

THE ANCESTRAL COPEPOD: TOWARDS A CONSENSUS
OF OPINION AT THE FIRST INTERNATIONAL CONFERENCE
ON COPEPODA

EDITED BY

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I N T R O D U C T I O N

During the First International Conference on Copepoda in Amsterdam two additional discussion sessions on the phylogeny of the copepods were organised by Prof. F. Dov Por and Prof. Jan H. Stock in response to an obvious need for more discussion time on this topic. The first of these developed into a collective analysis of the presumed characters of the hypothetical ancestor of the Copepoda as a whole. The characters were agreed upon largely by consensus and this 'ancestral copepod' is described and figured below. As a concept the ancestral copepod can be refined still further by more detailed consideration of features such as the maxillule, the maxilliped, and the armature of the appendages. Discussion of some of these points was curtailed because of the lack of available time, other omissions are due more to the impromptu and largely unprepared nature of the discussions.

The description is preceded by an edited transcript of the discussion, which is of considerable interest as it indicates firstly the reasoning behind the various decisions, secondly where the areas of uncertainty lie, and thirdly some profitable avenues for further research. Few editorial changes have been made other than grammatical changes necessary to avoid ambiguity, and the omission of repetitive statements. Any clarifications we have thought necessary are enclosed within brackets. Daniel F. Whybrew translated the German sections of the transcript (marked by an asterisk), and several participants helped to clarify inaudible sections of the recording.

T R A N S C R I P T

Por: Each one can try to draw his own views on the affiliations of the different groups in the form of a dendrogram. You have Dussart's scheme. I have also copies of my scheme which I showed on a slide. For my scheme I would like only to make one comment that I gave more or less in my lecture, relating to harpacticoid maxilliped types 2 and 3. Maxilliped 1 is the phyllopodial maxilliped, found in the Polyarthra, and is aberrant. Maxilliped 2 would be the stenopodial type. Maxilliped 3 is the typical maxilliped of the advanced harpacticoids, with a claw-like prehensile structure.

Ferrari: How did you define maxilliped type 2?

Por: We have in Polyarthra the phyllopodial type of maxilliped, but the second type is the more stenopodial, leg-like type of maxilliped, common to all except those phyllopodial types. So shall we try to connect these groups [on the blackboard] ? You can see that I have put here the Gymnoplea, not the Podoplea. Maybe I am wrong but I think the Podoplea is not a group, not a taxon. Who would like to start the discussion?

Boxshall: I would like to start in a slightly different way because my dendrogram would be very much like Kabata's [1979], published in his book. Perhaps most of us are familiar with it. The avenue I'd like to explore is trying to work out what combination of characters we might expect to find in the ancestral copepod stock. If we can agree on that, then perhaps it might be easier to determine what particular branches came off at which stage from that stock and its descendant stocks.

First of all the body - I am assuming that it has 5 cephalic somites [bearing the appendages A1, A2, Mnd, Mx1, Mx2], and 7 somites after that which bear limbs [Mxp, P1-P6]. Then 4 more somites, the last of which bears caudal rami.

Por: You said 5 cephalic somites was the ancestral condition. Do people agree on that?

Kunz: What is the "Oberlippe" [labrum]? Is this derived from one somite or more than one?

Boxshall: The labrum would be a ventral outgrowth from either the antennular or antennary somite. I am not sure which.

Stock: Antennary.

Por: What about the paragnaths?

Boxshall: Here [after the mandible] we have the paragnath. I think this is important because, looking at the muscles of the paragnaths and the muscles of the labium in siphonostomes, I think it is possible, although I have not investigated this fully, that the labium is derived from the fused paragnaths.

Stock: I still have one question. In an old fashioned book, Scott's Liverpool series memoir on the anatomy of *Caligus* [Scott, 1901], he shows that behind the [first] two pairs of appendages is a pair of spines that are innervated and could correspond to a somite that is lost in all other copepods, but is present in caligoids. In fact these postantennal spines are quite frequently present in that family. What is your opinion on that?

Boxshall: I think that with innervation one has to be careful whether these are motor nerves or merely sensory.

Stock: Sensory.

Boxshall: In my opinion, it is not an appendage.

Stock: I don't know whether these observations have ever been confirmed by later workers, or perhaps he was mistaken.

Ju-Shey Ho: That is the only publication so far.

Stock: Yes, the only one for fifty years.

Por: But somebody should look into it.

Boxshall: That was in *Lepeophtheirus pectoralis* - the postantennal process.

Serban: I think it possible that in the ancestry of copepods there are 8 thoracopods and in their evolution there is abdominalisation of the legs of the eighth, seventh, and sixth [somites].

Boxshall: I think this is possible. What about *Limnocletodes*? I have never seen one. What are these P7 [seventh limbs] someone once described?

Por: There is something very interesting with this. I have seen *Limnocletodes* many years ago from the Black Sea when I was not aware of this. But I did not see these appendages and what worries me is that Borutzky [1952] described these appendages in the female and they are absent in the male. I would usually expect them to be present in the male. So, those having *Limnocletodes* in their fauna should look at this.

Boxshall: It needs confirmation.

Por: Yes. I have a comment here. Not that I disagree but I think that the maxilliped, as far as we know in the different copepods, is so far specialised and evolved from a thoracic appendage that I think the fusion between the maxilliped-bearing somite and the head even, perhaps, preceded the separation of the copepods. It might be a very old event, general to a bigger taxon than the copepods.

Boxshall: Yes, perhaps. Even in mystacocarids the fusion is already taking place.

Ferrari: Also if you define copepods as having flexed the 4 swimming legs together it would almost leave out the maxilliped as functioning with the more primitive [metachronal] behaviour of the front [cephalic] legs.

Park: All the swimming legs function in the same way, forwards and backwards. However, the maxilliped movement is more like that of the mouthparts than of the legs.

Boxshall: They have no coupler [a functional intercoxal plate] - a basic difference.

Ferrari: Proceed first with the body somites. We can construct the legs later. How about flexing of the body?

Boxshall: I'd like to leave that for now.

Por: May I still ask about the problem of the caudal rami? Uropods or caudal rami? Uropods or a longitudinally split telson - what do you think?

Boxshall: I don't think they are uropods. It seems to me that the muscles going to it are the normal muscles at the end of the abdomen. They are the dorsal longitudinal trunk muscles and also

there are a pair of opercular muscles and 11 hindgut dilatator muscles in *Benthomisophría*. So there are lots of possible muscles there which are not appendage muscles. I would say that the features of the Canuellidae are advanced.

Stock: I am not too happy with the move of the maxilliped [to be appended to the cephalic series]. This is especially because of the presence between the maxillipeds of an intercoxal plate not present in the mouthparts, and indicating their thoracic origin.

Por: They certainly have a thoracic origin but this may be a pre-existing condition of the Copepoda.

Serban: In the evolution of the Copepoda there is cephalization of the anterior somites as in the extreme evolution of the primitive thoracopod 1 [P1] in some harpacticoids. A propos de l'origine de la morphologie actuelle des branches furcales, c'est le problème le plus difficile en ce qui concerne la reconstruction de la forme primitive des Copépodes. Je crois comme possible un phénomène tout-a-fait similaire à la céphalisation des segments antérieurs, donc un raccourcissement des segments abdominaux postérieurs, accompagné d'une scission successive des ceux-ci. Ainsi, chaque moitié d'un segment abdominal, en s'associant aux uropodes primitifs, a constitué les branches furcales actuelles. Par la suite, chaque paire de soies de celle-ci peut être considérée un vestige d'un segment abdominal primitif. Il y a des Copépodes qui font extrapoler cette évolution, en présentant une scission totale de leur dernier segment abdominal actuel, et en développant ainsi une sorte de super-branches furcales.

Por: About the uropods or furca - again the problem exceeds the Copepoda. Bowman [1971] based his comments on a very wide range of crustacean taxa. Schminke's [1976] criticism was not based on the point of view of the copepods. I never had the impression that Schminke's criticism was such a complete negation of Bowman's theories. So I think the problem has to be solved for the Crustacea as a whole. We cannot say that the copepods are something exceptional.

Tiemann: *[There is an additional problem - whether this last segment is in reality the same as the telson, since the anal opening is located here. If the furca is attached to this segment perhaps it is not a somite at all but rather the telson of the other Crustacea. This is discussed too little but it is not clear where the true furca of the crustaceans is located.]

Por: Bowman said that the telson in Copepoda is the anal operculum. In *Bryocyclops* there is a huge anal operculum extending between the caudal rami. So it is not impossible that the operculum is a reduced telson.

Stock: However, I think that in primitive crustaceans the anus terminates on the telson, whereas in copepods the operculum is just a flabby extension of the cuticle above the anal aperture but not having the anus on top. Secondly in all primitive crustaceans the telson is articulated from the last abdominal somite whereas in copepods it [the anal operculum] never is.

Por: We still have to consider the problem of the position of the genital openings - the problem of an abdomen or not.

Boxshall: I think it may be artificial to have an abdomen at all. Some primitive crustaceans do not. I prefer to call the somites thoracoabdominal, all 11 of them.

Stock: There is another solution, a functional one. Dividing the copepod body into cephalosome - the rigid anterior part, metasome - everything between it and the urosome, and urosome. Between the metasome and the urosome is the major articulation. At least in some copepods the major articulation is apparently at a different somite from others.

Por: Or not present at all.

Stock: When you see them alive there is an articulation.

Por: I have many vermiform harpacticoids without.

Stock: But when they move you see the articulation.

Por: No. They have a nematode-like movement.

Stock: The problem with the abdominal segments is that the genital segment, at least in cyclopoids, is a composite structure not just composed of a single somite, but must be a composite of more than one.

Boxshall: So it would be with one of these? The first of the following [somites].

Stock: I don't know.

Ferrari: Do we need a flexing point in order to allow the swimming legs to function in a non-metachronal rhythm? Are we going to have an articulation or can we get by without it? What would that mean in terms of functioning of the swimming legs?

Boxshall: It is difficult to say. I would guess that a metachronal rhythm of the swimming legs is ancestral, so the copepod stock had it originally, because they all have the same arrangement of the ventral body wall, with its strong remotor process and with the remotor muscles inserting on the body wall posterior to the limb base, not on the limb itself. They all have that. Schminke [pers. comm.] has observed the same structure in harpacticoids, Perryman 1961 found that in calanoids and I found that in misophrioids. It seems basic to the Copepoda. Traditionally the limb behind the first functional swimming leg has been reduced [i.e., P6 in gymno-pleans and P5 in podopleans], perhaps as a functional necessity as the metachronal beat starts with the last leg and works forwards.

Park: First I want to comment on the thoracoabdominal somites. In my opinion the ancestral copepod should have all similar body somites after the maxilliped-bearing somite, and the major articulation came [evolved] several times on different occasions. In the case of the legs we have to examine the innervation. I have examined the innervation in detail [in *Epilabidocera amphitrites*, see Park, 1966]. The copepod has interneurons, one pair running throughout the central nervous system. This pair of interneurons crosses just behind the pharynx so that the left side originates at the right antennule and the right side originates at the left antennule. They cross at the pharynx and run the entire course of the nerve cord. Each of these giant interneurons innervates motor axons of both the legs and the longitudinal muscles. All these muscles are apparently fired by a single stimulus at the antennules.

Whether the stimulus comes from the left or right antennule it would fire all the legs simultaneously.

Boxshall: They don't have to, as I have seen living cyclopoids [the poecilostome *Oncaea venusta*] swimming with legs 3 and 4 only. So they don't all have to beat simultaneously.

Park: Do they beat several times consecutively, or beat only once?

Boxshall: It happened repeatedly but not rapidly so. They beat once then a gap, then beat again.

Park: In calanoids the mouthparts vibrate continuously but all the legs are held before [protracted] while they are swimming so that in the case of the escape movement all the legs beat only once. Depending on the musculature the urosome swings left or right. If it swings one side the copepod moves the other way so that the direction of the escape movement was controlled by the urosome.

Boxshall: Strickler [1974] found the same thing, that the urosome was important for steering.

Park: Yes, steering. If we examine the innervation, all the motor fibres synapse with the interneurons so that the legs coupled by the coupler function as a unit. So, in my opinion, the stimuli can be received by either antennule and will transmit via the interneurons, so that all the motor fibres that synapse with the interneurons may be fired simultaneously. In that case the urosome swings either side, and all the legs which are held forwards beat with a single stroke and the copepod moves to either side.

Por: I don't know whether this discussion is crucial for our decision here. You have this thesis that there is no abdomen.

Boxshall: Well, an abdomen is defined arbitrarily.

Por: No. I think in Crustacea the definition is that the abdomen is behind the sexual openings. In that sense I think the copepods have an abdomen just like decapods or any other Crustacea.

Boxshall: But the genital openings move around so much within the Crustacea. In cirripedes the female opening is on the second [first] thoracic somite and the male opening is on the first abdominal somite. It is very plastic and I think it is artificial to rigidly stick to an abdomen which, in my view, is left over from insect morphology rather than fundamental to crustacean morphology.

Tiemann: * [We have to consider Lauterbach (1973) who studied the ground plan of the Crustacea intensively and documented the presence of legs on each somite in the primitive condition. We must begin with this condition and consider that the legs were continually more reduced: starting at the back and proceeding forwards. To begin with it is a primary continuum from the thorax to the abdomen and from there it would be reduced. The copepods had reached the stage where only the last 5 somites are reduced.]

Boxshall: Antennule uniramous, surely none will disagree. Many-segmented, perhaps some will disagree; 28 or 29 - something like that.

Por: Will someone comment on Sars' idea that the increase in antennular segment numbers is secondary?

Tiemann: * [I am of the opinion that a short antennule is the original state of the Copepoda. The reason for this opinion is that the groups related to the Copepoda all have short antennules.]

Por: Tiemann's idea is that the ancestor has short antennules, meaning also that it had a few segments and that the increase in numbers of segments is secondary.

Boxshall: I don't know how to prove either way.

Serban: * [I have another idea which I learned from Zimmerman (1959). That in the study of phylogenetic relationships one must first consider the phylogeny of the character and then the phylogeny of the character-group. I have started a study in which it may be possible to prove that the antennules of *Tachidius* are identical to those of the first nauplius of *Paracalanus*. Thus it is an idea that the antennules of harpacticoids are a neotenic form of the calanoid antennules. This does not necessarily mean that the calanoids themselves are primitive, but they have maintained a number of primitive characters and other groups have not. But one should be careful in making such a consideration.]

Por: This is an observation that the antennules of the harpacticoids might be a neotenic structure of the calanoid type.

Boxshall: I don't agree that it is of the calanoid type but I think the fact that you have long, many-segmented antennules in both gymnopleans and podopleans suggests perhaps that it is primitive. As, when a many-segmented antennule occurs in both groups there is a general plesiomorphic facies. In the new genera and species of misophrioids there is a biramous fifth leg which is very plesiomorphic and they also have a 27-segmented antennule. Also if you look at the muscles of an antennule of *Benthomisophria*, the levator muscle, a long muscle which originates in the mandibular somite, at least in the proximal portion inserts on every segment before inserting on the proximal rim of the last segment. But for a large number of proximal segments it inserts on every segment.

Por: How many?

Boxshall: I think 14 [out of 18] but I am not sure offhand. But I think this suggests the segments are real segments.

Stock: I think I have to support Boxshall's suggestion that a multi-articulate antennule is ancestral.

Por: How many segments?

Stock: Twenty-seven rather than 28 perhaps but this is not very important. I reach this conclusion by in-group comparisons in Hennig's sense. When I compare within the cyclopoids, and especially within the siphonostome cyclopoids, you see the highest number of antennular segments in the least modified genera. As was made clear by Giesbrecht [1899] in his monograph on the Gulf of Naples asterocherids, in which he showed that the degree of fusion of the antennular segments is correlated with reductions in the other appendages.

Tiemann: * [It may be the wrong time to mention this but it does not help much in terms of systematics. The antennule is often reduced, i.e., the number of segments is often reduced. Benthic animals often have short antennules. In the phylogeny of the copepods

there will often be parallel occurrences of such reductions. The fact that the primitive antennules were long is of little use in taxonomy. We still can't put all copepods with short antennules together in spite of this. It is probably not a homologous synapomorphy of these animals with short antennules. The above mentioned [trithek] scheme of Giesbrecht is convincing but even this does not help. We cannot progress with its help. We have to find the way back to synapomorphies.]

Por: What I would suggest is to leave this problem, as there is no consensus I think.

Boxshall: I think there is almost a consensus.

Por: I didn't develop my arguments further but I don't think it is necessary to discuss further the number of segments.

Boxshall: I think it is crucial when you think of the three different phylogenetic schemes we have seen during this week [Dussart's, *Por*'s, and Kabata's]. I think the antennule is very important.

Por: Then I would add only one more point. If we agree that the ancestral copepod was a benthic animal then that animal must have had a short antennule.

Boxshall: Why?

Por: Since all benthic harpacticoids do, that we know.

Boxshall: The benthic cyclopoids and *Misophris* don't.

Por: In the purely benthic cyclopoids, the freshwater *Bryocyclops* for instance, they have a shortened antennule. At least they do not have such high numbers [of segments].

Ferrari: But the benthic calanoids also have a large number of segments but a short antennule. Maybe we shouldn't try to work from the hypothetical environment just yet. That is too complicated.

Boxshall: Second antenna - biramous. Exopod . . .

Por: How many segments?

Boxshall: Up to eight.

Por: Endopodite?

. . . . : Three.

Boxshall: Mandible - biramous palp, well developed gnathobase.

Por: How many palp segments?

Boxshall: In one of the new misophrionids there are 6 exopod segments, but they only have 2 on the endopod. I don't know about calanoids.

Park: Yes, about 5- or 6-segmented exopod and 2-segmented endopod in calanoids.

Boxshall: Paragnaths - present. First maxilla - well developed gnathobase, biramous palp.

Por: I suggest we don't go into too many details on the first maxilla.

Boxshall: Second maxilla - uniramous.

Por: How many endites?

Park: Six.

Boxshall: So, six endites and a distal claw on the basis. Maxilliped - uniramous. Gurney in *Freshwater Copepoda* [1931] suggested 9 segments. Either 8 or 9, I don't know. Some of the misophrionids have 8.

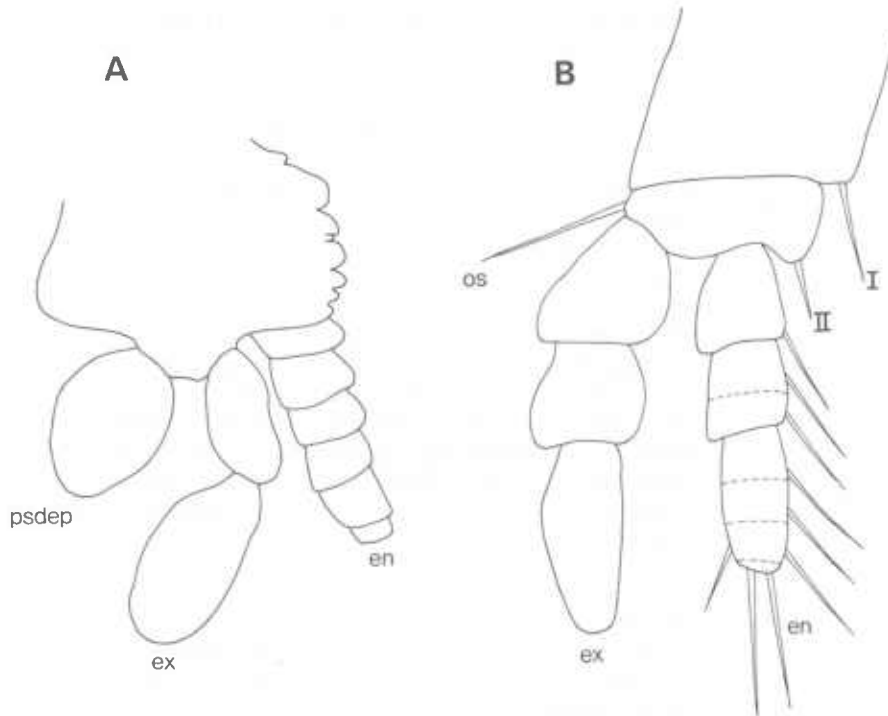


Fig. 1. [Part of the contribution by Itô.] A, generalised plan of a cephalocaridan trunk limb; B, generalised plan of a copepod swimming leg; (en = endopod, ex = exopod, os = outer seta, psdep = pseudopodite).

Por: The maxilliped again is too complicated and variable an appendage. I don't think we can decide at this stage.

Boxshall: Is this acceptable as a simple statement?

Por: Uniramous, yes, but not the number of segments.

Boxshall: Thoracic legs, P1 to P5 biramous.

Stock: Why do you omit the sixth leg?

Boxshall: I thought that would cause more argument. Can we deal with it separately?

Itô: I think the ancestral copepod [leg] is triramous. Sanders [1957] said that the copepod exopodite and endopodite accord with the cephalocaridan pseudopodite and exopodite [respectively]. This outer seta [os in fig. 1B] or spine is always present in harpacticoids. The maximum setation of the endopodite is 1, 2, 3, 2 [terminal] and 1. I believe that this basal seta corresponds to the cephalocaridan pseudopodite, copepodan exopodite to cephalocaridan exopodite, and copepodan endopodite to cephalocaridan endopodite.

Por: What do you make of the fact that the coxal segment also has a spine?

Stock: Here [position I in fig. 1B] is the coxal spine in cyclo-poids.

Itô: Sanders said copepodan exopodite and endopodite accord with cephalocaridan pseudopodite and exopodite. I don't think so because as far as I know in harpacticoid development the rudiment of the leg first appears as a seta or as a seta and two rudiments. [This basal seta could therefore correspond to the cephalocaridan pseudopodite.]

Stock: I am not sure that the presence of a spine corresponds to an original segment. I am not sure in other words, that each segment always carries only one spine. I have no indication for this but have many to the contrary - that a segment may have several spines.

Por: I suggest that we separate here the two problems. Itô has expressed two ideas; that the endopodite is originally many segmented and, the most crucial idea, the problem of the triramous limb.

Stock: This spine here is taken as an indication of the presence of a coxal segment and I am not sure that the presence of a spine is always indicative of a fused segment.

Por: What do you do with the coxal spine?

Stock: In all cyclopoids the coxal spine is here [position I in fig. 1B] except in siphonostome cyclopoids it is here [position II]. I don't know what this means.

Ferrari: In *Oithona* they have two of them, and both are present on the first leg.

Boxshall: I think this is very interesting. I don't want to comment on it at the moment but I think, as long as we accept that this structure [fig. 1B] was present in the ancestral copepod, for the purpose of the present argument we don't need to consider the homology of this spine further.

Por: So the conclusion is that whilst this may be true it exceeds, perhaps, the level of the Copepoda.

Boxshall: We only need start with this for the ancestral copepod.

Kunz: * [The finding of such setae is something that occurs very often on different parts, e.g., the mandible in Mesochridae can be very variable. In the most extreme case it can be reduced to a single seta. In Paramesochridae there is the tendency for the 3-segmented endopodite on P4 to be reduced. In the most extreme case it is reduced to a single seta. This occurs in the genus *Apodopsyllus* in which the endopodites of P2, P3, and P4 are reduced. But in some *Apodopsyllus* species a residual seta is found on the endopodites and in others, at least according to the literature, this seta is missing.]

Por: This is supporting Itô's idea. But still we have no proof that the reduction of the pseudopodite occurred within the Copepoda.

Boxshall: Can I add that they are joined by a coupler?

Ferrari: Are they still going to operate metachronally if they are joined by a coupler?

Boxshall: Yes.

Stock: Is this the intercoxal sclerite?

Boxshall: Or interpodal bar, yes.

Por: I think it would be better to call it the intercoxal plate.

Boxshall: I was using Manton's [1977] term coupler.

Stock: Coupler is used for reproductive structures.

Boxshall: Yes. This is very important because this structure was interpreted by Manton [1977] as crucial to the metachronal jumping type of locomotion in copepods. The whole of the structure of the metasome is quite rigid and geared to give strength and prevent unnecessary flexion during the jumping movement.

Ferrari: That's not metachronal rhythm.

Boxshall: Yes. There is a 2 millisecond gap between - leg 4 goes and it takes 4 milliseconds for its remotor swing. Two milliseconds later leg 3 goes.

Park: I still don't agree with that idea because the neuroanatomical structure doesn't support a metachronal movement. In the escape reflex they move all the legs simultaneously, this is supported. Also the coupler simply forms a unit so the legs form and move as a single unit.

[Eds.: Discussion of this topic was curtailed. Both Park and Boxshall agree that the intercoxal plate forms each leg pair into a single functional unit. The difference in opinion being: Boxshall: swimming legs beat metachronally starting with leg 4 and with a 2 millisecond delay between the commencement of swing of each leg pair. Park: the swimming legs beat simultaneously in the escape reflex as the single pair of giant interneurons synapsed to the motor nerves in each somite is too simple a system for a complicated behaviour such as metachronal beating.]

Stock: Can we put in an intercoxal plate for the maxilliped?

Por: Yes.

Boxshall: Sixth leg - uniramous and reduced?

Stock: Biramous. I base this on cyclopoids again. In some notodelphyids where P6 is large and developed as a big genital flap this is bilobed and each lobe bears several cuticular structures like spines or setae. This to my mind makes P6 biramous in the ancestor.

Por: In the gonopods of the Canuellidae too, in the most developed forms it is bilobed and each lobe has its own appendages and spine-like structures.

Humes: Even in the Lichomolgidae P6 has 2 setae.

Boxshall: These are all the limbs then.

Por: No. What about *Limmocletodes*, and the Canuellidae which have long inserted setae on the following abdominal somites.

Boxshall: We will have a query here.

Por: There might be a possibility that they are the reduced P7 and P8.

Boxshall: We need not just good scanning shots [SEM micrographs] of the urosome. We need to look internally at the muscles.

Stock: Is this what you have in *Limmocletodes*? Is that on the abdomen?

Boxshall: According to the literature [Smirnov, 1933; Borutzky, 1952] *Limmocletodes* has something here on the first of these somites [immediately behind that bearing the P6].

Stock: Behind the genital segment?

Boxshall: Yes, behind the genital segment. I would say that it had a heart. It is present in calanoids and in misophrioids.

Por: I don't know really what a heart is. Especially if you mention that it does not have lateral ostia [in *Misophría*]. It's just a simple part of the dorsal vessel.

Boxshall: Yes, it's a dorsal vessel.

Por: I would comment on the ecological or physiological value of such an organ. I would say that a bottom-living harpacticoid is anyhow very much adapted to living in an environment poor in oxygen. It is not permanently moving, permanently swimming like a calanoid. I think we should consider the reason to have developed a heart. There is a necessity for a heart in a calanoid, or even in a misophrioid. I don't know the significance of a heart in these small crustaceans, or whether it is a primitive or adaptive feature.

Tiemann: *[The heart is a crustacean characteristic. It is an articulate feature as well. It must therefore also be a basic copepod feature.]

Por: A dorsal vessel, yes. A heart, no.

Park: In Calanoida there is usually a well developed heart with ostia. In *Epilabidocera* it has only one ostium and also it has the anterior aorta which carries blood directly into the anterior region of the head where there is the brain and other systems.

Stock: This could be a rudiment of the dorsal vessel or heart. Or do you think this is a new formation?

Park: I don't know whether it is a rudiment of the primitive condition or specialised. Anyway, the calanoid has a well developed heart and aorta.

Por: Well, I would accept a pulsating dorsal vessel but a heart, definitely not.

Boxshall: I missed something. With the antennule in the male: it is primitively geniculate on both sides.

Ferrari: Yes. We should mention sexual dimorphism.

Stock: This is certainly true for in-group comparisons, such as within the cyclopoids.

Por: It is interesting here that one of the characters that makes calanoids much considered a monophyletic group is this innate tendency to asymmetry. Almost all calanoids have it.

Stock: Boxshall's statement certainly holds true for cyclopoids.

Ferrari: So we are going to have a symmetrical geniculate antennule. Is it going to be unigeniculate or digeniculate?

Boxshall: I don't know.

Por: Let's not go into it.

Park: What about mentioning the P5 specialisation in the male?

Boxshall: Not specialised.

Ferrari: No.

Boxshall: Primitively unspecialised, like the P4.

Park: We have to decide whether there is sexual dimorphism.

Por: The problem of one or two spermatophores and the mechanism of transmission of spermatophores is a very complex one and I would suggest perhaps to leave this problem aside.

Ferrari: I disagree with not considering at least what the male looked like. One of the fundamental problems with systematics is that too much attention has been placed on the female. You need a male in copepods and you must consider what he looked like because the female didn't evolve without one.

Boxshall: I have just written up these and there is probably no argument: no carapace, no compound eye. Reproductive system - everything paired and bilaterally symmetrical in both sexes; gonads, ducts, and openings all paired, plus spermatophore present.

Stock: Openings ventral.

Boxshall: Yes, ventral genital openings. Is that sufficient? Is that what you wanted to consider about the male? Primitively the P5 is simple, not modified.

Ferrari: Right, I would agree.

Por: What about the [sexually] dimorphic legs?

Boxshall: Not primitive.

Stock: Primitive copepods have males that are rather similar to the females, excepting sexual system features of course, but the legs are identical in the male and the female.

Por: The swimming legs?

Boxshall: No. All legs.

Stock: All legs including maxillipeds and P6.

Boxshall: Everything except the antennules.

Por: I tend to agree about all legs but somehow I think in every crustacean there must be a basic dimorphism which ensures fertilization.

Ferrari: But in the Cyclopidae, in *Cyclops*, they are perfectly capable of transferring the spermatophore with the tips of the fourth swimming legs [Hill & Coker, 1930], no specialisation there. So I think our male would do quite well in transferring the spermatophore, but I like the idea of him having a geniculate antennule. His swimming legs would do quite well to pick the spermatophore up and place it especially if his and her genital openings are ventral. It could transfer quite quickly without a specialised organ.

Por: So I think it is accepted that all the legs are the same.

Ferrari: Yes, except the antennules for which we have dimorphism.

Boxshall: The primitive developmental stages of our archicopepod - 6 naupliar stages, 5 copepodid stages and the adults.

. . . .: Is there moulting in the adult?

Boxshall: No, that is it. With a terminal moult for the adult. In *Lernaeocera* the adult female grows from 2 mm to 2.5 cm at maximum without moulting.

Stock: I know that many parasitic copepods can grow without moulting but I am not sure in some semiparasitic copepods if the moult is terminal or not.

Ju-Shey Ho: I have found two different sizes of female, small one and a big one, and they are both capable of laying eggs. From in vivo experiment it shows that the small female may grow into a large one.

Boxshall: With or without moulting?

Ju-Shey Ho: No moulting.

Boxshall: So would we agree on a terminal moult, then?

Por: Here I would like to comment on the problem of the nauplii. It could perhaps be a suggestion of this conference to go into the study of naupliar stages, since sometimes much phylogenetic importance is attached to naupliar structures. For instance, in Dussart's scheme he attached much importance to that, following the work of Björnberg [1972]. I believe we are today unable to say more except to make this recommendation.

Boxshall: There are few other characters left. The nervous system - a nauplius eye is present. The excretory system - an antennary organ in the nauplius and a maxillary organ in the adult. I think the misophrioid situation is unusual and provides a nice comparison with the normal situation.

Por: But we don't know what happens in the copepodid.

Boxshall: That's true. Somewhere it must change but I don't know where. Well, that is it.

DESCRIPTION OF THE ANCESTRAL COPEPOD

Body comprising 5 cephalic and 11 thoracoabdominal somites (fig. 2A, B). The five cephalic somites and the first (maxilliped-bearing) thoracoabdominal somite are fused to form a cephalosome covered by a dorsal shield. The second to seventh thoracoabdominal somites each bear a pair of biramous legs, and the eighth may possibly bear a pair of vestigial legs. The remaining thoracoabdominal somites are limbless although the anal somite bears the paired caudal rami, the homology of which is uncertain. They may represent either the paired uropods or the true caudal furca. The paired genital openings lie on the ventral surface of the seventh thoracoabdominal somite in both sexes.

Antennule uniramous, many-segmented; geniculate on both sides in the male. Antenna biramous with an exopod comprising up to 8 segments and an endopod of up to 3 segments. Labrum present. Mandible with well developed gnathobase and biramous palp comprising an exopod of up to 5 or 6 segments and an endopod of 2 segments. Paired paragnaths present. Maxillule with a well developed gnathobase and a biramous palp. Maxilla uniramous, with up to 6 endites and a distal claw on the basis. Maxilliped uniramous, with an intercoxal sclerite. Swimming legs 1 to 5 biramous, with 3-segmented rami. The legs of each pair are joined by an intercoxal plate (coupler) fused to the medial surfaces of both coxae. Sixth leg biramous, reduced but with an intercoxal plate. There is no sexual dimorphism in any of the appendages other than the antennules.

Circulatory system comprising a pulsating dorsal vessel which probably represents the crustacean heart. Nauplius eye present but lateral compound eyes absent. Excretory system comprising paired antennary glands in the nauplius stage and paired maxillary glands in the adult. Sexes separate; gonads, ducts, and genital openings

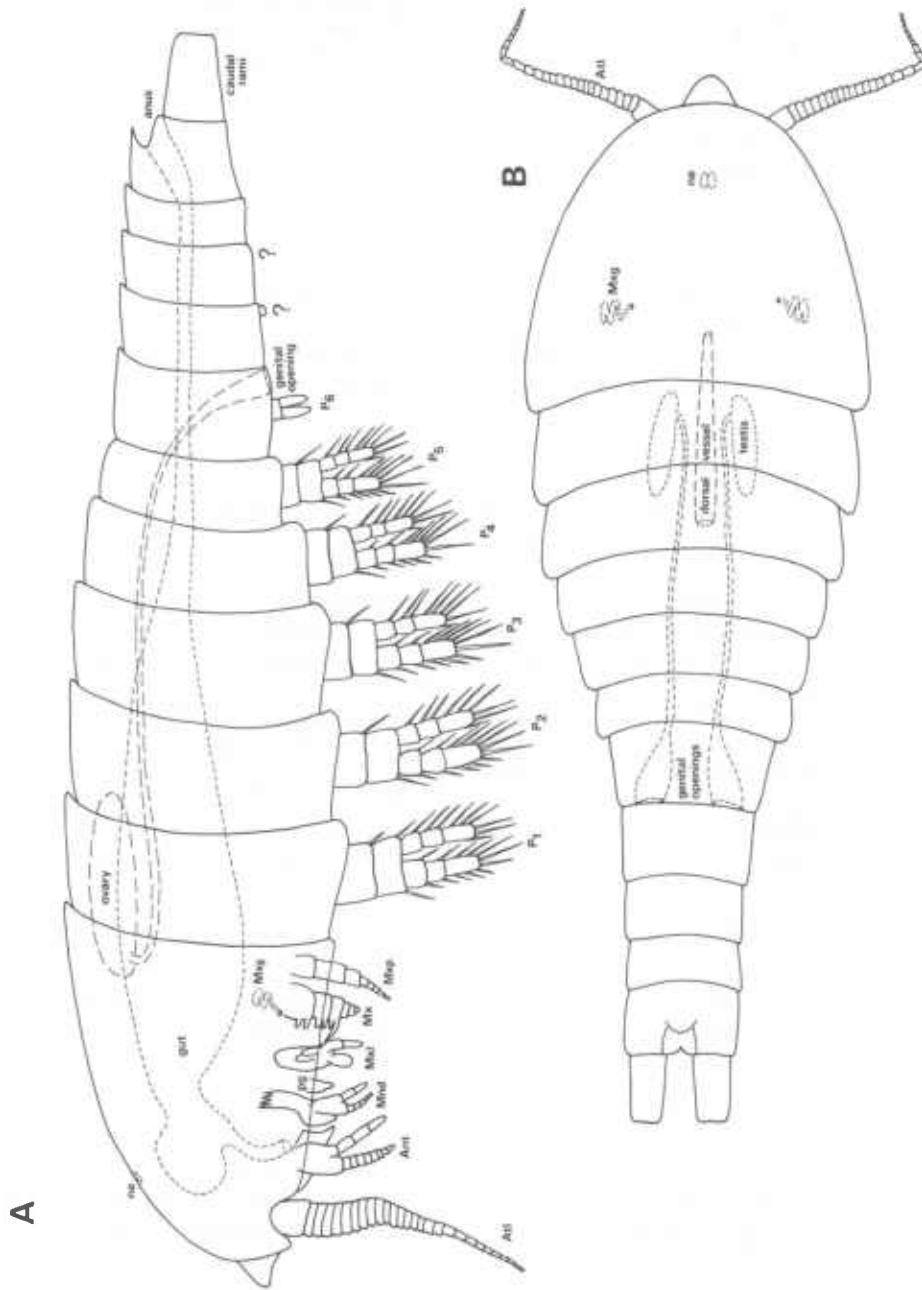


Fig. 2. The ancestral copepod: A, female, lateral; B, male, dorsal. There was no consensus on the number of antennary segments, the many-segmented condition figured was that favoured by a majority of active participants. (Ant = antenna, Atl = antennule, Mnd = mandible, Mx = maxilla, Mxg = maxillary gland, Mxl = maxillule, Mxp = maxilliped, ne = nauplius eye, pg = paragnath.)

paired in both sexes. Genital openings ventral and sperm transfer is by means of a spermatophore. Development proceeding from egg, through 6 nauplius and 5 copepodid stages, to the adult which does not continue to moult.

P O S T S C R I P T

This ancestral copepod is merely a compilation of the plesiomorphic characters exhibited by representatives of the various copepod groups. It is a generalised concept, not an actual organism, and several important functional considerations have been neglected in its construction. Its value lies in the information it provides - information upon which phylogenetic inferences can be based. Within the Copepoda many evolutionary trends (morphoclines) can be recognised and the construction of the ancestral copepod greatly helps one to determine the polarity of any morphocline from the ancestral to the derived condition.

An implicit assumption throughout much of the discussion was that primary evolutionary processes in copepods proceed towards fusion of body somites, and towards reduction in the segmentation and armature of the appendages by either fusion or loss. This trend towards quantitative reductions both in segmentation and in armature often has a pattern of qualitative increases in complexity superimposed on it, as in the case of the evolution of a highly specialised male fifth leg within the Calanoida. The formulation of this assumption into an evolutionary 'rule' would have significant repercussions on our consideration of copepod phylogeny. It would, for example, indicate the ancestral nature of the multiarticulate antennule rather than the reduced antennule as found in harpacticoids. The polarity of such morphoclines should be established individually on the basis of in-group and out-group comparisons rather than on the basis of a general dogma. Such a rule could clearly not apply to numbers of developmental stages as there is well documented evidence of the interpolation of an additional stage in the life history of some siphonostomatoids. Members of the genera *Caligus* and *Lepeophtheirus* have the equivalent of 6 copepodid stages before the adult (4 chalimus and 2 preadults), one more than the ancestral copepod.

It is generally accepted that the ancestral copepod was a benthic organism. We assume, as did Kabata (1979), that it lived on or near the surface of the substratum and not within it. Its generalised gnathostomous mouthparts would have enabled it to utilize a wide variety of food items, as in certain modern copepods like *Oithona nana*, which can employ these mouthparts both as a filtering mechanism for sieving relatively small particles and as a raptorial mechanism for grasping larger prey organisms (Lampitt, 1978).

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