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Review of methodological problems of 'Computer cladistics' exemplified with a case study on isopod phylogeny (Crustacea: Isopoda)

By J. W. Wägele

Abstract

Using a computerized phylogenetic analysis of the Isopoda (Crustacea: Peracarida) as source of typical errors and misunderstandings, problems that may occur in computer cladistics are reviewed. It is concluded that in addition to the errors that are possible in a conventional Hennigian analysis some specific methodological problems exist in computer cladistics. It is recommended that the OTU be replaced by the groundpattern concept. Tree statistics are not useful for comparing different competing hypotheses. Arguments ought to concentrate on the hypothetico-deductive steps of the analysis, i. e. on character analysis. The use of computers does not add objectivity to character analysis. Single outgroup taxa should not be used in assessing the character states of ingroups.

Concerning isopod phylogeny, it is argued here that the tail fan of the Isopoda can probably be derived from the eumalacostracan groundpattern and did not evolve de novo within the Isopoda.

Key words: Phylogenetic systematics – Computer cladistics – Isopod evolution – Eumalacostracan tail fan – Anatomy

1 Introduction

A recently published study on the phylogeny of the Isopoda based on the use of computer programs (Brusca and Wilson 1991) contains a number of peculiar hypotheses of relationships which are neither in accordance with traditional (typological) classification of the Isopoda nor with the results of a previous 'hand generated' phylogenetic analysis (Wägele 1989). A comparison of these two publications yields some interesting results on the methodological problems of computer cladistics, which are discussed in the following. It is not intended to present a complete list of all possible mistakes, but to discuss some important sources of errors and misunderstandings. The present study refers only to *morphological* data, the use of molecular data involves different problems.

The theory of phylogenetic systematics is undoubtedly becoming mature and excellent textbooks are available (e. g. Ax 1987; Sudhaus and Rehfeld 1992) for those willing to learn modern methods of biological systematics. Looking through the extensive literature one gets the impression that nearly every subject and all relevant ideas concerning cladistics have already been sufficiently discussed. Nevertheless it seems that a growing number of taxonomists is using computer programs for phylogenetic analyses of morphological data without being familiar with the strict logic of the Hennigian method:

"... phylogenetic analysis is frequently treated as a black box into which data are fed and out of which 'The Tree' springs" (Swofford and Olsen 1990: 411).

Several authors have criticized blind belief in computers (e. g. Crowson 1982), but a compilation of arguments based on Hennigian logic seems to be needed. Some arguments in favour of the use of computer programs are the easier and faster management of data, and the economization of brain-work. A typical statement: "For that fortunate handful of

systematists who study groups with only a few taxa, it is possible to reconstruct phylogenies the way HENNIG envisioned it – by hand. For everyone else, computer-implemented algorithms are indispensable" (SANDERSON 1990). Similarly BRUSCA and WILSON (1991) cannot imagine that a large taxon "can be ordered without a computer: ... an analysis of the 10 nominate isopod suborders alone requires assessments of 282 million possible trees ..."

These statements remind me of the fictitious botanist who refused to identify species of trees in a Canadian forest 'because there are too many trees'. In reality, with the identification of a single apomorphic character (or, in the analogy, of a single species of tree) a large number of alternatives are immediately excluded. Resignation in the face of an enormous diversity is not necessary. It is true that "... the number of possible trees increases rapidly with number of terminal taxa ..." (FARRIS 1981), but the number of possible trees *decreases* even faster with each recognized synapomorphy. This is the most powerful effect of phylogenetic systematics: the immeasurable diversity of life can be ordered into a surveyable number of natural units, and this is possible with the help of arguments that are not the result of a computer analyis. One should not forget that, for example, W. HENNIG (1969) was able to analyze major events of the phylogeny of insects 'by hand'.

The statement that "the hand generated method is a useful technique (only) for small, clear-cut data sets ..." (PRESCH 1989) can often be heard. This belief implies that there are better and less good data sets, and that a set of algorithms is able to improve the information content of the latter. But, as in statistics (garbage in, garbage out), the quality of the data has a definite influence on the quality of the results. If obvious autapomorphies are not known, the use of computer programs will not improve the state of our knowledge.

Another argument in favour of computer cladistics is its alleged objectivity: "... the systematist must proceed in a formal manner that allows for the examination of data without a priori assumptions. Utilizing computers ... [ ] ... provides the mechanism to remove the subjectivity during analysis" (PRESCH 1989: 188). Or, misunderstanding the Hennigian procedure: "WÄGELE's study ... was still based on an ad hoc hypothetical ancestral morphotype, the phylogenetic tree was computed by hand ..." (BRUSCA and WILSON 1991: 147). [In fact, the cited morphotype is a groundpattern of the Isopoda, reconstructed by analysis of the phylogeny of subordinated taxa after the reconstruction of the groundpatterns of these subordinated taxa (WÄGELE 1989), not ad hoc.]

Another misunderstanding of the same method: "One of the advantages of the available computer-assisted numerical techniques ... is that they treat each character independently" (BRUSCA and WILSON 1991: 149). (The Hennigian method always requires independence of characters.)

These and many other publications praise the use of computer programs. It is not the aim of this paper repeatedly to explain the methodology of phylogenetic systematics, but to discuss some methodological problems occurring in connection with computer cladistics.

2 Position of computer analysis within a phylogenetic study

"The cladistic analysis itself is relatively trivial: it is only summarizing the information already entirely contained within the characters ... [ ] ... the result ... is completely determined as soon as the data set is assembled" (NEFF 1986: 116).

This observation should be known to all those seeking the 'objectivity' of computer cladistics. To estimate the value of numerical methods that help to transform a data matrix into dendrograms one has to remember which steps are necessary in a phylogenetic analysis (Fig. 1):

1. Study of single individuals (representing single species).
2. Selection of characters
   - from species
   - or from groundpatterns of higher taxa (= result of a previous analysis).
3. Character analysis (assessment of homology and polarity, character weighting).
4. Assemblage of a data matrix.
5. Construction of dendrograms, selection of a hypothesis of relationships
   - or, in computer cladistics, calculation of equally most parsimonious dendrograms.
6. Test of dendrograms (with further characters, returning to step 1).
7. Examination of the plausibility of the hypothesis (comparison with data on ways of life, autecology, evolution of adaptations, biogeography, ontogeny, paleontology, reconstruction of an evolutionary scenario, etc.).

In this long series of operations the most important ones for the formulation of a hypothesis are steps 1 to 3. With step 4 the result is already fixed: "A hypothesis of synapomorphy is equivalent to a hypothesis of relationships . . ." (BRYANT 1989).

The hypothesis of hierarchical order of a dendrogram is therefore already contained in the data matrix. A good deal of biological knowledge is necessary for such an analysis

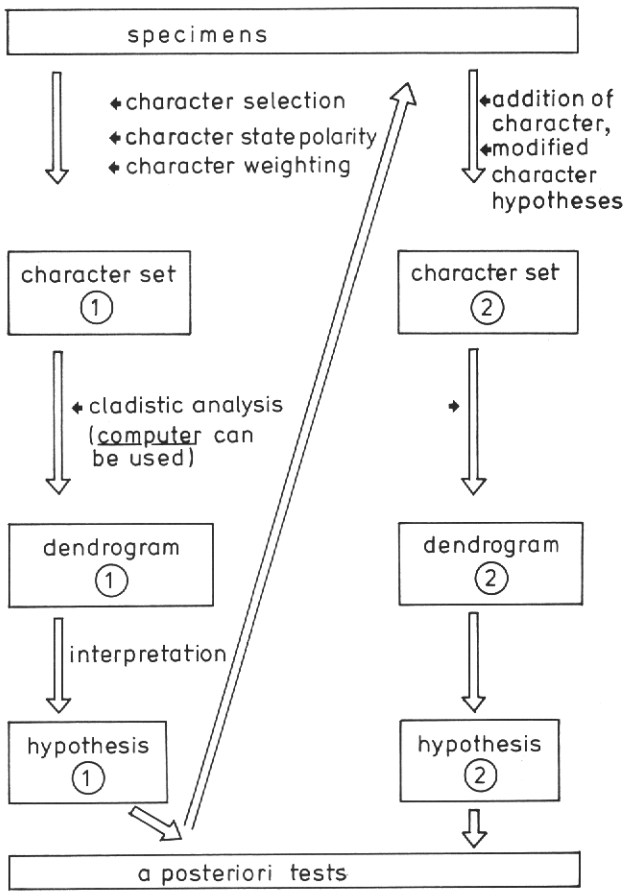


Fig. 1. Illustration of the path leading from specimen examination and character analysis to a phylogenetic hypothesis and indication of the position where computers can be used. Further discussion in the text

(e. g. on histological complexity and function of organs), e. g. to find indications for homology, wherefore a computer can not compete with the brain of a biologist. Of course "one's own training and background may effect the decisions made at each step ..." (PRESCH 1989), but each step is falsifiable with new arguments and the result is therefore a scientific hypothesis.

Like others before him, BRYANT (1989) correctly emphasizes the importance of the character analysis. This is the hypothetico-deductive part of a phylogenetic analysis, which leads to the compilation of the character set (steps 1 to 4). Cladistic analysis s.str. is inductive insofar as the results are contained in the data matrix (step 5). Phylogenetic relationships are not decided at this step. Step 5 is just a method of pattern description.

Step 7 should not be neglected. The result of a phylogenetic analysis is a hypothesis with information about relationships, but not the description of the evolution of a group: "... a genealogy does not explain by itself why one group acquires a new feature" (FARRIS 1982).

If on the basis of a dendrogram a plausible evolutionary scenario can be reconstructed (e. g. evolution of parasites in coevolution with their hosts), then probability increases in favour of that dendrogram. Incongruences cast doubt on the quality of the phylogenetic analysis.

3 The 'subjectivity' of computer cladistics

Though often criticized (e. g. CHARIG 1982; NEFF 1986; BRYANT 1989), the opinion that computer cladistics is a more objective method still prevails. The many steps necessary to compile a data set for a computerized cladistic analysis, inevitably require the same decisions, not arithmetically calculable, as in the analysis 'by hand' (see e. g. WHEELER 1986). This subjectivity arises from

- observational methods (e. g. taxonomic decriptions),
- selection of characters used for the analysis (an often unconscious character weighting),
- a priori hypotheses of monophyly (for the terminal taxa),
- hypotheses of character homology,
- a priori assessment of character polarity,
- character weighting,
- 'a posteriori' search for additional characters.

No algorithms exist for these steps (for the meaning of 'character weighting' see par. 6.3). WHEELER (1986) correctly remarks that not weighting in a numerical analysis is also a source of weighting, since each character gets the value 1. There is no objective reason for such equating of characters in a numerical analysis (see par. 6.3 and 8.5).

4 Outgroup taxa and a priori assumptions of phylogenetic relationships

In contrast to a Hennigian analysis, which can be carried out 'descending' step by step, starting with small taxonomic units (Fig. 4), numerical analysis must always begin with a complete data matrix for all terminal taxa. To assess character polarity an outgroup comparison is necessary. Usually taxa closely related to the ingroup are chosen as outgroups (but see also par. 6.7).

If an outgroup taxon is selected and not included in a phylogenetic analysis it is usually implicitly assumed that the ingroup is monophyletic and that the outgroup does not belong to this monophylum. This is a further example of a decision not based on the 'objectivity' of computer programs. The assumption can be verified, as usual, with Hennigian logic (searching for autapomorphies of the monophyla). But if we are looking for the mechanical 'objectivity' of an algorithm, we might believe that inclusion of the outgroup

in the data matrix would avoid an a priori hypothesis. Unfortunately, this step implies further a priori hypotheses, namely the monophyly of the included outgroup taxon and hypotheses of autapomorphy for characters of the outgroup. To code the outgroup characters, further outgroup comparisons are necessary.

The solution is either to work without computer cladistics and to reconstruct groundpatterns in a FIG/FOG analysis (FIG = functional ingroup, FOG = functional outgroup, see par. 6.7), to reconstruct first the phylogeny of smaller monophyla with species as terminal taxa, or to accept that a priori hypotheses (e. g. of monophyly of terminal taxa and of ingroup-outgroup taxon relationships) are unavoidable.

5 What is an OTU?

The concept of the OTU (= operational taxonomic unit) should be avoided, as it smokescreens the indispensable reconstruction of groundpatterns. OTUs are either single species or any other taxon, which always must be a monophylum, entities, whose characters can be coded in a data matrix. They can also represent groundpatterns ('basal node characters' or 'ancestral states') reconstructed in a previous analysis.

The characters of a single species are usually those found in taxonomic descriptions. Polymorphic characters cannot be used as long as the ancestral character state of the species is not known. A taxon other than the species is usually (but not necessarily correctly) coded without a priori analysis of phylogeny within it. This can lead to errors, namely whenever characters that are not present in the taxon's groundpattern are selected arbitrarily, such as autapomorphies of a subordinated species group (e. g.: vivipary is not a groundpattern character of the Mammalia).

An OTU can only be
- a single species, or
- the groundpattern of a monophylum (par. 6.7).

6 Character analysis

"... the errors introduced by character selection, coding, and scoring probably far exceed inaccuracies in the algorithms" (SANDERSON 1990).

6.1 What is a character?

A character is any discernible feature of a life-stage of a species (e. g. SUDHAUS and REHFELD 1992). It can be very simple or very complex, and if complex it can be divided into subunits, each of which is also a character. Complexity means high genetic information content. A character can be the locus of a single nucleotide or a long sequence, the result of a point mutation or of a long sequence of specific genomic changes. Character states can be regarded as modifications of a single character or as two characters, of which one is derived historically from the other one: despite different semantics the ontology is the same (see e. g. PLATTNICK 1979; RODRIGUES 1986).

6.2 Character valuation – an a priori source of mistakes

After the first step, namely identification of character homology, the assessment of character polarity is the second important operation during which errors can be made. An automatic determination of character polarity by selection of few outgroup taxa is implemented in many computer programs. To follow this routine is a logical mistake: only

the groundpattern of the ingroup contains the plesiomorphies that could be used for this procedure (see also par. 6.7). If a character or a transformation series are to be used in an analysis, character polarity must be assessed a priori. If in a transformation series analysis the hierarchical order of a given dendrogram is used to find the ancestral states of characters (see LIPSCOMB 1990), i. e. a posteriori, the result may fit into an existing hypothesis, but the hypothesis can not be corroborated with these characters: a posteriori polarity assessment leads to circular argumentation (see also WILEY 1975).

This does not mean that 'a posteriori' use of further characters suffers from circularity. To the contrary, a phylogenetic hypothesis can be tested with further independent synapomorphies (Fig. 1), i. e. with characters whose polarity has been found without reference to the existing hypothesis prior to the test of the latter (WILEY 1975; NEFF 1986). The fit of a synapomorphy into an existing hypothesis of phylogenetic relationships also seems to give more weight to the hypothesis of synapomorphy of the character in question (mutual illumination). Again, to avoid circularity, arguments of the hypothesis of synapomorphy should be independent of the hypothesis of relationships.

A priori character analysis is also indispensable in computer cladistics, for apomorphic states must be known in order to assemble a data matrix. No computer can carry out this work, and this is without doubt the most important step in a phylogenetic analysis (see par. 2). The following mistakes are possible: 1. plesiomorphic characters are scored as apomorphic, 2. convergencies or parallelisms are scored as synapomorphies, 3. synapomorphies are scored as plesiomorphic or non-homologous characters.

All 3 mistakes produce false hypotheses of relationship or weaken the argumentation in favour of a correct hypothesis.

Example: BRUSCA and WILSON's (1991) attitude towards assessment of character polarity was clearly stated (p. 184): "... the final analyses were done with all characters unpolarized, ..., and allowed to change in any direction. This procedure makes no assumptions as to what the primitive or derived states are for any characters in the data set." It then follows logically that the analysis is numerical, and not phylogenetic. In cases where character polarity was assessed a posteriori the authors are trapped in circular argumentation.

Concerning the evaluation of the varying outline of uropods the authors write (p. 179): "This character was analysed unordered in initial analyses." Indeed, initially the broad, flat uropods of the Isopoda, that resemble those of an eumalacostracan tail fan (see par. 7), were coded with 0 (plesiomorphic), styliform uropods with 1 (apomorphic). Character polarity was assessed a posteriori to fit the character into the resultant tree topology and to obtain a parsimonious dendrogram: as a result it was decided to consider the styliform uropods as plesiomophic, clearly a double mistake (see also par. 7): 1. character polarity was not determined a priori but adapted to tree topology, as a consequence 2. the plesiomorphic state (uropods forming a tail fan) was not identified correctly.

6.3 Character weighting: what are 'good' characters?

In a phylogenetic study only those characters that are inherited are of interest, i. e. characters that are (or are based on) genetic information. This is the reason why there are 'good' characters and less reliable characters: simple characters of low information content are more likely to evolve often than complex characters; gene sequences that are not expressed or are not functional are more likely to mutate stochastically than functional sequences and the corresponding morphological characters.

Character weighting should therefore be based on the probability that a new feature has evolved (see par. 8.5). Experience of taxonomists is a valuable source of information on character evolution. Thus some characters are very variable (e. g. setation in larger crustacean species, pigmentation), losses (negative characters) occur more easily than gains. Adaptive characters must be analyzed carefully for homology, since convergencies can be expected (see e. g. WHEELER 1986). Decisions to reject possibly weak characters (such as losses, pigment patterns, the absolute number of setae etc.) in a phylogenetic analysis are not at all ad hoc arguments but based on a rough estimation of probabilities that genetic

information evolves convergently. As long as these probabilities cannot be calculated statistically, an estimation of character complexity can help to formulate rules of thumb.

Weak characters might nevertheless "contain phylogenetically useful information on restricted parts of the phylogenetic tree" (STRAUCH 1984), i. e. they can be autapomorphies of smaller monophyla. For example, in several taxa of the Isopoda eyes are lost. This negative character occurs obviously convergently in deep-sea species and in epicontinental stygobionts. For single monophyla, corroborated with other autapomorphies, the reduction of eyes is an additional adaptive character of less weight than positive characters, but in accordance with a hypothesis of monophyly.

6.4 Carelessly defined characters

Superficial character selection or character description is the source of the following mistakes:

- two or more different and independent features of a species are summarized in 1 character (example a),
- two superficially similar but not homologous structures occurring in 2 different species are decribed as homologous (example b).

Example a: BRUSCA and WILSON (1991) describe as character Nr. 17 of their data matrix an apomorphy of terrestrial isopods: "Complex compound sensillar structures at the tips of the antennae and uropodal rami." The ultrastructure and physiology of the apical antennal sense organ is well known (e. g. SCHNEIDER 1973; ALEXANDER 1977; SEELINGER 1977, 1983). This organ is probably touch- and chemosensory. It consists of bundles of about 13 to 100 sensilla, each sensillum containing several unbranched dendrites. In contrast to aesthetascs the sensilla have dendritic sheaths around the outer segment, and the inner enveloping cell has a scolopale-like structure in the area of the ciliary segments. The cuticular cone surrounding the bundle of sensilla is a character only present in the 'higher' Oniscidea; in species of *Ligia*, for example, it is absent. This arrangement of aesthetasc-like contact-chemosensory sensilla seems to be unique to one group within the Oniscidea, but sensilla which are probably homologous are also present in aquatic species, in different arrangement.

This antennal sense organ has until now never been described from uropods; character Nr. 17 of BRUSCA and WILSON's data matrix is simply a careless homologization of an uropodal spine of unknown ultrastructure with a complex antennal organ. Fortunately, as long as this character is used as autapomorphy of the Oniscidea alone, it does not influence hypotheses of relationships.

Example b: BRUSCA and WILSON (1991: 182) present in their consensus tree, two parasitic taxa as sistergroups, namely the Epicaridea (= Bopyridae; parasites of crustaceans with sessile, epizoic adults) and the Gnathiidea (only larvae are parasites of fishes, adults do not feed). Superficially similar mouthpart structures (characters nr. 30, 31, 35, 91) are used as arguments. For example: "mandibles modified as elongate scythe-like structures with serrated cutting edge".

First of all, the slender mandibles of the two taxa occur in different ontogenetic stages. In bopyrids, namely in larvae and adults. In gnathiids on the other hand, they occur only in the so-called praniza-larvae, while adults have broad mandibles (in the males) or reduced mandibles (in the females) (Fig. 2). The long, acute mandible of larval gnathiids is a caenogenetic character. The adult male mandible is broader and resembles the mandible of *Protognathia*. And secondly, the shape of the mandible is rather different in the two taxa (see Fig. 2). Thus, in the larvae of gnathiids, the mandibles are elongated and surpass the front of the head considerably; they are embedded between labrum and hypopharynx; the tips are serrated medially, whereas in bopyrids the mandibles are very small (and therefore hitherto rarely illustrated), do not project beyond the head and have a tip, which in some species is spoon-like and serrated laterally (not medially; Fig. 2), while in other species the tip is bilobed with a tiny molar-like process and a larger, often ventromedially serrated incisor (see e. g. figures in BONNIER 1900). Bopyrid mandibles are certainly not "scythelike".

The bopyrid mandible is specialized as in cymothoids, where also a ventromedially directed apical part with cutting or biting edges occurs. According to WÄGELE (1989) bopyrid mouthparts can be derived from the form seen in cymothoids, (other morphological characters and the life cycle are further sources of synapomorphies), while gnathiid mouthparts fit into a character transformation series leading from cirolanid mouthparts via protognathiid mouthparts to those of gnathiids (WÄGELE and BRANDT 1988). Further apomorphies used by BRUSCA and WILSON to support the relationship Epicaridea (= Bopyridae) / Gnathiidae are negative characters (loss of molar, of mandibular palp, of maxillules).

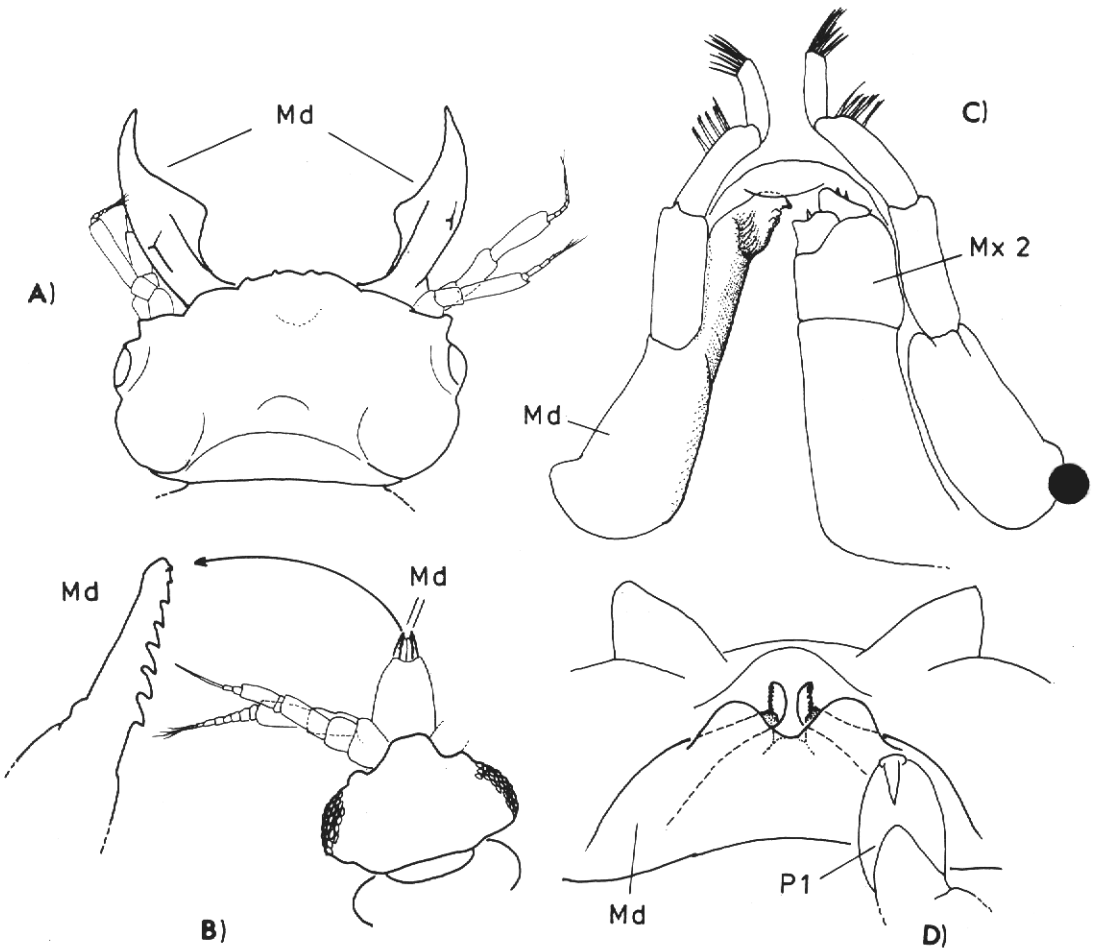


Fig. 2. Comparison of mandible form of bopyrid, cymothoid and gnathiid isopods. A and B: head of male (A) and of praniza larva (B) of *Gnathia calva* Vanhöffen, 1914 in dorsal view; detail of larval mandible (modified after WÄGELE 1987). C: Ventral view of mouthparts of an undetermined mediterranean *Aegathoa* (Cymothoidae); maxillipeds and right maxillae lacking. D: Ventral view of mouthpart cone of juvenile female *Clypeoniscus hanseni* Giard & Bonnier, 1893 (after GIARD and BONNIER 1893). Md: mandible; Mx2: second maxilla; P1: pereopod 1

In this example superficial similarity resulting from adaptations to haemophagy is mistaken for homology.

6.5 Seeming homoplasies

Seemingly homologous apomorphies of two taxa whose occurrence is incompatible with a phylogenetic hypothesis, can be evidence for the incorrectness of the hypothesis. But they can also be only seeming homoplasies, i. e. misinterpreted characters that only at first sight or at the present state of knowledge seem to be homologous: "... characters that violate the hierarchy will be primarily indications of errors in character identification, and only secondarily evidence of parallelism" (BRADY 1982).

The probability that homoplasies are misinterpretations is especially high in "weak characters" (see par. 6.3). For instance, comparing negative characters it is nearly impossi-

ble to find evidence for homology. Such homoplasies should have much less weight in tree statistics than positive characters (e. g. presence of a certain type of statocyst). A typical seeming homoplasy results from careless and superficial, simplistic description (STRAUCH 1984), e. g. 'winged forelimbs' in an analysis of tetrapod phylogeny.

Calculations of homoplasies in computer cladistics in no way reflect the probabilities of convergent character evolution but yield only a numerical description of incongruences between data matrix and dendrogram. The calculated homoplasy index of a dendrogram is not a measure of the quality of a hypothesis. Discussions should therefore concentrate on the quality of the characters used in a data matrix, a feature which cannot be culated with a homoplasy index.

Example: The mandibular palp is uniramous in the groundpattern of the Isopoda, with 3 articulations (WÄGELE 1989). The palp is absent in some groups. This negative character (loss of palps) does not occur frequently, however it is consistent within certain taxa, so that absence must be judged as a character of the groundpattern of each of these taxa, namely of the following groups: Bopyridae (= Epicaridea of the traditional classification), Gnathiidae (only a seta remaining on the male mandible), Oniscidea, Calabozoidea, Keuphyliidae, Lynseiidae, Valvifera (a single species possesses a palp: probably an atavism; see POORE and LEW TON 1990).

Without knowledge about the different genetic events behind these losses it is not possible to distinguish between homologies and convergencies (a posteriori arguments derived from a given dendrogram can of course be found, as discussed in par. 6.2). It is therefore also not helpful to use this negative character as a synapomorphy of two of the taxa listed above, as proposed by BRUSCA and WILSON (1991: 182) for the postulated sistergroup-relationship between Calabozoidea and Oniscidea.

As homology cannot be substantiated a priori for such negative characters, the danger of introducing mistakes into the analysis is great or, in this example, almost certain. The use of computer programs cannot help to avoid this mistake. The character appears as homoplasy, because convergent evolution can not be recognized a priori. So it would have been better not to use this character for the data matrix (though it could be mentioned as consistently present in certain taxa, without the necessity to state if it is a plesiomorphy or an autapomorphy).

6.6 Seeming autapomorphies

These are derived characters erroneously coded as an autapomorphy of a hypothetical monophylum. Sources for this mistake can be 1. an erroneous determination of homology (the similarity is a convergence; example a), 2. wrong determination of character polarity (the similarity is a plesiomorphy; also example a), 3. incomplete search for this character in possibly related taxa (the character is present in a larger monophylum and therefore a plesiomorphy; example b).

Example a: Two errors occur in the evaluation of the evolution of the eumalacostracan tail fan within the Isopoda as proposed by BRUSCA and WILSON (1991; further details in par. 7):
- the tail fan with its flattened uropods, a plesiomorphic similarity of several taxa, is, as already mentioned before, treated as synapomorphy, and
- different types of styliform uropods (convergent similarity) are homologized to postulate styliform uropods in the groundpattern of the Isopoda (see par. 7).

Example b: An example of an incomplete search for a character is the tricorn sensilla of oniscids. This example is also a case of careless, simplistic character definition (superficial similarity with unknown homology):

In contrast to VAN LIESHOUT (1983) and WÄGELE (1989), BRUSCA and WILSON (1991) place the tiny stygobiontic freshwater Calabozoidea in their dendrogram not as sistergroup of the Asellota, but of the terrestrial, air-breathing Oniscidea. One of the synapomorphies proposed is character 16 (p. 200): "with cuticular tricorn sensilla (1)". These small sensilla until now have been described only for oniscids, where they occur nearly everywhere, usually in fields of cuticular scales (plaques) (HOLDICH and LINCOLN 1974; HOLDICH 1984). The ultrastructure has only been described for *Oniscus asellus*, where a single central outer dendritic segment and a second cell wrapped around it have been found (PRICE and HOLDICH 1980). BRUSCA and WILSON (1991) claim to have seen these sensilla in the SEM pictures of *Calabozoa pellucida* published by VAN LIESHOUT (1983: Figs. 5d–e). But, on these photographs tricorns are certainly not visible. Instead there are only short hair-like sensilla. Short sensilla of this type inserting in fields of plaques are found in nearly all isopod taxa seen by the author (Fig. 3). Some look superficially

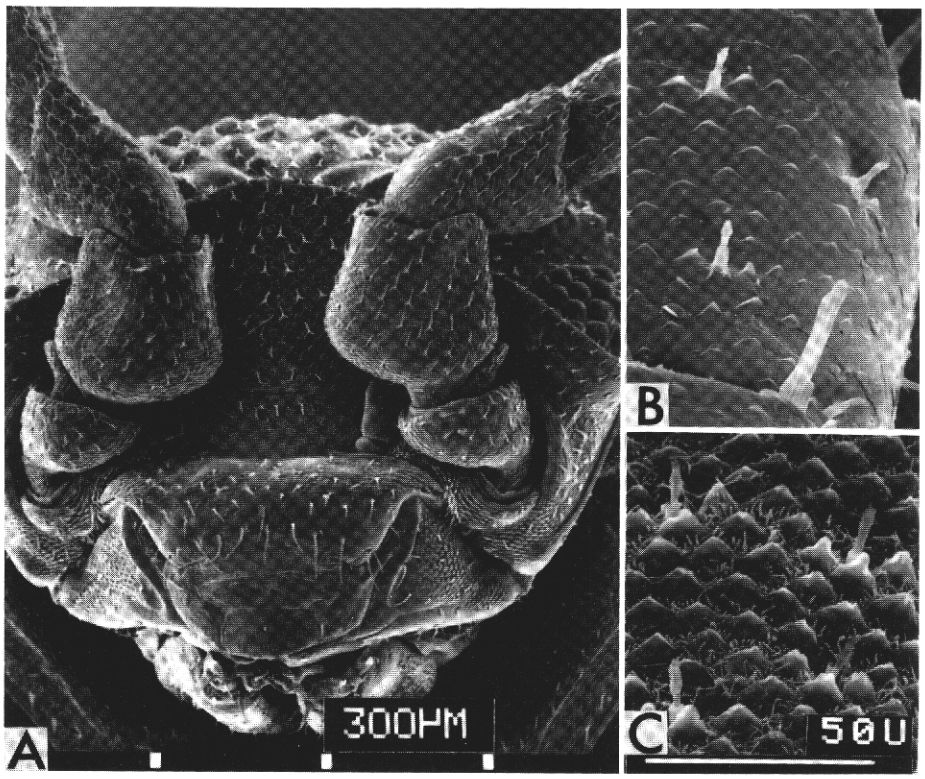


Fig. 3. Cuticular sensilla of isopods: A: Frontal view of head of *Porcellio scaber* Latreille, 1804; the hair-like structures in fields of cuticular scales are 'tricorns'. B and C: Cuticular scales and short tricorn-like sensilla are present in many isopods; here on the second article (C) and on the flagellum (B) of antenna 2 of *Idotea baltica* (Pallas, 1772)

like tricorns, while others are simple short hair-like sensilla. As long as ultrastructural data are not available, homology with oniscid tricorns is as probable as analogy. And: tricorns are at present not a specific feature occurring only in Calabozoidea and Oniscoidea.

6.7 Selection of outgroups and the reconstruction of groundpatterns

Prior to the cladistic analysis character analysis requires outgroup comparisons and – for terminal taxa – the reconstruction of groundpatterns. The outgroups are selected in order to find the polarity of the ingroup characters. This procedure can lead to the following errors prior to the computerized analysis (see e. g. MADDISON et al. 1984): 1. autapomorphic outgroup characters can be assessed as plesiomorphic for the ingroup, i. e. the true plesiomorphic state is not recognized; 2. parallel evolution of characters of the ingroup and of the outgroup can lead to wrong determination of ingroup plesiomorphic states (convergent apomorphy coded as plesiomorphy).

In some cases these mistakes can be avoided when more than a single outgroup taxon is compared with the ingroup. Ideally we should regard all species of the animal kingdom that do not belong to the monophyletic ingroup as outgroup: Contrary to widespread belief, character states of the ingroup groundpattern can be identified without knowing which taxon might be closely related, i. e. without designation of a special outgroup. Feathers of birds are an example – they are present in the Aves and nowhere else. To discuss crustacean characters:

Example: The homology of the *malacostracan pleon* has been the subject of long discussions. While this tagma is often called the abdomen, LAUTERBACH (1975) presents many arguments in favour of a homology with the caudal thorax of other crustaceans. But, to recognize the autapomorphy it is not necessary to decide which of these concepts is correct: even without knowing which segments of other crustaceans are homologous with the malacostracan pleon, and even without knowing which crustacean taxon is the sistergroup of the Malacostraca, it can be stated that the pleon is a complex autapomorphic character of the Malacostraca (see e. g. HESSLER 1983).

The foregoing example uses all remaining crustaceans as outgroup and shows that a character of the groundpattern can be found this way. For complex character sets a logical procedure necessary for the reconstruction of a groundpattern has been described by WATROUS and WHEELER (1981) as FIG/FOG analysis (see also MOOI 1989), which is equivalent to a descending analysis (SUDHAUS and REHFELD 1992). I can recommend this procedure with the modification that outgroups should be as many taxa as possible. The basic cognition is that relationships can only be derived from common groundpatterns (ancestral states in the basal node of a monophylum; Fig. 4): at least a single good autapomorphy in the groundpattern is necessary as evidence for monophyly.

Starting with a small taxonomic unit, the functional ingroup (FIG) , the monophyly of this unit must be substantiated and characters of the groundpattern of this FIG are reconstructed by comparison with the remaining, non-ingroup taxa, the functional outgroup (FOG). Only then a potential sistergroup can be compared with this first groundpattern. The next step is the reconstruction of the groundpattern of the larger monophylum composed of the initial ingroup and its sistergroup, i.e. the characters present in the node connecting the first monophylum with its sistergroup. Monophyly of that sistergroup must of course also be examined.

At the end of this descending reconstruction (Fig. 4) a groundpattern for the largest superordinated monophylum is obtained, using all remaining animals as outgroup, as in the above-mentioned example of the malacostracan pleon. Of course, for comparisons between the subordinated taxa these groundpattern characters must be coded as plesiomorphies (all-zero ancestor).

To use computer programs, prior to the assemblage of a data matrix groundpatterns must be reconstructed for all terminal taxa, whenever these are not species. To avoid mistakes, only groundpattern characters can be used for the data matrix.

At this point it is convenient to remark that the German term 'bauplan' should not be used in a phylogenetic analysis. Though frequently used in the sense of groundpattern in German literature, the bauplan concept, e. g. as used in BRUSCA and BRUSCA (1990), is not based on the Hennigian method. Such a bauplan is a mixture of all kinds of characters that occur within a taxon, selected without methodology, and therefore is not identical with the groundpattern of a taxon.

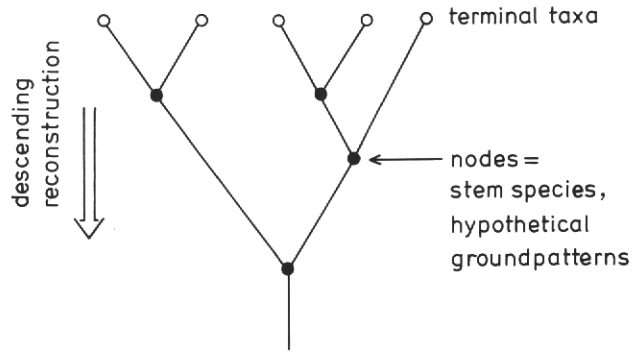
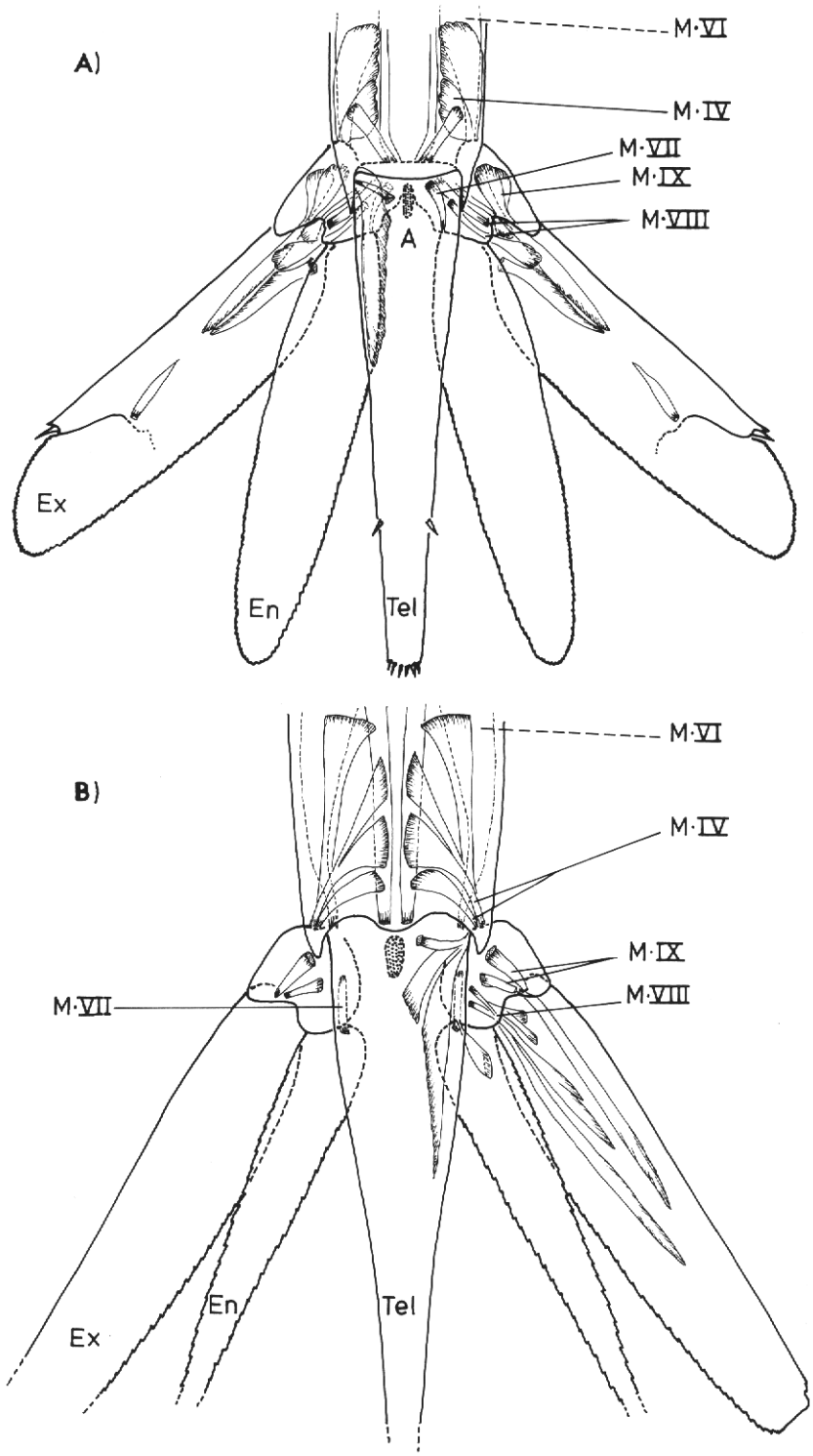


Fig. 4. Descending reconstruction and the position of groundpatterns. For details see text


A)
M·VI
M·IV
M·VII
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A
Ex
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B)
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M·VII
Ex
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7 The problem of the isopod tail fan

A major difference between the results of WÄGELE (1989) and of BRUSCA and WILSON (1991) concerns the interpretation of the isopod tail fan. While the author was and still is convinced that the tail fan is an old heritage derived from the eumalacostracan tail fan, BRUSCA and WILSON (1991) used the character as autapomorphy for a large group composed of the Flabellifera, Valvifera, Anthuridea, Gnathiidea and Bopyridae.

In 1981 WÄGELE showed that tail fan anatomy of several isopod taxa can be derived from a common groundpattern (see Fig. 6C). Fan-like uropods with a similar arrangement to those of some isopods (i. e. the uropod is lateral to the elongated telson, the endopod overlies the exopod, the sympod is short and inserts anteriorly, the anus is near the anterior border of telson: Fig. 5) occur e. g. in shrimps, euphausiids, and mysids. For this reason the tail fan of the Isopoda was homologized with that of the Eumalacostraca (WÄGELE 1989: 162). Figs. 6, 7 show that tail fan musculature of the Isopoda is less complex than that of other Eumalacostraca, especially due to the shortening of pleonite 6 and its fusion with the telson. Shrimps and euphausiids (Fig. 5) for example have strong muscles within the exopods and larger muscles in pleonite 6. Several muscles of the isopod tail fan (example in Fig. 7A) can be homologized with those of eucarids, and it is possible to derive all hitherto examined fan-like uropod-pleotelson arrangements of the Isopoda from the same groundpattern (WÄGELE 1981; Fig. 6C).

Styliform uropods have been proposed by BRUSCA and WILSON (1991) as a groundpattern character for the Isopoda. A first, still superficial comparison of the anatomy of isopods with styliform uropods suggests that muscle arrangements in these types of tails are not homologous. Phreatoicids (*Mesamphisopus capensis* in Fig. 6A and B) have in spite of their peculiar laterally compressed body plesiomorphies that hitherto were not seen in other isopods. Thus they have very large sympodal muscles M. IV and M. VI (M. V could not be discerned), which in contrast to other isopods are still 'shrimp like', i. e. they occupy laterally large areas corresponding to pleonite 6 and they insert serially, i. e. M. IV caudally of M. VI instead of dorsally and ventrally as in other isopods. Furthermore the dorsal pleotelson muscle M. III forms a broad fan very unlike the short M. III with only 3 branches known of other isopods.

For comparison the tail of an oniscid (*Ligia oceanica* Fig. 7B), also with styliform uropods, is shown. In it, 1. the uropods insert subterminally at both sides of the anus (not anteriorly as in *M. capensis*); 2. dorsal pleotelsonic muscles are reduced; 3. the sympodal muscles M. IV to M. VI are arranged as in Fig. 6C (not laterally and serially as in *M. capensis*). The sympodal muscle arrangement seems to be a synapomorphy of a large group of the Isopoda (of which many taxa have not yet been examined anatomically), while this character is plesiomorphic in the Phreatoicidea. This coincides well with the distribution of other characters (WÄGELE 1989).

It therefore must be concluded that the styliform uropods of phreatoicids and oniscids evolved independently. The tail of *Ligia oceanica* (Fig. 7B) can be derived from the pattern shown in Fig. 6C; modifications are the reduction of the telsonic part of the pleotelson (analogous with the Asellota, see Fig. 8), uropods are displaced caudally, have a still dorsoventrally flattened sympod and elongated, cylindrical rami. The tail of the phreatoicid *Mesamphisopus capensis* has a more shrimp-like muscle arrangement; the telsonic part is also reduced, but the uropods remain in their anterolateral position and the sympod is laterally compressed.

Fig. 5. Examples for eumalacostracan tail-fans in dorsal view. Only some prominent muscles are shown. A: *Hippolyte inermis* (Leach, 1819) (Decapoda); B: *Euphausia superba* Dana, 1852 (Euphausiacea). A: anus; En: uropodal endopod; Ex: uropodal exopod; M. IV to IX: muscles (see also Fig. 6C); Tel: telson

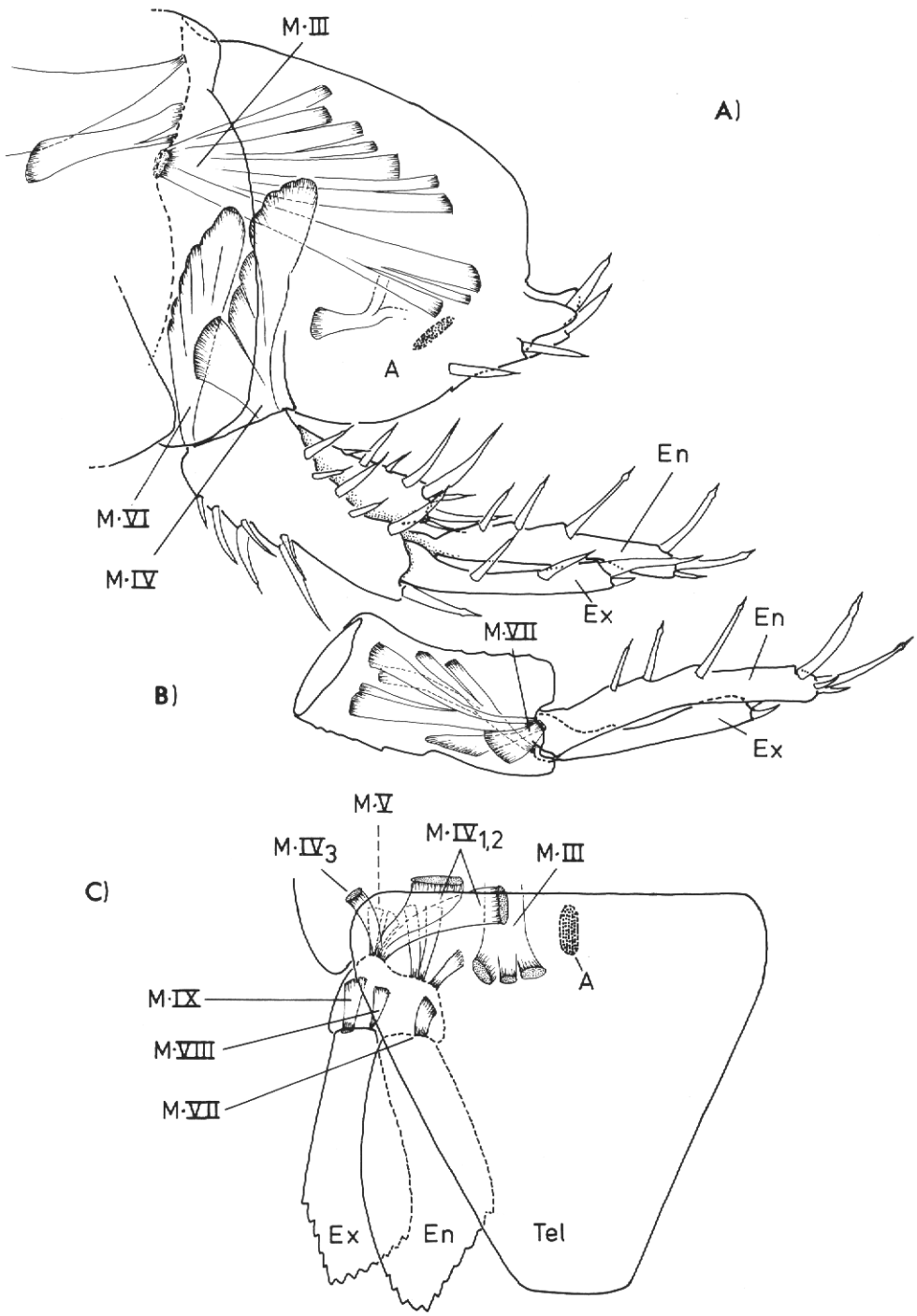

Fig. 6. A and B: pleotelson and uropods of *Mesamphisopus capensis* (Barnard, 1914) (Phreatoicidea). A: Prominent muscles and left uropod shown. B: Uropod in medial view. C: Schematic groundpattern of muscle arrangement in isopod tail fans (modified after WÄGELE 1981). A: anus, En: uropodal endopod; Ex: uropodal exopod; M. III to IX: muscles

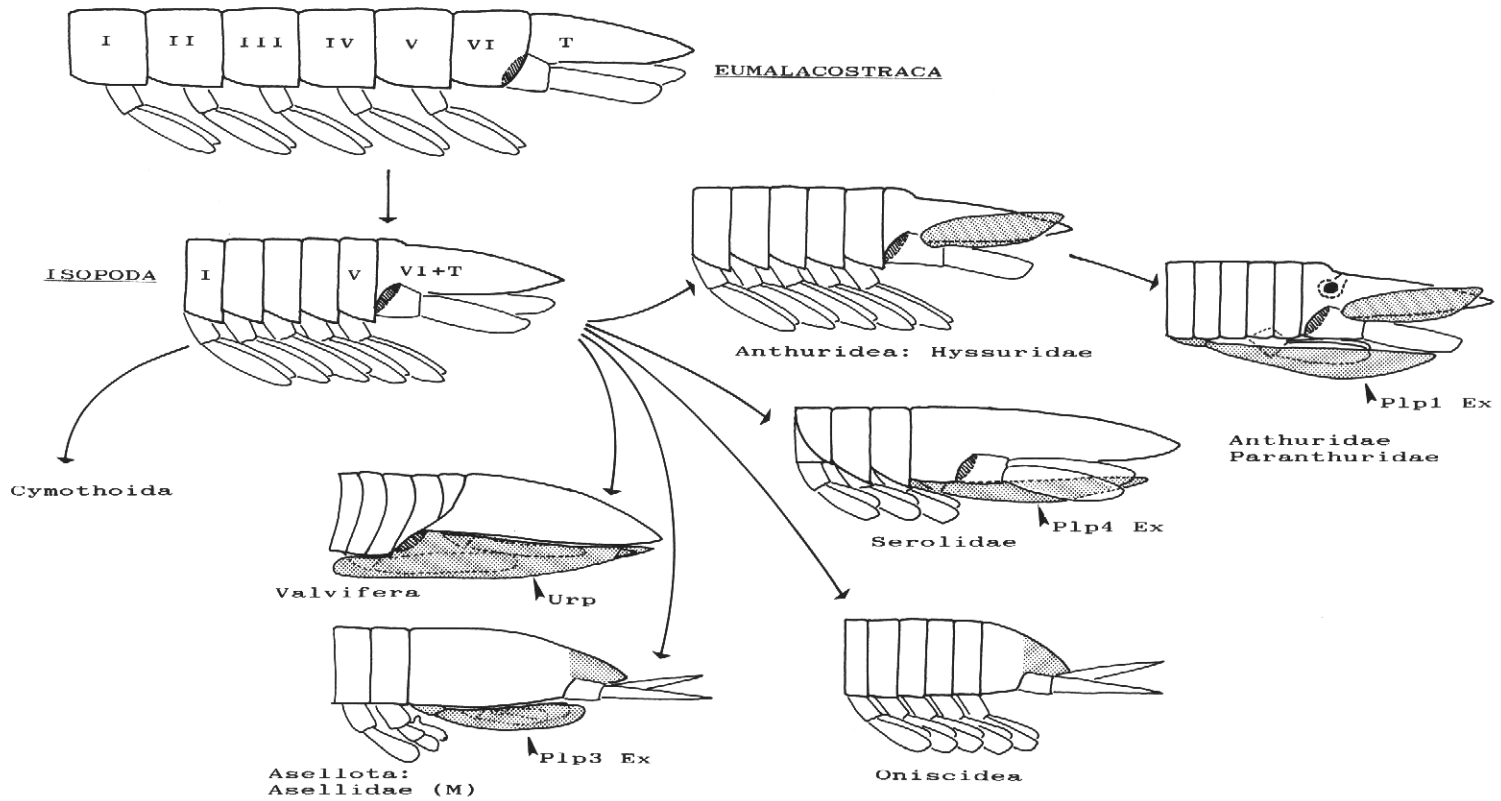

Fig. 8. Modifications of pleon and pleotelson within the Isopoda. Note similarity between the isopod groundpattern morphology and the caridoid facies (eumalacostracan groundpattern)

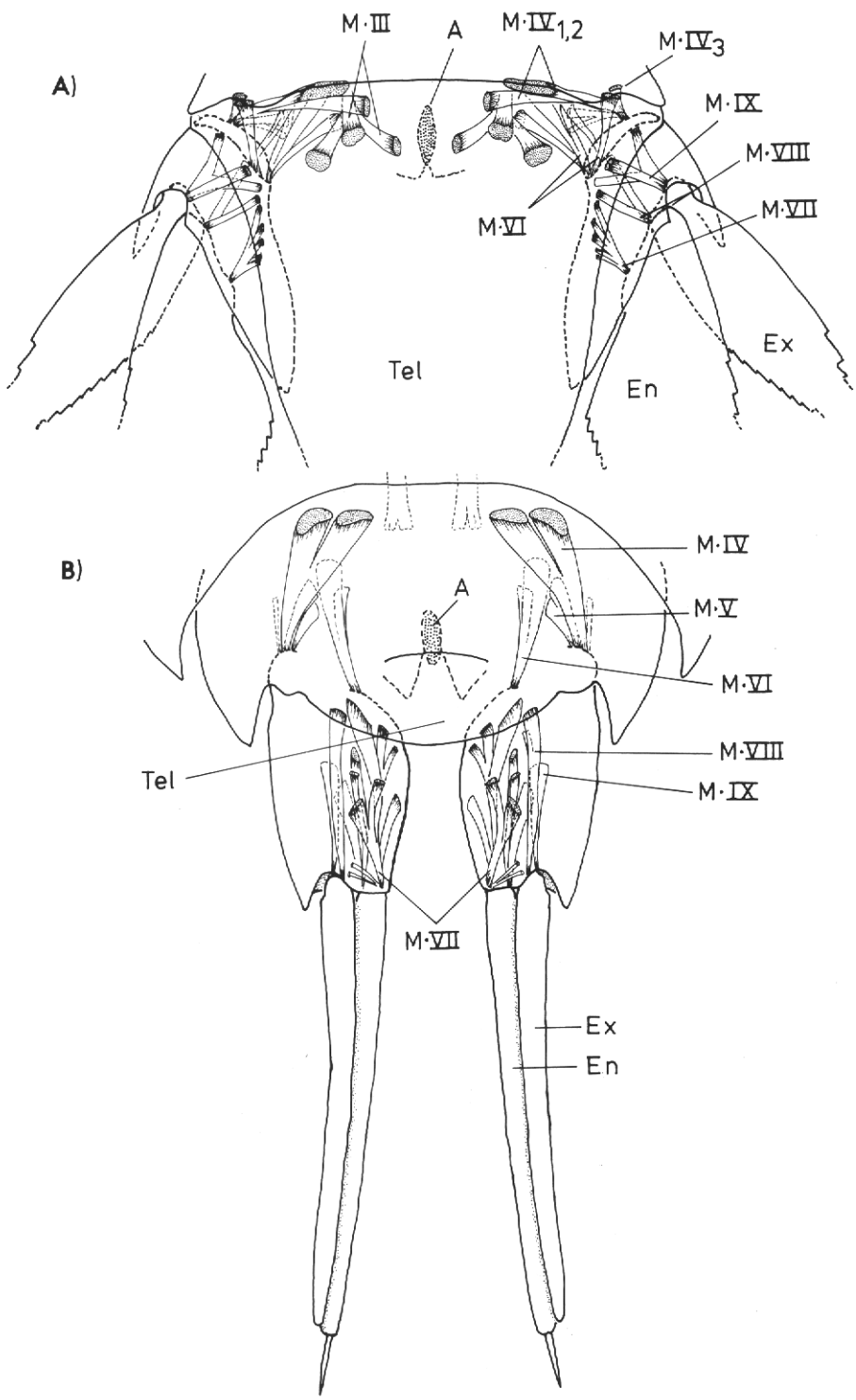

Fig. 7. A: Tail fan of *Cirolana* sp. (modified after WÄGELE 1981); B: Tail of *Ligia oceanica* (Linné, 1767). A: anus; En: uropodal endopod; Ex: uropodal exopod; M. III to IX: muscles

To derive the isopod tail fan from an isopod groundpattern with styliform uropods, as proposed by BRUSCA and WILSON, would first raise the problem that such a groundpattern must be reconstructed in full anatomical detail to avoid simplistic character definition. Such a groundpattern does not exist. Secondly, this hypothesis would imply a reversal or a "de novo" evolution of several features already present in other Eumalacostraca: 1. an elongation of the telsonic part of the pleotelson, 2. a more anterior position of the anus, 3. a flattening of the uropods, 4. a rearrangement of muscles, for example to the pattern seen in Fig. 6C.

At the present state of knowledge it is more parsimonious (meaning evolutionary, not methodological parsimony) to suppose that the complex morphology and anatomy of the tail fan evolved only once in the stem lineage of the Eumalacostraca, the groundpattern of the isopod tail fan being derived from it, while modifications of this groundpattern occurred in many taxa (Fig. 8). It must be remembered that such modifications of the eumalacostracan tail-fan are rather common, not only within the Isopoda but also in other taxa.

The Mysida and Lophogastrida prove that the eumalacostracan tail fan is present in shrimp-like Peracarida and therefore also in the peracarid groundpattern. Nevertheless this tail-fan is frequently modified within the Peracarida:

The Cumacea have cylindrical uropods with elongated sympods; the Tanaidacea have styliform elongated uropods with short sympods and multiarticulated rami; but flat uropods more similar to those of the eumalacostracan tail fan also occur in tanaids (fossil *Cryptocaris hootchi* Schram, 1974); bopyrid Isopoda, even according to the scheme proposed by BRUSCA and WILSON (1991), have tiny styliform uropods with cylindrical rami derived from a tail fan; in the Amphipoda it can be seen that also pleopods can evolve into styliform appendages.

Another argument supporting the hypothesis of an isopod groundpattern with a tail fan emerges when the pleon is considered as a functional unit (Fig. 8). The eumalacostracan tail fan is part of the tagma specialized for locomotion, and therefore can be discussed in a broader context: its evolution is correlated with the evolution of swimming behaviour and pleopod structure. Fig. 8 summarizes this correlation for isopod taxa: in species that swim regularly (e. g. Cymothoida) a tail fan and 5 pairs of similar pleopods are present as in other Eumalacostraca. Benthic species that live predominantly by climbing, crawling or burrowing have – as many other Eumalacostraca (e. g. WÄGELE 1981) – a modified pleon: uropods can be styliform (e. g. Asellota, Oniscidea), transformed into valves covering the respiratory chamber (Valvifera) or into a stopper used to close burrows or tubes (Anthuridea), while the telsonic part of the pleotelson can be reduced, usually when uropods are styliform and used as terminal antennae (Oniscidea, Asellota). In several taxa different pleopod pairs are enlarged to opercula that protect the respiratory surfaces ventrally.

8 Problems of cladistic analysis

The term cladistic analysis is used here for the transformation of a data matrix into a dendrogram or dendrograms.

8.1 Cladistic analysis without character valuation

An analysis based on undirected characters is a phenotypic, not a phylogenetic analysis. It has the same value as cluster analysis based on distance data, a typical procedure in numerical taxonomy. The following errors are inevitable in numerical cladistics:

- plesiomorphies are used to confirm monophyly,
- groundpatterns are not reconstructed,

– monophyly of terminal taxa is not investigated a priori,
– characters of low weight 'dilute' the effect of important apomorphies.
To avoid these mistakes, a priori character analysis is necessary: characters of high information content that allow us to distinguish between plesiomorphic and apomorphic states must be chosen (good characters: see par. 6.3).

8.2 Coding of taxa with unknown groundpatterns

Prior to the discovery of *Archaeopteryx* a bird could be defined as an amniote with feathers, with a bill that bears no teeth, and with an abbreviated caudal spinal column (among other features). Today it is a matter of convention whether birds are considered to have teeth and a long tail or not. The answer to the question "what is a bird?" can only be based on the definition of the taxon Aves. This is a definition of the name, not of the monophyla that exist in nature. In this context "to define" means, strictly speaking, to state (in theory), which species is the stem species of the taxon Aves, or (in practice), which autapomorphies should be present in the groundpattern of the taxon.

In this context 'groundpattern' is used in the sense of the character set reconstructed for the 'basal node' of the taxon's crown group (= extant species) (see e. g. Ax 1988). The distinction between a crown group and a stem lineage with fossils (see e. g. Ax 1987; LAUTERBACH 1989) is a useful convention. However, the discovery of a living *Archaeopteryx*, or, as it occurred, of a protognathiid isopod (WÄGELE and BRANDT 1988), would require a modification of the groundpattern character set of the crown group.

As stem species usually cannot be identified among fossils (Ax 1987), generally only the autapomorphies can be used to define a taxon. If birds are considered to have a shortened tail skeleton, then *Archaeopteryx* species clearly are not birds. It follows from this example that to characterize a taxon, its groundpattern must be reconstructed. This is also necessary because derived characters of subordinated taxa are not characters of all members of the ingroup.

Therefore the logical consequence of the need of a data matrix for a cladistic analysis is that an a priori reconstruction of the groundpattern of terminal taxa is necessary to find the correct characters. Another reason is that monophyly of terminal taxa must be verified. Each of these reconstructions is again a complete phylogenetic analysis, only on a smaller scale. For this reason the analysis must always proceed from the smaller to the larger taxonomic unit as explained in paragraph 6.7. Unfortunately the procedures of computer cladistics seduce one into assembling a data matrix without these a priori steps.

Example: 1. BRUSCA and WILSON (1991) tried to falsify the hypothesis of WÄGELE (1989) according to which the parasitic Bopyridae (Epicaridea of the traditional classification) can be derived in morphology, details of life cycle and mode of nutrition from the groundpattern of the parasitic Cymothoidae. One of the synapomorphic characters shared by these parasites is protandric hermaphroditism. BRUSCA and WILSON (p. 189) state that "epicarideans are not protandric hermaphrodites (they are facultative hermaphrodites)". This is true only for one group of the Bopyridae, namely the Bopyrinae. The bopyridium larvae of the Bopyrinae either develop male characters or they are immature; if the latter ones grow, they transform into females (review in WÄGELE 1989). Males of the Bopyrinae never reach the size of females. In contrast to the Bopyrinae, the life cycle of the remaining taxa (the former Cryptoniscoidea) begins (as far as known) with larvae (cryptoniscium) that become functional males and that later metamorphose into larger females (summary in WÄGELE 1989). So, in any case, in the groundpattern of the Bopyridae males are much smaller than females and can be considered as sexually mature larvae or young stages. The only difference between the Bopyrinae and the remaining taxa is that the Bopyrinae can adapt to the degree of infestation of their host and supress the male stage when no specimen of the species is present on the host, and to stay in the male stage when females are present. However REVERBERI and PITTOTI (1942) and REVERBERI (1947) have shown that at least in *Ione thoracica* (Montagu, 1808), males can transform into females when the female dies or is experimentally detached from its host, and also very young, immature females that have not grown to the adult size can become sexually mature males, while large females cannot. So, protandric hermaphrodism also occurs in the Bopyrinae. It is therefore only logical to suppose that

protandric hermaphroditism is part of the bopyrid groundpattern. As the morphology of the bopyrids can be derived from that of the Cymothoida (see e. g. BONNIER 1900; KUSSAKIN 1979; WÄGELE 1989), which also are protandric hermaphrodites, this hypothesis is plausible.

This mistake of BRUSCA and WILSON is the result of skipping an important step of phylogenetic analysis, namely the reconstruction of the groundpattern of the Bopyridae.

2. WÄGELE (1989) compared genera of the Sphaeromatidae and reconstructed some aspects of sphaeromatid evolution. One of the results was the postulation of a flat, disc-shaped body form in the groundpattern, a morphology seen in the less derived sphaeromatids and in related outgroups (Serolidae, Bathynataliidae, Plakarthriidae). Within the Sphaeromatidae in one line stepwise evolution of enrollment behaviour and morphological adaptations to enrollment can be observed; most species of upper littoral sphaeromatids belong to this more derived monophylum. BRUSCA and WILSON (1991: 200, 203) coded for this taxon (character nr. 7): "body not unusually broadened and flat (0)". This is clearly not a character of the groundpattern, though a character of most extant sphaeromatid species. No attempt was made to reconstruct this groundpattern; the authors even were aware that more data are necessary: "... a cladistic analysis ... of the Sphaeromatidae is greatly needed" (BRUSCA and WILSON 1991: 190). More correctly: an a priori phylogenetic analysis of the Sphaeromatidae is needed before the taxon can be used as terminal taxon in a cladistic analysis.

3. BRUSCA and WILSON (1991) try to prove that the dwarfish stygobiontic freshwater species *Calabozoa pellucida* Van Lieshout (1983) is closely related to the terrestrial isopods (Oniscidea). According to WÄGELE (1989) the Oniscidea have a large number of autapomorphies that are absent in *C. pellucida*. BRUSCA and WILSON however postulate a sistergroup relationship Calabozoidea/Oniscidea. One of the important synapomorphies they propose (p. 176, 177, 187) is character nr. 54: "male pleopod endopods 1 and 2 (only 2 in Ligiidae) elongate, styliform, participating together in the copulatory process". The following errors are contained in this single character definition:

– Different characters of two appendages (pleopod 1, pleopod 2) that, depending on the taxon, may or may not be a functional unit in copulatory behaviour, are combined to a single character: pleopod 1 does not participate in sperm transfer in most isopods; different modifications in the male sex are known also from taxa other than the Oniscidea (e. g. Valvifera). The structures of Plp1 and Plp2 should therefore be coded separately.

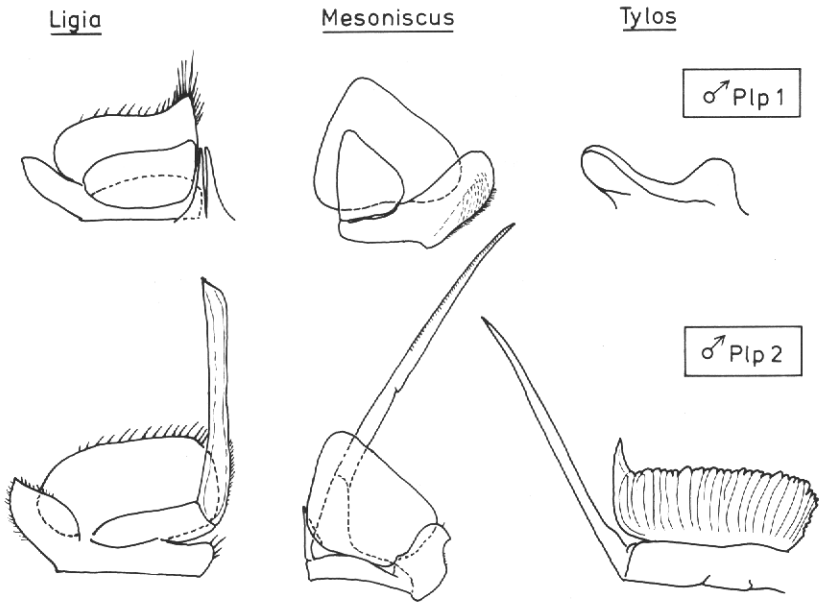

Fig. 9. Male pleopods of terrestrial isopods (Oniscidea), where pleopod 1 shows the plesiomorphic condition (endopod not a styliform copulatory organ). *Ligia oceanica* (Linné, 1767) (after SARS 1897), *Mesoniscus graniger* (Frivalsky, 1865) (after GRUNER and TABACARU 1963), *Tylos granulatus* Krauss (after KENSLEY 1974)

- Different character states of male pleopod 1 (i. e. not styliform in Ligiidae, but styliform in other taxa) are combined into a single character state.
- The homology of the copulatory structure of pleopod 1 in *Calabozoa* has not been verified. The male pleopod 1 is biramous (Brusca and Wilson 1991: Figs. 10A, B; Table 2), bearing a tiny medial article that due to its position must be the endopod, while the large exopod is elongated, styliform. Therefore the authors' character definition 'styliform endopod' is probably not correct. Strangely, on p. 187 they seem to have noted this: "... the copulatory part of the calabozoan first pleopod could be the exopod ..."! With this statement the presumed synapomorphy of Calabozoidea and Oniscidea becomes worthless.
- Furthermore, the styliform male endopod of pleopod 1 of the Oniscidea does not occur in the groundpattern of the taxon. To the groundpattern belongs a pleopod 1 rather similar to that of other isopods, namely with broad, lamellar rami as in pleopods 3 to 5 (Fig. 9). This plesiomorphic character state can be seen in the Ligiidae and Mesoniscidae; in the Tylidae pleopod 1 has no styliform ramus either, but the pleopod is much reduced in size and therefore derived in comparison with e. g. ligiids.

The absence of all unique autapomorphies of the Oniscidea in the Calabozoidea allows only a sistergroup relationship at most. If the character of pleopod 1 were a synapomorphy, it would be necessary to place *Calabozoa pellucida* within the Oniscidea, because the synapomorphy is not present in the oniscid groundpattern. But this single character would then have been in conflict with all other oniscid autapomorphies. Probability would thus have suggested a convergent evolution of the male pleopod 1 endopod, and the hypothesis of synapomorphy would have been rejected. Also, in view of the uncertain homology of this endopod, arguments in favour of a sistergroup relationship do not exist.

8.3 Coding of taxa of unknown monophyly

This problem is related to the previous one. If no attempt to reconstruct groundpattern characters has been made the danger of non-monophyly of a taxon is real. As a phylogenetic system can only be reconstructed for monophyletic terminal taxa, before the compilation of a data matrix monophyly of each taxon must be examined. This can have the consequence that extensive, detailed phylogenetic analyses become necessary for some of the subordinated taxa before the envisioned computerized cladistic study can be carried out.

Examples: It is risky to use taxa established in a traditional classification, because many of these are not monophyletic.

1. Brusca and Wilson (1991) coded two groups of terrestrial isopods, namely the "Ligiamorpha" and the "Tylomorpha". Nowhere do they explain the composition of these groups nor from where their data matrix characters have been selected. They have certainly not reconstructed the groundpatterns of these two taxa. The name Tylomorpha is derived from the family Tylidae, the Ligiamorpha from the Ligiidae. It therefore must be assumed that the authors place the Ligiidae within the Ligiamorpha together with the remaining Oniscidea (as many conservative oniscid taxonomists do; see e. g. Holdich et al. 1984). But the Ligiamorpha probably are not a monophyletic group. The Tylidae and Ligiidae may both belong to the Diplochaeta Vandel, 1943, which share several synapomorphies absent in the remaining Oniscidea (Wägele 1989). It would therefore be justified to state that the Tylidae are Ligiamorpha, if the name Ligiamorpha is used as synonym for the Diplochaeta. Brusca and Wilson did not test the monophyly of the Tylomorpha.

2. Another doubtful taxon is the "Mysidacea", used by Brusca and Wilson (1991) as the all-zero outgroup. Two very different groups belong to the Mysidacea, namely the Mysida and the Lophogastrida. The Mysida have apomorphic features that within the Peracarida are unique for the lineage leading to the Isopoda (e. g. modification of the respiratory mechanism, epipodial gills of pereopos are reduced) and they have unique autapomorphies (e. g. uropodal statocysts) absent in the Lophogastrida. The Lophogastrida are, if monophyly can be substantiated for this taxon, at most the sistergroup of a monophylum to which the Mysida and Isopoda belong. A groundpattern can not be reconstructed for the non-monophyletic Mysidacea, and therefore no basis for a coding as outgroup exists.

8.4 Wagner parsimony and reversals

As already stressed (par. 6.2) a phylogenetic system can only be reconstructed with the help of characters whose states have been found prior to the cladistic analysis. Any other procedure, such as the a posteriori character weighting discussed by PANKHURST (1991) can lead to circularity (NEFF 1986).

In contrast to molecular data, morphological characters can be so complex that back mutations or reversals are not very probable (e. g. BLACKBURN 1984). Though the phenomenon of atavism is real, only exceptionally are atavisms positively selected to become characters of a species. If reversals really are observed, they can only result from a new mutation, such as the loss of a supressing gene. So in reality these reversals are new apomorphic characters and should be coded as such whenever these correlations are known. Because reversals of complex morphological characters are improbable, the number of seeming reversals should be minimized in a phylogenetic analysis. The use of Wagner parsimony, that allows changes from apomorphic to plesiomorphic states, is therefore not to be recommended. The use of Wagner parsimony is an admission that the character set contains weak characters or that it was not possible to assess character polarity a priori.

BRUSCA and WILSON (1991) use Wagner parsimony explicitly to allow characters to change from 0 to 1 and from 1 to 0 ad libidum. A posteriori they derive character states from the most parsimonious dendrogram (see also example in par. 6.2), clearly a circular procedure.

8.5 Confusion of methodological with evolutionary parsimony

The principle of parsimony is an essential criterion for the selection of a scientific hypothesis. In phylogenetic studies two different parsimonies must carefully be distinguished: methodological parsimony used for dendrogram construction, and evolutionary parsimony estimated in character analysis.

Methodological or technical parsimony (see KLUGE 1984; descriptive parsimony sensu JOHNSON 1982; BRYANT 1989) is calculated with algorithms that select the shortest dendrogram(s) on the basis of a given data matrix. This is merely a statistical procedure for choosing among dendrograms, without biological implications (BRADY 1982). It is not useful for estimating evolutionary parsimony. This methodological parsimony nevertheless is in accordance with the observation that evolution is economical (see e. g. KLUGE 1984) in the sense that characters change stepwise and stay functional and that roundabout routes, such as repeated reversals, are less probable because they cost time and energy or require improbable convergent mutations. To choose the shortest dendrogram is therefore also a method employed in a conventional Hennigian analysis. This does not mean that the result of evolution is always the shortest or best solution (think of the peculiar evolution of the vertebrate circulatory system or of the returning to a marine way of life of several mammals).

An aspect of methodological parsimony is the calculation of dendrogram statistics that describe, for example, the number of character changes or tree length. The retention index for example, reflects "the degree to which similarities apparent in the data can be retained as homologies" (FARRIS 1989), while the consistency index is inversely proportional to the length of the tree. The distance between nodes of species that are ordered with the help of character transformation series is calculated as being 1 between each step, no matter how complex the changes from state 0 to 1 and from 1 to 2 are. There have been objections, such as to the use of the consistency index, which according to ARCHIE (1990) is dependent on the number of taxa and characters and on character state distributions. But more important is the fact that these statistics have nothing to do with evolutionary parsimony. The following parameters are not considered in this type of statistics: 1. the different probabil-

ity of evolution of complex characters in contrast to simple ones; 2. the different probability of parallel evolution of complex characters in contrast to simple ones.

None of these probabilities, which are the only ones relevant for evolution of characters, are estimated by arithmethic parsimony calculations. Even when an a priori estimate of complexity is used to give characters different weights, the numbers calculated by dendrogram statistics remain mere useful artifacts of the method. They are without biological implications, because no correlation exists between the absolute numbers and the evolution of organisms composed of an incalculable wealth of features.

Evolutionary parsimony (see KLUGE 1984; ontological parsimony sensu BRYANT 1989) cannot be calculated for historical events, but it can partly be roughly estimated. The probability that a new character evolves depends on 1. the number of mutations that are necessary to produce the new feature, 2. the probability that the new feature spreads in a population and is selected in a historical ecological situation.

Thus evolutionary parsimony is correlated with the laws studied by genetics, population genetics, and ecology. Some of these probabilities can be calculated for laboratory experiments, but probabilities for genetic drift cannot be calculated for the past. Nevertheless one aspect of evolutionary parsimony can be estimated, namely the probability that a series of mutations occurs. This has already been discussed above (character weighting, par. 6.3). In theory, the genetic background of character evolution can be analyzed, but this is not practicable. A rough comparative estimation of character complexity and of the adaptive value are the arguments available for character weighting.

In the Hennigian method estimation of evolutionary parsimony is used to decide 1. whether a character could have evolved more than once, 2. which of two competing hypotheses of synapomorphy is based on better evidence, 3. which of two competing hypotheses of sistergroup-relationship is based on more probable hypotheses of synapomorphy.

The estimated quality of characters and not the numbers calculated from tree statistics are used in decisions. Therefore a comparison of statistics of dendrograms from different authors is not an adequate criterion to estimate the quality of the hypotheses; the discussion must always concentrate on the quality of the characters. This is why a comparison of differences in "tree lengths" calculated for hypotheses of different origin (e. g. in BRUSCA and WILSON 1991: 186, 190) is, in my opinion, a confusion of methodological with evolutionary parsimony.

The confusion of arithmetic procedures with laws of evolution has led to the development of nonsense algorithms. SHAO and SOKAL (1990) for example want to distinguish between symmetrical (balanced) and asymmetrical (imbalanced) trees: "A suitable measure of tree balance is necessary to find out if a tree shape reflects patterns of speciation or possible biases." What selection factor has an influence on tree shapes?

It can be concluded that 1. methodological parsimony is useful to find the shortest dendrogram on the basis of a given data matrix, 2. tree statistics have no evolutionary information content, but 3. evolutionary parsimony is the only criterion that can be applied to discuss character weights and competing hypotheses of relationships.

8.6 Failure to recognize the encaptic order

This is another serious problem of computer cladistics that cannot be avoided if other analytical methods (as the FIG/FOG type of analysis) are excluded:

If in nature a smaller group is part of a superordinated larger one and if this fact is not known a priori, then both taxa will be coded separately in a data matrix. The result of the cladistic analysis is at best a sister-group relationship (Fig. 10) between the subordinated and the superordinated taxon. None of the available computer programs can recognize this encaptic order of the two taxa.

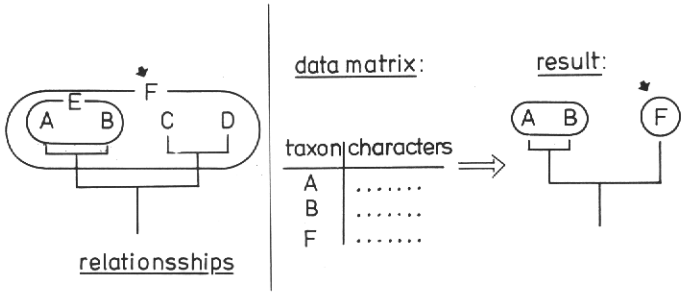

Fig. 10. A problem of computer cladistics: the encaptic order is not recognized

Example: WÄGELE (1983) produced a hypothesis on the origin of the Microcerberidae, tiny mesopsammal species occurring in freshwater interstices and in coastal groundwater. On the basis of several character transformation series and synapomorphies it was postulated that the Microcerberidae belong to a group that evolved in fresh water (the Aselloidea) and that therefore the taxon Microcerberidae must be considered to be a member of the Asellota. To prove that the Microcerberidae are not asellotes BRUSCA and WILSON (1991) coded both taxa (Asellota and Microcerberidae) separately. The false result is, of course, a sistergroup relationship.

This mistake cannot be avoided, but it can be corrected a posteriori: Whenever two taxa appear as sister groups in a cladogram calculated from a data matrix the possibility exists that they should be ordered encaptically. To test encaptic order versus sistergroup relationship the two taxa must be divided into their subordinated smaller monophyletic units and a separate analysis must show relationships between the smaller units.

This problem does not occur if a descendent analysis is done by hand, starting with small terminal taxa of corroborated monophyly (see par. 6.7).

8.7 Circular tree comparison

> "Some cladists belief that simplicity and truth are one and the same" (KLUGE 1984: 28).

The shortest tree is not necessarily the best one; short trees for example can be obtained decreasing the number of characters or of terminal taxa. Only on the basis of a given complete data set, are tree length or number of character changes to be seen as meaningful applications of methodological parsimony. But, as already discussed (par. 8.5), it is a mistake to compare tree lengths, when the alternatives are based on different data. This argumentation is circular (Fig. 11). Unfortunately the program McClade seduces the user into making such comparisons.

Example: "Each of these alternative trees was analysed with the program McClade, with the same data set used to construct our tree . . . [. . .] . . . All of these trees are longer and less parsimonious than the 16 shortest trees . . . summarized in our consensus tree . . ." (BRUSCA and WILSON 1991: 190). The mistake here is that the alternative trees (from different authors) are based on different character sets. It is the quality of characters which should have been compared!

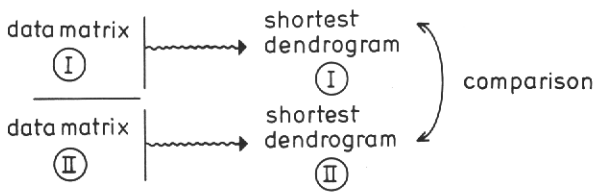

Fig. 11. Circular argumentation results from comparison of dendrograms based on different data sets (see text)

9 Confusion of systematization with classification

Like other sources of misunderstandings this one is not unique to computer cladistics. Arguments derived from classificatory demands should not be used in phylogenetic argumentation. Classification is not based on objective scientific arguments (see e. g. Ax 1987) but on conventions.

Example: As already mentioned, BRUSCA and WILSON (1991) tried to prove that the parasitic Bopyridae did not arise within the Cymothoida and they want to keep the bopyrids as a separate unit. They write (p. 189): "retaining the Epicaridea as a separate suborder ... has the further distinct advantage of not compressing the broad diversity of this group into a single highly heterogeneous family ..."

Obviously the authors do not question the monophyly of this group, but they want to place it in a higher category and support their proposed systematization with classificatory arguments.

10 The use of computer cladistics

Most of the sources of errors explained in this review can also occur in a classical Hennigian analysis. But it is the author's aim to show that in much-praised computer cladistics further specific sources of error occur. The belief of many users of computer programs, that they can objectively find sistergroup relationships and monophyletic groups without a priori assumptions, is a dream. The information that decides on relationships, namely the occurrence of synapomorphies, usually cannot be gained with computers. Therefore computers are normally not needed: with each valuable synapomorphic character a monophylum is identified.

However, after all the criticism that has been made, computer programs like Hennig'86 are still useful for one purpose. They serve to test the occurrence of alternative dendrograms that can be calculated from a data set for monophyletic terminal taxa.

It is no doubt possible that some alternative dendrograms are overlooked during a 'by hand' analysis. But the output of computer cladistics should be regarded as a mere statistical result, which needs biological interpretation, which can help to improve a previous hypothesis or to motivate the search for further characters. The value of different hypotheses of relationships can be estimated only on the basis of character evaluation and of the evolutionary plausibility of the hypothesis. It can never be settled by an arithmethical method that has been used to represent graphically a data set.

11 Conclusions

It is a mistake to belief that relationships of a large number of taxa can be explored only with computer programs. The number of possible taxa combinations decreases rapidly with each correctly identified synapomorphy. The latter must be found anyway without the help of computers.

Computer programs can be used only in one of several steps of a phylogenetic analysis, namely for the graphical representation of information contained in a data matrix and for calculation of tree statistics based on methodological parsimony.

Character analysis and examination of the plausibility of the hypothesis of relationships must be carried out by a trained biologist on the basis of Hennigian logic and the theory of evolution.

For the assemblage of a data matrix a priori hypotheses are unvoidable: namely hypotheses of synapomorphy, of monophyly of terminal taxa, of exclusion of outgroup taxa from the ingroup.

The term OTU should be avoided and replaced by species or by groundpatterns of monophyla.

Important sources of errors occur during character analysis, i. e. prior to the cladistic analysis. These are the same errors as in conventional phylogenetic analysis.

Character weighting is unavoidable to distinguish between characters of high information content and long evolutionary history and characters of low information content. Also computer cladists, like those who work "by hand", must distinguish between useful and meaningless characters.

Characters should be defined carefully and in detail to avoid the artificial fusion of non-homologous or of independent characters into one meaningless character.

The presence of apomorphic characters in all ingroup and outgroup taxa must be checked carefully to avoid the coding of a plesiomorphy of a subordinated taxon as an apomorphy.

It is not necessary to select a taxon as outgroup. This procedure can lead to mistakes in assessment of character polarity. It is safer to regard all non-ingroup taxa as outgroup, whenever ingroup monophyly has been corroborated. Groundpatterns of monophyla can be reconstructed even when a sistertaxon is not known.

The comparison of taxa can only be carried out with the groundpatterns of the taxa. The term 'bauplan' should be replaced by 'groundpattern'.

Cladistic analysis without character valuation is not a method of phylogenetic systematics but of phenetical comparison (e. g. of numerical distances between taxa). The use of Wagner parsimony and the use of unpolarized characters is therefore not recommended. When character reversals occur in a dendrogram, character states should be checked for homology since reversals are very rare in nature.

A posteriori character state polarization leads to circular argumentation whenever these characters are used to corroborate a hypothesis of relationships.

If relationships of taxa of unknown groundpatterns or monophyly are analysed, characters cannot be coded correctly.

Methodological parsimony is not the same as evolutionary parsimony and can therefore not be used to compare hypotheses based on different character sets.

Comparisons of statistics for dendrograms based on different data sets are meaningless. Only comparisons of character qualities have evolutionary significance. Comparison of lengths of dendrograms taken from different analyses in relation to a single data matrix leads to circular argumentation. It is character sets, not tree lengths, which must be compared.

Algorithms calculating dendrograms on the basis of a data matrix cannot recognize encaptic order in the analysed terminal taxa.

Arguments based on classificatory convenience cannot be used in a phylogenetic analysis.

The use of computer programs is recommended only to supplement the conventional procedure of a phylogenetic analysis, namely to explore patterns of relationships calculated from a given data set. The results must be discussed on the basis of character weights and the plausibility of dendrograms should be tested.

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Zusammenfassung

Methodische Probleme der Computer-Kladistik, erläutert am Beispiel einer Fallstudie der Phylogenese der Isopoda (Crustacea)

Eine mit Computerprogrammen durchgeführte Analyse der Phylogenese der Isopoda (Crustacea: Peracarida) wird als Quelle für Beispiele charakteristischer Fehler und Mißverständnisse der „Computer-Kladistik" genutzt. Zusätzlich zu den Fehlern, die in der konventionellen Hennig-

schen Analyse auftreten können, gibt es weitere spezifische Probleme. Es wird empfohlen, das Konzept des OTU durch das Grundmuster zu ersetzen. Statistiken der Klassifikation der Datenmatrix erlauben keine Aussage über die Qualität konkurrierender Hypothesen; Argumente müssen sich vielmehr auf die Merkmalsanalyse konzentrieren. Die Nutzung der Computer erhöht damit nicht die Objektivitat der Analyse. Es wird weiterhin empfohlen, zur Bestimmung der Merkmalsausprägung nicht ein ausgewähltes Taxon als Außengruppe zu verwenden. Zur Phylogenese der Isopoda werden neue Argumente und Daten vorgestellt, die – entgegen der Vorstellung einer de novo evolutiven Entwicklung – die Herkunft des Schwanzfächers der Isopoden aus dem Grundmuster der Eumalacostraca stützen.

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Author's address: Prof. Dr. J. W. WÄGELE, Abt. Systematik und Morphologie der Tiere, Fakultät für Biologie, Universität Bielefeld, P.O.B. 100131, D-33501 Bielefeld, Germany