1998. P. A. Selden (ed.). *Proceedings of the 17th European Colloquium of Arachnology*, *Edinburgh 1997*.

Elucidating the historical process of phylogeny: Phylogenetic Systematics versus cladistic techniques

Otto Kraus

Zoologisches Institut und Zoologisches Museum,
Universität Hamburg, Martin-Luther-King-Platz 3,
D–20146 Hamburg, Germany

Summary

The method of Phylogenetic Systematics *sensu* Hennig is compared with cladistic methods (especially pattern cladistics) and also with recent approaches in molecular phylogenetics. Homology (in its original sense) should be established carefully. Characters should not be treated as being of equal value. Homology in complex characters can be established with more reliability than in simple yes/no situations. Functional morphology is regarded as an important tool for understanding the direction in which evolutionary transformation occurred. *A priori* weighting of characters is favoured. Examples are presented in order to demonstrate that pattern/computer cladistic procedures, including *a posteriori* weighting, may be less efficient in elucidating the unique process of phylogenetic branching, including a proper understanding of evolutionary novelties. Until now, approaches in molecular phylogenetics are regarded as unreliable.

Introduction

The terms "classification" and "system" are frequently used as synonyms. English-speaking zoologists almost exclusively say that they classify. But in contrast to a "system", "classification" in its original sense is the formation of groups according to similarity. The arrangement of the higher categories of spiders published by Roewer (1942: 133–144) in the first volume of his *Katalog der Araneae* forms a good example of this kind of an approach. Typically, families, subfamilies and other categories of the Linnean hierarchy are numbered. Classifications (or "systems") of this kind were and still are useful for purposes of information retrieval, including the arrangement of collections.

But during the course of the second half of this century, primarily typological classifications were increasingly abandoned, and the term "system" has come to be associated with the hierarchic arrangement of closed descent communities, i.e. of monophyletic units. This approach goes back to Hennig (1950, see also 1966). He introduced the demand that classifications should be replaced, step by step, by *phylogenetic systems*. The hierarchic arrangement of the taxa in a system of this kind should be congruent with phylogenetic branching events and hence should reflect sister group relationships. According to this demand, the reconstruction of the historical process of phylogeny in a certain group appears to be primary basic research, and establishing a phylogenetic system is a secondary step of transcription.

Accordingly, the primary question is how phylogenetic relationships can be determined with the highest degree of reliability.

Approaches

Relying on similarity and character expressions *as such* may cause misconceptions. This is true in any case—also in approaches at molecular levels. Some examples are really striking. Consider the long-established distinction of two subgroups of the Araneomorphae: the Ecribellata and the Cribellata. This concept was already falsified by Lehtinen (1967). Later, Coddington & Levi (1991: 571) spoke of the "collapse of the Cribellata". But there are many other, less obvious, instances. As an example, one could mention a presumed taxon

"Apulmonata" Firstman, 1973 for all those subgroups of the Arachnida having tracheae as respiratory organs instead of book lungs (see also Weygoldt & Paulus, 1979: 189). Apparently, the observation that even in spiders tracheae originated more than once (Levi, 1967) and the failure of Petrunkevitch's concept of a group "Apneumonomorphae" (1933) were not taken into account. By now, there is evidence that respiratory systems of this kind even originated four to five times independently in the taxon expressly called Tracheata (see Hilken, 1998). Examples of this kind sufficiently demonstrate potential shortcomings associated with too simple, purely typological approaches—approaches without sound studies in order to ensure homology.

Phylogenetic Systematics

In his original approach, Hennig expressly stated that, in Phylogenetic Systematics, characters should *not* be treated as being equal. As early as 1950 he had clearly expressed the view that the weight of characters should be taken into consideration. He established the "Criterion of the Complexity of Characters". This means that the presence of organs having complex structures is of higher value for inferring phylogenetic relationship than the presence of single, more-or-less simple characters. In the first case, the identity in complex structural, and hence functional, details provides sound arguments for assuming that parallel evolution is unlikely. In the latter case, it may be difficult or even impossible to decide whether parallel development has occurred or not.

Let me illustrate this approach by referring to the spider family Oecobiidae. Two taxa were previously considered to represent separate families, the oecobiids and the urocteids; the first was classified among the Cribellata, the second was placed in the Ecribellata. When Baum (1972) established their sister-group relationship, she was able to base this conclusion on several complex characters: special conformities in structures of the highly complicated internal female genitalia (Fig. 1); unique specialization, including function, of the anal tubercle and of the posterior spinnerets; and identity in remarkable details of the prey-capture behaviour (see Crome, 1957; Glatz, 1967).

In contrast, the approach of Phylogenetic Systematics may also be used to test the validity of previously assumed relationships. As an example, I take the concept of a taxon called "Arachnida". It is generally believed that it originated from aquatic ancestors by terrestrialization. This was apparently correlated with the transformation of original book gills into book lungs. But it was not realized that Millot's comparison of the opisthosomal appendages (1949:

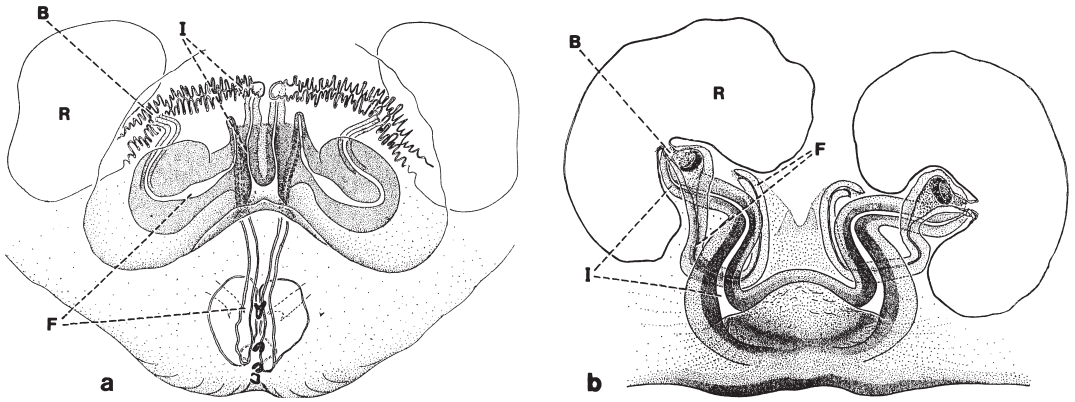

Fig. 1: Comparison of vulval structures: **a** in the Oecobiinae (*Oecobius cellariorum* (Dugès, 1836)) and **b** in the Urocteinae (*Uroctea durandi* (Latreille, 1809)) indicates phylogenetic relationship of the taxa. Note thin-walled receptacula (R) and unique bypass (B) between introductory duct (I) and fertilization duct (F), permitting direct sperm transfer from I to F without prior storage of sperm in R. From Baum (1972).

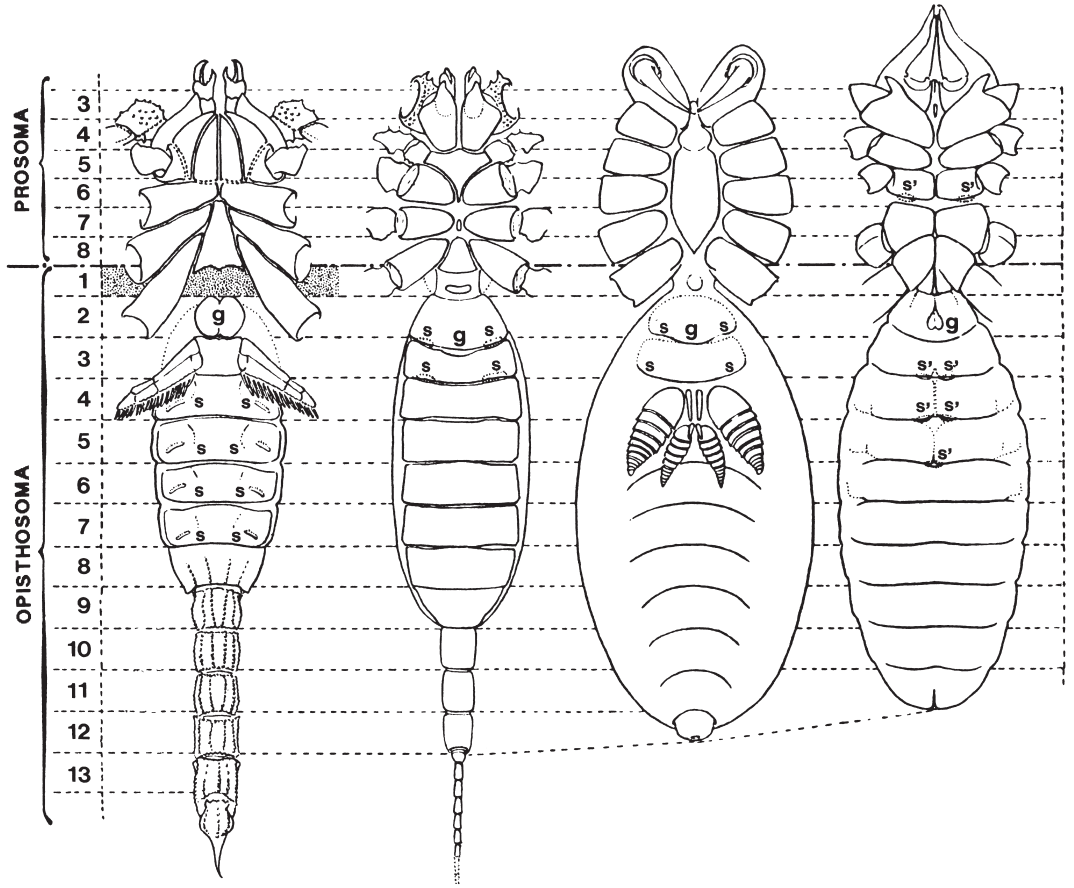

Fig. 2: Comparison of the position of book lungs (s) in Scorpiones, Uropygi, Araneae (Mesothelae) and spiracles (s') in Solifugae in relation to the the position of the genital orifice (g) and the occurrence of other types of transformed appendages of different opisthosomal segments: combs in scorpions, two succeeding pairs of biramous appendages still maintained in spiders (spinnerets). Modified from Millot (1949).

fig. 52) already demonstrated *in*homology—at least between the respiratory organs of terrestrial scorpions and the Tetrapulmonata (= Lipoctena with Uropygi + Amblypygi + Araneae, and including the Trigonotarbida + Ricinulei) (Fig. 2). Scorpions did maintain the pre-epipodites of the appendages of the third opisthosomal segment, the combs. But exactly these parts of an originally biramous pair of appendages were transformed into the second pair of book lungs in the tetrapulmonate Lipoctena! Whereas terrestrial scorpions transformed the appendages of the opisthosomal segments 4 to 7 into paired book lungs—perhaps more than once (see, e.g., Selden & Jeram, 1989)—the biramous state of the appendages of segments 4 and 5 was maintained in the ground pattern of the Araneae. This explains the presence of eight spinnerets in two rows still present in species of the genus *Liphistius*. The conclusion is that scorpions and Lipoctena transformed quite different pairs of appendages into book lungs. Hence, the presence of this type of respiratory organ, as such, cannot be regarded as a synapomorphy of the "Arachnida"—despite the fact that structural details of such book lungs are almost identical. This interpretation is in accordance with views expressed by Selden & Jeram (1989: 309). They regarded book lungs (and also trichobothria) as products of convergence.

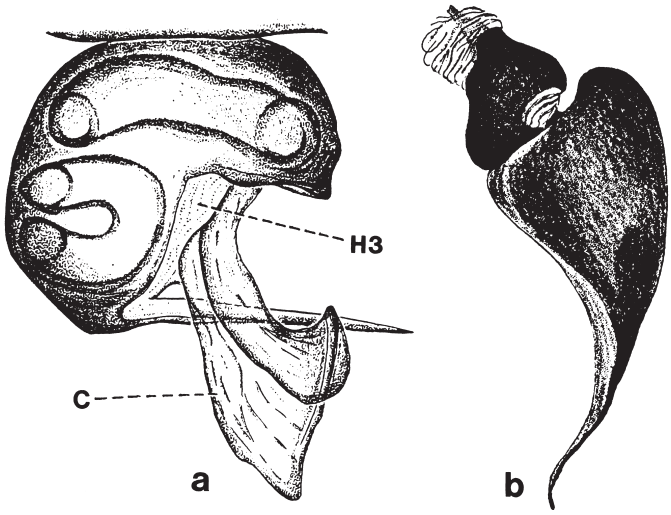

Fig. 3: Male bulbs: **a** of a representative of the Atypidae (*Atypus* sp.); and **b** of an avicullariid spider *(Eurypelma* sp.). Note that original conductor (C) and terminal haematodocha (H3) were maintained in a, but were lost in b. a from Kraus & Baur (1974), b from Comstock (1967).

The examples briefly presented here were chosen in order to illustrate that the phylogenetic systematicist tries to understand structural and functional aspects of potential characters first, including homology, biological significance, and behaviour. In other words: *a priori* weighting is favoured. This includes an understanding of functional morphology insofar as, for example, an increase of efficiency may indicate the direction in which transformation occurred.

Cladistic analysis

In contrast to Phylogenetic Systematics, parsimony is generally regarded as one of the guiding principles in cladistic approaches. Even more important: *a priori* weighting is regarded as a subjective, and hence, an *un*scientific approach. As many characters as possible are coded in a data matrix. Polarity is inferred by comparison with an outgroup to be selected. By using computer programs they are secondarily, i.e. *a posteriori*, identified as synapomorphies or homoplasies, respectively. The results obtained may considerably depend on the selection of the outgroup. In the Atypidae, male bulbs are piriform and have a conductor guiding the embolus. The cladogram produced will depend on the decision whether an outgroup with or without a conductor is chosen (Fig. 3).

In principle, this effect may also influence regular analyses carried out "by hand". But the pure selection of an outgroup can be supplemented in this case by a scientific concept of the underlying ground pattern.

This can be illustrated by referring to the traditional distinction between orthognathy and labidognathy in the arrangement of spider chelicerae. It is now almost certain that both orthognathy (in a strict sense) and labidognathy are specializations in different directions, whereas plagiognathy should be regarded as forming part of the ground pattern of spiders (Kraus & Kraus, 1993).

The limited potential of cladistic approaches may be illustrated by another example. Orb-weaving spiders of the family Tetragnathidae lack an epigynum. This may be coded as haplogynous, a stage commonly regarded to be plesiomorphic. The bulbs of the male pedipalps are piriform. Some authors still maintain the view that this also is a plesiomorphic feature (e.g. Foelix, 1992: 119). But it is much more probable that piriform bulbs originated secondarily by fusion (Kraus, 1984: 379) and represent an advanced specialized type of construction. With regard to the female genital structures, the fact that representatives of *Tetragnatha* and related genera developed cheliceral coupling mechanisms permits two alternative explanations: (1) that tetragnathids "invented" the cheliceral coupling mechanism, so there was no need to produce an epigynal/pedipalpal coupling mechanism in order to safeguard sperm transfer; or (2) that tetragnathids shifted secondarily to a new type

of coupling mechanism; an epigynum was no longer needed and was completely reduced.

The evolution of piriform bulbs in males seems to be reasonable in both cases. But it is well known that tetragnathids have an unpaired median receptaculum, in addition to paired lateral spermathecae (see Wiehle, 1963). This median receptaculum is also used for the storage of sperm (Uhl *et al*., 1992: 255). Unpaired receptacula (Kraus, 1978) are also present in most subtaxa of the Haplogynae (see Coddington & Levi, 1991: fig. 2). This may well be an argument for alternative (a): tetragnathids may have maintained haplogynous vulval structures, and never had an epigynum.

The examples are presented with the intention of demonstrating that sound studies in the field of comparative and functional morphology, homology included, cannot be replaced by numerical computer procedures.

One of the main arguments for using techniques of this kind is the belief that subjectivity during the course of an analysis would be excluded by avoiding *a priori* assumptions, and that trees obtained would be objectively falsifiable. But what seems to be much more important from the point of view of the phylogenetic systematicist is that alternative cladograms may be produced by methods of cladistic analysis which could remain unrecognized when an analysis is carried out "by hand"; see Wägele (1994) for further details.

Molecular phylogenetics

The number of studies in molecular phylogenetics is rapidly increasing. Only some examples are mentioned here as they include statements on the phylogenetic position of chelicerate groups.

Ballard *et al*. (1992) used data derived from 12S Ribosomal RNA sequences. They published two different trees (fig. 3). In a strict consensus tree (resulting from a maximum parsimony analysis), they presented spiders and scorpions as the sister group of all non-chilopod mandibulates. In a second (neighbour-joining) tree, the same representatives of the chelicerates are presented as the sister group of the Onychophora! Could it be that phylogenies inferred depend on the procedure used?

In their paper on arthropod phylogeny, Wheeler *et al*. (1993) published a tree (fig. 6) derived from 18S rDNA data with a high degree of irresolution, but with a cephalopod occurring as the closest relative of clitellate worms. In another cladogram derived from ubiquitin sequence data, the arachnids studied appear to be more closely related to onychophorans of the genus *Peripatus* than to another velvetworm of the genus *Peripatopsis*. It should be mentioned that ubiquitin sequence data may not be informative at all for an analysis of branching events which happened in very early Palaeozoic times. Finally, the authors produced what they call a consensus cladogram derived from molecular *and* morphological data (fig. 9), and this seems to be quite reasonable.

Friedrich & Tautz (1995) presented another ribosomal DNA phylogeny (18S and 28S rDNA sequences). According to their results, chelicerates are the closest relatives to what they call Myriapoda, and both groups together are regarded as the sister group to crustaceans + hexapods. But they missed out the millipedes altogether. Giribet *et al*. (1996) also used 18S rDNA and rRNA gene sequences and concluded that a Chilopoda + Arachnida line would form the sister group of a Hexapoda + Crustacea line.

These examples permit the conclusion that the major part of evidence derived from molecular data is considerably different from what has been found by using traditional methods. In part, discrepancies even between molecular approaches may be caused by differences in processing the data. Wägele & Stanjek (1995) re-examined the work presented by Ballard *et al*. (1992). They used the same data and concluded that ". . .with bootstrapping alone, or with counting the branch lengths, the reliability of trees inferred from sequences cannot be described properly"; they continued that "Variations of the alignments are as important as the selection of appropriate tree-constructing algorithms. . .". Similar results were obtained by Backeljau *et al*. (1993) when they checked a cladistic analysis of metazoan relationships presented by Schram (1991).

In general, the impression is that, until now, phylogenies which were exclusively based on molecular sequence data do not seem to be very reliable. Various trees even proved to be contradictory. This may be because sequence data *as such* have no polarity. The principle of homology

can hardly be applied. As demonstrated by Wägele & Wetzel (1994), similarities may just have a single origin; they may also be caused by convergency and parallelism. On the other hand, dissimilarities may be due, for example, to reversals and may have extremely low "signal value".

Conclusion

The evidence presented and discussed here demonstrates that the most reliable insight into phylogenetic branching events continues to be obtained by using methods of comparative and functional morphology at high scientific and technical standards. Information on the direction of evolutionary changes may be derived from studies on the adaptive value of character transformations.

One may ask why conclusions based on sound research in the field of morphology apparently continue to remain superior to results obtained by cladistic procedures and by molecular phylogeny. A possible answer may be that the morphological approach is primarily based on peculiarities of the functioning phenotype—the real subject of natural selection. Molecular phylogeny may be close to reductionism.

References

BACKELJAU, T., WINNEPENNINCKX, B. & DE BRUYN, L. 1993: Cladistic analysis of metazoan relationships: a reappraisal. *Cladistics* **9**: 167–181.

BALLARD, J. W. O., OLSEN, G. J., FAITH, D. P., ODGERS, W. A., ROWELL, D. M. & ATKINSON, P. W. 1992: Evidence from 12S ribosomal RNA sequences that onychophorans are modified arthropods. *Science, N.Y.* **258**: 1345–1348.

BAUM, S. 1972: Zum "Cribellaten-Problem": Die Genitalstrukturen der Oecobiinae und Urocteinae (Arach.: Aran.: Oecobiidae). *Abh. Verh. naturw. Ver. Hamburg N.F.* **16**: 101–153.

CODDINGTON, J. A. & LEVI, H. W. 1991: Systematics and evolution of spiders (Araneae). *A. Rev. Ecol. Syst.* **22**: 565–592.

COMSTOCK, J. H. 1967: *The spider book*. Ithaca: Cornell University Press.

CROME, W. 1957: Bau und Funktion des Spinnapparates und Analhügels, Ernährungsbiologie und allgemeine Bemerkungen zur Lebensweise von *Uroctea durandi* (Latreille); (Araneae, Urocteidae). *Zool. Jb.* (*Syst.*) **85**: 501–672.

FOELIX, R. F. 1992: *Biologie der Spinnen*. 2nd ed. Stuttgart, New York: Thieme.

FRIEDRICH, M. & TAUTZ, D. 1995: Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. *Nature, Lond.* **6**: 165–167.

GIRIBET, G., CARRENTA, S., BAGUNA, J., RIUTORT, M. & RIBERA, C. 1996: First molecular evidence for the existence of a Tardigrada + Arthropoda clade. *Molec. Biol. Evol.* **13**: 76–84.

GLATZ, L. 1967: Zur Biologie von *Oecobius annulipes* (Araneae, Oecobiidae). *Z. Morph. Tiere* **61**: 185–314.

HENNIG, W. 1950: *Grundzüge einer Theorie der Phylogenetischen Systematik*. Berlin: Deutscher Zentralverlag.

HENNIG, W. 1966: *Phylogenetic systematics*. Urbana: University of Illinois Press.

HILKEN, G. 1998: Vergleich von Tracheensystemen unter phylogenetischem Aspekt. *Verh. naturw. Ver. Hamburg N.F.* **37**: 5–94.

KRAUS, O. 1978: *Liphistius* and the evolution of spider genitalia. *In* P. Merrett (ed.). *Arachnology.* Symposia of the Zoological Society of London, No. 42. London and New York: Academic Press: 235–254.

KRAUS, O. 1984: Male spider genitalia: evolutionary changes in structure and function. *Verh. naturw. Ver. Hamburg N.F.* **27**: 373–382.

KRAUS, O. & BAUR, H. 1974: Die Atypidae der West-Paläarktis. Systematik, Verbreitung und Biologie (Arach.: Araneae). *Abh. Verh. naturw. Ver. Hamburg N.F.* **17**: 85–116.

KRAUS, O. & KRAUS, M. 1993: Divergent transformation of chelicerae and original arrangement of eyes in spiders (Arachnida, Araneae). *Mem. Qd Mus.* **33**: 579–584.

LEHTINEN, P. T. 1967: Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Annls zool. fenn.* **4**: 199–467.

LEVI, H. W. 1967: Adaptations of respiratory systems of spiders. *Evolution, Lancaster, Pa.* **21**: 571–583.

MILLOT, J. 1949: Classe des Arachnides [some parts with André, Berland, Vachon]. *In* P.-P. Grassé (ed.). *Traité de zoologie, anatomie, systématique, biologie, Tome VI, Onycophores, Tardigrades, Arthropodes, Trilobitomorphes, Chélicérates*. Paris: Masson et Cie: 263–892.

PETRUNKEVITCH, A. 1933: An inquiry into the natural classification of spiders, based on a study of their internal anatomy. *Trans. Conn. Acad. Arts Sci.* **31**: 303–389.

ROEWER, C. F. 1942: *Katalog der Araneae von 1758 bis 1940*. Bremen: Paul Budy.

SCHRAM, F. R. 1991: Cladistic analysis of metazoan phyla and the placement of fossil problematica. *In* A. M. Simonetta & S. Conway Morris (eds.). *The early evolution of Metazoa and the significance of problematic taxa*. Cambridge: Cambridge University Press: 35–46.

SELDEN, P. A. & JERAM, A. J. 1989: Palaeophysiology of terrestrialisation in the Chelicerata. *Trans. R. Soc. Edinb., Earth Sci.* **80**: 303–310.

UHL, G., SACHER, P., WEISS, I. & KRAUS, O. 1992: Europäische Vorkommen von *Tetragnatha shoshone* (Arachnida, Araneae, Tetragnathidae). *Verh. naturw. Ver. Hamburg N.F.* **33**: 247–261.

WÄGELE, J. W. 1994: Review of methodological problems of 'computer' cladistics exemplified with a case study on isopod phylogeny (Crustacea: Isopoda). *Z. Zool. Syst. EvolForsch.* **32**: 81–107.

WÄGELE, J. W. & STANJEK, H. 1995: Arthropod phylogeny inferred from partial 12S+ RNA revisited: monophyly of the Tracheata depends on sequence alignment. *Z. Zool. Syst. EvolForsch.* **33**: 75–80.

WÄGELE, J. W. & WETZEL, R. 1994: Nucleic and sequence data are not *per se* reliable for inference of phylogenies. *J. nat. Hist.* **28**: 749–761.

WEYGOLDT, P. & PAULUS, H. F. 1979: Untersuchungen zur Morphologie, Taxonomie und Phylogenie der Chelicerata. I: Morphologische Untersuchungen; II: Cladogramme und die Entfaltung der Chelicerata. *Z. Zool. Syst. EvolForsch.* **17**: 85–200.

WHEELER, W. C., CARTWRIGHT, P. & HAYASHI, C. H. 1993: Arthropod phylogeny: a combined approach. *Cladistics* **9**: 1–39.

WIEHLE, H. 1963: Spinnentiere oder Arachnoidea (Araneae). XII: Tetragnathidae, Streckspinnen und Dickkiefer. *Tierwelt Dtl.* **49**: i–viii + 1–76.