle. The larvae of Spintheridae are unknown; those of Amphinomidae are of rostraria type, with large, subsegmented, ciliary filtering palps (Mileikovsky, 1961); their frontal pair of food-collecting appendages reminds us the large grasping frontal appendages of the most basal arthropods (dinocarids). In addition, the dinocarid setal blades may be derivatives of the lamellate notopodia with embedded setae of their *Spinther*-like polychaete ancestors.

Metagenesis, the alternation of an asexual generation of sessile polyps and a sexual generation of swimming medusae, characteristic of Hydrozoa and Scyphozoa, was reduced in Anthozoa, but underlying genetic mechanisms were retained. Various groups of Triploblastica display catastrophic metamorphosis, where the adult does not inherit the larval body. The only logical explanation for this phenomenon was proposed by John Beard (1892): "…Metazoan development appears to me to be by means of an alternation of generations, in that from the fertilized egg there arises an organism, the larva, upon which, in one way or another according to the circumstances of each case, a new form, the adult or imago, takes its origin." In cases of non-catastrophic metamorphosis or direct development, an organism combining larval and adult features has a synthetic nature. The gametophyte and sporophyte generations in Metaphyta do not merge due to different ploidy, but there was no such obstacle to the fusion of sexual and asexual generations in the life cycles of Metazoa.

If Articulata and other lineages of Triploblastica descended from Cnidaria, then metamorphosis in their life cycles is a legacy of metagenesis. Alternation of generations, suppressed in Anthozoa, was subsequently restored, transformed and somewhat inverted in the metamorphosis of their direct descendants, Articulata. Ciliated larvae lack gonads like polyps, but they display some features (e.g. ciliary bands) found in medusae (Mackie *et al*., 1989; Jordano *et al*., 2024).

A few final remarks (not intended to be novel). The phylogeny of higher taxa is more of a ladder of grades and subgrades than a phylogenetic lawn. To reach a higher organization level, a lineage must pass through the previous level. Reaching a higher level often correlates with colonization of a new adaptive zone. Just as white light, passing through a prism, is split into a spectrum, the descendants of a group that has overcome some barrier and entered a new adaptive zone may further evolve both towards progressive improvement and towards regressive simplification of body plans. Morphological regress is common and can lead to biological progress. Worm-, myriapod- and snake-like body plans are secondarily simplified, regressive, arising due to the transition to hidden habitats. Transformations of body plans occur through heterochronies and heterotopies. The structures that appear to be lost are just suppressed, and may be subsequently restored in modified form.

Acknowledgements. For discussion of the views expressed here, I am grateful to the late Claus Nielsen and other participants in the International Symposium on the Relationships of Major Arthropod Groups in London (1996) and other symposia where my concept was presented.

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Responsible editor A.Yu. Sinev