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Millipede phylogeny: how much do we know and what is it good for?

Abstract: Phylogenetic (cladistic) studies on millipedes, as well as cladogram-based analyses of millipede biogeography and evolution, are reviewed, from analyses at supraordinal level to those dealing with species of a single genus. Taxon-biogeographical and area-biogeographical analyses of the superfamily Nemasomatoidea are presented in detail as an example.

Key words: Diplopoda, phylogeny, cladistics, biogeography

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INTRODUCTION

Facing the breathtaking diversity of species of living organisms on Earth, many representatives of at least one of these species want to know how this biodiversity has evolved: which species are most closely related to which other species, and in what sequence did they acquire their particular characteristics? Such *phylogenetic* or *cladistic* studies have been conducted for more than a century, but it was not until the formalisation of the method of phylogenetic systematics by HENNIG (1950, 1966) that phylogenetics passed beyond the almost purely speculative stage and into an analytical one. Since then, the method has been the subject of massive development, including computerisation of the analysis and inclusion of molecular characters. Today a cladistic analysis, with hypotheses on relationship depicted in the form of cladograms, and with the indication of apomorphies (shared derived, inherited traits) for taxa, is a core ingredient of many systematic studies. For an introduction to the cladistic method, see KITCHING et al. (1998).

The present paper presents an overview of existing cladistic analyses of millipede taxa, as well as of biogeographical and evolutionary analyses based on millipede cladograms. As an example, an original cladogram-based biogeographical analysis of the julidan superfamily Nemasomatoidea is included.

EARLY PHYLOGENETIC STUDIES ON MILLIPEDES

Although it was Hennig's writings that marked the beginning of modern phylogenetics, this does not mean that earlier authors did not hypothesize about phylogeny. For example, VERHOEFF (1900) presented a diagram of phylogenetic relationships between what was then subgenera of the julid genus *Pachyiulus* (Fig. 1).
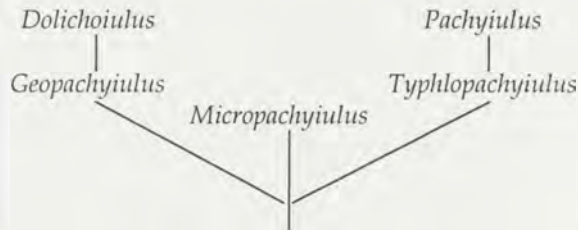

Fig. 1. Phylogenetic relationships between subgenera of *Pachyiulus* as presented, but not otherwise commented upon, by VERHOEFF (1900).

CLADISTIC STUDIES ON MILLIPEDES

Hardly surprising, the first myriapodologist to adopt Hennig's method was another German, namely KRAUS (1966) who in his *magnum opus* 2 on the African family Odontopygidae presented Hennigian argumentation schemes for spirostreptidean families (Fig. 2), odontopygid subfamilies, and some genera of odontopygids. The next cladistic study on record was that of ENGHOFF (1981) who analysed relationships between families of the order Julida (cf Fig. 6).

Since then, a number of publications have dealt more or less cladistically with the entire order Diplopoda or with various subordinate millipede taxa. There are numerous examples where authors have used cladistic argumentation, and/or have presented phylogenetic hypotheses in the form of cladograms, but have not carried out a cladistic character analysis in the strict sense (e.g. ENGHOFF & GOLOVATCH 1995, JEEKEL 1985, MAURIÈS 1987, SHELLEY 1994). The following review is not exhaustive with respect to such contributions, but an attempt has been made to mention all studies which include a proper cladistic analysis, be it by hand or using one of the several available cladistic computer programs.

The analyses mentioned have been done manually except where noted. Employment of molecular characters, notably DNA sequences, in cladistic studies has become

extremely prevalent in the last years and is even, but unwarrantedly, regarded as a *sine qua non* for phylogenetics by some. The molecular aspect of phylogenetics has, however, not yet spread to diplopodology. The only exception is that one or a few millipedes species have been included as class representatives in some molecular studies of higher-level relationships of arthropods (e.g., EERNISSE 1998, FRIEDRICH & TAUTZ 1995, GIRIBET & RIBERA 1998, WHEELER 1998, WHEELER *et al.* 1993).
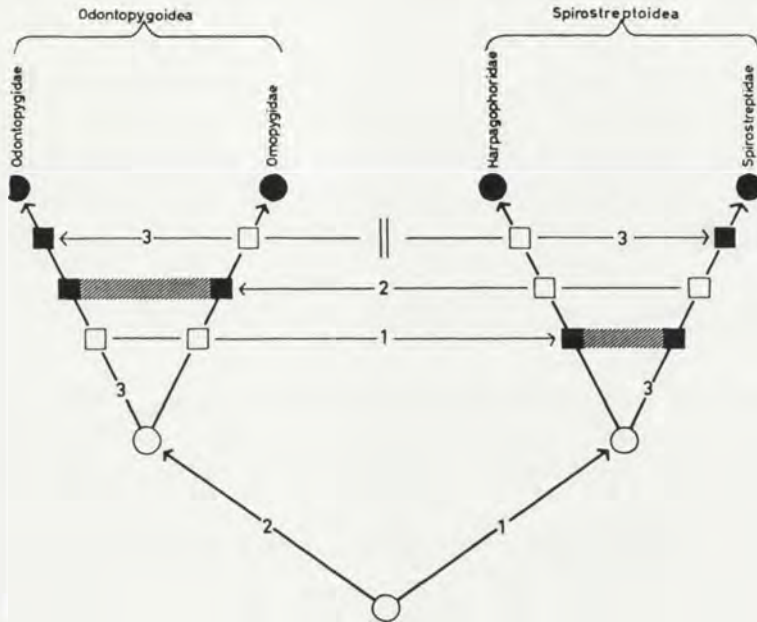

Fig. 2. Cladogram of spirostreptidean families. This cladogram is in the form of a "Hennigian argumentation scheme" in which the characters discussed in the text are shown as variously shaded bars. From KRAUS (1966).

The class Diplopoda

ENGHOFF (1984a) analyzed supraordinal relationships of millipedes, recognizing as monophyletic the traditional groups Penicillata and Chilognatha, Pentazonia and Helminthomorpha, Colobognatha and Eugnatha, and Nematophora, Merocheta and Juliformia. Enghoff's cladogram was refined by DOHLE (1988) who argued for a sister-group relationships between Merocheta and Juliformia, and by ENGHOFF *et al.* (1993) who resolved ordinal relationships within Pentazonia and Nematophora (Fig. 3).

Callipodida

WANG (1996) presented a computer-aided cladistic analysis of the Paracortinidae. All three genera and seven known species of this endemic Chinese family were included (Fig. 4).
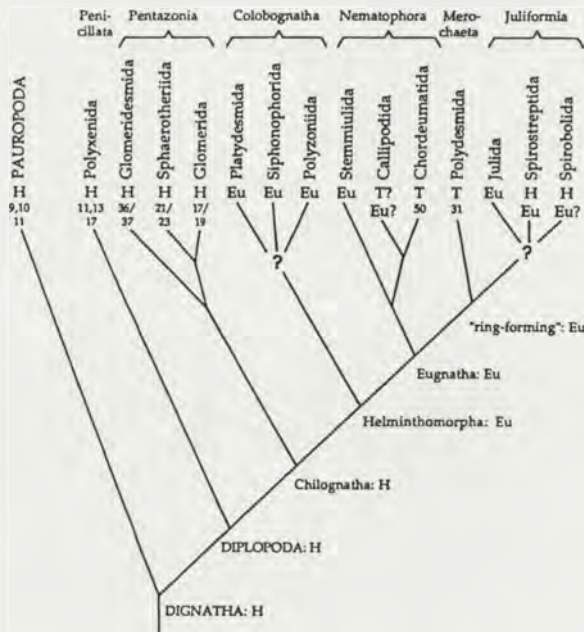
Fig. 3. Cladogram of millipede orders, with modes of anamorphosis indicated. Eu: euanamorphosis; H: hemianamorphosis; T: teloanamorphosis. From ENGHOFF et al. (1993).
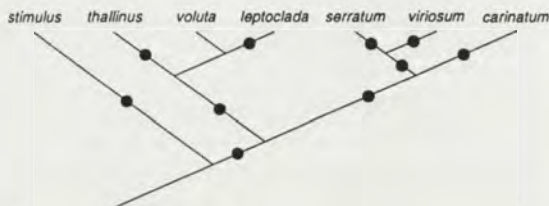

Fig. 4. Cladogram of species in the callipodid family Paracortinidae. Dots indicate apomorphies. From WANG (1996).

Chordeumatida

SHEAR (1990) analyzed relationships between the 34 species of *Diplomaragna* (Diplomaragnidae), using a computer programme (Fig. 5).

Julida

ENGHOFF (1991) revised his analysis of julidan families from 1981, this time also using a computerised method. A total of 15 families was included (Fig. 6). A second follow-up is in preparation by Shultz, Regier and Enghoff, using molecular characters and also considering internal relationships in the Julidae.
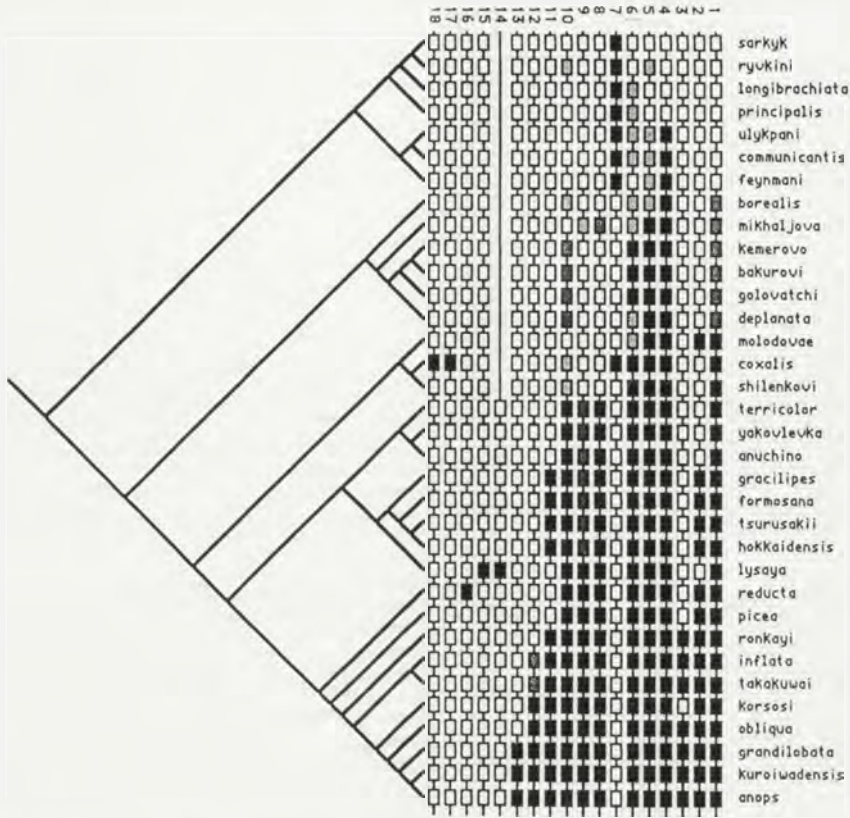
Fig. 5. Cladogram of species of *Diplomaragna*. The character matrix forming the basis of the analysis is illustrated to the right of the cladogram. From SHEAR (1990).

Several lower-level analyses of genus- and species-level relationships within the Julida have been published:

- The seven genera of Nemasomatidae (ENGHOFF 1985).
- The four genera of Blaniulidae-Nopoiulinae (ENGHOFF 1984b, 1990b).
- The 13 tribes of Julidae (Fig. 7, see also ENGHOFF 1996a concerning basal julid phylogeny), the five genera of Cylindroiulini, and the species of *Enantiulus* and *Allajulus* (READ 1990, computer-aided analysis).
- The numerous species of the *Cylindroiulus madeirae*-group (Julidae) (ENGHOFF 1982, see also READ 1989).
- The 12 species of the *Nepalmatoiulus birmanicus*-group (Julidae) (ENGHOFF 1987)
- The numerous species of the julid genus *Dolichoiulus* (ENGHOFF 1992, computer-aided analysis).

Fig. 6. Cladogram of families of Julida. From ENGHOFF (1991).

- The six genera and six species-groups of the julid tribes Paectophyllini and Calyp-
  tophyllini (ENGHOFF 1995a, computer-aided analysis).

Spirostreptida

The first and so far only analysis to follow up on Kraus' pioneering work in this
order is that on 23 southern African species of *Doratogonus* by HAMER & SLOTOW
(2000).

Polydesmida

SIMONSEN (1990) analyzed relationships between the four suborders of Polydes-
mida and the 16 families of suborders Polydesmidea and Dalodesmidea. His most
remarkable result was that the Dalodesmidae seem to occupy a phylogenetically sub-
ordinate position within the Polydesmidea (Fig. 8).

A few lower-level analyses have also been published:

- The tribes of the eastern Nearctic Xystodesmidae and the genera of one of these,
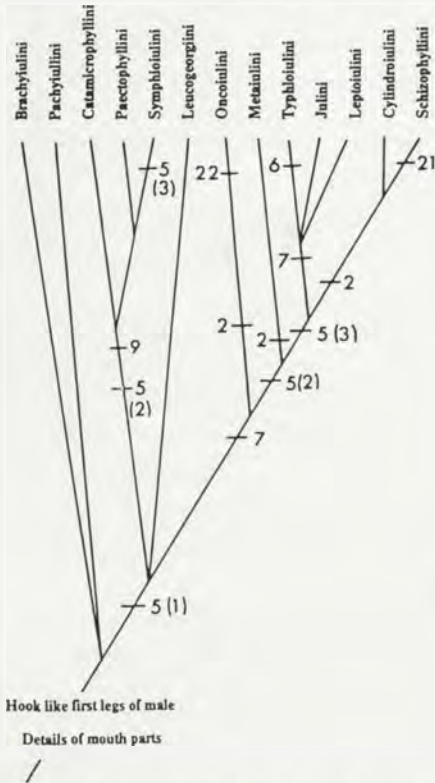 the Apheloriini (SHELLEY & WHITEHEAD 1986).

Fig. 7. Cladogram of tribes of Julidae. Numbers refer to apomorphies. From READ (1990).
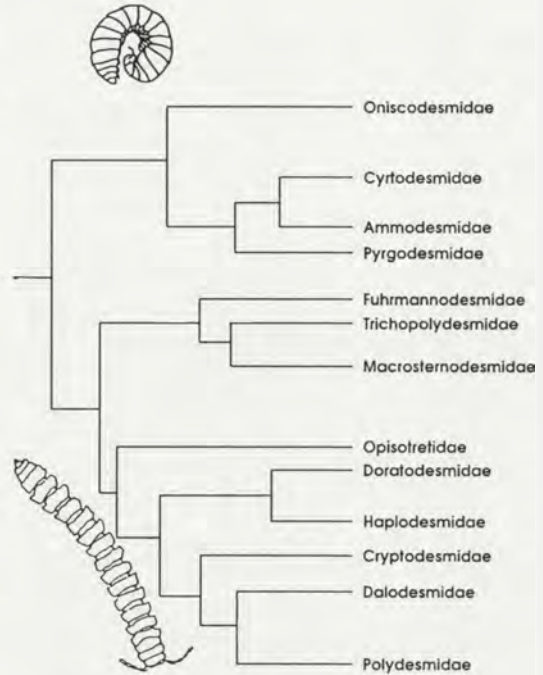
Fig. 8. Cladogram of families of Polydesmidea. From SIMONSEN (1990).

- The numerous species of the paradoxosomatid genus *Tylopus* (GOLOVATCH & ENGHOFF 1993, computer-aided analysis).
- The 19 species of the paradoxosomatid genus *Desmoxytes* (GOLOVATCH & ENGHOFF 1994, Fig. 18, computer-aided analysis).
- Thirty-seven representative species of the very large genus *Polydesmus s.l.*, resulting in a splitting of this collective genus into 6 cladistically defined genera (DJURSVOLL *et al*. 2000).

USES OF PHYLOGENIES: CLADOGRAM-BASED BIOGEOGRAPHY

Although a cladogram can never be more than a hypothesis, each cladogram can be said to bring us a step forward towards full insight into the evolution of the study group, *in casu* millipedes.

The cladogram by itself tells part of the story of millipede genealogy but a cladogram can be used in several ways to obtain further insight. One of the most wide-

spread uses of cladograms is for historical biogeography. It is important to keep in mind that biogeography is a very comprehensive discipline and that cladograms are only useful for particular subdisciplines. It is also important to keep in mind that when hypotheses of relationships between taxa are wholly or partly based on geographical distribution (e.g. SHELLEY & WHITEHEAD 1986), a subsequent biogeographical analysis will be biased by circular reasoning and should therefore be avoided.

The methodology of cladogram-based biogeography is very much a matter of debate. For recent reviews of some of the available methods, see BIONDI (1998), HUMPHRIES & PARENTI (1999), MORRONE & CARPENTER (1994), and MORRONE & CRISCI (1995).

The starting point for a cladogram-based biogeographical analysis is a *taxon-area cladogram* (Fig. 9). Here, distribution areas have simply been added to the taxon names on the cladogram. A taxon-area cladogram can be viewed in two ways.
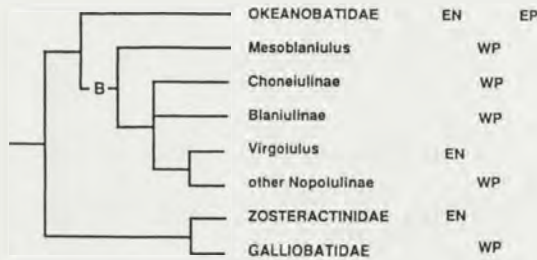

Fig. 9. Taxon-area cladogram for Blaniuloidea. B = Blaniulidae. The distribution of the taxa in the Eastern Nearctic (EN), Western Palaearctic (WP) and Eastern Palaearctic (EP) is shown. From ENGHOFF (1993).

First, the distribution areas may be viewed as information about the taxa, and one can try to trace the distributional history of the group under study. This is what most diplopodologist biogeographers have done. In most such *taxon biogeographic* studies on millipedes authors merely have "explained" in a narrative form the distributional history of the animals taking the cladistic information into account. This is true of KRAUS' study of Spirostreptidea (1966), ENGHOFF'S of Nemasomatidae (1985), SHEAR'S of *Diplomaragna* (1990), and WANG'S of Paracortinidae (1996). WANG (1996) referred to Hennigs progression rule (HENNIG 1966), an early cladistic biogeographical method which has subsequently been refined/replaced. ENGHOFF (1993) used the concept of "cladistic subordinateness" to infer routes of dispersal of julidan millipedes (e.g., Fig. 10) and later (1995a) used the "ancestral area analysis" method of BREMER (1992) to infer the area of origin of paectophylline and calyptophylline julids to be in Turkey.

An alternative view of a taxon-area cladogram is to consider the included taxa and the cladogram as information about the areas they inhabit. This information can then be used to infer the historical connections between the areas, an approach known as *area biogeography*. Thus SIMONSEN (1990, 1992) used his phylogenetic analysis of

Polydesmidea in a narrative reconstruction of the history of Eastern Gondwanaland. There is a number of analytical methods available for transforming a taxon-area cladogram into a *resolved area cladogram* (e.g. Fig. 16). This approach is warranted in particular when a hierarchical pattern of area relationships can be supposed as, e.g., in the case of the southern landmasses (Fig.11). The only case where millipedes have been involved in an analytical area biogeographical study so far has been ENGHOFF's (1995b) analysis of area relationships in the Holarctic region. This study was based on phylogenies of 73 animal groups including five millipede groups.
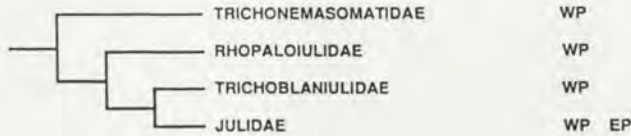

Fig. 10. Taxon-area cladogram for Juloidea. The family Julidae occupies a cladistically subordinate position; therefore the occurrence of the family in the Eastern Palaearctic (EP) is regarded as resulting from dispersal from the Western Palaearctic (WP). From ENGHOFF (1993).
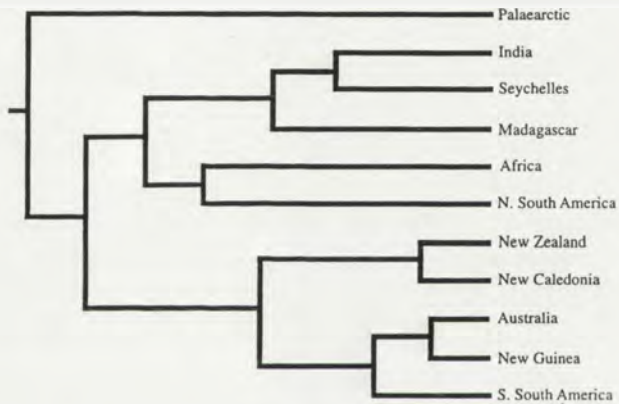

Fig. 11. Geological area cladogram of the southern (Gondwanan) landmasses. From JOHANSON (1998).

AN EXAMPLE OF A CLADOGRAM-BASED BIOGEOGRAPHICAL ANALYSIS:
THE NEMASOMATOIDEA

To illustrate how taxon and area biogeographical analysis is practically done, we may have a look at the Nemasomatoidea. This superfamily of small, juliformian milli-pedes occurs in all four main divisions ("infraregions") of the Holarctic region (Figs 12–13). A taxon-area cladogram of the group was presented by ENGHOFF (1993), and, in a somewhat simplified form, by ENGHOFF (1995b), see Fig. 14.
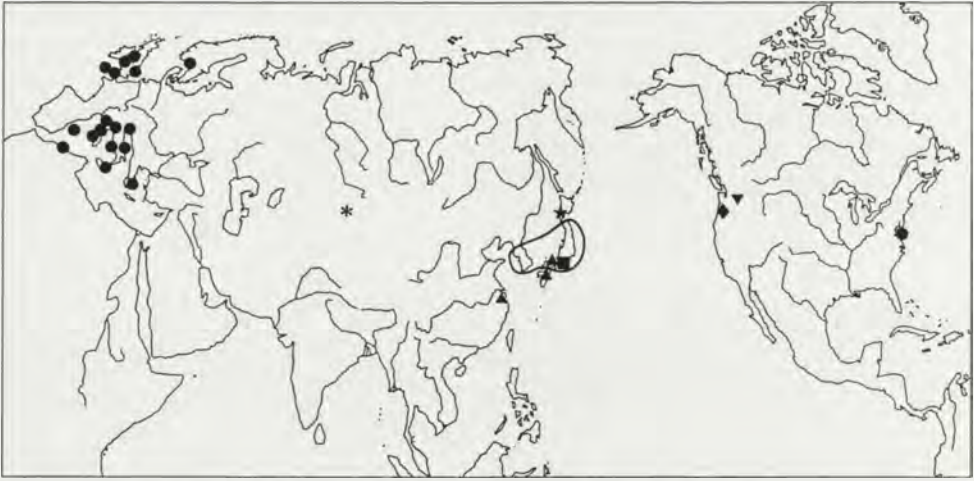
H. Enghoff

Fig. 12. Distribution of Nemasomatoidea except *Nemasoma* and *Orinisobates*. Diamond: Telsonemasoma-
tidae; inverted triangle: Chelojulidae; star: Pseudonemasomatidae; encircled area: *Antrokoreana*; asterisk:
Basoncopus; square: *Dasynemasoma*; triangles: *Sinostemmiulus*, dots: *Thalassisobates*. From ENGHOFF (1993).

Fig. 13. Distrbution of the nemasomatid genera *Nemasoma* and *Orinisobates*. 1: *N. varicorne* C. L. KOCH,
1847; 2: *N. caucasicum* (LOHMANDER, 1923); 3: *O. kasakstanus* (LOHMANDER, 1933); 4: *O. sibiricus* (GULIČKA,
1963); 5: *O. gracilis* (VERHOEFF, 1933); 6: *O. microthylax* ENGHOFF, 1985; 7: *O. n.sp.*; 8: *O. soror* ENGHOFF,
1985; 9: *O. expressus* (CHAMBERLIN, 1941); 10: *O. utus* (CHAMBERLIN, 1912); 11: *O. nigrior* (CHAMBERLIN,
1943). From ENGHOFF (1993).

From a taxon biogeographic point of view we might ask: what was the most likely distribution of the inferrred ancestors on the cladogram (i.e., the ancestor of all *Orinisobates* species, the ancestor of *Orinisobates* + *Nemasoma*, the ancestor of *Orinisobates* + *Nemasoma* + *Sinostemmiulus*, etc.)? The best method for hypothesizing the ancestral distributions is dispersal-vicariance analysis (DIVA), developed by RONQUIST (1996, 1997). DIVA finds those ancestral distributions that require the lowest number of postulated dispersals and extinctions whereas speciations, be they allopatric (vicariances) or sympatric, are regarded as "cost-free" (*cf* below). The result of the DIVA analysis of the taxon-area cladogram in Fig. 14 is shown in Fig. 15. The cladogram in Fig. 15 suggests that the Nemasomatoidea were originally an amphi-Beringian (WN+EP) group, that most of the subsequent differentiation took place in the eastern Palaearctic, and that the occurrence of nemasomatoids (except for the "Chelojulidae etc." clade) in the Nearctic and in the western Palaearctic is due to dispersal from the eastern Palaearctic.

```
        ┌──────── CHELOJULIDAE etc.   WN
    ┌───┤          PSEUDONEMA-                    EP
    │   └          SOMATIDAE
    │      ┌────── Antrokoreana +                 EP
   ─┤ N─┤  └────── Dasynemasoma                   EP
    │   │  ┌────── Thalassisobates      EN WP
    │   └──┤  ┌─── Sinostemmiulus                 EP
    │      └──┤    Nemasoma              WP
    │         │    "O." soror                     EP
    │         └┐   O. kasakastanus +              EP
    │         ┌┴┐  O. expressus +      WN
    └─────────┴─┴  O. nigrior           EN

N = NEMASOMATIDAE, O. = Orinisobates
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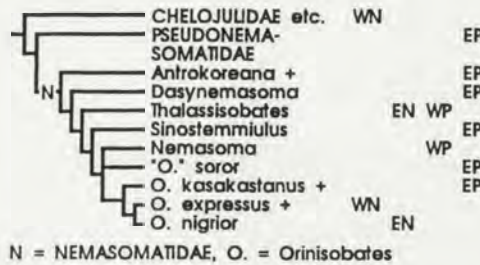
Fig. 14. Taxon-area cladogram for Nemasomatoidea. Some branches have been deleted from the original cladogram (cf. ENGHOFF 1993), viz. *Basoncopus* and five species of *Orinisobates*. This was done in order to minimize the number of polytomies since these cannot be handled by the programs used for analysis. EN: eastern Nearctic; EP; eastern Palaearctic; WN: western Nearctic; WP: western Palaearctic. From ENGHOFF (1995b).

Focussing on areas instead of millipedes, we can ask: what can the Nemasomatoidea tell us about the history of the four Holarctic infraregions? To answer this question, we can use my preferred method, the WISARD algorithm (ENGHOFF 1996b). The Nemasomatoidea occur in all four infraregions and the question now is, which of the 15 possible resolved area cladograms for four areas (Fig. 16) are supported by the Nemasomatoidea. The "null hypothesis" is that the ancestral nemasomatoidean was distributed over all four infraregions and that the present distribution of the various subgroups is a result of subsequent geographical splitting, vicariance, of the ancestor. It is, however, clear that vicariance cannot be the whole explanation, since there are several instances of more than one taxon occurring in the same infraregion. Also, one taxon occurs in more than one infraregion. To account for the observed pattern, additional processes have to be taken into account. The WISARD algorithm considers three such processes: non-vicariant (sympatric) speciation, extinction and dispersal. The
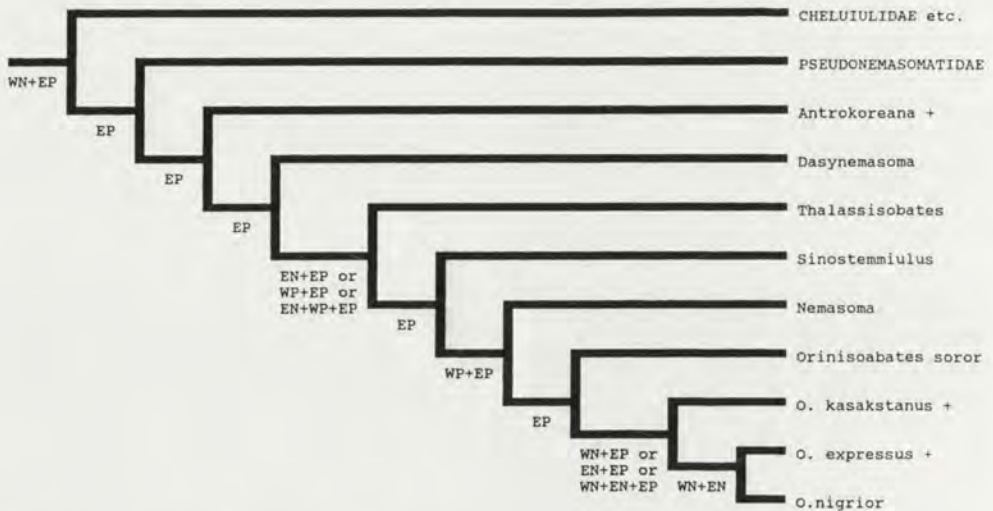
Fig 15. Results of DIVA analysis of the Nemasomatoidea. For each ancestor, the most probable distribution(s) is/are indicated. Note that there are three equally probable distributions of the ancestor of *Orinisobates kasakstanus + expressus + niger,* and also of the ancestor of *Thalassisobates + Sinostemmiulus + Nemasoma + Orinisobates.* Area codes as in Fig. 14. The deletion of certain branches from the original cladogram (see legend to Fig. 14) may have influenced the outcome of the DIVA analysis: if one and not both of the two *Orinisobates* species in WN (*O. expressus* and *O. utus*) was the sister species to *O. nigrior,* there would be only one most probable distribution of the ancestor of these three species + their sister group (which would in any case occur in EP), viz., WN+EP. The trichotomy between *Orinisobates soror, Nemasoma* and the remaining *Orinisobates* species has, for the sake of demonstration, been resolved in favour of monophyly of *Orinisobates.*

fifteen possible resolved area cladograms are tested in relation to the three processes, and if a resolved area cladogram can be found that requires the minimum number of instances of all three processes, this is the preferred one. Sympatric speciation and extinction can be analyzed with the computer program COMPONENT version 2.0 (PAGE 1993). Dispersal is minimized by hand by deleting all occurrences of each area, except one, in all possible combinations. The results of the WISARD analysis is shown in Table. It appears that no resolved area cladogram minimizes all three criteria, but there are two which minimize two criteria, and these are therefore those best supported by the Nemasomatoidea. Both these resolved area cladograms include a "sister area" relationship between the western and eastern Nearctic subregion. If the same resolved area cladograms were found to be supported by other groups of animals or plants, this would provide strong biogeographical evidence that the western and eastern Nearctic share a common history not shared by the Palaearctic subregion.
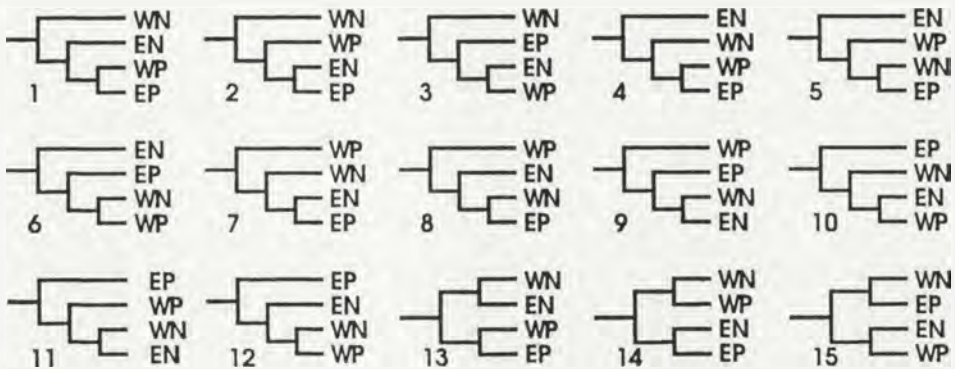
Fig. 16. The 15 possible resolved area claodgrams for the four Holarctic infraregions. Area codes as in Fig. 14. From ENGHOFF (1995b).

OTHER USES OF PHYLOGENIES

Just as one may trace the distribution of a group of organisms through time by ana-lyzing a cladogram, e.g., with DIVA (see above), one may trace the evolution of any other attribute of the organisms on their cladogram. Technically, one speaks of opti-mization of characters or attributes on the cladogram (DIVA analysis can accordingly be called optimiziation of areas on a cladogram). The recent literature is full of studies where this or that attribute is optimized on a cladogram of a particular plant or animal group, see, e.g. GRANDCOLAS (1997).

For millipedes there are so far very few such studies: e.g. ENGHOFF (1990a) traced charac-ters on a cladogram of millipedes to recon-struct the groundplan of the subclass Chilogna-tha. ENGHOFF et al. (1993) traced the mode

Table. Results of WISARD analysis of the Nemasomatoidea. Numbers refer to Fig. 16. **Bold** numbers are the preferred resolved area cladograms.

Criterion minimized	Sympatric speciations (Duplications)	Extinctions (Losses)	Dispersal
Resolved area cladograms minimizing this criterion	9	11, 10	9, 11, 1, 2, 3, 5, 6, 12, 15

of anamorphosis on a cladogram of millipedes (Fig. 3) and concluded that the ances-tral millipede was hemianamorphotic. ENGHOFF & BÁEZ (1993) used a cladogram of part of the julid genus *Dolichoiulus* to infer that the occupation of the laurel forests (laurisilva) of Tenerife by *Dolichoiulus* is secondary in relation to occupation of more open habitats because laurisilva species are cladistically subordinate in relation to open-land species. GOLOVATCH & ENGHOFF (1994) mapped the evolution of paratergal shape in the "dragon millipedes", genus *Desmoxytes* (Paradoxosomatidae) on a clado-gram (Fig. 17). In this case there is the problem that paratergal shape was among the
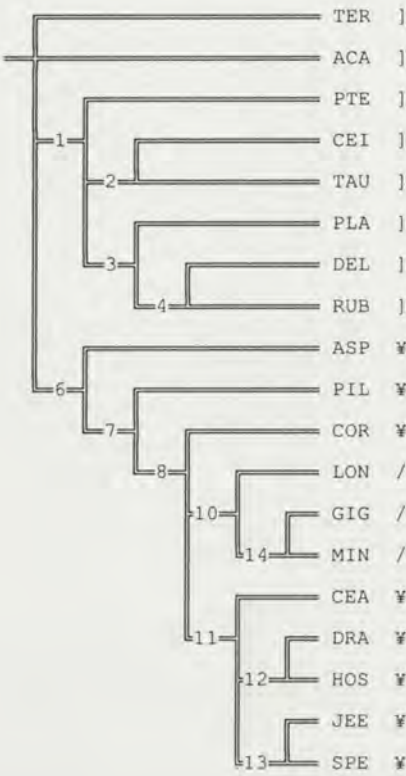
Fig. 17. Shape of paraterga in the para-doxosomatid genus *Desmoxytes* mapped on a cladogram.]: wing-shaped paraterga; ¥: antler-shaped paraterga; /: spine-shaped paraterga. From GOLOVATCH and ENGHOFF (1994).

characters used to construct the cladogram and there therefore is a risk of circular reasoning: some species may form a clade on the cladogram because they have a particular paratergal shape, and because they form a clade, the particular paratergal type is regarded as having evolved only once from another type. To avoid this problem, the cladistic analysis should have been re-run with the paratergal character removed from the chartacter matrix.

An important use of cladograms which has to my knowledge not been applied to millipede so far, is for conservation evaluation, see, e.g., several papers in FOREY *et al.* (1994).

CONCLUSION

There are those who believe that for a group so poorly known as the millipedes, phylogenetic analysis is a waste of effort. And it is true indeed that as new taxa are being described, and new characters examined, the existing phylogenies are bound to change. It is also true that in some cases, our observations seem unamenable to cladistic analysis. For example, SHELLEY & WHITEHEAD (1986) described what they called mosaic evolution in the xystodesmid genus *Sigmoria*. The patterns of colour and shape Shelley and White-head observed in this genus did not suggest a set of hierarchical relationships and the authors therefore considered a cladistic analysis of the genus premature.

Even though problem cases like *Sigmoria* may some day be resolved (e.g. using molecular characters), and even if the most unlikely situation should one day arise that we will have described all millipede species and will have performed sound phylogenetic analyses of them all, we will never be able to say that we know the truth about millipede phylogeny. All we can do is to present our best estimates. But such estimates are a precious tool if we want to understand the evolutionary and geographical history of millipedes. At a more general level, phylogenetic estimates help us to understand how the living organisms populating Earth, and the communities and intereactions they take part in, have come to be what they are today, and how we can optimize their conservation in our rapidly changing world.

ACKNOWLEDGMENTS

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