

New view on the relationships of Copepoda within Maxillopoda (Crustacea)

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According to P.P. Ivanov, body somites are formed in two ways, by segmentation of the germinal bands and by the activity of the growth zone. The growth zone appears posterior to the 4th postantennular somite and divides the body into 2 parts, the group of anterior protosomites (anterior to the growth zone) and the group of posterior protosomites (posterior to the growth zone). The somites formed by the growth zone (eusomites) are disposed between the anterior and posterior groups of protosomites. The precise position of the growth zone may be confirmed by the study of concentrations of mitoses. Sometimes one may determine the position of the growth zone by the loss of at least one eusomite and its limbs behind the anterior protosomite and its limbs, or by a variability in the number of thoracic somites (as in Branchiopoda). The number of trunk somites may be reduced by halting early the segmentation of the hind part of the germinal bands and/or the activity of the growth zone.

On the basis of the number of trunk somites, Maxillopoda are usually subdivided into 2 groups. The first group have 11 trunk somites including the telson: Copepoda, Ascothoracida, Mystacocarida, Skaracarida (*Skara* as an exception with 12 trunk somites), Facetotecta with no more than 10 trunk somites including the telson, and certain ostracodan groups (Myodocopida, Cyliandroberididae, Platycopida, Cytherellidae). The second group have only 4-7 trunk somites (including the telson): Branchiura, Cirripedia, and Podocopida among Ostracoda. Tantulocarida are very similar to Copepoda in the structure of adult males and tantulus larvae, differing only in secondary characters: fusion of 2 (not 1) somites with the cephalosome and fusion of urosomal somites posterior to genital one. The development of Mystacocarida (a representative of the first group) demonstrates that the 1st-3rd trunk somites are formed by the growth zone. The coincidence in the number of trunk somites among most members of the first group leads me to conclude that 3 eusomites are present in all taxa of that group. Development in Cirripedia and Branchiura demonstrates the absence of eusomites inasmuch as all the definitive somites appear simultaneously during the molt to the cypris larva. The incomplete homology of trunk somites together with other characters leads me to regard these 2 groups as the classes Ascothoraciodes and Halicyniodes in the recently proposed classification of the Crustacea (Starobogatov, 1988); these names have priority over other ones. This does not exclude the hypothesis of a common ancestor for both of the above-mentioned classes, nor for the Crustacea as a whole.

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For a phylogenetic analysis it is necessary to decide which characters could have appeared independently several times and what structures should be considered as homologous. Strictly speaking, the problem of homology should be analyzed from the position of Popper's (1973) hypothetical-deductive method. The hypothesis of homology is the initial hypothesis which we must try to falsify (disprove), and accordingly, exposure of non-homology is the main task of character analysis.

The concept of primary (ontogenetic) heteronomy of the segmented animals proposed by

P.P. Ivanov is one of the most basic concepts of homology for a large school of zoologists, mostly Russians. This concept was elaborated in 7 papers and monographs (Ivanoff, 1912, 1928, 1933, 1937, 1940, 1944, 1945). Unfortunately, only two papers were published outside of the Soviet Union (in Germany), in 1928 and 1933, while the remaining ones were published in Russian. Probably this is why Western morphologists either ignore or have never been exposed to the concept. The dates of the cited references show that until 1945 the concept took over 33 years to work out. Naturally, when this

concept was first developed it appeared that some of its rules applied not to all segmented organisms but to limited taxa only (e.g. to errant Polychaeta).

The most important aspect of primary heteronomy is the difference between somites of different origin. The first type (larval somites) are formed by the enlargement and subsequent segmentation of the germinal bands (i.e. mesodermal structures formed by the teloblasts). The second type (postlarval somites) are formed by the activity of the growth zone. These ideas, well accepted by Russian morphologists, are often based on particular characters that apply to one taxon but not to others. It is widely accepted, for instance, that larval somites are disposed only anterior to postlarval ones because the growth zone is supposedly always disposed anterior to the pygidium (which cannot be regarded as a somite). However, Ivanov himself observed in a centipede and a migratory locust that some larval somites are disposed posterior to the growth zone. It is also generally accepted that gonad formation and the process of regeneration are realized only in the part of body that is formed by postlarval somites. But there are some groups of segmented animals devoid (primarily or secondarily) of a growth zone and postlarval somites. To this category belong the leeches and the Nerillidae. Where then are the gonads in such group formed and from what part of the body is regeneration realized, if not from larval somites?

The current state of the concept of primary heteronomy is as follows.

1. Somites of adult segmented animals belong to two basically different types designated by Ivanov as larval and postlarval somites. The body of an animal may be formed by larval and postlarval somites (primary heteronomy), or by larval somites only. The latter case may be primary (as in leeches) or secondary (as in Nerillidae of the Annelida and *Argulus* among Crustacea). In order to escape any confusion with the larval development, I (Starobogatov, 1992) have proposed to substitute these names: larval somite = protosomite; postlarval somites = eusomites.

2. Protosomites (= larval somites) are more archaic in the evolutionary sense than eusomites (= postlarval somites). This is proved by the existence of segmented animals primarily devoid of eusomites. The opposite opinion is based only on the trochophore of *Polygordius neapolitanus* (Fraip.), which is devoid of segmentation during all its pelagic life. However, the larva of the other species of the

same genus, *P. lacteus* Schn., has at least 3 somites (Woltereck, 1904).

3. Simultaneous formation of somites is evidence in favour of their being protosomites. However, the opposite statement, that somites formed non-simultaneously are eusomites, is incorrect; there are many cases when the protosomites are formed step-by-step.

4. The head of Crustacea has been said to consist of 4-6 protosomites. The difference in number is not a matter of biology, but depends on the point of view of the author who interpreted the segmental composition of the head. The earlier interpretation of the segmental composition of the head is akron plus 4 somites, bearing antennae, mandibles, maxillulae and maxillae. More recently the following segmental composition has become widely accepted: acron plus 5 somites (bearing antennules – maxillae). Some authors (e.g. Melnikov & Rasnitsyn, 1984) recognize of rudimentary acron plus 6 somites: labral in Arthropoda or metatrochal in Polychaeta, followed by antennular – maxillary. I also accept the structure of the head composed of 6 components, but the labral somite is, in my opinion, not a somite but a part of the body equal in status to the whole segmented part (Starobogatov, 1988). The 6 above-mentioned components are typical of all Arthropoda in spite of the situation in the Chelicerata, where two hind protosomites bear the first two pairs of walking legs. In order to escape a discussion about the number of anterior protosomites, I use below the number of postmaxillary somites only. Representatives of certain crustacean groups (e.g. Ostracoda) have leg-shaped maxillae, which are often regarded as a pair of thoracopods. It should be mentioned that the somite bearing these limbs is marked by the opening of maxillary excretory gland.

5. The number of both protosomites and eusomites shows a trend of diminishment. The number of protosomites is reduced by the early end of the process of growth and segmentation of germinal bands. The number of eusomites is reduced due to the early end of activity of the growth zone. Sometimes the growth zone remains active later than normal. This leads to an increase in the number of thoracic somites in the anostracan *Polyartemia* and in two genera of Pantopoda (*Decalopoda* and *Dodecalopoda*). In general, though, a greater number of either protosomites or eusomites is a pleiomorphic character.

Somites of different origin evidently cannot be regarded as homologous, but only a few methods may be applied for elucidating the position of the growth zone. The positions of the

proto- and eusomites in an arthropodan or annelidan body may be exposed by different methods, both direct and indirect. The direct methods involve very difficult study of the development of the animal in vivo (e.g. Melnikov, 1970) or in the course of a traditional embryological study, or by the study of the distribution of mitoses. In the last case, it is possible to stop the mitoses by colchicine and later to study the disposition of cells undergoing mitoses. One may also study the mitoses autoradiographically using thymidine marked by tritium.

Indirect methods are easier but can be applied in a few especially suitable cases only. The number of thoracic somites in Anostraca is 11-19 (in different genera), but the number of abdominal ones is always 9. The variability in the thorax can be explained by different periods of activity of the growth zone. Representatives of Cladocera (excluding polyphemids and *Leptodora*) have 4-6 eusomites (in different genera) and 1 (postabdomen) posterior protosome. Representatives of Cirripedia gain all their body segments simultaneously during the molt to the cypris-larva (Walley, 1969), which can only be explained by the complete absence of a growth zone and eusomites. The same is true for the development of *Argulus*. It should be kept in mind that the simultaneous appearance of all groups of somites is real evidence that these somites are protosomes. On the other hand, in many other cases the protosomes are formed step-by-step.

Studies of the development of *Hemimysis* (see Manton, 1928), *Nebalia* (see Manton, 1934), and *Limnadia* (see Anderson, 1967) support the above-discussed concept. The growth zone appears near the developing telson and produces 8 eusomites anteriorly. At the same time, the posterior parts of the germinal bands remaining near the telson become segmented step-by-step, forcing the telson hindwards behind 6 posterior protosomes in *Nebalia* and 5 in *Hemimysis*. Afterwards the telson acquires the definite structure of the anal somite. Almost the same takes place in *Limnadia*, but with a different number of eusomites. In *Limnadia* the growth zone is disposed anterior to the postabdomen and produces 22 eusomites anteriorly. As for Anderson's (1969) data about *Tetraclita*, the interpretation is not clear to me and at the same time there is Walley's (1969) work on the development of *Balanus*, from which it is evident that the formation of all somites happens simultaneously.

Mystacocarida demonstrate a peculiar case (Fig. 1). The 3rd postmaxillary somite (somite of thoracopod 2) drops behind the 4th. When

rudiments of limbs (i.e. thoracopod 3) appear at the 3rd metanaupliar stage, there is no trace of thoracopod 2. Later (at the 4th and 5th metanaupliar stages) thoracopods 3 are developed but thoracopods 2 are rudimentary. This may be interpreted as heterochrony of development in the last-appearing eusomite and the first posterior protosome, which is situated directly behind the former; this permits me to localize the position of the growth zone.

The systematics of the Crustacea is in a "statu nascendi" now. Different carcinologists accept various number of classes (or subclasses when Crustacea as a whole is regarded as a class): from 10 (Monod & Forest, 1996) or 9 when three recently discovered groups were still unknown (Gruner & Deckert, 1956) to 6 (Bowman & Abele, 1982), and even 4 (Dall, 1956 and – in another combination – Starobogatov, 1988); for a review see Monod & Forest (1996). A cause of such a variation among scholars is the division of this multisomited group into 2-3 classes and partially (excluding Ostracoda) or completely uniting paucisomited groups into the sole class Maxillopoda.

The groups composing the class Maxillopoda are united by the following synapomorphies (Boxshall & Huys, 1989, pp. 135 and 137): (1) uniramous antennules, (2) 7 pairs of trunk limbs, (3) no more than 13 trunk somites, (4) male gonopore on the 7th trunk somite, (5) presence of tapetal cells in the nauplius eye. The 2nd and 4th characters are absent in Mystacocarida, the males of which have the genital opening on the 4th trunk somite (the somite bearing the 3rd thoracic limbs), and there are only 5 trunk limbs: maxillipeds and 4 pairs of thoracic limbs. *Skara* (Fig. 2) has only one pair of trunk limbs corresponding to maxillipeds (Müller & Walossek, 1985). It is possible that the same situation is present in *Leuroleberis*.

In my opinion, in the study of phylogenetic relationships it is necessary to distinguish between characters connected with the parasitic mode of life, i.e. those that may appear independently and sometimes in parallel, and basic characters that represent the general morphology of the animal. For example, many representatives of the parasitic Copepoda differ from the free-living ones much more than Amphipoda differ from Isopoda.

Tantulocarida (Fig. 5) is another example of the influence of the parasitic mode of life. In the so-called sexual male the cephalosome is completely identical to that of Copepoda but with the 2nd trunk somite in addition to the 1st fused with the cephalosome. Furthermore, the positions of the genital (the 7th trunk) somite

stages

1	2	3	4	5	6	7	ad	
L	L	L	L	L	L	L	L	antennules
L	L	L	L	L	L	L	L	antennae
L	L	L	L	L	L	L	L	mandibles
l	l	l	L	L	L	L	L	maxillules
		l	l	l	l	L	L	maxillae
			l	l	L	L	L	maxillipeds
			l	l	L	L	L	thoracopods 1
			l	l	L	L	L	thoracopods 2
t		l	L	L	L	L	L	thoracopods 3
	t			l	L	L	L	thoracopods 4
		t						
			t					
				t				
					t	T	T	telson

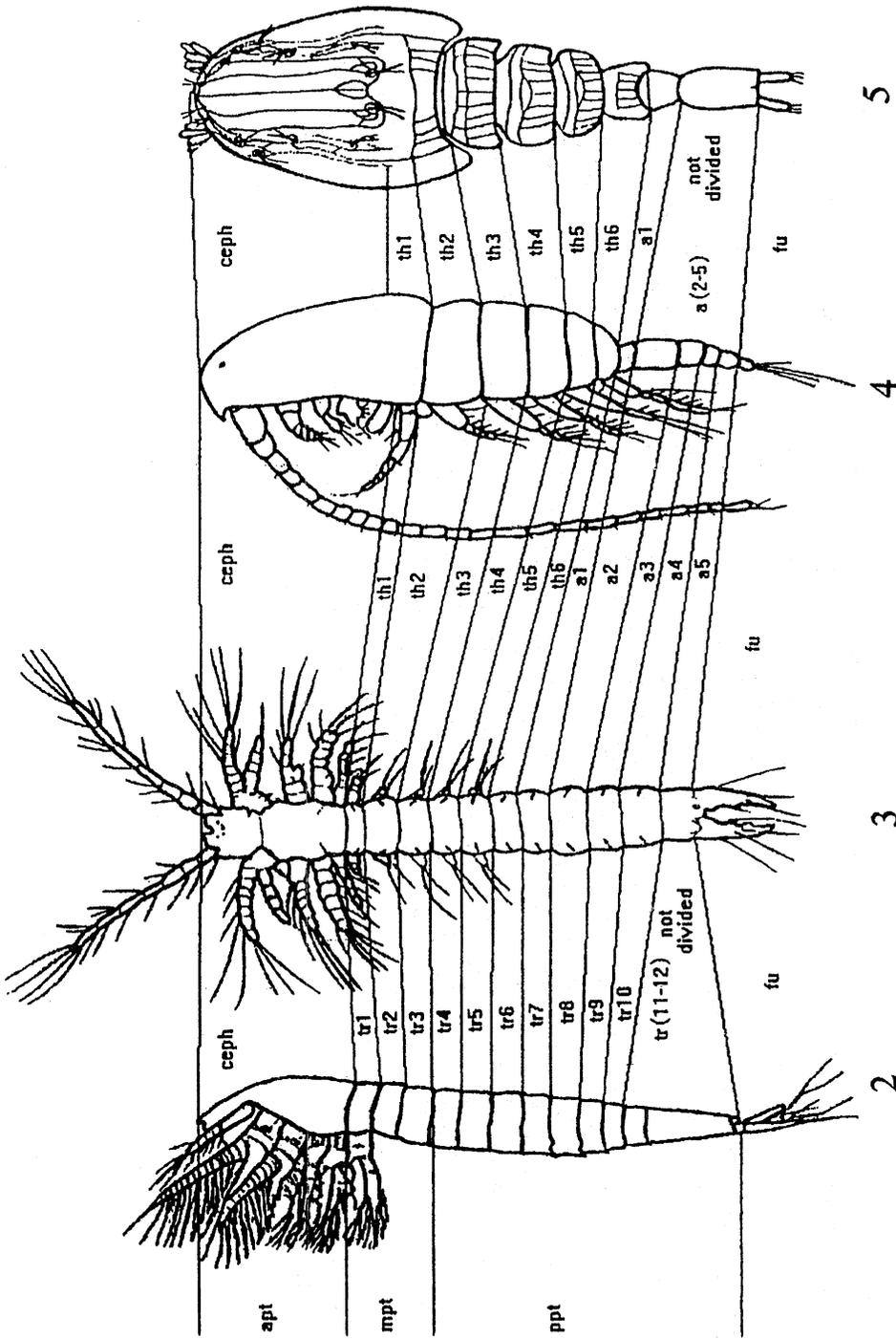
Fig. 1. Development of Mystacocarida (after Boxshall & Defaye, 1996). Upper line – metanaupliar stages. *l*, *L* – limbs; *t*, *T* – telson. Small letters – weakly developed; capital letters – well developed; empty squares – absence of limbs.

coincide in both groups. It is interesting that the position of the male genital somite unites a series of groups (Figs 2-9) discussed below, and it is probable that this character as well as the type of trunk segmentation are synapomorphies for these groups. The subdivision of the body into a fused cephalosome not covered by a true carapace, limb-bearing somites of metasome, and a narrow urosome (but with two somites instead of 5) may also be regarded as synapomorphies of Tantulocarida and Copepoda. On the other hand Tantulocarida differ from Copepoda (especially Calanoida in which the 7th somite is the 1st, not the 2nd, somite of the urosome). I suppose that the demarcation between the wide mesosome and narrow urosome anterior to the genital somite is a pleiomorphic character present also in Ascothoracida. The shortening of the urosome, absence of cephalosomal limbs, and presence of oral disc are connected with a parasitic mode

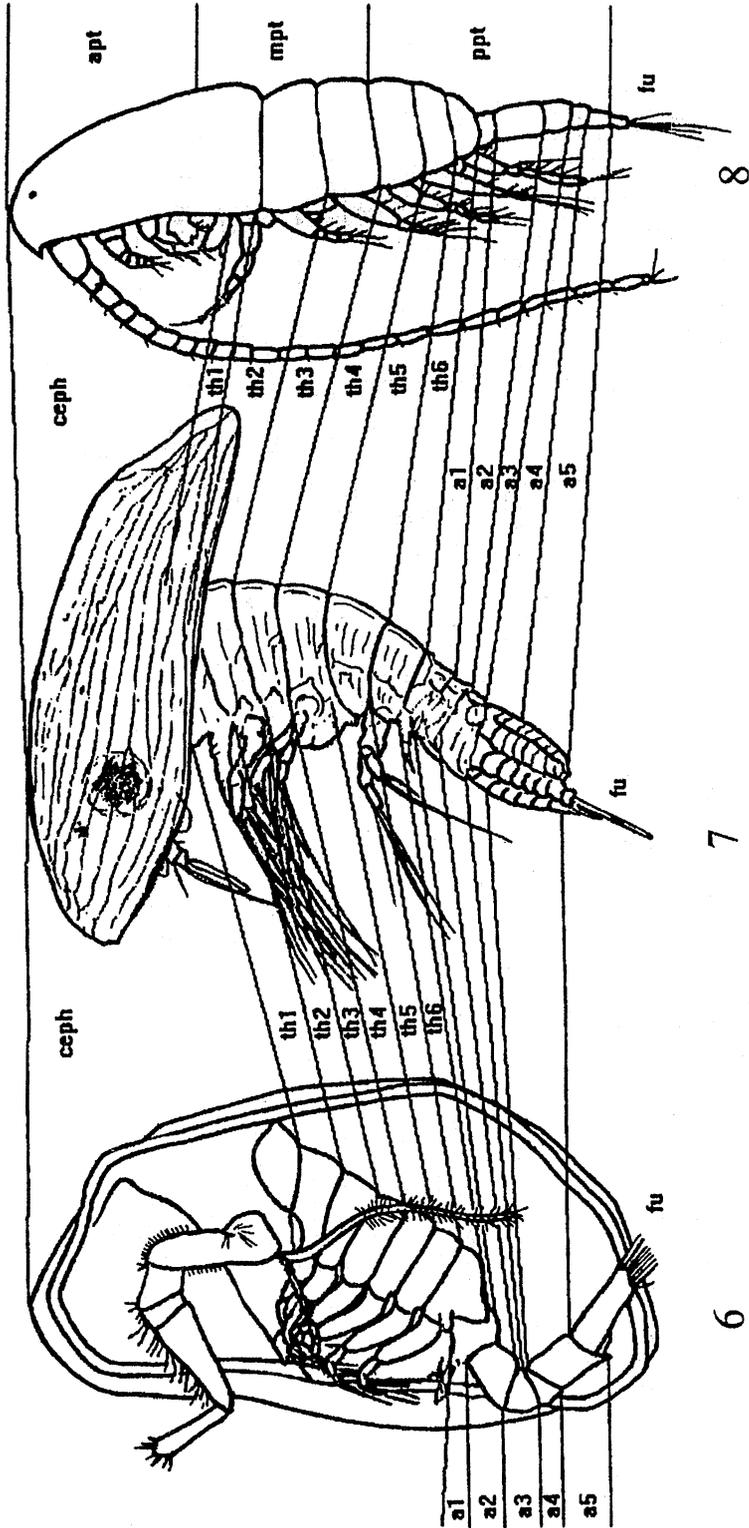
of life. Absence of cephalosomal appendages (including the 1st and 2nd trunk limbs) is connected with the life-cycle in which tantulus larva and paedomorphic male (similar to the larva) do not feed themselves.

Figures 2-9 clearly demonstrate coincidence in the number of trunk somites (11 including telson), with only *Skara* having 11 trunk somites anterior to the telson. In my opinion, coincidence in the number of all somites is a consequence of the coincidence of both eu- and protosomites in the discussed groups and especially Skaracarida, Mystacocarida, and Copepoda.

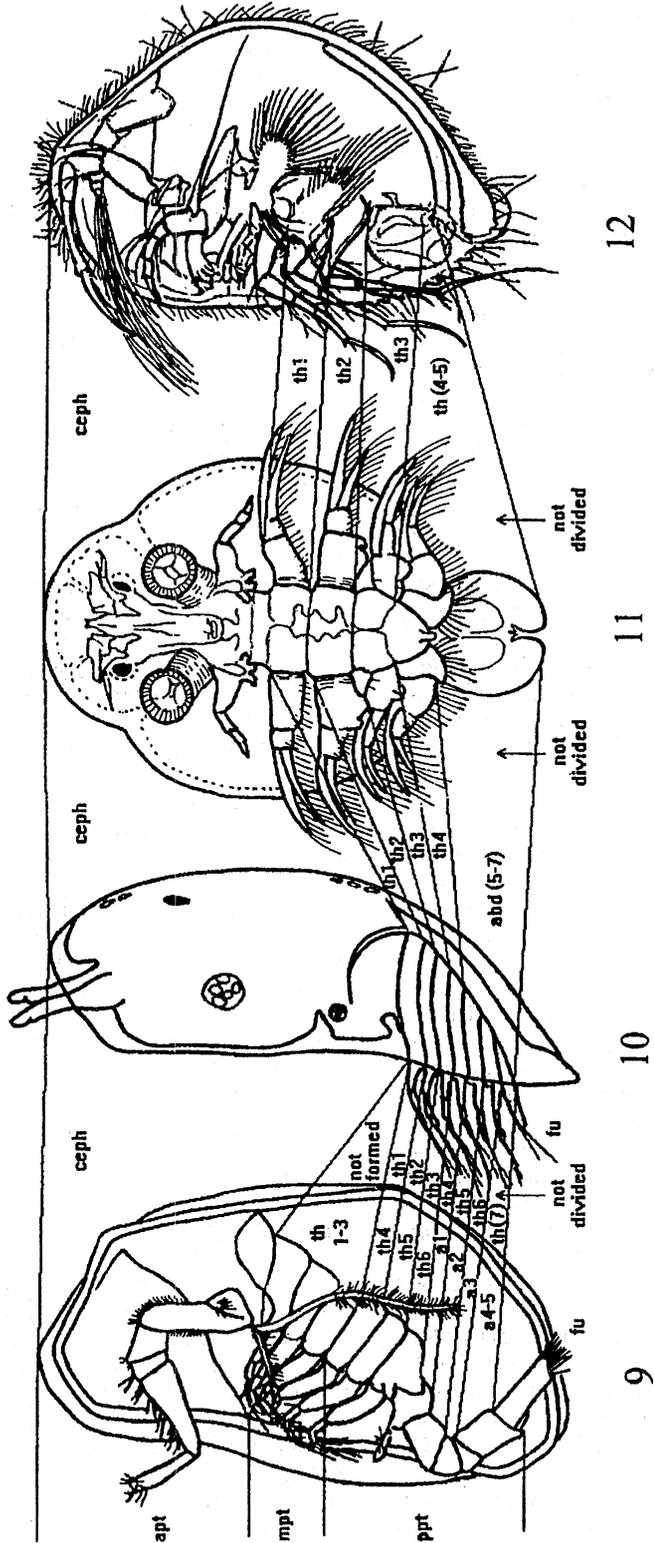
The order Skaracarida was established by Müller & Walossek (1985) for two Cambrian species, *Skara annulata* Müll. and *S. minuta* Müll. & Wal. I use for the analysis the later species only because there is a contradiction between the text and the picture: "The major features of the trunk are the same in both species such as: 11 segments, the first with a soft tergite and



Figs 2-5. Scheme of corresponding postmaxillary somites in certain groups of Maxillopoda. 2, Skaracarida (*Skara*); 3, Mystacocarida (*Derocheilocaris*); 4, Copepoda (*Calanus*); 5, Tantulocarida (paedomorphic male of *Microdegius*).



Figs 6-8. Scheme of corresponding postmaxillary somites in certain groups of Maxillopoda. 6, Ascothoracida (male of *Synagoga*); 7, Facetotecta (larva of male of *Hansenocaris*); 8, Copepoda (male of *Calanus*).



Figs 9-12. Scheme of corresponding postmaxillary somites in certain groups of Maxillopoda. 9, Ascothoracida (male of *Synagoga*); 10, Cirripedia (cypris-larva of *Trypetesa*); 11, Branchiura (*Argulus*); 12, Ostracoda (male of *Bairdia*).

limbs; a long telson, jointed furcal rami..." (ibid., p. 15). However, the former species is depicted (ibid., fig. 3) with 13 trunk somites plus telson. *Skara* has some characters plesiomorphic for the group under discussion (Maxillopoda with eusomites): the additional 8th somite anterior to the telson, a cephalic shield (probable reduced carapace), and biramous postantennular limbs. Moreover, a reduced cephalic shield is present in Mystacocarida. Absence of trunk limbs except maxillipeds is an autapomorphy of *Skara*. However, *Skara* is more similar to Mystacocarida than to any other crustacean group and may be placed provisionally with Mystacocarida. Besides the synapomorphy of Mystacocarida and Skaracarida there are autapomorphies of Mystacocarida: position of the male genital somite (4th postmaxillary one), peculiar shape of rudimentary cephalic shield, uniramous maxillules and maxillae, and somewhat reduced, uniramous thoracopods.

Figures 3, 5, 6 demonstrate the coincidence in the number of postmaxillary somites in Ascothoracida, Facetotecta (assuming a fusion of 2 somites), and Copepoda. As in the above-discussed case, possession of equal numbers of postmaxillary somites is evidence in favour of coincidence in the number of eu- and protosomites, i.e. 3 and 8 respectively including the telson.

Ascothoracida are usually united with Cirripedia on the basis of a bivalved carapace (at least in larvae), presence of compound eye in the cypris-larva, at most tiny buds of post-mandibular limbs in the nauplius-larva, the use of antennules for attachment, presence of oral cone, absence of antennae (except in nauplius-larva) and the connection of frontal filaments with the compound eye (as in cypris-larvae of Rhizocephala). All these characters except the first one are connected either with settling on substrate or with attaching to a host and can appear independently and in parallel. Presence of a carapace formed by the maxillary somite is a plesiomorphic character in all crustaceans. Initially the carapace was shield-like (*Triops*, *Argulus*, and in early stages of the ostracod *Manawa* (Swanson, 1989, 1990)), but it was further folded into a cylindrical form (Decapoda), or folded in half but not subdivided into two valves (Cladocera), or, it subdivided, either into two valves, or two valves separated by median plate (Conchostraca, Ascothoracida, cypris-larva of Cirripedia, Phyllocarida, Ostracoda). In addition, it has been reduced to various degrees independently in many groups. The carapace may shorten into a cephalic

shield (Cephalocarida, *Skara*), be reduced to the dorsal side of the cephalosome, devoid of segmentation and not particularly thick (Copepoda) or disappear completely (Anostraca). Comparing Ascothoracida (Fig. 9) with cypris-larvae of Cirripedia (Fig. 10) one notes that the number of postmaxillary somites is 11 in the first group and only 7 (including the reduced telson, to which the furcal rami are attached) in cirripedian cypris-larvae. Doubtless, the later case is connected with the absence of a growth zone and eusomites and the presence of protosomites which can form simultaneously (Walley, 1969). In addition, that nauplius of Ascothoracida is devoid of fronto-lateral horns and all somites of cirripedian cypris-larvae are homonomous; the later condition is contrary to Ascothoracida, in which there are 6 somites in the thorax bearing thoracic limbs, and a 5-somite, limbless abdomen. The male genital somite is also different in both groups (6th postmaxillary somite in Cirripedia and 7th in Ascothoracida). All the characters discussed above are evidence in favour of separation of Ascothoracida from Cirripedia, the former group being close to Copepoda, but the later belonging to the complex of crustaceans without eusomites.

Facetotecta (Fig. 6) is a poorly studied group known from larva only (Itô, 1990, 1991; Grygier, 1996). It may be explained either by living the adult representatives of the order in extremely uncommon biotopes or by their parasitic mode of life. However, it is evident from Figs 3-6 that the segmentation of Facetotecta almost coincides with those of Ascothoracida and Copepoda (only the 1st and 2nd somites are fused). This similarity becomes clearest when comparing the position of the male genital somite or the division of the trunk into limb-bearing, 6-somite thorax and a limbless, 5-somite abdomen. Besides this, the Facetotecta as well as the Ascothoracida are devoid of fronto-lateral horns and compound eyes are absent. Strong differences between the Facetotecta and Ascothoracida and Cirripedia lie in the presence of a undivided cylindrical carapace of the larva (although it is named cypris Y). It is characteristic that abdominal somites and sometimes 4 posterior thoracic ones are not attached to the mantle. A peculiar character of Facetotecta is the complicated sculpture of the carapace. All the above constitutes some evidence in favour of their taxonomic relationships with Ascothoracida.

It is impossible to find direct phylogenetic relationships between two recent paucisomitic groups of Crustacea: Branchiura and Cirripedia. Absence of eusomites could have originated independently and a large (in com-

parison with the body) carapace also could have appeared independently. I propose for the discussion on the phylogenetic relations of these groups to add an extinct (Carboniferous – Triassic) paucisomitic group, the Halicyniformii. For a discussion concerning the structure of *Halicynyne* see Starobogatov (1988). These animals have a shield-like carapace covering not only the telson, but also seven postmaxillary (or postmaxillulary) somites and the homonomous limbs on all trunk somites have both an exo- and endopodite. This group may be ancestral to the 2 paucisomitic recent groups mentioned above, each having originated from the Halicyniformii independently. Branchiura can be connected directly with a *Halicynyne*-like ancestor as a result of oligomerization of the body somites to 5 (including the telson) and the presence of some characters connected with a parasitic mode of life. Cirripedia maintain 7 somites including the telson. The telson is not mentioned in descriptions of Cirripedia, but the part of the body to which the furcal rami are attached in cypris-larvae makes me insist that a rudimentary telson is present. I suppose, contrary to the widely accepted opinion, that the definitive form of the earliest Cirripedia was identical with cypris-larvae and the formation of the peduncle and the armature of the capitulum are secondary processes involving transformation of the antennulae and the strengthening of the bivalved carapace by calcareous plates. This is evident from the organization of *Cyprilepas* and free-living males of Rhizocephala.

The most difficult problem is connected with Ostracoda. The representatives of this taxon are divided into two groups. The first one is represented by the forms with 11 trunk somites including telson: Copepoda, Ascothoracida, Mystacocarida, Skaracarida (*Skara* as exception with 12 trunk somites), Facetotecta with at most 10 somites including telson and certain ostracodan groups (Myodocapida, Cyllindroleberididae, Platycopida, Cytherellidae). Representatives of the second group have only 4-7 somites including the telson: Branchiura, Cirripedia, Ostracoda Podocopida and Tantulocarida. The group containing species with 11 trunk somites including the telson have the segmentation similar to that of Copepoda and Ascothoracida. Podocopida having 4 trunk somites including the telson are similar in segmentation to Branchiura and cypris-larvae of free-living males of Rhizocephala.

It is important to admit that Maxillopodan-Ostracodan complex of Crustacea is easily divided into 2 main groups: one of them have 3 or 4 eusomites and complete set of protosomites, whereas the representatives of the

second group have no eusomites. These groups may be named Calaniodes and Lepadiodes.

Formerly I (Starobogatov, 1988) regarded Ostracoda as paucisomitic crustaceans having 4 (5) trunk somites, contrary to Howe's et al. (1973) data concerning segmentation of the body in platycopids, and included this group into the class Halicyniodes together with Branchiura and Cirripedia. However, Swanson's (1993) and Vannier's et al. (1996) papers clearly demonstrate that a part of ostracods cannot be regarded paucisomitic (11 trunk somites including telson in platycopids and 11 or 12 in Cyllindroleberididae). There is no other case when groups with eusomites and groups without them are present in the same class. On the other hand, the most archaic ostracods, the recent *Manawa* (see Swanson, 1989, 1990) and the Cambrian Phosphatocopida (see Müller, 1979) are paucisomitic, with 4-5 trunk somites. This diversity in ostracod segmentation may be explained by different hypotheses beginning from that of simple polymerization of trunk somites to that of polyphyly of Ostracoda: those having 4-5 trunk somites are related to Phosphatocopida and *Manawa*, and those with 11 (12) trunk somites are related to Ascothoracida.

In connection with the discussed problems, I nearly agree with the cladogram of relationships within Maxillopoda published by Boxshall & Huys (1989). In my opinion, only two alterations are necessary. As discussed above, Tantulocarida has to be placed near the Copepoda as the separate superorder Basipodelliformii (Starobogatov, 1988). Ascothoracida must be separated from Cirripedia and, probably together with Facetotecta, be placed very near the base of the right branch of the cladogram. After these two displacements, the representatives of the right branch agree in the number of proto- and eusomites as well as (except Mystacocarida) in the number of praegenital trunk somites. It is clear that the concept of primary heteronomy of segmented animals permits us to understand the cause of variation in the number of postmaxillary somites.

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