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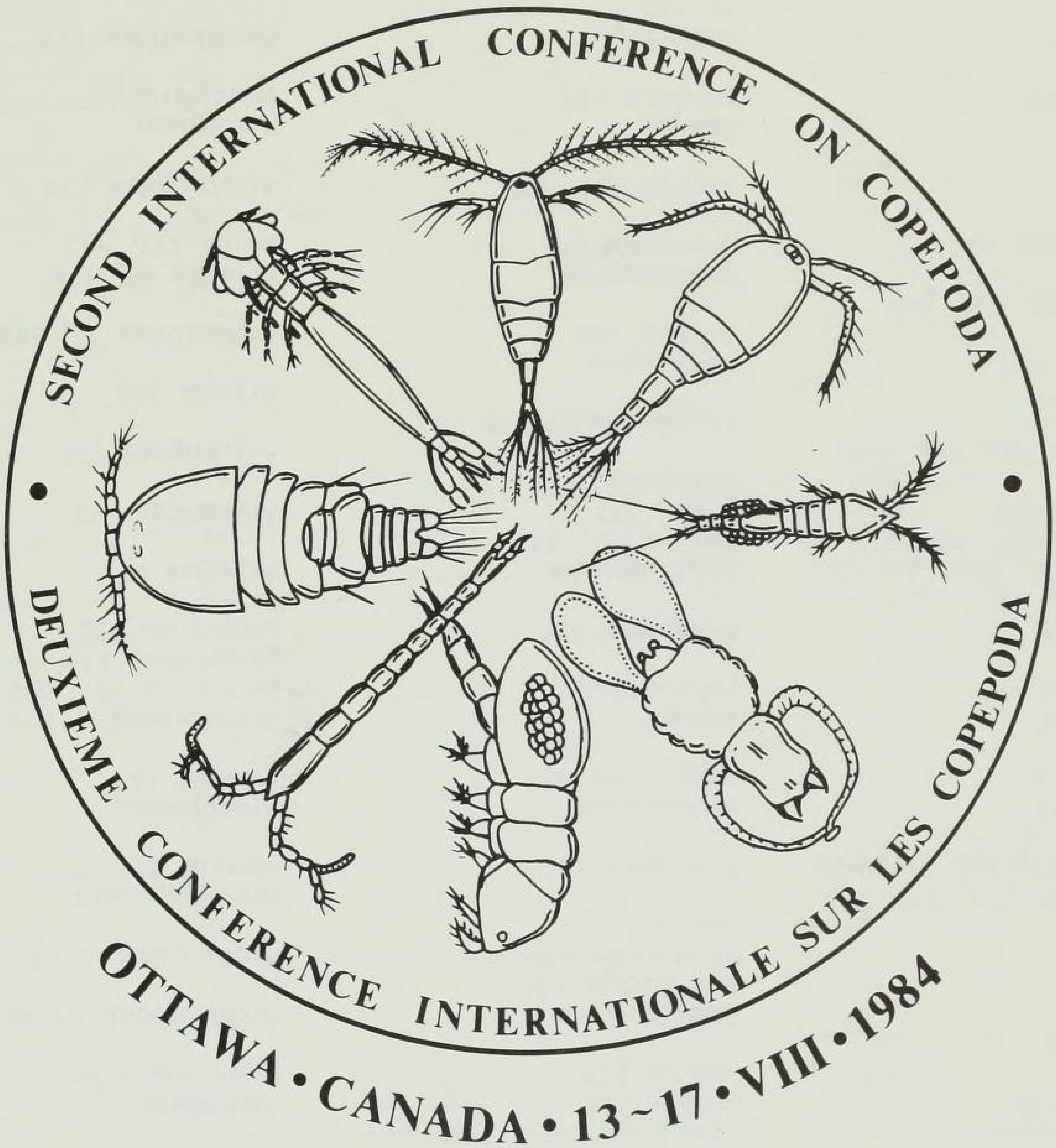

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DISCUSSION

Edited by *Z. Kabata*

F.D. Por: I have a few comments. My first comment is related to the antiquity of copepods. In my view, we should definitely think of a very early origin of the copepods and not of a Mesozoic one, as suggested by Brian (Dr. Marcotte). I would refer to a very recent paper on the fossil microcrustaceans from the Cambrian, so-called "ersten Crustaceen", described by Müller. These are obviously microcrustaceans, meiobenthic beasts, very small, millimetre-sized and clearly showing many archicopepodid characters, or characters intermediate between copepods and Ascothoracida. We are clearly dealing with a very, very old, at least Cambrian, group when we speak of copepods.

Now, this brings us to Cambrian environments. It is clear that during the Cambrian the fresh waters were not yet inhabited. So freshwater copepods must be younger. I daresay that the phyto-environment, the algal flora, was not yet developed at that time. In general, modern algae are later than the Cambrian, and of course the pelagic environment, open ocean environment, was not in being in the Cambrian. The algae as we know them are probably Mesozoic, dating back to the time when diatoms and coccoliths appear. Therefore, we have to speak of bottom-living, small animals eating detritus, or whatever was available. I think we cannot go to the present big groups to find something near to the copepods, neither to the cyclopoids, nor the calanoids, and probably not to the majority of the harpacticoids. Since copepods are very old, I think we have to find a few small groups of "living fossils". They might be the mormonilloids or some of the primitive harpacticoids.

It's clear that the calanoids, at least the open sea calanoids, are a new, Cretaceous group. The majority of freshwater cyclopoids, because they show a very nice separation between gondwanic and laurasian groups, are also late, post-Triassic. We might, however, here and there, have also very old inhabitants of fresh-water, of course, probably not earlier than Devonian. They might be parastenocarids or similar groups, and again here we have to find some living fossils. In general, when we speak of cyclopoids, the majority of calanoids and the vast majority of harpacticoids, that is harpacticoids which have grasping P1, grasping maxillipeds, these are late-comers that had arrived after phyto-environments of the globe became well developed. This means they had to be post-Cambrian.

Z. Kabata: Thank you, Prof. Por. Well, we have been shown only yesterday an early Cretaceous parasitic copepod which was extremely well developed. It does take some time to develop this kind of form. This would rather favour the theory of an earlier origin. Perhaps Brian (Dr. Marcotte) would like to say something about that.

B.M. Marcotte: The only comment is that phytoflagellates occurred in the Devonian for the first time, so that there were at least some materials in the phytoplankton for planktonic organisms to ingest. Interestingly enough, the diatoms occurred in the Cretaceous at periods of turbidity maxima, organisms with specialized pigment systems to absorb wavelengths of light that occurred in turbid water, so it kind of buffers the thing. As to the origin of the copepods in the Cambrian, I do not know. I am cautious, though, because copepod-like limbs do occur, for example, in Scourfield's branchiopod-like creature and elsewhere. It could be that at least the thoracic limbs, the swimming-type limbs of copepods, do occur convergently in several crustacean groups. I just don't know enough about the microfossils in the Cambrian, except I haven't seen a copepod there yet. I have seen things that share some say I have seen one. I would more likely expect one in the Silurian-Devonian. In the Silurian you start having a lot of creatures leaving the sea and going into fresh-water. The first freshwater ostracods occur in the Devonian to lower Carboniferous. Things are getting out, I presume, of a turbid ocean, of an ocean that is anoxic and getting crowded, and presumably coastal environments are very competitive at that point, if they were not before. I don't know.

J.-S. Ho: I have some comments to make on that. The palaeontologists tell us of the so-called Permo-Triassic bottleneck. This means that between 80% and 95% of marine organisms died off during that period, let's call it Permo-Triassic. In other words, only very few marine organisms made it through the Palaeozoic and into the Mesozoic. Whether the copepods are one of the surviving groups we do not know because we don't have the fossil records. Therefore, if we must rely on the fossil records, I would say it is hopeless.

B.M. Marcotte: I think you can. There is this notion that the Permo-Triassic boundary extinguished all kinds of organisms. In fact it didn't. The extinction of most filter-feeding organisms, most organisms dependent upon symbiotic algae (or at least presumed to have been dependent upon them), the complementary origin of deposit-feeding bivalves, the extinction of visually foraging organism, whether they are nautiloids or trilobites, all begin at the Ordovician and continue without interruption to the Permo-Triassic boundaries. It is true that there was something that stopped a lot of organisms, like trilobites, but things that were foraging visually, or filter-feeding, were having real problems long before, 150 million years before and longer. This gets back to this notion that oceans may have been getting more turbid, that vision was becoming a limiting resource for foraging, filter-feeding was a problem and animals became deposit-feeders or chemoreceptive. The last of the trilobites to exist with primitive eyes were in clear tropical waters. So, at any rate, there is more to the story than simply an extinction at the Permo-Triassic boundary. There is a great lot of detail, if you look at sensory modalities instead of looking only at the number of genera. You see a lot more of what has been going on earlier.

Z. Kabata: Geoff (Dr. Boxshall), have you any comments?

G.A. Boxshall: I would have to agree on the ancient origin of at least an ancestral type of copepods. Müller found some very interesting microcrustaceans in his Cambrian-Austin. The nauplius stage of one of them will be shown tomorrow in Geoffrey Fryer's talk. I oppose Maxillopoda as a taxon. There are taxa described by Müller in 1983 that conform precisely to the 5-6-5 cephalon-thorax-abdomen (or 5-7-4, depending on how you divide the trunk into thorax and abdomen). Both of these can be accommodated into the maxillopodan plan. There are animals in Müller's paper which have exactly this plan: a cephalon of 5 segments, with 5 paired appendages and a large labrum; there is a thorax with 6 pairs of biramous thoracopods, and there are 4 or 3 segments in the urosome, the first of them bearing the genital openings. No, I don't like the Maxillopoda, but you can't argue against the facts.

Z. Kabata: Thank you. Does it exhaust our discussion of this question? Dr. Schminke?

H.K. Schminke: The trouble is, we all think they are Crustacea, these ones that have been discovered by Müller. In fact, Lauterbach is beginning to question whether they are really Crustacea. Now, what are the synapomorphies of Crustacea? Really, what are the definite characters that define Crustacea as opposed to the rest of the arthropods? When you go back and include the fossil forms, it becomes very difficult to define Crustacea. I mean, there are lots of characters by which we define Crustacea but most of them are plesiomorphic if you compare them. I can't go into the details of Lauterbach's analysis, still it is not always quite clear whether all these forms we now call Crustacea are really crustacean. Before we use them in our discussions, we have to wait and analyse them and see if they are not something else. Because actually they are very far back in times when Crustacea evolved. Perhaps they were other groups which were near to the crustaceans or sister groups to Crustacea. Consequently, I think they don't tell us very much for the moment. Brian (Dr. Marcotte) said, that in the Permo-Triassic we had only large crustaceans. When I visited Müller in Bonn, he told me that he discovered them also in other periods of the Earth's history, I mean not only back in the Devonian. These minute things have been discovered also in later deposits. So, small crustaceans have always been there. It is not as if we had small ones, then bigger ones and then, by neoteny, smaller ones again. Being small is certainly an advantage, I agree with you. But neoteny is not the only way to become small. So I don't think this is convincing evidence that neoteny plays an important role in becoming a copepod. We should always keep in mind that there are quite different means for becoming small. Another thing is that, for example, Tisbe could be a model for a very primitive crustacean. You said that when they feed, their mouthparts look pretty much the same as the mouthparts of other groups, but this could be convergent. I think that similarity just doesn't tell us they are the same or that this is something that could be ancestral to other types. I think we have to look deeper into this and find new evidence, such evidence, for instance, as that Geoff (Dr. Boxshall) had proposed today. It is so difficult and there are so many aspects relating to different talks today that I do not know how we should proceed. Perhaps we should discuss different talks, one by one. How should we proceed?

Z. Kabata: If we do that, we will inevitably leave something out of the discussion. Perhaps we better let anybody with anything particularly pressing on his mind speak out, whatever the topic. Unfortunately, whatever we do, we are not going to cover everything. Dr. Björnberg, you had a question?

T. K. S. Björnberg: It is unfortunate that during all this discussion no one mentioned nauplii. It is unfortunate, because nauplii bring in evidence which in a way goes completely against a lot of what Andronov proposed. For instance, Clausocalanus, Microcalanus, Ctenocalanus, Calanus and all the calanids and paracalanids, all have the same nauplius. I am sorry, I have not discovered this. This was discovered by Oberg in 1906, and there is the work of Marshall and Orr, Mary Lebour and of many old-timers who worked on all these nauplii. They have been known at least since 1906. They are exactly alike, even their musculature is alike. They move in the same way. I cannot believe that there was a convergence of naupliar forms in these different species and genera. They can only be distinguished at first sight by their size and even then one has to look well at them, because there are several genera that have nauplii of the same size. This is why I think that there is something wrong with Andronov's classification. I am sorry to be repetitive, but you do have to look at the nauplii. When you do, you find that you cannot separate Clausocalanus and clausocalanids from the calanids and paracalanids. Calocalanids also have the same nauplius, but it is a little longer than the rest, so that it moves a little differently. It is not top-heavy like the nauplii of Calanus, Clausocalanus, Danocalanus and Paracalanus. It does not somersault but rather moves a little way and then gives a little somersault; then it does it again in the same way. So, if you want to separate anything, you might separate calocalanids. I would not do it myself, I think they are well placed together with paracalanids and calanids. The one group that from the point of view of nauplii cannot be broken up are the clausocalanids. They must belong together in one group with Calanus and Paracalanus and (if you do not want to split) also Calocalanus. Unfortunately, Megacalanus has no known nauplius. At any rate, once you know that these nauplii are so very much alike, it would be going a bit against the evidence of nature to separate animals with identical developmental stages. According to Williamson, and he has been generally acknowledged for his work on larvae, it is absolutely important that one considers all stages of development when one studies taxonomy of anything at all. I try to defend my nauplii by saying that most of the copepods in the world never reach the adult stage, they are eaten while still in the nauplius stage. A good reason why nauplii should be considered. There is one more thing: If you want to split anything, there is a big group that is considered homogeneous but on naupliar evidence is splitable. You can split the eucalanids. This group has two different nauplii, completely different even in their movements, their behaviour and their musculature. On the one hand, you have Rhincalanus and Eucalanus, the Eucalanus elongatus group which has nauplii derivable from those of the calanids. Hence, they must be very closely related to the calanids. On the other hand, you have Eucalanus pileatus, Eucalanus crassus which Fleminger placed in a different group. He set up four groups: Eucalanus elongatus, E. attenuatus, E. pileatus and E. subtenuis. The E. elongatus group is completely different from all the others because it has a nauplius exactly like that of Rhincalanus. There are minor differences between them only in the symmetry of the mouth. All the others have nauplii definitely far more similar to those of Centropages. The adult forms must have converged, because the nauplii are completely different, even in their movements.

Z. Kabata: Hands are rising all over the place. I think I should ask Dr. Park to comment, because calanoids were his subject. Perhaps he has a short comment.

T. S. Park: I do not have much experience with the nauplii. I really cannot make any valid comment because Dr. Björnberg has already substantiated her own evidence. However, I believe that the planktonic stages have their own specializations or their adaptations. As far as I can see, nauplii are simple when compared with adults. I believe that the adult structures also show a great deal of specialization, but if we select certain appendages we will find that primitive features are maintained by all groups. Only certain groups show some similarity of synapomorphies. Those similarities are similar specializations and they can be selected for classifying or for tracing phylogenies.

Z. Kabata: Thank you. Geoff (Dr. Boxshall), have you a comment?

G. A. Boxshall: I think you (Dr. Björnberg) are tending to fall into a trap in reverse to that we are falling into. You base your conclusions on nauplii, we do ours on adults. We obviously have to meet halfway. But I am very suspicious in many ways of naupliar evidence, because not so many are well known. In your lecture the other day you drew attention to the fact that nauplii of Longipedia and Canuella were sufficiently different to separate them from all the other harpacticoids, perhaps even to remove them from the group. Or am I taking it further than you would? When you consider the adults, there are good synapomorphies that link the harpacticoids together. Primarily the fusion of the endopod and the basis in the fifth leg, which forms a baso-endopod. It is a structure unique to the harpacticoids, is present in the longipedids and canuellids and in Oligoarthra, the other harpacticoids. It is a good, clean synapomorphy. On the other hand, some of the factors that we are looking at and that make longipedid nauplii so different are all plesiomorphic. If you adhere to a cladistic methodology, you cannot construct phylogenies on primitive characters, you have to look for advanced ones. There are enough advanced characters to produce a scheme of relationships for all the eight copepod orders. I think we ought to look at the nauplii as well and see if they have synapomorphies that support these arguments. But, looking at the adults we know there are synapomorphies to link them all in coherent, congruent (I use an "in" term) scheme.

Z. Kabata: Dr. Schminke, you have a comment?

H. K. Schminke: Actually, I want ask a few questions. Now, Dr. Ho, could we take another look at your "straw man"? (My first question about synapomorphies of harpacticoids has already been answered.) Now, it shows that you have synapomorphies mostly on the right-hand side. Let us take the Cyclopinidae the first family what is the synapomorphy of that family, because without one it is not a clear monophyletic grouping.

J.-s. Ho: I was asked to do this back in March. I did not have much time to go through all characteristics I could pick. So I restricted myself to the cephalosomatic appendages, that is why I have in the list from the first antenna all the way down to the maxilliped. I didn't take into consideration the swimming legs, fifth leg or any other characteristic. So if I have those, I think it will show somewhere here. On this line, on that line of the archinotodelphyids, on the line of the notodelphyids. By the way, in the notodelphyids there you can plug one in, right there, which is the brood pouch. That is the only one which has a brood pouch. None of the others have it. This is just an indication that if I have enough or many characteristics I can show something there. The time limit did not allow me to go through them all.

K. Schminke: All right, this is, then, a preliminary scheme, isn't it? It is a preliminary system, because if you have on the other side antenna two without exopod, this reduction is not a very strong character in my opinion. Yet, you have a lot of conclusions drawn from this table. This is why I thought it was more important than it appears to be now.

J.-S. Ho: In answer to your question about the reduction of the exopod in the second antenna, it came up because I made a comparison with the misophrioids and they have the exopod, which this group doesn't have. This showed the synapomorphy of the entire cyclopoids.

H.K. Schminke: Geoff, I have a question for you. You said that the Siphonostomata are monophyletic. Yet there are other people who say they are polyphyletic. Now, how many species of siphonostomes have you studied? I believe the way to do it would be to ask the people: which are the different groups that are considered to have originated polyphylogenetically, and then study one species in each of these groups. If they show the character you have shown, I think I will be convinced. But just one, (it is only one that you have studied, isn't it?) cannot be accepted as a definitive end of the discusssion.

G. A. Boxshall: That is a rotten question. I have looked at three. One of them is somewhat primitive, Hyalopontius is definitely more primitive than Pontoeciella which is an invertebrate-inhabiting form, and caligids. Those two from the two different categories of host type can be linked together as advanced siphonostomes, and the other one is a plesiomorphic siphonostome. There are other characters that link the siphonostomes, they do have another synapomorphy in the entire phylogenetic scheme. If you have taken off some of your other groups first, by the time you get there, there is another one and that is your exopod again, of the antenna.

F. D. Ferrari: I would like to ask the panellist to look into the future instead of the past and think along other lines. Several years ago Max Hecht wrote an important paper on the evolution in which he suggested that the patterns of reduction contained the least evolutionarily significant information, especially if the underlying genetic systems are widespread, leading to many parallel origins. We also today have widespread evidence of the genetic systems which can add elements in arthropods. So, looking into the future 100 years from now, when your sons and daughters sit here to analyze copepods, will they still be making use of somewhat evolutionarily uninformative seuqences of reduction?

G. A. Boxshall: In our little postscript from Amsterdam we said that the implicit assumption is made that evolution in copepods and Crustacea generally proceeds through reduction, fusion and loss. I agree. Hecht said in that NATO paper that reduction and loss are the worst categories of character that you can use, but there is nothing else. Evolution seems to go that way. There is very little evidence of the addition of novel structures in the evolution of copepods, such structures as there are tend to be rather small and specialized like the pigment blob in Pleuromamma and various other particular items you can choose but say the fifth leg of the calanoid male. It is a highly modified, specialized grappling apparatus but it hasn't any additional elements. It's got superficial complexity superimposed upon its existing trimerous, biramous structure. It has no new elements as far as I am aware.

F. D. Ferrari: That escapes the point. The point is we can have reduction and then a re-addition and I think that there are genetic factors that enable you to do that.

G. A. Boxshall: If you say evolutionary reversals are commonplace then I say that until we have evidence from the geneticists and biochemists that this is common we have to take things at face value. Otherwise you have no system at all.

I have a phylogenetic scheme for the whole Copepoda based almost solely on reduction characters.

Voice from the floor: Could you tell us about it?

G. A. Boxshall: That was not a planted question, Mr. Chairman, is it appropriate to show this scheme as another "straw man"(Fig. 1)?

Z. Kabata: Please do.

G. A. Boxshall: One or two people have already seen this, but I have made some slight modifications. It has been pointed out to me that I have my basi-endopod in a wrong place, but we will get to that. Right.

Character 1. The apomorphy for the Calanoida is the prosome-urosome articulation position. It's a good character for the Gymnoplea and it serves to diagnose the Calanoida. Character 2, therefore, is going to be the differing position of the prosome-urosome articulation in Podoplea; the latter comprising the rest of the Copepoda. So far no reduction. Character 3, there is a reduction. This is a loss of a separate distinct coxoexite on the first maxilla. Calanoids have one, it doesn't have an articulation but it has a suture at the base and it has a muscle, an extrinsic muscle that originates up in the body and passes right through the precoxa-coxa and into the exites. In all podopleans the exite is incorporated into the coxal segment. In many of the groups you have a cluster of setae there but in none that I am aware of do you have a suture line separating the exite from the coxa. The misophrioids (I did not put them all in) have the carapace and that will do. I thought that the separation of misophrioids as a sister group of the rest of the Podoplea was going to be a problem, but I found three characters which I was very pleased with at the time, though I discover now that it should only be two. First is loss of the heart. The heart is retained in misophrioids and calanoids but none of the others have a heart - Character 4. Character 5 is the loss of a separate articulated endopod on the fifth leg. One misophrioid, Misophriopsis, has this separate endopod, none of the others do. Character 6 is the fusion

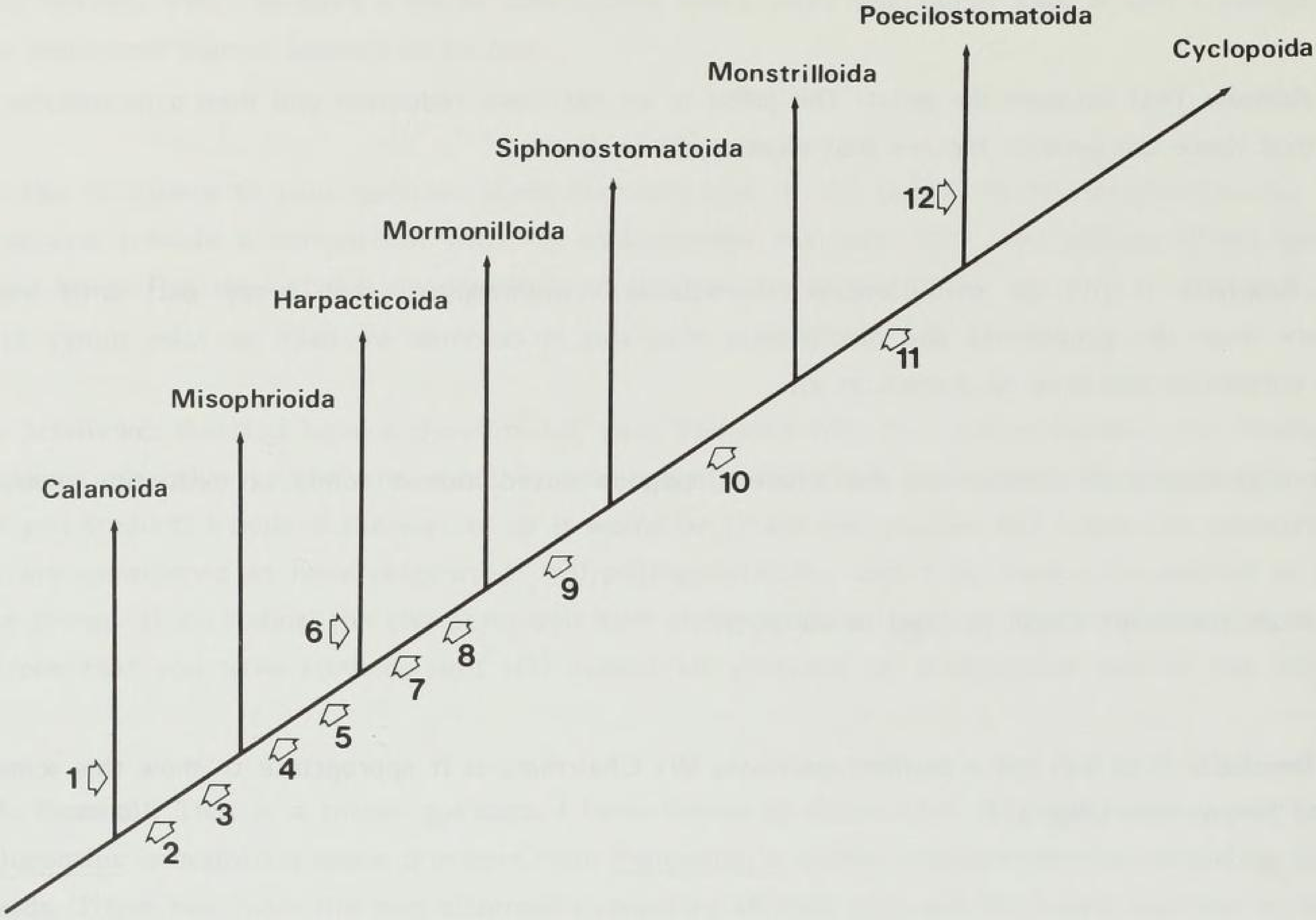

Figure 1. *Significant characters in copepod phylogeny*

1. *Prosome-urosome junction between thoracic somites 6 and 7*
2. *Prosome-urosome junctions between thoracic somites 5 and 6*
3. *Loss of separate maxillulary exite with basal suture*
4. *Partial fusion of gential somite and first abdominal somite to form genital double somite with suture*
5. *Loss of heart*
6. *Possession of baseoendopod on fifth leg*
7. *Complete fusion of genital and first abdominal somites to form genital complex without suture*
8. *Loss of endopod of fifth leg*
9. *Reduction of antennary exopod to 1 segment*
10. *Loss of antennary exopod*
11. *Female genital openings lateral or dorsolateral*
12. *Falcate mandible*

of what's left of the endopod with the basis so the baso-endopod is in fact a synapomorphy of the harpacticoids. Here, where I have it, it becomes a synapomorphy of all the rest; it is lost later on. Characters 7 and 8 are synapomorphies for all the rest. Seven is the complete fusion of the genital segment and the first abdominal segment. To my knowledge in all of these, from the harpacticoids onwards, there is no suture line separating these two segments. They completely fuse into a genital complex. They are partially fused in the harpacticoids, but you often have a suture line left, indicating quite clearly that it was a functional articulation fairly recently in their ancestry. Character 8 is a non-starter because I had to move the baso-endopod, but we have one synapomorphy there that is a reasonable one; it is a fusion not a loss. We have removed the first three and what we are left with is a mixture of three well-defined groups: the mormonilloids, these funny, little, planktonic, sexless jobs; the monstrilloids which we haven't mentioned, a token parasitic group. Their nauplii are internal parasites of polychaetes and the adults are free-swimming and planktonic. You can't use them much because they have a first antenna and swimming legs and nothing in between. However, character 9, which is a synapomorphy linking all these and separating the mormonilloids, is the reduction of the antennary exopod to at most two segments. In fact, I think it is an exopod reduced to one segment. I don't know of examples of two but there are possibilities. Mormonilloids still retain eight. They still have a very well developed antennary exopod. Now it starts to get a bit tricky. In siphonostomes we have a synapomorphy for the mandible, but I found it rather difficult to separate from here clearly. Character 10 which I have to use with apologies is the loss of the antennary exopod. Poecilostomes, cyclopoids, and monstrilloids do not have an antennary exopod. The logical flaw here is that monstrilloids do not have an antenna, but when you are desperate you will use anything. The monstrilloids have not really been incorporated into any coherent system, because they lack so many characters. What characters they do have tend to be unique. Character 11, and I was not too sure about it, for me was the lateral or dorsolateral position of the genital openings of the female. Cyclops, if you can visualize it, has these paired egg sacs coming out dorsally. The ancestral plesiomorphic position of the copepods is ventral genital openings. Poecilostomes and cyclopoids, as far as I am aware (and that's not very far) have either lateral or dorsal, or maybe that is a mixed character, but not ventral, anyway. That brings us right up to the poecilostomes and cyclopoids. As Prof. Stock has said the separation here is not particulary clear. I just have this falcate mandible, the lash of the mandibular gnathobase, but the order of separation might only be subordinal if all of these are ordinal, but there are clearly two lineages there. It ist just a question of disagreeing at what level they should be classified.

I am prepared to be shot down now, because there is a number of groups that I know almost nothing about.

Dr. Z. Kabata: Any comments?

T.K.S. Björnberg: I think in all this we haven't yet considered an important factor, which is that the oldest group in the world will not show any more primitive forms. It will present a lot of forms which are extremely adapted to different niches and it also has the greatest number of species. It has had time to adapt to the pressures of the environment and to different kinds of habitats and different modes of life. I think this is something we should think about and not only from the naupliar evidence but also from the number of species. The nauplii of the cyclopoids, the Poecilostomatoida and the Siphonostomatoida are very much alike. They are also most primitive, from the point of view of the Urcrustacean. Judging by the number of species that form this group, which has now been separated into three, if I were asked to vote which one is the oldest: the Calanoida, Harpacticoida or the Cyclopoida plus Poecilostomatoida and Siphonostomatoida, I would vote for the last one because they have the greatest number of species adaptations. They have invaded all the possible habitats and they are well established in all of them. They have invaded the free living marine ambient, they are parasitic and commensal, they are also found in freshwater in great quantity, and they are living in the benthos. This is something to think about.

Z. Kabata: Thank you Dr. Björnberg. You have touched upon a fascinating topic. We are talking now about rates of evolution and various other things. Would anybody like to comment? Prof. Por, you wanted to comment?

F.D. Por: Just a question. You know that I like my Canuellidae very much. They are supposed to occupy a primitive position. What do you think of the separate thoracic segment?

G.A. Boxshall: The segment bearing the first leg? It is entirely separate in the misophrioids as well.

F.D. Por: All right, but this puts the Canuellidae in a position separate from other Harpacticoida.

G. A. Boxshall: None of these characters refer to the incorporation of the first pedigerous somite.

F.D. Por: But you could use it.

G.A. Boxshall: It is too convergent, it happens in all the lineages that I know of.

F.D. Por: I see. Thank you.

Z. Kabata: There are two or three more comments. Dr. Schminke, please.

H.K. Schminke: I would like to comment on Dr. Björnberg's remarks just now. She was saying that because they had radiated into all habitats, they should be the oldest. Now, look at other groups of animals. If for instance you look at the mites, within the Arachnida they are certainly the group that has radiated the most, yet it is not the most primitive. Also you can take the flies within the insects. Flies have radiated practically everywhere yet they are not the most primitive and oldest insects. And take the ophiurids among the echinoderms, which are the most widespread in different habitats and, as far as I know, are not the most primitive. So I don't think that radiation is a good sign for telling us which should be the oldest and which should be the youngest. It's just a matter of striking the right situation and the right time and they radiate into these niches regardless of the period when this has happened.

Z. Kabata: Thank you Dr. Schminke. We have time for two or three more questions, or comments. Dr. Hulsemann, please.

K. Hulsemann: I think that one could argue the other way around and say if a group has spread very much these are all members of the groups that are still surviving and if we have just one or two of a group or very few numbers, others may have died off. So, it would be just the opposite.

D. Soto: It seems to me that all the apomorphies in this case are reductions and fusions, so you can almost predict that the future evolution of the copepods is going to a very simple situation, almost a one cell condition. There is no place for reversion, it seems. I wonder if some of the problems are because of that, because reversions have not been considered as an evolutionary possibility.

G.A. Boxshall: I am open-minded. I can consider anything but you have to work with the characters you have. It is possible there are reversions but what can you do? You have to use the characters there are. If you find other characters that are better, that show noncongruents and therefore convergence or reversions, that's fine. You have to set up to disprove it and the onus is on you to disprove it, otherwise we will have no system at all. I agree some of the characters down here (in the diagram) are reasonable, they are fusions. You can at least work out the homologies when you have got fusions. In the first antenna you have armature elements that can help you to identify what segments you are dealing with, it can give you homologies right through. For example, in the vast majority of calanoids the primitve segments 2, 3, and 4 are all fused into a triple segment, and segment 2 has three sets of armature elements. Now, these are really nice homologies that link some of the groups, but there is nothing else. I have puzzled over this long and hard, 20 minutes. I really couldn't come up with anything else.

J.-s. Ho: This character reversal and the homoplasy which is a synonym of convergence and parallelism and used to be a "systematist's nightmare" are the things we would like to forget about in doing cladistic analysis. Recently they have been trying to take that into consideration, so I think that in perhaps 2 or 3 years from now we will see that there is a good way of analyzing character reversal. How do we explain when it happens?

Taisoo Park: In calanoids, of course, specialization seems to be the trend, but the crucial thing is the reduction of the appendages, the same time there is an increase in the complexities within a group. Such as the undinellids. If you know male Undinellidae, you know that they are primitive in every aspect, but the male's leg is enormously complex as it is also in the Centropagidae. Centropages retains very primitive features, but there are many species in Centropagidae, including the species that I have studied, Epilabidocera, in which the antennules and the fifth pair of legs become extremely complex. These complexities go in parallel with increased complexity of behaviour.

Z. Kabata: Thank you. We have time for only one more question. Dr. Sieg.

J. Sieg: I would like to make a comment on reduction. I think it is very bad when people start to think that structures which have been lost may come back. I have seen many such structures that I had been told have come back, but wherever I have analyzed these structures very carefully, I have found that they were different structures of quite different origin. So they were not homologous. As we normally have to compare characters, we always have to compare homologous characters and not analogous ones. If you pick the wrong structure and compare it with another one you will never arrive at a system which works.

Z. Kabata: Thank you very much, Dr. Sieg. I am afraid that we will have to terminate this interesting discussion.

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DISCUSSION

Edited by Z. Kabata

F.D. Por: I have a few comments. My first comment is related to the antiquity of copepods. In my view, we should definitely think of a very early origin of the copepods and not of aMesozoic one, as suggested by Brian (Dr. Marcotte). I would refer to a very recent paper on the fossil microcrustaceans from the Cambrian, so-called "ersten Crustaceen", described by Muller. These are obviously micro-crustaceans, meiobenthic beasts, very small, millimetre-sized and clearly showing many archicopepodid characters, or characters intermediate between copepods and Ascothoracida. We are clearly dealing with a very, very old, at least Cambrian, group when we speak of copepods.

Now, this brings us to Cambrian environments. It is clear that during the Cambrian the fresh waters were not yet inhabited. So freshwater copepods must be younger. I daresay that the phyto-environment, the algal flora, was not yet developed at that time. In general, modern algae are later than the Cambrian, and of course the pelagic environment, open ocean environment, was not in being in the Cambrian. The algae as we know them are probably Mesozoic, dating back to the time when diatoms and coccoliths appear. Therefore, we have to speak of bottom-living, small animals eating detritus, or whatever was available. I think we cannot go to the present big groups to find something near to the copepods, neither to the cyclopoids, nor the calanoids, and probably not to the majority of the harpacticoids. Since copepods are very old, I think we have to find a few small groups of "living fossils". They might be the mormonilloids or some of the primitive harpacticoids.

It's clear that the calanoids, at least the open sea calanoids, are a new, Cretaceous group. The majority of freshwater cyclopoids, because they show a very nice separation between gondwanic and laurasian groups, are also late, post-Triassic We might, however, here and there, have also very old inhabitants of fresh-water, of course, probably not earlier than Devonian. They might be para-stenocarids or similar groups, and again here we have to find some living fossils. In general, when we speak of cyclopoids, the majority of calanoids and the vast majority of harpacticoids, that is harpacticoids which have grasping PI, grasping maxillipeds, these are late-comers that had arrived after' phyto-environments of the globe became well developed. This means they had to be post-Cambrian.

Z. Kabata: Thank you, Prof. Por. Well, we have been shown only yesterday an early Cretaceous parasitic copepod which was extremely well developed. It does take some time to develop this kind of form. This would rather favour the theory of an earlier origin. Perhaps Brian (Dr. Marcotte) would like to say something about that.

B.M. Marcotte: The only comment is that phytoflageliates occurred in the Devonian for the first time, so that there were at least some materials in the phytoplankton for planktonic organisms to ingest. Interestingly enough, the diatoms occurred in the Cretaceous at periods of turbidity maxima, organisms with specialized pigment systems to absorb wavelengths of light that occurred in turbid water, so it kind of buffers the thing. As to the origin of the copepods in the Cambrian, I do not know. I am cautious, though, because copepod-like limbs do occur, for example, in Scourfield's branchiopod-like creature and elsewhere. It could be that at least the thoracic limbs, the swimming-type limbs of

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copepods, do occur convergently in several crustacean groups. 1 just don't know enough about the microfossils in the Cambrian, except I haven't seen a copepod there yet. I have seen things that share some say I have seen one. I would more likely expect one in the Silurian-Devonian. In the Silurian you start having a lot of creatures leaving the sea and going into fresh-water. The first freshwater ostracods occur in the Devonian to lower Carboniferous. Things are getting out, I presume, of a turbid ocean, of an ocean that is anoxic and getting crowded, and presumably coastal environments are very competitive at that point, if they were not before. I don't know.

J.-S. Ho: I have some comments to make on that. The palaeontologists tell us of the so-called Permo-Triassic bottleneck. This means that between 80% and 95% of marine organisms died off during that period, let's call it Permo-Triassic. In other words, only very few marine organisms made it through the Palaeozoic and into the Mesozoic. Whether the copepods are one of the surviving groups we do not know because we don't have the fossil records. Therefore, if we must rely on the fossil records, I would say it is hopeless.

B.M. Marcotte: I think you can. There is this notion that the Permo-Triassic boundary extinguished all kinds of organisms. In fact it didn't. The extinction of most filter-feeding organisms, most organisms dependent upon symbiotic algae (or at least presumed to have been dependent upon them), the complementary origin of deposit-feeding bivalves, the extinction of visually foraging organism, whether they are nautiloids or trilobites, all begin at the Ordovician and continue without interruption to the Permo-Triassic boundaries. It is true that there was something that stopped a lot of organisms, like trilobites, but things that were foraging visually, or filter-feeding, were having real problems long before, 150 million years before and longer. This gets back to this notion that oceans may have been getting more turbid, that vision was becoming a limiting resource for foraging, filter-feeding was a problem and animals became deposit-feeders or chemoreceptive. The last of the trilobites to exist with primitive eyes were in clear tropical waters. So, at any rate, there is more to the story than simply an extinction at the Permo-Triassic boundary. There is a great lot of detail, if you look at sensory modalities instead of looking only at the number of genera. You see a lot more of what has been going on earlier.

Z. Kabata: Geoff (Dr. Boxshall), have you any comments?

G.A. Boxshall: I would have to agree on the ancient origin of at least an ancestral type of copepods. Muller found some very interesting microcrustaceans in his Cambrian-Austin. The naupiius stage of one of them will be shown tomorrow in Geoffrey Fryer's talk. I oppose Maxillopoda as a taxon. There are taxa described by Mùller in 1983 that conform precisely to the 5-6-5 cephalon-thorax-abdomen (or 5-7-4, depending on how you divide the trunk into thorax and abdomen). Both of these can be accommodated into the maxillopodan plan. There are animals in Muller' s paper which have exactly this plan: a cephalon of 5 segments, with 5 paired appendages and a large labrum; there is a thorax with 6

pairs of biramous thoracopods, and there are k or 3 segments in the urosome, the first of them bearing the genital openings. No, I don't like the Maxillopoda, but you can't argue against the facts.

Z. Kabata: Thank you. Does it exhaust our discussion of this question? Dr. Schminke?

H.K. Schminke: The trouble is, we all think they are Crustacea, these ones that have been discovered by Muller. In fact, Lauterbach is beginning to question whether they are really Crustacea. Now, what are the synapomorphies of Crustacea? Really, what are the definite characters that define Crustacea as opposed to the rest of the arthropods? When you go back and include the fossil forms, it becomes very difficult to define Crustacea. 1 mean, there are lots of characters by which we define Crustacea but most of them are plesiomorphic if you compare them. I can't go into the details of Lauterbach' s analysis, still it is not always quite clear whether all these forms we now call Crustacea are really crustacean. Before we use them in our discussions, we have to wait and analyse them and see if they are not something else. Because actually they are very far back in times when Crustacea evolved. Perhaps they were other groups which were near to the crustaceans or sister groups to Crustacea. Consequently, I think they don't tell us very much for the moment. Brian (Dr. Marcotte) said, that in the Permo-Triassic we had only large crustaceans. When I visited Muller in Bonn, he told me that he discovered them also in other periods of the Earth's history, I mean not only back in the Devonian. These minute things have been discovered also in later deposits. So, small crustaceans have always been there. It is not as if we had small ones, then bigger ones and then, by neoteny, smaller ones again. Being small is certainly an advantage, I agree with you. But neoteny is not the only way to become small. So I don't think this is convincing evidence that neoteny plays an important role in becoming a copepod. We should always keep in mind that there are quite different means for becoming small. Another thing is that, for example, Tisbe could be a model for a very primitive crustacean. You said that when they feed, their mouthparts look pretty much the same as the mouthparts of other groups, but this could be convergent. I think that similarity just doesn't tell us they are the same or that this is something that could be ancestral to other types. I think we have to look deeper into this and find new evidence, such evidence, for instance, as that Geoff (Dr. Boxshall) had proposed today. It is so difficult and there are so many aspects relating to different talks today that I do not know how we should proceed. Perhaps we should discuss different talks, one by one. How should we proceed?

Z. Kabata: If we do that, we will inevitably leave something out of the discussion. Perhaps we better let anybody with anything particularly pressing on his mind speak out, whatever the topic. Unfortunately, whatever we do, we are not going to cover everything. Dr. Bjôrnberg, you had a question?

T. K. S. Bjôrnberg: It is unfortunate that during all this discussion no one mentioned nauplii. It is unfortunate, because nauplii bring in evidence which in a way goes completely against a lot of what Andronov proposed. For instance, Clausocalanus, Microcalanus, Ctenocalanus, Calanus and all the calanids and paracalanids, all have the same nauplius. I am sorry, I have not discovered this. This was discovered by Oberg in 1906, and there is the work of Marshall and Orr, Mary Lebour and of many old-timers who worked on all these nauplii. They have been known at least since 1906. They are exactly alike, even their musculature is alike. They move in the same way. I cannot believe that there was a convergence of naupliar forms in these different species and genera. They can only be distinguished at first sight by their size and even then one has to look well at them, because there are several genera that have nauplii of the same size. This is why I think that there is something wrong with Andronov's classification. I am sorry to be repetitive, but you do have to look at the nauplii. When you do, you find that you cannot separate Clausocalanus and clausocalanids from the calanids and paracalanids. Calocalanids also have the same nauplius, but it is a little longer than the rest, so that it moves a little differently. It is not top-heavy like the nauplii of Calanus, Clausocalanus, Danocalanus and Paracalanus. It does not somersault but rather moves a little way and then gives a little somersault; then it does it again in the same way. So, if you want to separate anything, you might separate calocalanids. I would not do it myself, I think they are well placed together with paracalanids and calanids. The one group that from the point of view of nauplii cannot be broken up are the clausocalanids. They must belong together in one group with Calanus and Paracalanus and (if you do not want to split) also Calocalanus. Unfortunately, Megacalanus has no known nauplius. At any rate, once you know that these nauplii are so very much alike, it would be going a bit against the evidence of nature to separate animals with identical developmental stages. According to Williamson, and he has been generally acknowledged for his work on larvae, it is absolutely important that one considers all stages of development when one studies taxonomy of anything at all. I try to defend my nauplii by saying that most of the copepods in the world never reach the adult stage, they are eaten while still in the nauplius stage. A good reason why nauplii should be considered. There is one more thing: If you want to split anything, there is a big group that is considered homogeneous but on naupliar evidence is splitable. You can split the eucalanids. This group has two different nauplii, completely different even in their movements, their behaviour and their musculature. On the one hand, you have Rhincalanus and Eucalanus, the Eucalanus elongatus group which has nauplii derivable from those of the calanids. Hence, they must be very closely related to the calanids. On the other hand, you have Eucalanus pileatus, Eucalanus crassus which Fleminger placed in a different group. He set up four groups: Eucalanus elongatus, E. attenuatus, E. pileatus and E. subtenuis. The E. elongatus group is completely different from all the others because it has a nauplius exactly like that of Rhincalanus. There are minor differences between them only in the symmetry of the mouth. All the others have nauplii definitely far more similar to those of Centropages. The adult forms must have converged, because the nauplii are completely different, even in their movements.

Z. Kabata: Hands are rising all over the place. I think I should ask Dr. Park to comment, because calanoids were his subject. Perhaps he has a short comment.

T. S- Park: I do not have much experience with the nauplii. I really cannot make any valid comment because Dr. Bjôrnberg has already substantiated her own evidence. However, I believe that the planktonic stages have their own specializations or their adaptations. As far as I can see, nauplii are simple when compared with adults. I believe that the adult structures also show a great deal of specialization, but if we select certain appendages we will find that primitive features are maintained

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by all groups. Only certain groups show some similarity of synapomorphies. Those similarities are similar specializations and they can be selected for classifying or for tracing phylogenies.

Z. Kabata: Thank you. Geoff (Dr. Boxshall), have you a comment?

G. A. Boxshall: I think you (Dr. Bjôrnberg) are tending to fall into a trap in reverse to that we are falling into. You base your conclusions on nauplii, we do ours on adults. We obviously have to meet halfway. But I am very suspicious in many ways of naupliar evidence, because not so many are well known. In your lecture the other day you drew attention to the fact that nauplii of Longipedia and

Canuella were sufficiently different to separate them from all the other harpacticoids, perhaps even to remove them from the group. Or am I taking it further than you would? When you consider the adults, there are good synapomorphies that link the harpacticoids together. Primarily the fusion of the endopod and the basis in the fifth leg, which forms a baso-endopod. It is a structure unique to the harpacticoids, is present in the longipedids and canuellids and in Oligoarthra, the other harpacticoids. It is a good, clean synapomorphy. On the other hand, some of the factors that we are looking at and that make longipedid nauplii so different are all plesiomorphic If you adhere to a cladistic methodology, you cannot construct phylogenies on primitive characters, you have to look for advanced ones. There are enough advanced characters to produce a scheme of relationships for all the eight copepod orders. I think we ought to look at the nauplii as well and see if they have synapomorphies that support these arguments. But, looking at the adults we know there are synapomorphies to link them all in coherent, congruent (I use an "in" term) scheme.

Z. Kabata: Dr. Schminke, you have a comment?

H. K. Schminke: Actually, I want ask a few questions. Now, Dr. Ho, could we take another look at your "straw man"? (My first question about synapomorphies of harpacticoids has already been answered.) Now, it shows that you have synapomorphies mostly on the right-hand side. Let us take the Cyclopinidae the first family what is the synapomorphy of that family, because without one it is not a clear monophyletic grouping.

J.-s. Ho: I was asked to do this back in March. I did not have much time to go through all characteristics I could pick. So I restricted myself to the cephalosomatic appendages, that is why I have in the list from the first antenna all the way down to the maxilliped. I didn't take into consideration the swimming legs, fifth leg or any other characteristic. So if I have those, I think it will show somewhere here. On this line, on that line of the archinotodelphyids, on the line of the notodelphyids. By the way, in the notodelphyids there you can plug one in, right there, which is the brood pouch. That is the only one which has a brood pouch. None of the others have it. This is just an indication that if I have enough or many characteristics I can show something there. The time limit did not allow me to go through them all.

K. Schminke: All right, this is, then, a preliminary scheme, isn't it? It is a preliminary system, because if you have on the other side antenna two without exopod, this reduction is not a very strong character in my opinion. Yet, you have a lot of conclusions drawn from this table. This is why I thought it was more important than it appears to be now.

J.-S. Ho: In answer to your question about the reduction of the exopod in the second antenna, it came up because I made a comparison with the misophrioids and they have the exopod, which this group doesn't have. This showed the synapomorphy of the entire cyclopoids.

H.K. Schminke: Geoff, I have a question for you. You said that the Siphonostomata are monophyletic Yet there are other people who say they are polyphyletic. Now, how many species of siphonostomes have you studied? I believe the way to do it would be to ask the people: which are the different groups that are considered to have originated polyphylogenetically, and then study one species in each of these groups. If they show the character you have shown, I think I will be convinced. But just one, (it is only one that you have studied, isn't it?) cannot be accepted as a definitive end of the discussssion.

G. A. Boxshall: That is a rotten question. I have looked at three. One of them is somewhat primitive, Hyalopontius is definitely more primitive than Pontoeciella which is an invertebrate-inhabiting form, and caligids. Those two from the two different categories of host type can be linked together as advanced siphonostomes, and the other one is a plesiomorphic siphonostome. There are other characters that link the siphonostomes, they do have another synapomorphy in the entire phylogenetic scheme. If you have taken off some of your other groups first, by the time you get there, there is another one and that is your exopod again, of the antenna.

F. D. Ferrari: I would like to ask the panellist to look into the future instead of the past and think along other lines. Several years ago Max Hecht wrote an important paper on the evolution in which he suggested that the patterns of reduction contained the least evoiutionarily significant information, especially if the underlying genetic systems are widespread, leading to many parallel origins. We also today have widespread evidence of the genetic systems which can add elements in arthropods. So, looking into the future 100 years from now, when your sons and daughters sit here to analyze copepods, will they still be making use of somewhat evoiutionarily uninformative seuqences of reduction?

G. A. Boxshall: In our little postscript from Amsterdam we said that the implicit assumption is made' that evolution in copepods and Crustacea generally proceeds through reduction, fusion and loss. I agree. Hecht said in that NATO paper that reduction and loss are the worst categories of character that you can use, but there is nothing else. Evolution seems to go that way. There is very little evidence of the addition of novel structures in the evolution of copepods, such structures as there are tend to be rather small and specialized like the pigment blob in Pleuromamma and various other particular items you can choose but say the fifth leg of the calanoid male. It is a highly modified, specialized grappling

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apparatus but it hasn't any additional elements. It's got superficial complexity superimposed upon its existing trimerous, biramous structure. It has no new elements as far as I am aware.

F. D. Ferrari: That escapes the point. The point is we can have reduction and then a re-addition and I think that there are genetic factors that enable you to do that.

G. A. Boxshall: If you say evolutionary reversals are commonplace then I say that until we have evidence from the geneticists and biochemists that this is common we have to take things at face value. Otherwise you have no system at all.

I have a phylogenetic scheme for the whole Copepoda based almost solely on reduction characters.

Voice from the floor: Could you tell us about it?

G. A. Boxshall: That was not a planted question, Mr. Chairman, is it appropriate to show this scheme as another "straw man" (Fig. 1)?

Z. Kabata: Please do.

G. A. Boxshall: One or two people have already seen this, but I have made some slight modifications. It has been pointed out to me that I have my basi-endopod in a wrong place, but we will get to that. Right.

Character 1. The apomorphy for the Calanoida is the prosome-urosome articulation position. It's a good character for the Gymnoplea and it serves to diagnose the Calanoida. Character 2, therefore, is going to be the differing position of the prosome-urosome articulation in Podoplea; the latter comprising the rest of the Copepoda. So far no reduction. Character 3, there is a reduction. This is a loss of a separate distinct coxoexite on the first maxilla. Calanoids have one, it doesn't have an articulation but it has a suture at the base and it has a muscle, an extrinsic muscle that originates up in the body and passes right through the precoxa-coxa and into the exites. In all podopleans the exite is incorporated into the coxal segment. In many of the groups you have a cluster of setae there but in none that I am aware of do you have a suture line separating the exite from the coxa. The misophrioids (I did not put them all in) have the carapace and that will do. I thought that the separation of misophrioids as a sister group of the rest of the Podoplea was going to be a problem, but I found three characters which

I was very pleased with at the time, though I discover now that it should only be two. First is loss of the heart. The heart is retained in misophrioids and calanoids but none of the others have a heart - Character k. Character 5 is the loss of a separate articulated endopod on the fifth leg. One misophrioid, Misophriopsis, has this separate endopod, none of the others do. Character 6 is the fusion

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Poecilostomatoida

Monstrilloida

Siphonostomatoida

Mormon

illoida

Harpac

ticoida

Misophrioida

Calanoida

/°*

60

y^

10

Sb 8

7

121)

Cyclopoida

10

Figure J. Significant characters in copepod phylogeny

1. Prosome-urosome junction between thoracic somites 6 and 7

2. Prosome-urosome junctions between thoracic somites 5 and 6

3. Loss of separate maxillulary exite with basal suture

4. Partial fusion of gential somite and first abdominal somite to form genital double somite with suture

5. Loss of heart

6. Possession of baseoendopod on fifth leg

7. Complete fusion of genital and first abdominal somites to form genital complex without suture

8. Loss of endopod of fifth leg

9. Reduction of antennary exopod to 1 segment

10. Loss of antennary exopod

11. Female genital openings lateral or dorsolateral

12. Falcate mandible

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of what's left of the endopod with the basis so the baso-endopod is in fact a synapomorphy of the harpacticoids. Here, where I have it, it becomes a synapomorphy of all the rest; it is lost later on. Characters 7 and 8 are synapomorphies for all the rest. Seven is the complete fusion of the genital segment and the first abdominal segment. To my knowledge in all of these, from the harpacticoids onwards, there is no suture line separating these two segments. They completely fuse into a genital complex. They are partially fused in the harpacticoids, but you often have a suture line left, indicating quite clearly that it was a functional articulation fairly recently in their ancestry. Character 8 is a non-starter because I had to move the baso-endopod, but we have one synapomorphy there that is a reasonable one; it is a fusion not a loss. We have removed the first three and what we are left with is a mixture of three well-defined groups: the mormonilloids, these funny, little, planktonic, sexless jobs; the monstrilloids which we haven't mentioned, a token parasitic group. Their nauplii are internal parasites of polychaetes and the adults are free-swimming and planktonic. You can't use them much because they have a first antenna and swimming legs and nothing in between. However, character 9, which is a synapomorphy linking all these and separating the mormonilloids, is the reduction of the antennary exopod to at most two segments. In fact, I think it is an exopod reduced to one segment. I don't know of examples of two but there are possibilities. Mormonilloids still retain eight. They still have a very well developed antennary exopod. Now it starts to get a bit tricky. In siphonostomes we have a synapomorphy for the mandible, but I found it rather difficult to separate from here clearly. Character 10 which I have to use with apologies is the loss 1 of the antennary exopod. Poecilostomes, cyclopoids, and monstrilloids do not have an antennary exopod. The logical flaw here is that monstrilloids do not have an antenna, but when you are desperate you will use anything. The monstrilloids have not really been incorporated into any coherent system, because they lack so many characters. What characters they do have tend to be unique. Character 11, and I was not too sure about it, for me was the lateral or dorsolateral position of the genital openings of the female. Cyclops, if you can visualize it, has these paired egg sacs coming out dorsally. The ancestral plesiomorphic position of the copepods is ventral genital openings. Poecilostomes and cyclopoids, as far as I am aware (and that's not very far) have either lateral or dorsal, or maybe that is a mixed character, but not ventral, anyway. That brings us right up to the poecilostomes and cyclopoids. As Prof. Stock has said the separation here is not particulary clear. I just have this falcate mandible, the lash of the mandibular gnathobase, but the order of separation might only be subordinal if all of these are ordinal, but there are clearly two lineages there. It ist just a question of disagreeing at what level they should be classified.

I am prepared to be shot down now, because there is a number of groups that I know almost nothing about.

Dr. Z. Kabata: Any comments?

T.K.S. Bjôrnberg: I think in all this we haven't yet considered an important factor, which is that the oldest group in the world will not show any more primitive forms. It will present a lot of forms which are extremely adapted to different niches and it also has the greatest number of species. It has had time to adapt to the pressures of the environment and to different kinds of habitats and different

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modes of life. I think this is something we should think about and not only from the naupliar evidence but also from the number of species. The nauplii of the cyclopoids, the Poecilostomatoida and the

Siphonostomatoida are very much alike. They are also most primitive, from the point of view of the Urcrustacean. Judging by the number of species that form this group, which has now been separated into three, if I were asked to vote which one is the oldest: the Calanoida, Harpacticoida or the Cyclopoida plus Poecilostomatoida and Siphonostomatoida, I would vote for the last one because they have the greatest number of species adaptations. They have invaded all the possible habitats and they are well established in all of them. They have invaded the free living marine ambient, they are parasitic and commensal, they are also found in freshwater in great quantity, and they are living in the benthos. This is something to think about.

Z. Kabata: Thank you Dr. Bjôrnberg. You have touched upon a fascinating topic. We are talking now about rates of evolution and various other things. Would anybody like to comment? Prof. Por, you wanted to comment?

F.D. Por: Just a question. You know that I like my Canuellidae very much. They are supposed to occupy a primitive position. What do you think of the separate thoracic segment?

G.A. Boxshall: The segment bearing the first leg? It is entirely separate in the misophrioids as well.

F.D. Por: All right, but this puts the Canuellidae in a position separate from other Harpacticoida.

G. A. Boxshall: None of these characters refer to the incorporation of the first pedigerous somite.

F.D. Por: But you could use it.

G.A. Boxshall: It is too convergent, it happens in all the lineages that I know of.

F.D. Por: I see. Thank you.

Z. Kabata: There are two or three more comments. Dr. Schminke, please.

H.K. Schminke: I would like to comment on Dr. Bjôrnberg's remarks just now. She was saying that because they had radiated into all habitats, they should be the oldest. Now, look at other groups of

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animals. If for instance you iook at the mites, within the Arachnida they are certainly the group that has radiated the most, yet it is not the most primitive. Also you can take the flies within the insects. Flies have radiated practically everywhere yet they are not the most primitive and oldest insects. And take the ophiurids among the echinoderms, which are the most widespread in different habitats and, as far as I know, are not the most primitive. So I don't think that radiation is a good sign for telling us which should be the oldest and which should be the youngest. It's just a matter of striking the right situation and the right time and they radiate into these niches regardless of the period when this has happened.

Z. Kabata: Thank you Dr. Schminke. We have time for two or three more questions, or comments. Dr. Hulsemann, please.

K. Hulsemann: I think that one could argue the other way around and say if a group has spread very much these are all members of the groups that are still surviving and if we have just one or two of a group or very few numbers, others may have died off. So, it would be just the opposite.

D. Soto: It seems to me that all the apomorphies in this case are reductions and fusions, so you can almost predict that the future evolution of the copepods is going to a very simple situation, almost a one cell condition. There is no place for reversion, it seems. I wonder if some of the problems are because of that, because reversions have not been considered as an evolutionary possibility.

G.A. Boxshall: I am open-minded. I can consider anything but you have to work with the characters you have. It is possible there are reversions but what can you do? You have to use the characters there are. If you find other characters that are better, that show noncongruents and therefore convergence or reversions, that's fine. You have to set up to disprove it and the onus is on you to disprove it, otherwise we will have no system at all. I agree some of the characters down here (in the diagram) are reasonable, they are fusions. You can at least work out the homologies when you have got fusions. In the first antenna you have armature elements that can help you to identify what segments you are dealing with, it can give you homologies right through. For example, in the vast majority of calanoids the primitve segments 2, 3, and U are all fused into a triple segment, and segment 2 has three sets of armature elements. Now, these are really nice homologies that link some of the groups, but there is nothing else. I have puzzled over this long and hard, 20 minutes. I really couldn't come up with anything else.

J.-s. Ho: This character reversal and the homoplasy which is a synonym of convergence and parallelism and used to be a "systematist's nightmare" are the things we would like to forget about in doing cladistic analysis. Recently they have been trying to take that into consideration, so I think that in perhaps 2 or 3 years from now we will see that there is a good way of analyzing character reversal. How do we explain when it happens?

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Taisoo Park: In calanoids, of course, specialization seems to be the trend, but the crucial thing is the reduction of the appendages, the same time there is an increase in the complexities within a group. Such as the undinellids. If you know male Undinellidae, you know that they are primitive in every aspect, but the male's leg is enormously complex as it is also in the Centropagidae. Centropages retains very primitive features, but there are many species in Centropagidae, including the species that I have studied, Epilabidocera , in which the antennules and the fifth pair of legs become extremely complex. These complexities go in parallel with increased complexity of behaviour.

Z. Kabata: Thank you. We have time for only one more question. Dr. Sieg.

J. Sieg: I would like to make a comment on reduction. I think it is very bad when people start to think that structures which have been lost may come back. I have seen many such structures that I had been told have come back, but wherever I have analyzed these structures very carefully, 1 have found that they were different structures of quite different origin. So they were not homologous. As we normally have to compare characters, we always have to compare homologous characters and not analogous ones. If you pick the wrong structure and compare it with another one you will never arrive at a system which works.

Z. Kabata: Thank you very much, Dr. Sieg. I am afraid that we will have to terminate this interesting discussion.