Studies in Corinnidae: cladistic analysis of 38 corinnid and liocranid genera, and transfer of Phrurolithinae

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This paper studies the phylogeny of the spider families Liocranidae and Corinnidae as they have been delimited to date, using an exemplar approach. In the analysis, 40 species belonging to 24 liocranid and 14 corinnid genera are scored for 157 morphological characters. The genera *Clubiona* (Clubionidae) and *Gnaphosa* (Gnaphosidae) are used as outgroups. Under implied weighting, a single fittest tree is found. This hypothesis seriously challenges the presently prevailing classification of the former Clubionidae *sensu lato*. The subfamily Phrurolithinae (Liocranidae) turns out to be the sister group of Trachelinae and is transferred to Corinnidae. In the interest of taxonomic stability, no radical rearrangement of the families constituting Clubionidae *sensu lato* is proposed, as it is felt that the present results should first be further corroborated by additional, more elaborate analyses on an even larger data set.

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Introduction

Although the elucidation of spider phylogeny and the elaboration of higher level spider taxonomy have made considerable progress in recent years, the subdivision of Dionycha is still unclear (Coddington & Levi 1991; Griswold *et al*. 1999). In addition, the assignment of genera to families within this group of two-clawed spiders remains open to debate, especially in the former Clubionidae *sensu lato*. The spider family Clubionidae *sensu lato*, as defined by Simon (1897, 1898, 1903), was a large taxon comprising 182 genera, divided into seven subfamilies: Selenopinae, Sparassinae, Clubioninae, Cteninae, Liocraninae, Micariinae and Corinninae. Simon (1897: 20–22) listed some diagnostic characters for Clubionidae, but many of these characters do not apply to all the groups included, while some also apply to many other spider families. Simon's clubionid genera were mainly grouped together on the basis of the absence of any of the distinctive characters typical of other large spider families, and no synapomorphies have ever been proposed for this diverse assembly.

Groups were gradually split off from these Clubionidae '*sensu lato*' and, to date (Platnick 1997), the Clubionidae '*sensu stricto*' are only a small leftover of 24 genera, after Lehtinen (1967) raised the former subfamilies Corinninae and Liocraninae to family rank. Unfortunately, no synapomorphies have been established which unequivocally corroborate the present-day Clubionidae, Liocranidae and Corinnidae as monophyletic taxa, although several proposals have been made.

Clubionidae have been defined by the absence of cylindrical gland spigots, but this loss has not been documented for all clubionid genera, and it is also recorded in several other families (Kovoor 1987; Platnick 1990).

As far as the family Liocranidae is concerned, the presence, on the anterior pairs of legs, of modified ventral leg bristles with a peculiar basal socket has been proposed as synapomorphic for at least the subfamilies Liocraninae and Phrurolithinae (Ubick & Platnick 1991). However, similar, although not identical, scopula-like leg bristles are found in *Clubiona* Latreille, 1804, *Gnaphosa* Latreille, 1804, *Corinna* C. L. Koch, 1842 and many other genera, and the large, erectile bristles described by Ubick & Platnick (1991) are certainly not encountered in all genera grouped as Liocranidae by Platnick (1997). Additional synapomorphies have been proposed, but none seems to apply to all the genera that are presently attributed to the family (Platnick & Baptista 1995; Platnick 1997). Flattened female posterior median spinnerets (Dippenaar-Schoeman & Jocqué 1997) are not encountered in genera such as *Agroeca* Westring, 1861 or *Liocranum* L. Koch, 1896. The presence of a male palpal median apophysis (Lehtinen 1967) does not hold for Phrurolithinae (Ubick & Platnick 1991) and is, in fact, characteristic for most

entelegyne spiders. The presence of numerous paired ventral spines on the anterior tibiae and metatarsi (Platnick & Ubick 1989; Platnick & Baptista 1995) likewise is not restricted to Liocranidae alone.

For the family Corinnidae, Penniman (1985) proposed the absence of a male palpal median apophysis and the presence of a dorsal abdominal scutum in males as synapomorphies. However, as Bonaldo (1997) points out, several genera presently placed in Corinnidae possess a palpal median apophysis: *Ianduba* Bonaldo, 1997, *Mandaneta* Strand, 1932, *Procopius* Thorell, 1899 and *Pseudocorinna*, Simon 1910. Abdominal sclerotization, on the other hand, occurs in a wide variety of spider families and is most probably of little value for macrotaxonomy (Platnick 1975). The presence of three large cylindrical gland spigots in a triangular arrangement on female posterior median spinnerets and two large cylindrical gland spigots on female posterior lateral spinnerets has also been proposed as a synapomorphy for Corinnidae (Dippenaar-Schoeman & Jocqué 1997; Ramírez *et al*. 2000). As discussed below, Trachelinae most probably do not have three, but four or five, cylindrical gland spigots on female posterior median spinnerets. Bonaldo (1997) proposed the presence, on the tarsi, of a trichobothrial base with an elongated ridge traversing a lowered plate as a synapomorphy for Corinnidae. However, the presence or absence of this feature, which is only observable with scanning electron microscopy (SEM) at high magnification, has not been systematically inventorized within Corinnidae, and certainly not outside that family. Neither has the variability of this structure been adequately studied: the morphology of corinnid tarsal trichobothrial bases in some published photographs (Platnick 1975: figs 6 and 8) does not always look convincingly different from similar trichobothrial bases in *Cybaeodes* Simon, 1878 (Platnick & Di Franco 1992: fig. 9) or *Hortipes* Bosselaers & Ledoux, 1998 (Ledoux & Emerit 1998: fig. 5), both Liocranidae, or, for that matter, from a normal spider trichobothrial base (Foelix 1979: fig. 55). In summary, no valid synapomorphies for Clubionidae, Corinnidae or Liocranidae seem to be known to date.

Nevertheless, three subfamilies of Corinnidae (Corinninae, Castianeirinae and Trachelinae) and one of the subfamilies of Liocranidae (Phrurolithinae) are clearly defined and most probably supported by valid synapomorphies. It has already been taken into consideration that these subfamilies might have to be raised to familial rank (Deeleman-Reinhold 2001). Corinninae have a coiled sperm duct in the male palpal tegulum and a highly branched male palpal tibial apophysis (Platnick & Baptista 1995); Castianeirinae have a typical pear-shaped male palpal bulbus with a looped sperm duct and without median apophysis or conductor, as well as a sclerotized abdomen (Reiskind 1969) and female posterior median spinnerets bearing three large cylindrical gland spigots in a triangular arrangement (Dippenaar-Schoeman & Jocqué

1997); Trachelinae have leg cusps, combined with a strong reduction in spination on legs III and IV (Platnick & Shadab 1974); Phrurolithinae have a male palpal ventral femoral apophysis, simple tarsal claws, reduced leg spination on legs III and IV, often combined with numerous ventral spines on tibiae and metatarsi I and II, and flattened female posterior median spinnerets bearing many cylindrical gland spigots in two rows (Penniman 1985; Platnick & Ubick 1989). On the other hand, the remaining subfamilies named in the past are either very poorly defined, such as Liocraninae and Oedignathinae, or almost certainly artificial, such as Cybaeodinae (Bosselaers & Jocqué 2000b).

Given the lack of taxonomic stability described above, it comes as no surprise that many transfers have been proposed recently (since Platnick 1997). *Neoanagraphis* Gertsch & Mulaik, 1936 has been transferred from Clubionidae to Liocranidae by Vetter (2001), and *Sphingius* Thorell, 1890 has been transferred from Corinnidae to Liocranidae by Deeleman-Reinhold (2001). *Cambalida* Simon, 1910, *Messapus* Simon, 1898 and *Thysanina* Simon, 1910 have been transferred from Liocranidae to Corinnidae by Bosselaers & Jocqué (2000a), and *Arushina* di Caporiacco, 1947 and *Olbus* Simon, 1880 have been transferred from Clubionidae to Corinnidae by Bosselaers & Jocqué (2000a) and Ramírez *et al*. (2000), respectively. *Titiotus* Simon, 1897 has been transferred from Liocranidae to Tengellidae by Platnick (1999). Another genus, *Anachemmis* Chamberlin, 1920, has been removed from synonymy with *Titiotus* by Platnick (1999) and also transferred to Tengellidae. *Montebello* Hogg, 1914, until now classified in Liocranidae, has been found to belong in Gnaphosidae by V.I. Ovtsharenko (personal communication, 1998). Two more genera should no longer be listed under Liocranidae: *Mardonia* Thorell, 1897, because the type specimen of *Mardonia fasciata* Thorell, 1897 is considered to be a juvenile of an as yet unidentified species of *Seramba* Thorell, 1887 (Sparassidae) by Deeleman-Reinhold (2001), and *Palaetyra* Simon, 1898 which has been synonymized with *Otacilia* Thorell, 1897 by Deeleman-Reinhold (2001).

Because of the high level of homoplasy in spider cladograms (Griswold *et al*. 1999), it is doubtful that unreversed synapomorphies, which can serve as diagnostic criteria for entire families, exist for all monophyletic groups which may be discovered within the former Clubionidae *sensu lato*. However, in spite of this somewhat dim prospect, it seems straightforward that only the execution of careful cladistic analyses of this diverse assemblage can allow us to make progress towards unravelling the probably complex phylogeny of this group.

Materials and methods

Specimens were studied under a stereomicroscope equipped with an eyepiece grid by means of incident light. Feathery

hairs, claw tufts and cleared vulvae were observed with a compound microscope using transmitted light. Vulvae were cleared in methyl salicylate, and the vulvae illustrated were photographed in several focal planes under a compound microscope. The photographs of these optical sections were subsequently used for the execution of the drawings.

Specimens examined with a Philips XL-20 scanning electron microscope were dehydrated in acetone, critical point dried in carbon dioxide and sputter coated with gold prior to observation. Spinneret gland spigot terminology follows Kovoor (1987), Coddington (1989) and Platnick (1990).

Cladistic analyses were performed using the computer programs Pee-Wee 2.6 (Goloboff 1997a), NONA 1.6 (Goloboff 1997b), TNT 0.1 beta (Goloboff *et al.* 2000) and PAUP 4.0 beta 4a (Swofford 1999). Optimization of character states and printing of the preferred tree were performed using Winclada 0.9.99 m beta (Nixon 2000).

The following abbreviations are used throughout the text: AER, anterior eye row; ALE, anterior lateral eyes; ALS, anterior lateral spinnerets; AME, anterior median eyes; ci, consistency index; do, dorsal; es, extra steps; fe, femur; ID, insemination duct; MA, median apophysis of the male palp; MOQ, median ocular quadrangle; mt, metatarsus; pa, patella; PER, posterior eye row; PLE, posterior lateral eyes; pl, prolateral; PLS, posterior lateral spinnerets; plv, prolateral ventral; PME, posterior median eyes; PMS, posterior median spinnerets; rc, rescaled consistency index; ri, retention index; rl, retrolateral; rlv, retrolateral ventral; ST1, spermatheca 1 (closest to fertilization duct); ST2, spermatheca 2; ta, tarsus; ti, tibia; ve, ventral; vt, ventral terminal.

Abbreviations of personal and institutional collections (curators in parentheses) are as follows: AMNH, American Museum of Natural History, New York (N. Platnick); CCD, Collection Christa Deeleman; CJB, Collection Jan Bosselaers; CJK, Collection Johan Van Keer; CJM, Collection John Murphy; FMNH, Field Museum of Natural History, Chicago (P. Sierwald); MCN, Museu de Ciências Naturais, Porto Alegre (E. Buckup); MNHN, Muséum National d'Histoire Naturelle, Paris (C. Rollard); MRAC, Royal Museum for Central Africa, Tervuren (R. Jocqué); NCA, National Collection of Arachnida, Pretoria (A. Dippenaar-Schoeman); RBINS, Royal Belgian Institute of Natural Sciences, Brussels (L. Baert); UCR, Entomology Research Museum, University of California, Riverside (R. Vetter); ZMUC, Zoological Museum University of Copenhagen (N. Scharff).

Phylogenetic analysis
Taxon choice
Rather than representing the genera studied by their ground-plan or hypothetical 'common ancestor' (Bininda-Edmonds *et al.* 1998), exemplar species were chosen as terminal taxa in

our cladistic analysis. Representing a higher taxon by a hypothetical ground plan, which is the list of optimized character states at the basal node of that taxon, implies that the results of a cladistic analysis of the taxon concerned are available. However, only one of the genera studied in the present work, *Hortipes*, has ever been subject to a cladistic analysis (Bosselaers & Jocqué 2000b). As a result, it is not possible to hypothesize, in a reliable way, the primitive character states for most genera included. In addition, reconstructions of character states at the basal node of a clade inevitably have to remain highly hypothetical under all circumstances, as they are dependent not only on the distribution of character states among terminals of the ingroup, but also on the structure of the outgroup (Maddison *et al.* 1984).

Moreover, terminal taxa used in a higher level cladistic analysis are implicitly assumed to be monophyletic, while it is doubtful whether some of the genera treated in this work, e.g. *Medmassa* Simon, 1887 and *Agroeca*, are at all monophyletic. Representing such a genus by a hypothetical groundplan, or by a survey of all or part of its constituent species (the 'democratic' or 'intuitive' method) as a substitute for such a groundplan, can introduce serious errors in the resulting cladogram (Bininda-Edmonds *et al.* 1998; Prendini 2000; Yeates 1995). For these reasons, exemplar species were chosen as terminal taxa in our cladistic analysis. An exemplar approach has the clear advantage of presenting an empirically verifiable data matrix that can be used and improved by future workers (Griswold 1993).

In the present analysis, the type species of a genus was chosen as exemplar taxon where possible. However, in order to guarantee completeness of the data set, the availability of sufficiently intact male and female specimens of many of the rarer taxa was of prime importance in the selection of exemplar taxa. For three genera, two exemplar species were scored. Specimen data for the exemplar taxa examined can be found in the Appendix.

The ingroup of the analysis consists of representatives of 38 genera considered to belong to either Liocranidae or Corinnidae. Their family affiliations, following prevailing opinions, are indicated in the Appendix. These affiliations follow Platnick (1997), adapted with the transfers cited in the 'Introduction' section and taking into account that *Agraecina striata* (Kulczynski, 1882) has been transferred to *Liocranoeca* by Wunderlich (1999).

Two genera constitute the outgroup. *Clubiona* was chosen because it is the type genus of Clubionidae, the family of which Liocranidae and Corinnidae were previously considered to be subfamilies. *Gnaphosa*, the type genus of Gnaphosidae, was selected because this family can be considered to be representative for Gnaphosoidea, which Coddington & Levi (1991) place as the sister group of a clade grouping Liocranidae and Corinnidae in their cladogram of Araneomorphae.

Gnaphosidae share with corinnid and liocranid genera sexually dimorphic PMS, frequent occurrence of irregularly shaped PME, wandering habits and absence of any type of catching webs (Platnick 1990; Coddington & Levi 1991). Penniman (1985) derived a cladogram in which Gnaphosidae is the sister group of a clade consisting of Corinninae, Castianeirinae, Trachelinae and Phrurolithinae.

Character coding and description

A series of 157 characters (114 binary and 43 multistate) was coded for the 43 exemplar taxa chosen. Character state numbering does not imply plesiomorphy or apomorphy, because character polarity is derived during cladogram search by outgroup comparison (Watrous & Wheeler 1981; Maddison *et al.* 1984; Kitching *et al.* 1998). Only phylogenetically informative characters were included in the data matrix, in order not to inflate the consistency index artificially as a result of the inclusion of autapomorphies (Kitching *et al.* 1998). Autapomorphies that were excluded from the analysis are listed here as an aid for other workers, as these characters are potential synapomorphies which might be of interest in future analyses on larger numbers of taxa (Glenner *et al.* 1995; Prendini 2000). The following autapomorphies were excluded from the data matrix, exemplar taxa having these autapomorphies being added in parentheses: femur II plv and rlv spines present (*Hortipes luytenae*); male mt I and II pl spines present (*Agraecina lineata*); metatarsus I and II vt spine present (*Lessertina mutica*); female palpal pa rl spine present (*Cambalida coriacea*); small teeth in front of cheliceral promarginal hairs (*Lessertina mutica*); small teeth between promarginal and retromarginal cheliceral tooth rows (*Lessertina mutica*); male abdominal ve tuft of setae (*Cambalida coriacea*); female ALS cylindrical (*Gnaphosa lucifuga*); metatarsal do oval array of setae (*Hortipes luytenae*). Where necessary (characters 4, 5, 58, 59, 81, 82, 102, 103, 113, 114, 122, 123, 125, 126, 127, 135, 136, 137, 138, 139, 153 and 154), characters were scored with character states hierarchically related, as advocated by Hawkins *et al.* (1997), even though this necessitated coding missing entries due to character inapplicability in

some instances (Maddison 1993). Because spiders are many-legged creatures and heavy leg spination is present in a number of the genera studied, a substantial proportion of the characters used (46 out of 157) refer to leg spines. Establishing homology between individual spider leg spines is notoriously difficult over a range of genera as wide as examined in this work. Fortunately, in a number of cases, such as the dorsal femoral spines (characters 14–22), there can be little doubt about homology and the presence of individual spines could be scored. However, in other cases, establishing homology of individual spines was problematic (characters 27, 29, 30, 37, 39, 40, 41, 42, 45, 47, 48, 51, 53 and 54). Rather than dismissing this probably important information altogether, it was decided to score these characters as multistate characters describing numbers of spines on a surface of an article.

The characters used in the analysis are listed and discussed below. The 26 characters with state changes illustrated in Fig. 5 (see later) are indicated by an asterisk.

1. Male retrocoxal hymen: (0) absent; (1) present. This character was first described by Raven (1998) as the 'retrocoxal window'. It is a weak spot, in most cases hyaline and lens-shaped, on the retrolateral face of coxa I. R. J. Raven (personal communication, 2000) presently prefers the term 'retrocoxal hymen' for this feature.

2. Female retrocoxal hymen: (0) absent; (1) present (Fig. 1A).

3*. Trochanter notch: (0) absent; (1) present (Fig. 1B). While trochanters III and IV of many of the species studied have a shallow, indistinct notch of varying depth, legs I and II allow evaluation of the absence or presence of a sharp trochanter notch without ambiguity.

4*. Rows of bristles with modified tips in ventral scopulae of legs I and II: (0) present; (1) absent. Many of the genera studied have rows of bristles, implanted in basal, cup-like sockets, ventrally on ta, mt and often ti of legs I and II. The tips of these plumose bristles are spatula-, spoon- or club-shaped.

5*. Rows of bristles with special basal sockets and modified tips in ventral scopulae of legs I and II: (0) small; (1) large and erectile.

Fig. 1 A. *Scotinella minnetonka*, female, retrocoxal hymen. —B. *Castianeira occidens*, female, trochanter I. —C. *Scotina gracilipes*, male, pa I, rl. —D. *Liocranum rupicola*, female, pa I, rl. —E. *Agroeca brunnea*, male, ta IV. —F. *Neoanagraphis chamberlini*, male, ta IV. —G. *Trachelas schenkeli*, male, ti and mt I. —H. *Cybaeodes marinae*, male, ta IV. —I. *Orthobula calceata*, female, ta I. —J. *Corinna nitens*, female, mt and ta IV. —K. *Meriola decepta*, male, sternum, ve. —L. *Messapus martini*, male, ta I. —M. *Scotina celans*, female, chelicerae, frontal. —N. *Hesperocranum rothi*, female, endite, ve. —O. *Liocranoeca striata*, male, endite, ve. —P. *Medmassa proxima*, female, carapace, lateral. —Q. *Phrurolithus festivus*, female, chelicerae, frontal. —R. *Rhaeboctesis secundus*, female, chilum. —S. *Pseudocorinna* sp., male, chilum. Scale bar: A, C, I, 0.50 mm; L, Q, S, 0.60 mm; G, H, M, N, O, 0.75 mm; B, E, 1.00 mm; D, R, 1.25 mm; F, K, P, 1.50 mm; J: 2.0 mm. Abbreviations: aa, additional tegular apophyses; at, apical hair tuft; bb, basal bulge of cymbium; cd, coiled sperm duct; co, conductor; eb, embolus; ee, epigastric sclerite extension; en, entrance of ID; es, epigastric sclerite; fa, femoral apophysis; fg, femoral groove; hk, lateral epigynal hook; ho, epigynal hood; im, inframamillary sclerite; is, intercoxal sclerite; it, inflated tegulum; la, labyrinth-like ID; lt, lateral eye tubercle; ma, median apophysis; pa, rl patellar apophysis; pb, pleural bars; pt, precoxal triangle; rh, retrocoxal hymen; s1, ST1; s2, ST2; sc, epigynal scape; se, serrula; sh, shaggy hair at fang base; sl, subtegular locking lobe; sp, epigynal septum; st, subtegulum; ta, tibial apophysis; tk, tegular knob; tl, tegular locking lobe; tn, trochanter notch; tp, palpal tibial pl lobe; vs, ventral sclerite.
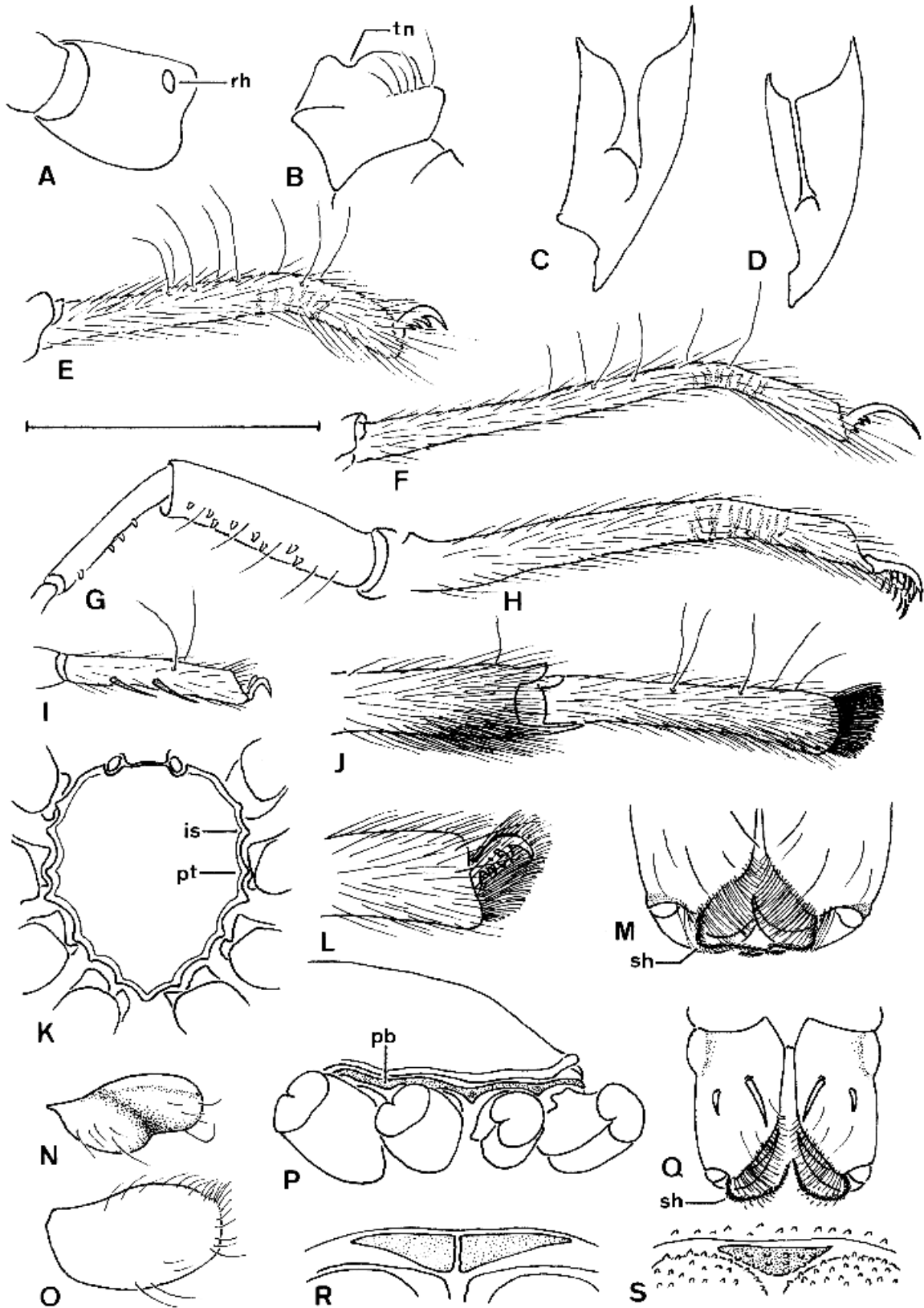
The bristles described under character 4 can be small, i.e. hardly larger than normal scopulae, or large and erectile, and with a peculiar basal socket, as described by Ubick & Platnick (1991).

6. *Patellar indentation of leg I and II*: (0) narrow (Fig. 1D); (1) wide (Fig. 1C). The patellar indentation is a slit-like membranous indentation on the rl side of the pa. May be very narrow or rather wide (Simon 1892: 22; Ledoux & Canard 1991: fig. 15(A,B)).

7*. *Patellar indentation of leg I and II, length*: (0) > 40% of pa length; (1) < 35% of pa length.

8. *Patellar indentation of leg IV*: (0) narrow; (1) wide.

9*. *Bent male leg IV ta*: (0) absent; (1) present. The tarsi of legs IV are bent in a characteristic way in the males of a number of classic liocranid genera (Fig. 1E,F,H). Wunderlich (1999) already mentioned this peculiar tarsal morphology.

10*. *Spination on ti, mt and ta of legs I and II*: (0) normal spines; (1) leg cusps (Fig. 1G). Instead of normal spines, a number of tracheline genera have very short, mostly blunt, dark spines in a ventral row on tibiae, metatarsi and tarsi, called leg cusps (Platnick & Shadab 1974: 3; Platnick & Ewing 1995: 2–4).

11. *Tarsal spines*: (0) absent; (1) present (Fig. 1I).

12. *Femur I plv spines*: (0) absent; (1) present.

13. *Femur I rlv spines*: (0) absent; (1) present.

14. *Femur I basal do spine*: (0) absent; (1) present.

15. *Femur I median do spine*: (0) absent; (1) present.

16. *Femur I apical do spine*: (0) absent; (1) present.

17. *Femur III basal do spine*: (0) absent; (1) present.

18. *Femur III median do spine*: (0) absent; (1) present.

19. *Femur III apical do spine*: (0) absent; (1) present.

20. *Femur IV basal do spine*: (0) absent; (1) present.

21. *Femur IV median do spine*: (0) absent; (1) present.

22. *Femur IV apical do spine*: (0) absent; (1) present.

23. *Female fe I and II rl spines*: (0) absent; (1) present.

24. *Male fe IV pl and rl spines*: (0) absent; (1) present.

25. *Patella III rl spine*: (0) absent; (1) present in female only; (2) present in both sexes.

26. *Patella IV rl spine*: (0) absent; (1) present.

27. *Male ti I plv spines*: (0) absent; (1) one to three; (2) four to six; (3) seven or more. Tibial and metatarsal ventral spines are not counted as 'ventral spine pairs' because the numbers of spines on the prolateral and retrolateral ventral ridge of these articles are often not equal and, even when they are, the plv and rlv spines are not always paired. In order to better describe the actual ventral spination of ti and mt, spines on plv and rlv ridges are counted separately.

28*. *Male ti I rlv spine number*: (0) similar to plv spine number, at most one or two spines more or less; (1) much less, e.g. none or one as compared to three or more. Males of many tracheline genera have a large number of plv leg cusps on ti I and very few or no rlv ones.

29. *Female ti I plv and rlv spines*: (0) absent; (1) one to three; (2) four to six; (3) seven or more.

30. *Tibia II plv spines*: (0) absent; (1) one to three; (2) four to six; (3) seven or more.

31. *Tibia II rlv spine number*: (0) similar to plv spine number; (1) much less than plv spine number; (2) at least two spines more than plv spine number.

32*. *Tibia III plv and rlv spines*: (0) present; (1) absent.

33. *Tibia IV plv and rlv spines*: (0) absent; (1) present.

34*. *Female ti III do spines*: (0) absent; (1) present.

35*. *Tibia IV do spines*: (0) absent; (1) present.

36. *Male ti IV rl spines*: (0) absent; (1) present.

37. *Metatarsus I and II plv spines*: (0) absent; (1) one; (2) two or three; (3) four or more.

38*. *Metatarsus I and II plv and rlv spination*: (0) identical in both sexes; (1) spines restricted to males.

39. *Metatarsus I and II rlv spines*: (0) absent; (1) one; (2) two or three; (3) four or more.

40. *Metatarsus III plv and rlv spines*: (0) absent; (1) one spine; (2) two; (3) three.

41. *Metatarsus IV plv and rlv spines*: (0) absent; (1) one spine; (2) two; (3) three.

42. *Male mt IV rl spines*: (0) absent; (1) one or two; (2) three or four; (3) five or more.

43. *Metatarsus III and IV ve terminal spines*: (0) absent; (1) present on mt IV only; (2) present on mt IV in both sexes and on mt III in females only; (3) present on mt III and IV in both sexes.

44. *Male palpal fe pl spines*: (0) present; (1) absent.

45. *Male palpal fe do spines*: (0) absent; (1) one spine; (2) two.

46. *Male palpal pa pl spines*: (0) absent; (1) present.

47. *Male palpal ti pl spines*: (0) absent; (1) one spine; (2) two; (3) three; (4) four.

48. *Male palpal ti do spines*: (0) absent; (1) one spine; (2) two.

49. *Spines on male palpal ta pl edge*: (0) absent; (1) present.

50. *Female palpal fe pl spines*: (0) absent; (1) present.

51. *Female palpal fe do spines*: (0) absent; (1) one spine; (2) two or more.

52. *Female palpal pa pl spines*: (0) absent; (1) present.

53. *Female palpal ti pl spines*: (0) absent; (1) one spine; (2) two; (3) three; (4) four.

54. *Female palpal ti do spines*: (0) absent; (1) one spine; (2) two.

55. *Female palpal ta plv spines*: (0) absent; (1) present.

56. *Leg formula*: (0) leg IV longest; (1) leg I longest.

57. *Feathery hairs*: (0) absent; (1) present.

58. *Metatarsal ventral terminal preening brush on legs III and IV*: (0) absent; (1) present (Fig. 1J).

59. *Metatarsal ventral terminal preening brush on legs III and IV*: (0) sparse; (1) dense.

60*. *Ventral scopulae on ti I and II*: (0) absent; (1) present.

61. *Metatarsal ve scopulae*: (0) absent; (1) present.

62. Tarsal ve scopulae: (0) absent; (1) present.

63. Claw tufts: (0) absent (Fig. 1E,F,H,I); (1) present (Figs 1 J,L and 2N). When present, claw tufts may be thick and dense, as in *Messapus* (Fig. 1L), or reduced to a few club-shaped hairs, as in *Phruronellus* Chamberlin, 1921 (Fig. 2N) or *Apostenus* Westring, 1851.

64*. Tarsal claw of leg IV: (0) pectinate (Fig. 1E,F,H,L); (1) smooth (Figs 1I and 2N).

65. Precoxal triangles in male: (0) absent; (1) present (Fig. 1K). Precoxal triangles are small triangular sclerites surrounding the sternum, their tips facing the bases of the coxae (Penniman 1985: 16). They may be free, or fused with the sternum (Fig. 1K).

66. Precoxal triangles in female: (0) absent; (1) present.

67. Intercoxal sclerites in male: (0) absent; (1) two pairs: between coxae I and II and between coxae II and III; (2) three pairs (Fig. 1K). Intercoxal sclerites are small triangular or elongated sclerites surrounding the sternum, their tips penetrating between the coxae of the legs. They may be free, or fused with the sternum (Fig. 1K).

68. Intercoxal sclerites in female: (0) absent; (1) two pairs: between coxae I and II and between coxae II and III; (2) three pairs.

69*. Pleural bars: (0) isolated; (1) longitudinally fused (Fig. 1P). Pleural bars are narrow, horizontal sclerites between coxae and carapace ('pièces épimériennes' of Simon 1892: 11). May be fused among each other, with intercoxal sclerites and/or with carapace.

70*. Carapace and pleural bars: (0) separate (Fig. 1P); (1) fused (Fig. 2E).

71*. Sternum and carapace: (0) separate (Fig. 1P); (1) fused (Fig. 2E).

72*. Sternum and plagula: (0) separate; (1) fused. The plagula is a triangular sclerite situated on the ve side of the petiolus. It may be fused with the sternum (Simon 1892: figs 15–18; Ledoux & Canard 1991: figs 13 and 14).

73. Sternal border: (0) simple; (1) rebordered.

74. Sternum and carapace: (0) smooth; (1) tuberculate.

75. Number of promarginal cheliceral teeth in male: (0) two; (1) three; (2) more than three.

76. Number of retromarginal cheliceral teeth in male: (0) two; (1) more than two. This character, as well as character 78, cannot be scored in *Gnaphosa lucifuga* (Walckenaer, 1802): the genus *Gnaphosa* has a toothed comb instead of teeth on the cheliceral retromargin of males and females.

77. Number of promarginal cheliceral teeth in female: (0) two; (1) three; (2) more than three.

78. Number of retromarginal cheliceral teeth in female: (0) two; (1) more than two.

79. Long shaggy hair in front of fang base: (0) absent; (1) present. Many of the ingroup genera bear, at the base of the cheliceral claw, a shaggy hair that is clearly distinct from other hairs at the cheliceral promargin in being as long as the fang itself and bent at a right angle just beyond its origin (Fig. 1M,Q). Platnick (2000: 10) has already mentioned this type of seta for Lamponidae.

80*. Cheliceral macrosetae: (0) absent; (1) present. A number of phrurolithine genera have at least one large, spine-like seta frontally on the basal article of the chelicera (Fig. 1Q).

81. Chilum: (0) absent; (1) present. The chilum is a small sclerite at the base of the chelicerae, below the clypeus. The chilum can be median and entire, or bilateral, in which case it is wholly or partly bipartite (Jocqué 1991).

82. Chilum extension: (0) bilateral (Fig. 1R); (1) median (Fig. 1S).

83. Endites, ve depression: (0) absent (Fig. 1O); (1) present (Fig. 1N). A transverse ve depression of the endites, typical of Gnaphosidae, is also found in several of the ingroup genera.

84. General shape of endites: (0) with external lateral notch (Fig. 1N); (1) semicircular; (2) parallel-sided (Figs 1O and 2A).

85. Serrula: (0) conspicuous (Fig. 2A); (1) reduced.

86. Apical maxillar hair tuft: (0) absent (Fig. 1N,O); (1) present (Fig. 2A). Many of the taxa studied have a dense tuft of hair on the anterior tip of the endites.

87. Height of fovea as compared to the rest of the carapace in lateral view: (0) fovea is highest part: carapace slanting (Fig. 2B); (1) fovea as high as cephalic part: flat carapace (Fig. 2C); (2) fovea lower than cephalic part: carapace bulging (Fig. 2E).

88. Clypeus slope: (0) vertical (Fig. 2C); (1) slanting forwards (Fig. 2B); (2) slanting backwards (Fig. 2E).

89. Clypeus height: (0) smaller than diameter of AME; (1) equal to diameter of AME; (2) larger than diameter of AME.

90. Curvature of AER, from front: (0) procurved; (1) straight.

91. Curvature of AER, from above: (0) procurved; (1) straight; (2) recurved.

92. Curvature of PER, from front: (0) procurved; (1) straight.

93. Curvature of PER, from above: (0) procurved; (1) straight; (2) recurved.

94. Diameter of AME as compared to ALE: (0) smaller; (1) equal; (2) larger.

95. Diameter of PME as compared to PLE: (0) smaller; (1) equal; (2) larger.

96. Diameter of AME as compared to PME: (0) smaller; (1) equal; (2) larger.

97. Shape of PME: (0) circular, identical to shape of other eyes (Fig. 2G); (1) angular (Fig. 2F) or markedly elliptic.

98. Shape of MOQ: (0) wider in front; (1) rectangular (Fig. 2F); (2) wider posteriorly (Fig. 2G).

99. Lateral eye tubercle: (0) absent; (1) present (Fig. 2E,G).

100. Retina of AME: (0) not restricted; (1) restricted to median portion of eyes (Fig. 2F). The occurrence of this peculiar type
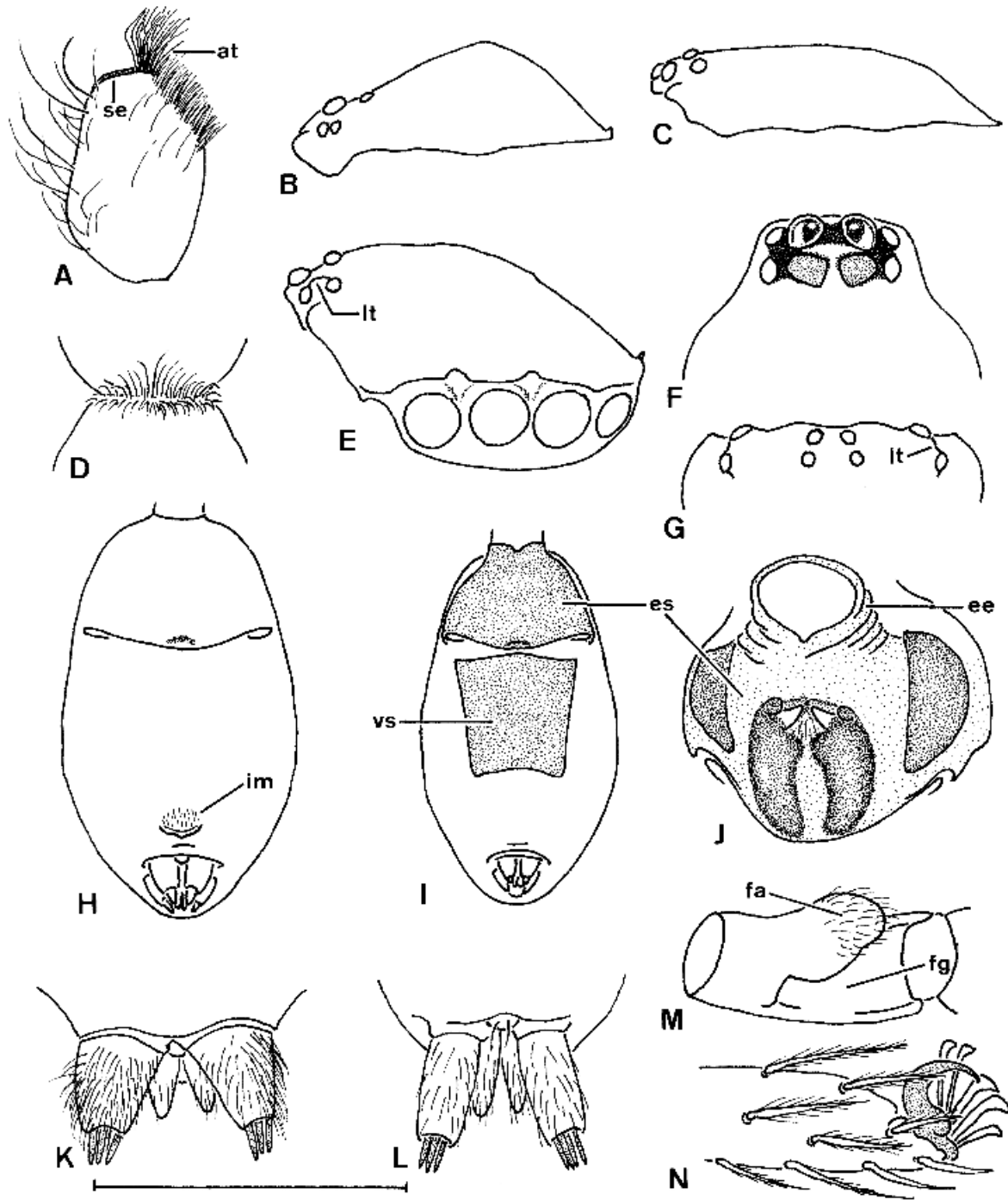
Fig. 2 A. *Coryssiphus praeusta*, female, endite, ve. —B. *Hortipes luytenae*, female, carapace, lateral. —C. *Mesiotelus cyprius*, female, carapace, lateral. —D. *Liocranum giersbergi*, female, frontal end of abdomen, dorsal. —E. *Oedignatha scrobiculata*, female, carapace, lateral. —F. *Piabuna nanna*, female, eye region, do. —G. *Lessertina mutica*, male, eye region, do. —H. *Messapus martini*, male, abdomen, ve. —I. *Castianeira occidens*, male, abdomen, ve. —J. *Teutamus fertilis*, female, frontal end of abdomen, plv. —K. *Agroeca brunnea*, male, ALS, ve. —L. *Agraecina lineata*, male, ALS, ve. —M. *Phrurolithus festivus*, male, left palpal fe, ve. —N. *Phruronellus formica*, female, distal end of ta IV. Scale bar: N, 0.20 mm; F, M, 0.50 mm; A, B, K, L, 1.00 mm; J, 1.25 mm; E, H, I, 1.50 mm; C, 2.25 mm; G, 2.50 mm; D, 3.0 mm. Abbreviations: see Fig. 1.

of AME, described by Chamberlin & Ivie (1933: 41) as 'face upwards more than forward', is rather common and also homoplastic among liocranid and corinnid genera. Platnick & Baptista (1995) described it for *Attacobius* Mello-Leitão, 1925 and Bosselaers & Jocqué (2000b) for *Hortipes*.

101*. Curved strong hairs frontally on abdomen: (0) present (Fig. 2D); (1) absent.

102. Male do scutum: (0) absent; (1) present.

103. Male do scutum size: (0) small (less than half the length of the abdomen); (1) large.

104. Male ve sclerite: (0) absent (Fig. 2H); (1) present (Fig. 2I). The abdominal sclerite nomenclature used follows Reiskind (1969).

105. Male epigastric sclerite: (0) absent (Fig. 2H); (1) present (Fig. 2I).

106. Male epigastric sclerite extension surrounding base of petiolus: (0) absent; (1) present.

107. Male inframamillary sclerite: (0) absent (Fig. 2I); (1) present (Fig. 2H).

108. Male ALS shape: (0) conical (Figs 2K, 7A and 9A); (1) cylindrical (Fig. 2L).

109. Male ALS separation: (0) tangent or close; (1) widely separated.

110. Male PMS shape: (0) slender (Figs 7C and 9C); (1) stout, subtriangular.

111. Male PLS separation: (0) by about half their length; (1) by more than their length.

112. Enlarged piriform spigots on male ALS: (0) absent; (1) present (Fig. 2K,L).

113. Female do scutum: (0) absent; (1) present.

114. Female do scutum size: (0) small (less than half the length of the abdomen); (1) large.

115. Female epigastric sclerite: (0) absent; (1) present (Fig. 2J).

116. Female epigastric sclerite extension surrounding base of petiolus: (0) absent; (1) present (Fig. 2J).

117. Female inframamillary sclerite: (0) absent; (1) present.

118. Female ALS separation: (0) tangent or close; (1) widely separated.

119*. Female PMS shape: (0) slender, conical (Fig. 7D); (1) large compressed (Fig. 8E,F); (2) medium-sized, subtriangular (Figs 8B–D, 9D); (3) gnaphosoid, i.e. split into an anterior part bearing aciniform and minor ampullate gland spigots and a posterior part bearing cylindrical gland spigots, as described in Platnick (1990: fig. 1).

120*. Arrangement of large spigots on female PMS: (0) none; (1) a single one (Fig. 7D); (2) two in a transverse row (Fig. 8B); (3) three in a triangle (Figs 8C,D and 9D); (4) four or five in two rows (Fig. 8F); (5) more than five in two rows (Fig. 8E).

121. Female PLS separation: (0) by about half their length; (1) by more than their length.

122. Ventral femoral apophysis of male palp: (0) absent; (1) present (Fig. 2M).

123. Position of male palpal ve femoral apophysis: (0) basal; (1) median (Fig. 2M); (2) terminal.

124. Retrolateral groove on male palpal fe: (0) absent; (1) present (Fig. 2M).

125. Male palpal tibial apophysis: (0) absent; (1) present.

126. Position of male palpal tibial apophysis: (0) retrolateral terminal (Fig. 3A,B,D,G,I); (1) retrolateral-dorsal terminal (Fig. 3C); (2) retrolateral-ventral median; (3) retrolateral median (Fig. 3F).

127. Male palpal tibial apophysis shape: (0) simple, pointed (Fig. 3F,G,I); (1) with bifid tip; (2) stout, with many tips; (3) large and sickle-shaped (Fig. 3C); (4) bifid, complex (Fig. 4G); (5) a sharp, notched ridge; (6) large and stout, blunt tipped (Fig. 3B).

128. Tip of cymbium: (0) wide and short (Fig. 3D); (1) narrowed and long (Fig. 3A–I).

129*. Tegular knob: (0) absent; (1) present (Fig. 3C). The tegular knob is a sclerotized distal knob on the tegulum of some phrurolithine genera (Penniman 1985: 23).

130. Tegular locking lobe: (0) absent; (1) present (Fig. 3D). Tegular and subtegular locking lobes were first mentioned from Lycosoidea by Griswold (1993).

131. Subtegular locking lobe: (0) absent; (1) present (Fig. 3D).

132. Inflated tegulum: (0) absent; (1) present (Fig. 3C).

133*. Pear-shaped bulbus: (0) absent; (1) present (Fig. 3E). A simple, smooth, pear-shaped bulbus is typical of Castianeirinae.

134*. Coiled sperm duct: (0) absent; (1) present (Fig. 3B,E).

135. Conductor: (0) absent; (1) present.

136. Conductor texture: (0) sclerotized; (1) membranous. The homology of the various tegular apophyses of the male palp is still not fully elucidated for most spiders. A hyaline appendage, immovably attached to the tegulum and facing the embolus tip, is considered to be a conductor in our analysis, while a sclerotized appendage which is flexibly attached to the tegulum via a thin membrane is considered to be a median apophysis (Sierwald 1990; Griswold 1993)

137. Conductor shape: (0) simple lamella with blunt or sharp tip (Fig. 3D,G,I); (1) centrally implanted on tegulum, anvil-shaped (Fig. 3F); (2) complex, large (Fig. 3B).

138. Median apophysis: (0) absent; (1) present.

139. Median apophysis shape: (0) relatively short and stout base, simple tip (Fig. 3G); (1) long, thin and pointed (Fig. 3F,I); (2) flattened, wide, robust.

140. Embolus shape: (0) relatively short, stout and pointed, apically inserted on tegulum (Fig. 3C); (1) long, thin and sickle-shaped (Fig. 3B,I); (2) long and thin, encircling tegulum (Fig. 3F,H); (3) broad and ribbon-like (Fig. 3D,G); (4) long and thin, passing behind tegulum (Fig. 3A); (5) corkscrew-shaped (Fig. 3E).

141. Additional tegular apophyses: (0) none; (1) large ones at embolus base (Fig. 3B,D,G). In some genera, such as *Agroeca*,
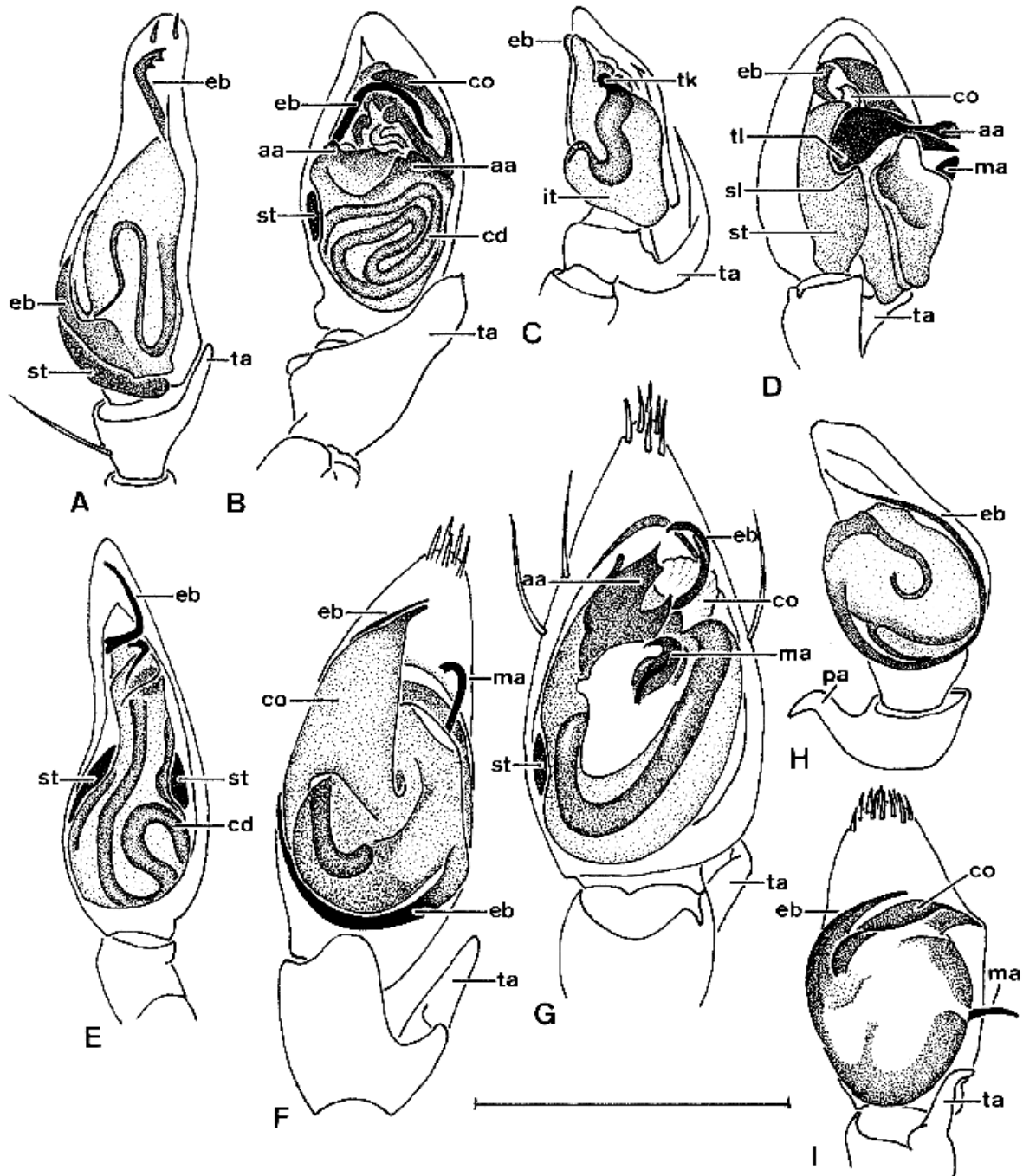
Fig. 3 A. *Cetonana martini*, male, left palp, ve. —B. *Corinna nitens*, male, left palp, ve. —C. *Phrurotimpus alarius*, male, left palp, ve. —D. *Agroeca brunnea*, male, left palp, plv. —E. *Copa benina*, male, right palp, ve. —F. *Lessertina mutica*, male, left palp, ve. —G. *Rhaeboctesis secundus*, male, left palp, ve. —H. *Trachelas schenkeli*, male, right palp, ve. —I. *Medmassa proxima*, male, left palp, ve. Scale bar: H, I, 0.50 mm; A, C, F, G, 0.75 mm; D, 1.00 mm; E, 1.50 mm; B, 3.00 mm. Abbreviations: see Fig. 1.

Corinna and *Liocranum*, the tegulum bears one or more additional apophyses that are immovably attached to it and situated near the base of the embolus.

142. Subtegulum as observed in ventral view of male palp:

(0) hidden (Fig. 3F,H); (1) pl (Fig. 3A,D); (2) pl and rl median (Fig. 3E); (3) rl.

143. Retrolateral apophysis of male palpal pa: (0) absent; (1) present (Fig. 3H).
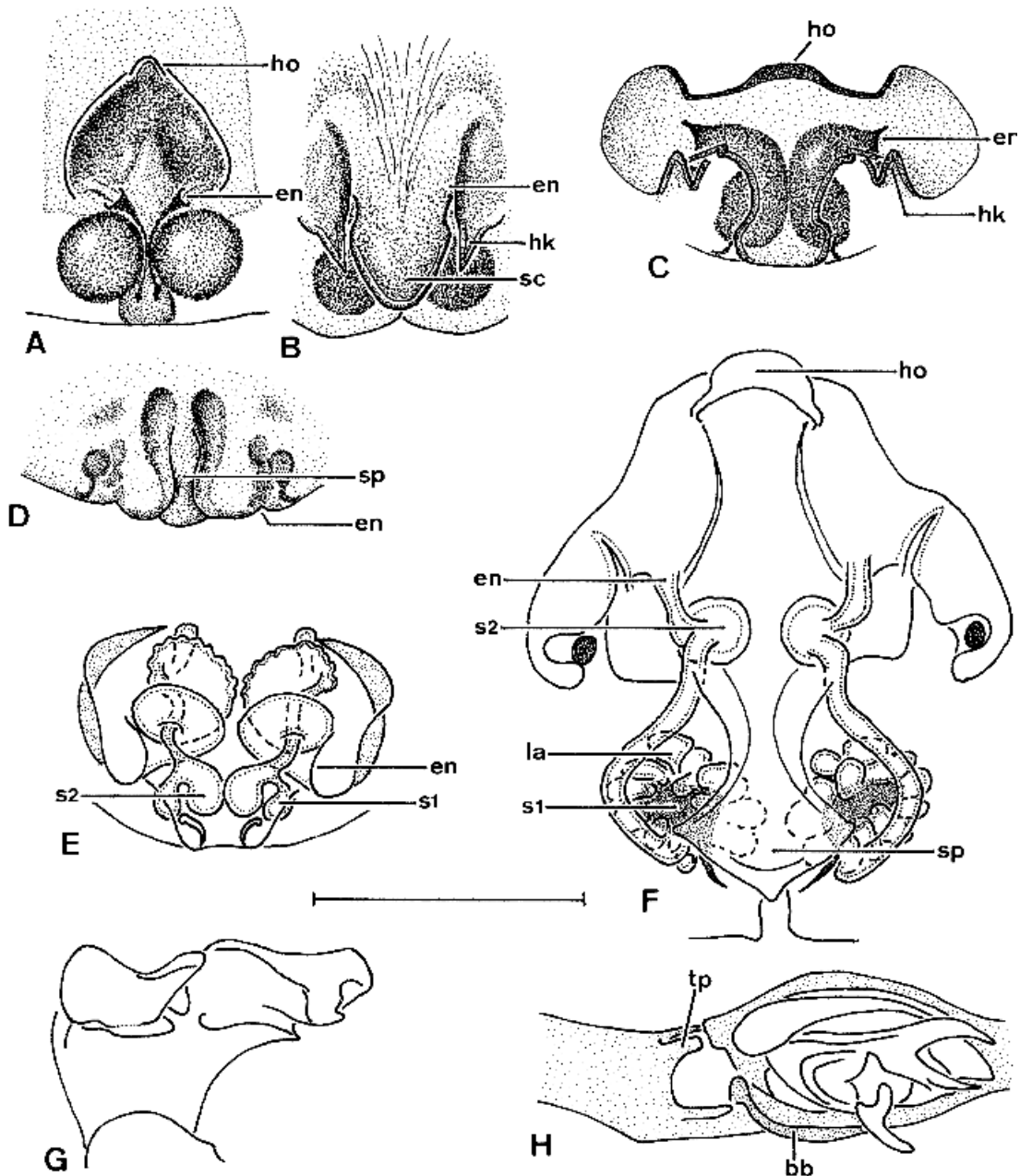
Fig. 4 A. *Sphingius gothicus*, female, epigyne, ve. —B. *Neoanagraphis chamberlini*, female, epigyne, ve. —C. *Cybaeodes marinae*, female, epigyne, ve. —D. *Medmassa proxima*, female, epigyne, ve. —E. *Cetonana martini*, female, vulva, ve. —F. *Rhaeboctesis secundus*, female, vulva, ve. —G. *Creugas bajulus*, male, distal end of palpal ti, rlv. —H. *Mesiotelus cyprius*, male, left palp, ve. Scale bar: E, F, 0.30 mm; A–D, 0.50 mm; H, 0.60 mm; G, 1.00 mm. Abbreviations: see Fig. 1.

144. Bunch of stiff setae on cymbium tip: (0) absent; (1) present (Fig. 3F,G,I).

145. Basal rl bulge with thickened rim on cymbium: (0) absent; (1) present (Fig. 4H).

146. Epigynal sclerotization: (0) weak; (1) substantial.

147. Epigynal central depression: (0) absent; (1) present (Fig. 4A).

148. Epigynal scape: (0) absent; (1) present (Fig. 4B).

149. Anterior epigynal hood: (0) absent; (1) present (Fig. 4A,C,F).

150. Epigynal septum: (0) absent; (1) present (Fig. 4D,F). The septum is a thin, median, longitudinal sclerite bisecting the epigyne.

151. Lateral epigynal hooks: (0) absent; (1) present (Fig. 4B,C).

152. Position of ID entrances: (0) anterior (Fig. 4A–C,E,F); (1) posterior (Fig. 4D); (2) median (Bosselaers & Jocqué 2000a: figs 3d and 4h). The entrances of the ID have been scored as anterior when they are situated in front of ST1, as posterior when situated behind ST1 and as median when lying in the same transversal plane as ST1.

153. Spermathecae 2: (0) absent; (1) present (Fig. 4E,F).

154*. Size of ST2: (0) smaller than ST1; (1) as large as ST1 (Fig. 4F); (2) larger than ST1 (Fig. 4E).

155. Shape of ID: (0) short and simple; (1) solenoidally coiled (Fig. 4E; Bosselaers & Jocqué 2000a: fig. 2f); (2) labyrinth-like and wrapped around ST1 (Fig. 4F).

156. Terminal pl lobe on male palpal ti: (0) absent; (1) present (Fig. 4H). Ubick & Platnick (1991) mentioned this character for *Hesperocranum* Ubick & Platnick, 1991, *Liocranum* and *Mesiotelus* Simon, 1897.

157. Claw on female palp: (0) reduced; (1) fully developed.

Results

The matrix of character states can be found in Table 1. All characters were run unordered in the analyses performed. Contrary to the opinion of Kluge (1997a,b), we believe that differential character weighting is necessary in phylogenetic reconstruction using parsimony analysis. Not all characters used in a phylogenetic analysis have the same information content and predictive value and, as a result, an equally weighted analysis can certainly not be considered unweighted. As a matter of fact, we feel that equal weighting of characters is a very improbable weighting scheme. Weighting, when applied by appropriate *a posteriori* methods, will give more weight to those characters that are more consistent with the initial heuristic cladograms. These are the characters that are most useful for cladistic inference (Farris 1969). Cladograms obtained by attributing *a posteriori* weights to characters based on their relative degrees of homoplasy on a set of heuristic trees explain the data better than cladograms in which an extra step in a very homoplastic character is considered as important as an extra step in a character which fits the tree topology almost perfectly.

Two *a posteriori* weighting methods are widely used in order to obtain cladograms with greater explanatory power. In successive approximations, character weighting (Farris 1969, 1989; Carpenter 1988) by an iterative procedure is followed, in which the characters are given weights based on a statistic (in most methods either ci or rc), attributed to those characters on a pooled initial set of shortest trees, obtained under equal weights. Data are reanalysed under these *a posteriori* weights and the procedure is repeated until a stable solution, i.e. a set of self-consistent cladograms, is obtained. In implied weighting (Goloboff 1993), characters are attributed weights in a non-iterative way by maximizing the sum of their Goloboff fits, defined as $k/k + es$, where k is a concavity constant (Goloboff 1997a). The implied weighting method is preferred here because it finds trees in one stage and, as a result, the solution obtained is not influenced by the initial weights attributed to the characters (Kaila 1999); self-consistency of the final cladograms is not defined with respect to a pooled set of topologies (Harbach & Kitching 1998); the fit function used does not have a lower bound of zero and so the chance of dismissing evidence by entirely excluding characters is minimized; and the method does not down-weight multistate characters (Goloboff 1993).

Implied weighting on the data in Table 1 was performed in PeeWee 2.6, with the default value for the concavity constant ('conc 3') in effect. A single fittest tree (Fig. 5) with fit 755.5 and a length of 964 steps was found in 221 of the 500 random addition sequences executed (command 'mult*500', using 'max*' was not necessary). The same solution was obtained under 'amb=' and 'amb-', indicating that no spurious resolution due to unsupported (Coddington & Scharff 1994; Wilkinson 1995) or ambiguously supported (Nixon & Carpenter 1996) branches was present. The unique tree found under 'conc 3' is also similar to the trees found under equal and successive weighting (see below). Implied weighting was performed in PAUP 4.0 beta 4a as well, with 'pset goloboff=yes; hsearch addseq=random nreps=500'. The default value for the concavity constant 'gk=2' was used, which is identical to 'conc 3' in PeeWee (Bosselaers & Jocqué 2000b). A single fittest tree, identical to the 'conc 3' PeeWee tree, was found in 188 out of 500 random addition sequences. PAUP, which calculates fit values more accurately and with a different order of magnitude and sign than PeeWee, gave the following statistics for this tree: fit, −75.895; length, 964; ci, 0.234; ri, 0.558; and rc, 0.131. With 'pset gpeewee=yes' in effect, emulating PeeWee, a fit of −755.5 was obtained.
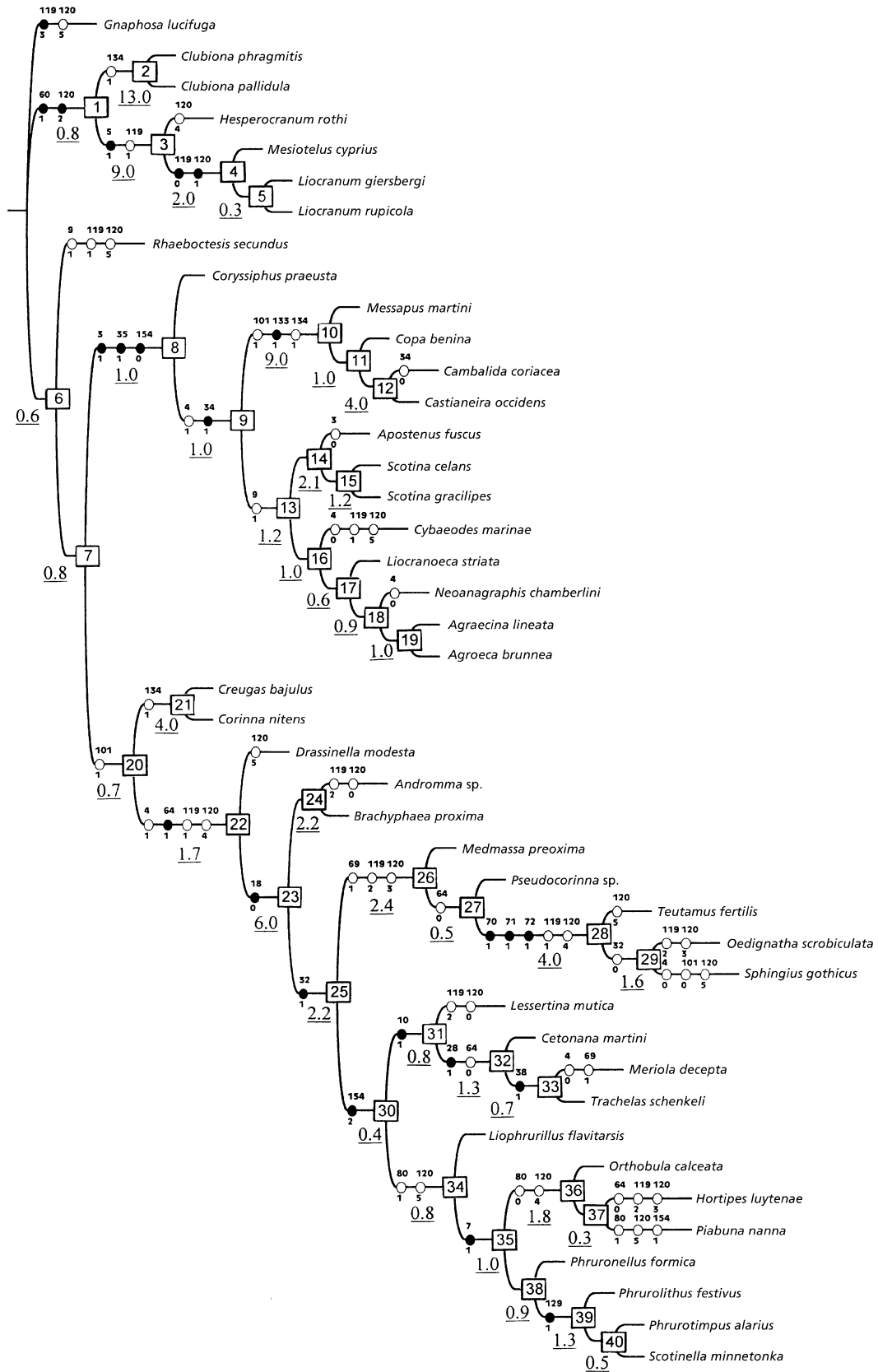
The data set in Table 1 was also analysed under the other concavity settings (1, 2, 4, 5 and 6) available in PeeWee. It turned out that the results obtained were sensitive to the concavity constant used. Under 'conc 2', three trees with fit 633.6 and lengths 964, 965 and 965 were found, one of them being identical to the single 'conc 3' tree and the other two differing by small rearrangements in clade 16 (node numbers are indicated in Fig. 5). Under 'conc 1', two trees with fit 461.1 and length 977 were found, in which clade 1 occupies two alternative positions, resulting in a basal trichotomy in their consensus. Because, under this very low concavity value, implied weighting weighs so strongly against homoplastic characters that excessive weight is given to a small set of mutually consistent characters, this solution is not preferred. Under both 'conc 4' and 'conc 5', the same unique tree, with length 945 and fits 845.0 and 915.0, respectively, was found. This tree shows clade 1 as the sister clade to a large, mostly pectinate clade grouping all other genera, an arrangement that does not reveal much interesting information about relationships

Table 1 Character–taxon matrix.

	Goloboff fit	ri	ci	Steps
1	0.21	0.27	0.08	12
2	0.20	0.37	0.08	13
3	0.75	0.90	0.50	2
4	0.38	0.64	0.17	6
5	1.0	1.0	1.0	1
6	0.50	0.50	0.25	4
7	1.0	1.0	1.0	1
8	0.75	1.0	0.50	2
9	1.0	0.50	0.50	2
10	1.0	1.0	1.0	1
11	0.43	0.60	0.33	3
12	0.60	0.67	0.20	5
13	0.60	0.89	0.33	3
14	0.50	0.67	0.25	4
15	1.0	1.0	1.0	1
16	0.43	0.50	0.20	5
17	0.38	0.50	0.17	6
18	0.50	0.79	0.25	4
19	0.38	0.72	0.17	6
20	0.60	0.89	0.33	3
21	0.75	0.67	0.67	3
22	0.75	0.80	0.50	2
23	0.25	0.61	0.25	12
24	1.0	1.0	1.0	1
25	0.21	0.50	0.21	14
26	0.25	0.21	0.21	12
27	0.50	0.50	0.50	5
28	0.75	0.92	0.40	2
29	1.0	0.75	0.50	3
30	0.60	0.78	0.33	2
31	1.0	0.89	0.50	1
32	1.0	1.0	1.0	1
33	0.43	0.67	0.20	5
34	0.38	0.74	0.38	8
35	0.38	0.58	0.38	10
36	0.30	0.70	0.30	7
37	0.43	0.79	0.43	7
38	0.27	0.69	0.27	11
39	0.38	0.90	0.38	8
40	0.60	0.67	0.67	3
41	0.60	0.74	0.29	7
42	0.38	0.38	0.11	9
43	0.27	0.50	0.24	17
44	0.38	0.52	0.50	13
45	0.27	0.31	0.15	8
46	0.19	0.63	0.13	6
47	0.21	0.69	0.30	6
48	0.30	0.78	0.17	
49	0.38		0.38	
50	0.43		0.43	

Taxa (rows, top to bottom):

- Trachelas schenkeli
- Teutamus fertilis
- Sphingius gothicus
- Scotinella minnetonka
- Scotina gracilipes
- Scotina celans
- Rhaeboctesis secundus
- Pseudocorinna sp.
- Piabuna nanna
- Phrurotimpus alarius
- Phruronellus formica
- Phrurolithus festivus
- Orthobula calceata
- Oedignatha scrobiculata
- Neoanagraphis chamberlini
- Messapus martini
- Mesiotelus cyprius
- Meriola decepta
- Medmassa proxima
- Liophrurillus flaitarsis
- Liocranum rupicola
- Liocranum giersbergi
- Liocranoeca striata
- Lessertina mutica
- Hortipes luytenae
- hesperocranum rothi
- Gnaphosa lucifuga
- Drassinella modesta
- Cybaeodes marinae
- Creugas bajulus
- Coryssiphus praeusta
- Corinna nitens
- Copa benina
- Clubiona pallidula
- Clubiona phragmitis
- Cetonana martini
- Castianeira occidens
- Cambalida coriacea
- Brachyphaea proxima
- Apostenus fuscus
- Andromma sp.
- Agroeca brunnea
- Agraecina lineata

Character columns numbered 1–51 across the bottom.

Table 1 *Continued*

Table 1 *Continued.*

and that also differs substantially from the solutions obtained under 'conc 3' and under equal and successive weighting. The single tree with fit 973.4 and length 946, which was found under 'conc 6', differs even more from these trees and was not further considered.

The single implied weighting tree obtained under 'conc 3' is our preferred solution. It is illustrated in Fig. 5. In Table 1, the last four columns give the number of steps and, rounded to two significant digits, ci, ri and the Goloboff fit (Goloboff 1993) for each character on this preferred tree. Cladogram robustness for the implied weighting tree was examined by calculating Bremer support (Bremer 1988, 1994) in PeeWee. With 'bsupport 26', 15 580 trees with fit between 752.9 and 755.5 were found. Bremer supports higher than 2.6 were calculated heuristically in steps of 1.0 by calculating trees down to a certain suboptimal fit value using the 'sub' command, storing 5000 trees in memory using 'hold 5000' and calculating their strict consensus in order to determine which branches were collapsed. The procedure was repeated several times for each step and the consensus trees found were checked for differences in order to avoid missing collapsed branches for a certain fit value. Moreover, the entire calculation was checked in PAUP, emulating PeeWee as described above, calculating suboptimal trees using the 'keep' command and storing 5000 trees each time using 'set maxtrees = 5000 increase=no'. Bremer support values are indicated below the branches in Fig. 5.

For the sake of comparison, an equally weighted analysis of the data matrix was performed in PAUP with 'hsearch addseq = random nreps = 1000' (heuristic search with tree bisection and reconnection swapping and 1000 random addition sequences). A single island of four shortest trees (927 steps) was found in 57 out of 1000 random addition sequences. When the number of random addition sequences was increased to 10 000, no additional islands were found. Collapsing branches with a minimum length of zero with 'condense collapse=minbrlen' keeps the same four trees, indicating that, as a result of the high number of characters as compared to the number of terminals, no spurious resolution due to unsupported or ambiguously supported branches is present. NONA 2.0 found the same four trees, even when the number of random addition sequences was set to 10 000 ('mult*10000', 'amb=' as well as 'amb-'). The data set was also analysed using TNT 0.1 beta, an experimental program analysing large data sets with new tree searching technologies. Because our data set is still relatively small for TNT, only tree drifting was applied (Goloboff 1999: 425) with 100 random

addition sequences, 25 cycles and allowing 30 changes. Shortest length (927 steps) was hit 72 times out of 100 and no shortest trees not found by the other programs were discovered. PAUP gives the following statistics for the set of four shortest trees: ci, 0.244; ri, 0.580; rc, 0.141; Goloboff fit between −73.388 and −73.674. The strict consensus tree of the set of shortest trees is illustrated in Fig. 6A. It is similar to the preferred implied weighting tree, but differs in the insertion of clade 3 and the placing of individual genera such as *Cybaeodes* and *Rhaeboctesis*.

Successive weighting was performed on the set of shortest trees found. Weighting based on ci is preferred to rc- or ri-based successive weighting in this respect: contrary to rc and ri, ci cannot reach a lower bound of zero, and therefore the chance of dismissing evidence by entirely excluding characters is minimized (Goloboff 1993). Moreover, successive weighting based on rc does not necessarily give higher weights to less homoplastic characters (Goloboff 1991). On the other hand, ci-based weighting makes multistate characters less influential, because an extra step represents a smaller fraction of the total change on a tree if a character has more states (Goloboff 1993). Successive weighting based on ci (Farris 1969; Carpenter 1988) was executed in PAUP with 'reweight index = ci hsearch addseq = random nreps = 200'. The program stabilized after two iterations on a tree with weighted length 226.0, ci 0.321, ri 0.640, rc 0.205 and Goloboff fit −28.028. When weights are reset to one, this tree has length 930, ci 0.243, ri 0.578, rc 0.141 and Goloboff fit −74.238. Successive weighting based on ci was also executed in NONA with 'run[swt amb-mult*50'. After two iterations, the program stabilized on the same tree as PAUP, for which NONA calculated a weighted length of 22 336. The unique ci-based successive weighting tree found by both programs is illustrated in Fig. 6B. It is similar to the preferred implied weighting tree.

Discussion

A list of character state changes, under ACCTRAN optimization, at the nodes of the preferred tree can be found in Table 2. Node numbers are indicated in Fig. 5. It is obvious that homoplasy is high in the data matrix: only 14 out of 157 characters are completely free of homoplasy on the preferred tree and only 54 character state changes are non-homoplastic under ACCTRAN optimization. Sanderson & Donoghue (1989: fig. 1) found, based on regression coefficients calculated on the basis of data from 60 cladistic analyses, that 43 taxa yield, on average, ci values of about 0.35, while all the trees found

Fig. 5 Preferred, strictly supported cladogram obtained under implied weighting for 40 liocranid and corinnid species and three outgroup species. State changes are indicated on the tree for 26 out of 157 characters (see text); non-homoplasious state changes are in black, homoplasious state changes in white. Nodes are numbered on the tree. Underlined figures below branches are Bremer support values (as PeeWee fit values).
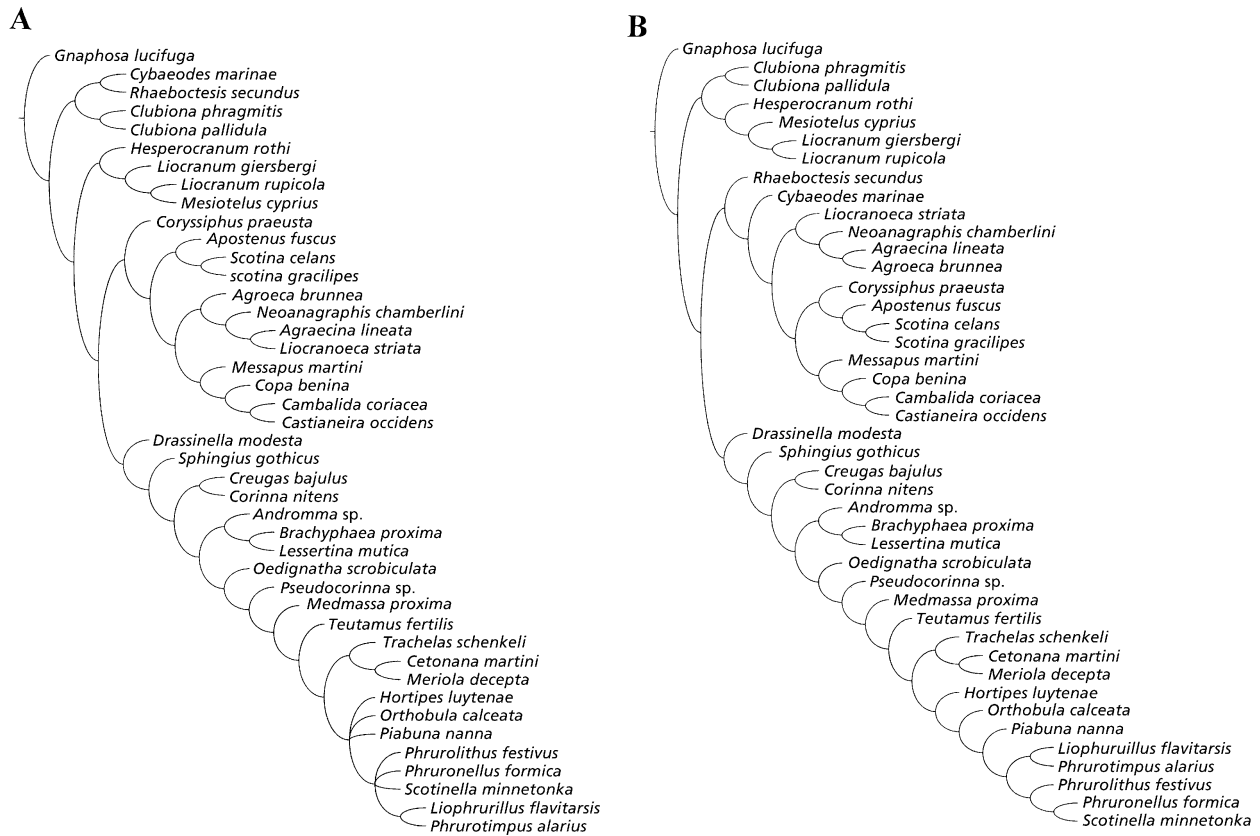
A

B

Fig. 6 A. Strict consensus of four most parsimonious trees found under equal weighting for the data set. —B. Single solution found for the data set under successive weighting based on ci.

for the present data matrix, differentially weighted or equally weighted, have ci values lower than 0.25. Quite a few characters which have been reported as valuable in the study of the relationships of other spider groups proved unreliable as indicators of relationships among the genera studied in this analysis, due to high homoplasy. The most striking examples are briefly discussed here.

Retrocoxal hymen (characters 1 and 2): this was considered to be of taxonomic value in Miturgidae and Corinnidae by Raven (1998). We found the presence of this structure to be highly homoplastic among the genera we studied. In addition, the retrocoxal hymen is only present in males (*Hesperocranum*) or females (*Agraecina* Simon, 1932, *Liocranum*, *Mesiotelus* and *Messapus*) in some taxa. Deeleman-Reinhold (2001) describes similar findings. Feathery hairs (character 57): these were consistently present in the castianeirine genera studied (clade 10), as reported before by Reiskind (1969), but no phylogenetic information could be discovered in their distribution among other genera. The corinnine *Creugas bajulus* (Gertsch, 1942) has feathery hairs, but no trace of them can be found in *Corinna nitens* (Keyserling, 1891), a

species that is closely related (Bonaldo 1996) to the extremely rare *Corinna rubripes* C. L. Koch, 1842, type species of the genus *Corinna*. Precoxal triangles: we cannot confirm the claim of Penniman (1985) that the presence of precoxal triangles defines a clade including Gnaphosidae, Clubionidae, Corinninae, Castianeirinae, Trachelinae and Phrurolithinae. Characters 65 and 66 are homoplastic in our ingroup and precoxal triangles are absent in *Gnaphosa lucifuga*, the type species of *Gnaphosa*. Eye characters (characters 90–100): although considered to be important by many of the earlier arachnologists, the eye characters studied in this analysis turned out to be very homoplastic. Female PMS shape and spigot arrangement (characters 119 and 120): due to technical limitations and restrictions in the number of specimens available, we could not study the female PMS of all genera in the matrix by SEM. However, general PMS shape and the number of large spigots present can be clearly observed under a stereomicroscope. Female PMS characters were homoplastic among the genera studied and did not yield synapomorphies supporting large clades. Because character states 0–5 of character 120 represent a series of an increasing

Table 2 Character state changes at the nodes of the preferred tree (Fig. 5). Characters have been optimized favouring reversals over parallel gain ('ACCTRAN' optimization, 'fast' in Winclada). Non-homoplasious character state changes are indicated by '*'; entirely non-homoplasious characters are indicated by '**'. Ambiguous optimizations are given in italics.

Node 1: 46:0, *52:0, 58:1*, 60:1**, 89:0, *120:2*, 146:0*
Node 2: 16:1, 26:1, 59:1, 63:1, 75:2, 94:1, 97:0, 108:1, 112:1, 127:1*, 134:1, 138:0, 152:1, 153:1
Node 3: 5:1**, *19:0, 22:0*, 43:1, 50:0, 54:2, 79:1, *81:1*, 119:1, 140:0, 141:1, 145:1, 156:1
Node 4: 2:1, 43:3, 47:4, *48:1, 52:1*, 57:1, 89:1, 90:1, 95:0, 119:0*, 120:1*, 128:1, 149:1
Node 5: 27:2, 29:2, 30:2, *40:3, 81:0*
Node 6: 37:2, *39:2, 48:1*, 54:2, *57:1, 67:1, 68:1, 73:1*, 111:1, 121:1*, 128:1
Node 7: 27:2, 29:2, *30:2*, 43:1, *53:3*, 63:1, 79:1, 84:2, *93:0*, 94:1, *97:0, 102:1*, 138:0
Node 8: 2:1, *3:1*, 35:1**, 43:3, 65:0, 66:0, *67:0, 68:0, 73:0, 87:0, 154:0*
Node 9: 4:1, *30:1*, 34:1*, *53:2, 61:0*
Node 10: 16:1, 27:1, 29:1, 47:2, *54:1*, 58:1, 75:0, *79:0, 94:2, 98:1*, 101:1, 117:1, 125:0, 133:1**, 134:1, 140:5, 142:2, *152:1*
Node 11: *2:0*, 61:1, *66:1*, 73:1, *77:0*, 105:1, 113:1, 115:1, 152:2*
Node 12: *59:1*, 67:1, *94:1, 98:2*, 103:1, 104:1, 106:1, 116:1
Node 13: 9:1, *63:0*, 94:0, *96:0, 128:0*, 138:1
Node 14: 1:1, 12:1, 30:2, 40:1, *50:0, 57:0*, 62:0, 81:1, 86:0, 130:1, 131:1
Node 15: 6:1, 16:1, *29:3*, 42:3, *102:0*, 140:3, 146:0, 153:1
Node 16: *2:0, 31:1*, 41:3, *53:3, 87:1*, 108:1, 109:1, 135:1, *149:1*
Node 17: 26:1, 27:1, 29:1, 40:3, 42:3, 43:0, 53:4, *96:1, 102:0*
Node 18: 16:1, 25:2, *31:0*, 47:4, *87:0, 140:2, 149:0*
Node 19: 2:1, 112:1, 131:1, 145:1, 150:1
Node 20: *42:1, 47:2, 48:0*, 49:0, 58:1, 59:1, 67:2, *87:2*, 101:1, 105:1, *139:1*, *152:1*
Node 21: 43:3, 76:1, 78:1, *79:0*, 85:1, 96:2, 98:0, 115:1, 127:4, 134:1, 135:1, 136:0, 137:2, 141:1, 142:2
Node 22: 4:0, *24:0, 41:1*, *43:0*, 44:1, 50:0, 61:0, 62:0, 64:1*, *97:1*, 103:1, *114:1*, 119:1, *120:4*
Node 23: 15:0, 18:0**, 19:0, 21:0*, 22:0, 45:0, 47:0, 51:0, 53:1, 54:0, *55:0, 57:0*, 91:1, *142:0*
Node 24: 1:1, 2:1, *41:2*, 67:1, *79:0*, 82:0, 85:1, 96:2, 102:0, 121:0, 127:4
Node 25: *12:1*, 14:0*, *17:0*, 20:0*, *27:3*, 32:1*, *37:3*, 40:1, 42:0*, *46:0, 74:1*, 136:0
Node 26: 29:3, 30:3*, 68:2, 69:1, 84:0, 88:2, *97:0*, 98:0, 99:1, 107:1, 115:1, *119:2, 120:3*, 135:1, *142:1*, 156:1
Node 27: *39:3, 46:1, 47:1*, 64:0, *94:2, 96:2, 106:1*, 116:1, *139:2*
Node 28: *54:1*, 55:1, 70:1**, 71:1**, 72:1**, *83:1, 85:1, 97:1*, 98:1, *113:1*, 119:1, 120:4, 152:0, 156:0
Node 29: 12:0, 14:1, 17:1, 20:1, *29:2*, 30:2, *32:0, 39:2*, 45:1, 47:2, 49:1, 51:1, 53:3, *94:1, 96:1*, 98:2, 104:1
Node 30: 40:0, 41:0, *54:1, 68:0, 93:1*, 126:1, *152:0*, 154:2*
Node 31: 10:1**, *12:0, 29:1*, 30:0, 39:0, *56:1, 79:0*, 126:2, 137:1*, 140:2, 155:1*
Node 32: *11:1*, 28:1**, *47:1*, 49:1, 55:1, 64:0, 68:1, 89:1, *91:2, 92:1*, 93:2, *142:1, 143:1*, 153:1
Node 33: 33:0, 36:0, 38:1**, 68:2, 79:1, 146:0, *155:0*
Node 34: 33:0, 36:0, *45:1, 51:1*, 67:0, 73:0, *74:0, 80:1*, 81:1, 86:0, 87:0, *94:0*, 120:5, 122:1
Node 35: 7:1**, *27:2, 59:0, 84:0*, 107:1, *115:1, 117:1*, 132:1, *153:1*
Node 36: *45:0, 51:0, 52:0, 53:0, 54:0, 80:0*, 83:1, 100:1, *120:4*, 123:2**, *126:0, 140:2*
Node 37: 6:1, 8:1, 93:0, 94:2, 98:1, *115:0, 117:0*, 146:0
Node 38: 57:1, 124:1, 127:3*, 131:1, 140:0, *142:1*
Node 39: *65:0, 84:2, 98:1, 128:0*, 129:1**
Node 40: 1:1, 2:1, 6:1

number of large gland spigots, the possibility exists that they constitute a transformation series of internested homologies. For that reason, the implied weighting analysis with 'conc 3' was also performed with the states of character 120 ordered from 0 to 5. A single tree was found, identical to the tree found with all character states unordered. The same unique preferred tree was also found when character 120 was inactivated. Nevertheless, a prevalence of a single type of large spigot arrangement could be observed in certain clades: subtriangular PMS with a triangular arrangement of large spigots (characters 119:2, 120:3) in clade 8, and large, compressed PMS with large spigots in two rows (characters 119:1, 120:5) in clade 34, which groups most phrurolithine genera. Tegular

and subtegular locking lobes (characters 130 and 131): although these characters provided interesting phylogenetic information in the study of Lycosoidea (Griswold 1993), no large-scale phylogenetic pattern could be deduced from them in our context.

However, in contrast to the characters discussed above, a number of characters do fit the tree well and unambiguously support interesting clades, as discussed below.

Trochanter notch (character 3): only present in clade 8, reversed in *Apostenus* and polymorphic in *Scotina gracilipes* (Blackwall, 1859). Rows of bristles with modified tips (character 4): plesiomorphic in the groups studied. The bristles are absent in clade 9 (reversed in *Cybaeodes* and *Neoanagraphis*)

and clade 22 (reversed in *Sphingius* and *Meriola* Banks, 1895). The bristles are large and erectile (character 5) in clade 3. A short indentation on pa I and II (character 7): synapomorphic for clade 35, which groups most phrurolithine genera and *Hortipes*. Bent tarsi (character 9): present in clade 13, and paralleled in *Rhaeboctesis* Simon, 1897. Leg cusps (character 10): restricted to clade 31, the tracheline genera. An rl spine on pa IV (character 26): present in clade 17, paralleled in *Clubiona*. An unequal number of plv and rlv spines on male ti I (character 28): synapomorphic for the tracheline genera grouped in clade 32. A ti III without plv and rlv spines (character 32): restricted to clade 25, although reversed in *Oedignatha* Thorell, 1881 and polymorphic in *Sphingius* and *Cetonana* Strand, 1929. A do spine on female ti III (character 34): synapomorphic for clade 9 (reversed in *Cambalida*). A do spine on ti IV (character 35): synapomorphic for clade 8. Prolateral spines on male palpal fe (character 44): absent in clade 22 (reversed in *Pseudocorinna*) and in *Cambalida*. Tibial ve scopulae (character 60): restricted to clade 1. Smooth tarsal claws (character 64): present in clade 22, but reversed to pectinate claws in clades 27 and 32, and in *Hortipes*. Longitudinally fused pleural bars (character 69): present in clade 26 and paralleled in *Meriola*. Sternum, plagula, pleural bars and carapace fused (characters 70, 71 and 72): synapomorphic for clade 28, which groups three heavily armoured genera. Curved strong hairs frontally on abdomen (character 101): absent in clade 10 and clade 20 (reversed in *Sphingius*). Large male do scutum (character 103): present in clade 12 and clade 22, where applicable. Male palp with ve fe apophysis (character 122): present in clade 34 (reversed in *Hortipes*), paralleled in *Drassinella* Banks, 1904 and *Trachelas* L. Koch, 1866. Inflated tegulum (character 132): present in clade 35 (reversed in *Hortipes*), paralleled in *Teutamus* Thorell, 1890. Pear-shaped bulbus (character 133): this well-known synapomorphy for Castianeirinae (clade 10) is confirmed here. Coiled sperm duct (character 134): paralleled in clade 2 (*Clubiona*), clade 10 and clade 21. Large ST2 (character 154:2): synapomorphic for clade 30 (where applicable), reversed in *Piabuna*.

The most striking features of the preferred tree are three large clades: clade 1, clade 8 and clade 20.

Clade 1 groups *Clubiona* and three liocranid genera, *Hesperocranum*, *Mesiotelus* and *Liocranum*. The four genera unambiguously share the absence of a pl spine on the male palpal pa (character 46:1), the presence of ve scopulae on ti I and II (character 60:1, non-homoplastic), a narrow clypeus (character 89:0, transformed to 89:1 at node 4) and the presence of a simple, membranous conductor (characters 135:1, 136:1 and 137:0). *Clubiona* differs from the other three genera by the presence of an apical do spine on fe I, III and IV (characters 16:1, 19:1 and 22:1), the presence of a single do spine on female palpal ti (character 54:1), the presence of claw tufts

(character 63:1), the absence of a long, shaggy, bent hair in front of the fang base (character 79:0), AME as large as ALE (character 94:1), circular PME (character 97:0), cylindrical male ALS with enlarged piriform spigots (characters 108:1 and 112:1), subtriangular female PMS bearing two large spigots in a transverse row (characters 119:2 and 120:2), a bifid male palpal ti apophysis (character 127:1, non-homoplastic), a coiled sperm duct (character 134:1), the absence of MA (character 138:0), a sickle-shaped embolus without basal apophyses (characters 140:1 and 141:0), the absence of a retrolateral thickened rim on the cymbium (character 145:0), an epigyne with posterior entrances (character 152:1), the presence of ST2 (character 153:1) and the absence of a pl terminal lobe on male palpal ti (character 156:0). The most striking feature uniting *Clubiona* with *Liocranum* and *Mesiotelus* was discovered by studying the spinneret structure with SEM. It is known that Clubionidae lack cylindrical gland spigots (Kovoor 1987; Platnick 1990), while Liocranidae and Corinnidae, as currently defined, are reported to possess them. However, when observed under a stereomicroscope, the female PMS of *Liocranum* and *Mesiotelus* species look quite different from those of other liocranid or corinnid genera: they are slender and conical and bear only one large spigot. Observed with SEM, this spigot turns out to be a minor ampullate gland spigot (Fig. 7C,D). Moreover, the microscopic structure of the male and female PMS of *Mesiotelus* turns out to be very similar to that observed in *Clubiona* (Fig. 8A,B). Contrary to the presently held view, no cylindrical gland spigots are present on the female PMS and PLS of *Liocranum* and *Mesiotelus* (Fig. 7A–F). On the other hand, the female PMS and PLS of several other genera presently considered to belong to Liocranidae and Corinnidae do possess cylindrical gland spigots (Figs 8C–F, 9A–F). The presence of cylindrical gland spigots was not included as a character in the data matrix, because it was not possible to perform SEM on all the genera studied. *Hesperocranum* does not fit well in the picture outlined above: it does have cylindrical gland spigots (Ubick & Platnick 1991). In the present analysis, *Hesperocranum* branches off at the base of clade 3 as the most parsimonious solution. Future work will eventually confirm or challenge the present placing of this enigmatic genus.

Clade 8 encompasses four castianeirine genera (clade 10), seven '*Agroeca*-like' nearctic and palaearctic genera (clade 13) and the enigmatic South African genus *Coryssiphus* Simon, 1903. The clade is supported by the presence of a trochanter notch (character 3:1, reversed in *Apostenus*), a do spine on ti IV (character 35:1, non-homoplastic), a ve terminal spine on mt III and IV (character 43:3, reversed at node 17), the absence of precoxal triangles (characters 65 and 66, reversed in *Cybaeodes* and *Castianeira* Keyserling, 1879 for both sexes, *Messapus* for males and *Copa* Simon, 1885 for females), the
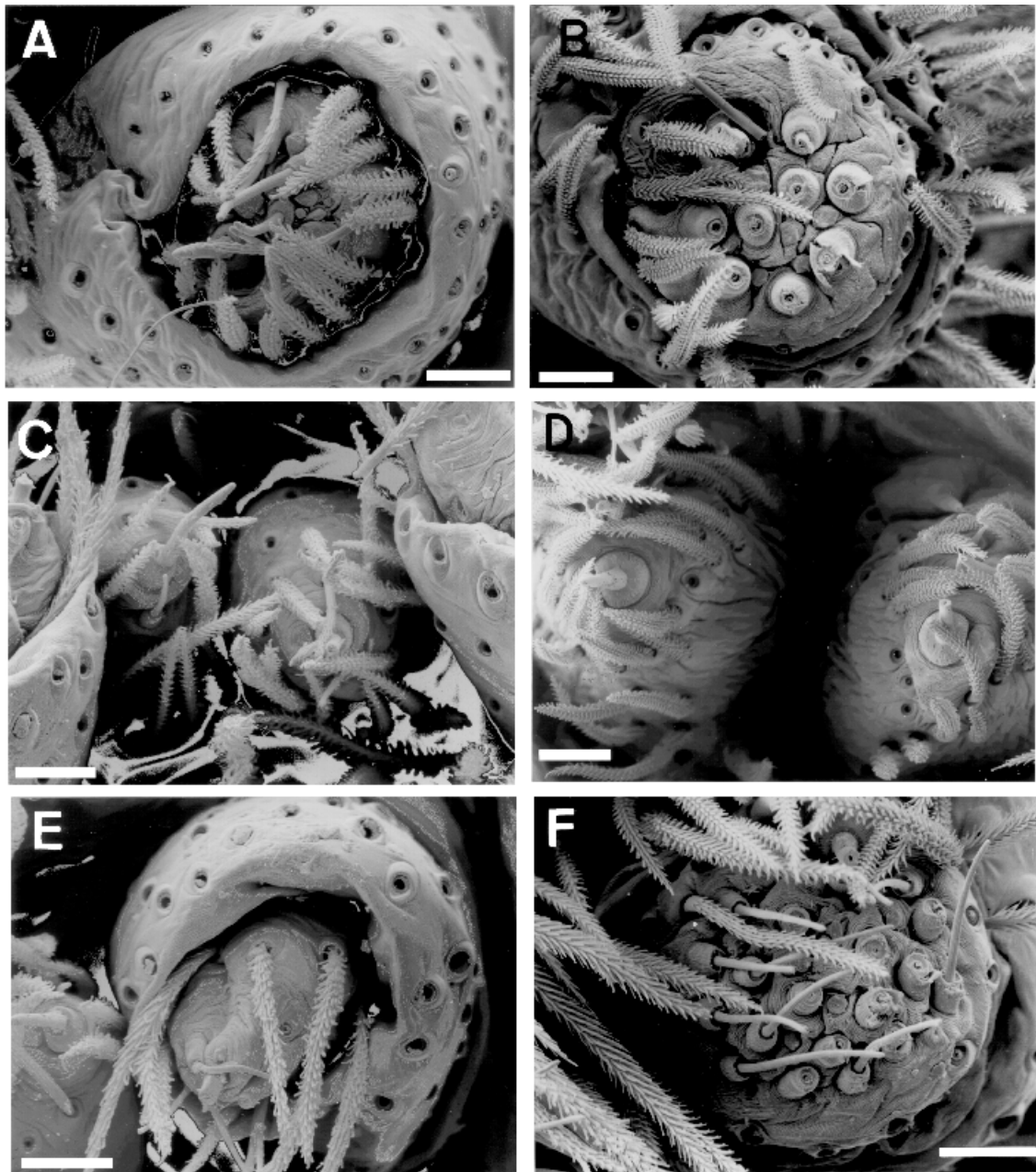
Fig. 7 A–F. *Mesiotelus cyprius*. —A. Male ALS. —B. Female ALS. —C. Male PMS. —D. Female PMS. —E. Male PLS. —F. Female PLS. Scale bars, 20 µm.

absence of intercoxal sclerites (characters 67 and 68, also reversed in *Cybaeodes*, and at node 12 for males), a slanting carapace (character 87:0) in most species and small ST2 (character 154:0) where applicable. Clade 9, which equals clade 8 with *Coryssiphus* excluded, is additionally character-ized by the absence of rows of bristles with modified tips (character 4:0, reversed in *Cybaeodes* and *Neoanagraphis*) and the presence of a do spine on female ti III (character 34:1,

non-homoplastic). Clade 10 (the castianeirine genera) can be distinguished from the remainder of clade 8 by a series of characters: two pl spines on male palpal ti (character 47:2), absence of curved strong hairs frontally on abdomen (char-acter 101:1), presence of female inframamillary sclerite (char-acter 117:1, reversed in *Castianeira occidens*), absence of male palpal ti apophysis (character 125:0), pear-shaped bulbus (character 133:1, non-homoplastic), coiled sperm duct
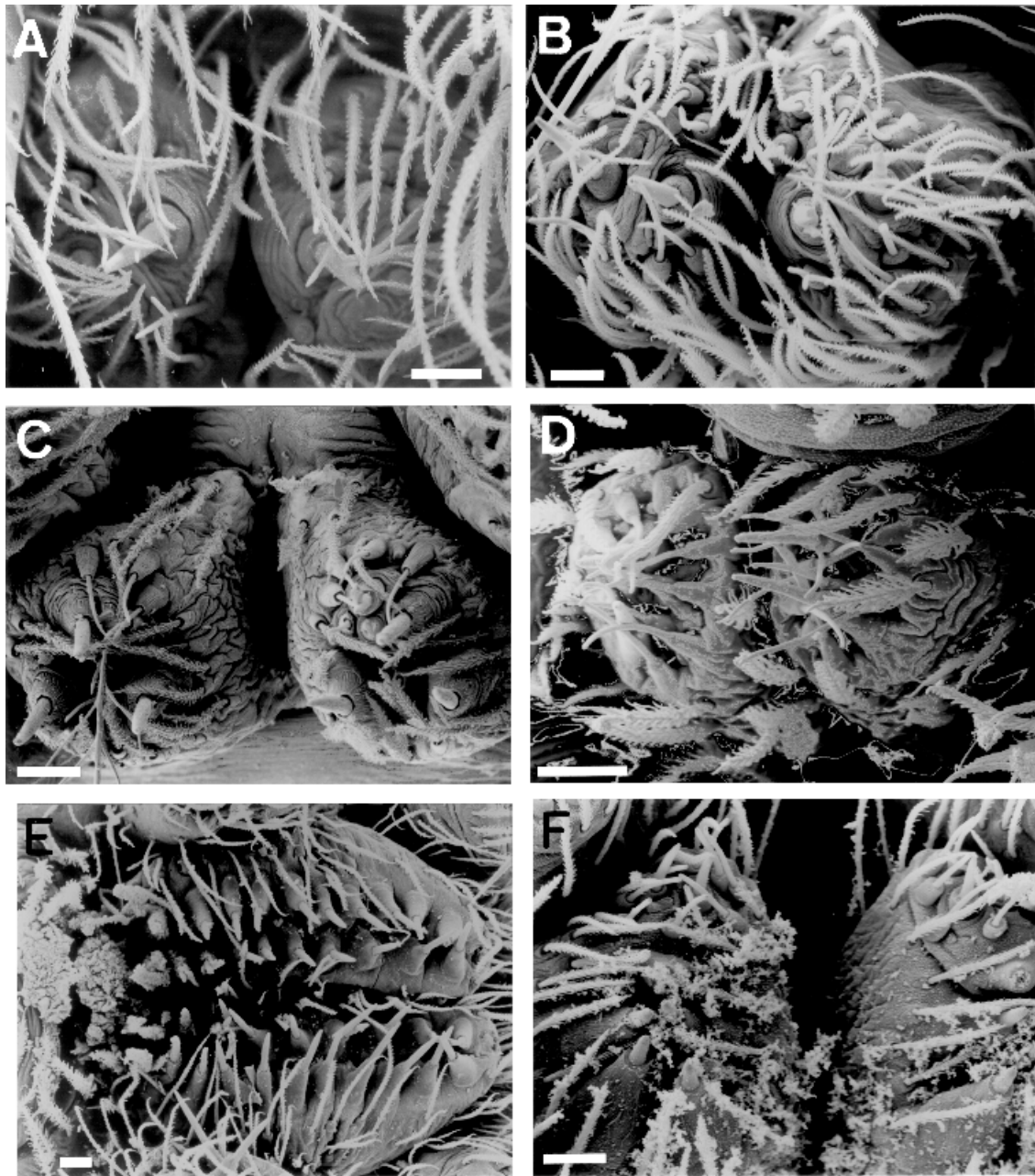
Fig. 8 A, B. *Clubiona phragmitis*. —A. Male PMS. —B. Female PMS. —C. *Scotina celans*, female PMS. —D. *Oedignatha scrobiculata*, female PMS. —E. *Teutamus fertilis*, female PMS. —F. *Meriola decepta*, female PMS. Scale bars, 20 μm.

(character 134:1), subtegulum pro- and retrolaterally pro-truding (character 142:2, paralleled in clade 21) and median entrances of vulva (character 152:2, unknown in *Messapus*). Clade 13, encompassing the '*Agroeca* group' of genera, is supported by the following synapomorphies: presence of bent tarsi (character 9:1, paralleled in *Rhaeboctesis*), AME smaller than ALE (character 94:0, transformed to 94:1 in *Neoana-*

graphis) and presence of a median apophysis (character 138:1). The latter character is regained here, having been lost at node 7 (Table 2). Within clade 13, clade 16 is characterized by the presence of a conductor (character 135:1) and the repeated occurrence of widely separated, cylindrical male ALS bearing enlarged piriform spigots (characters 108:1, 109:1 and 112:1).
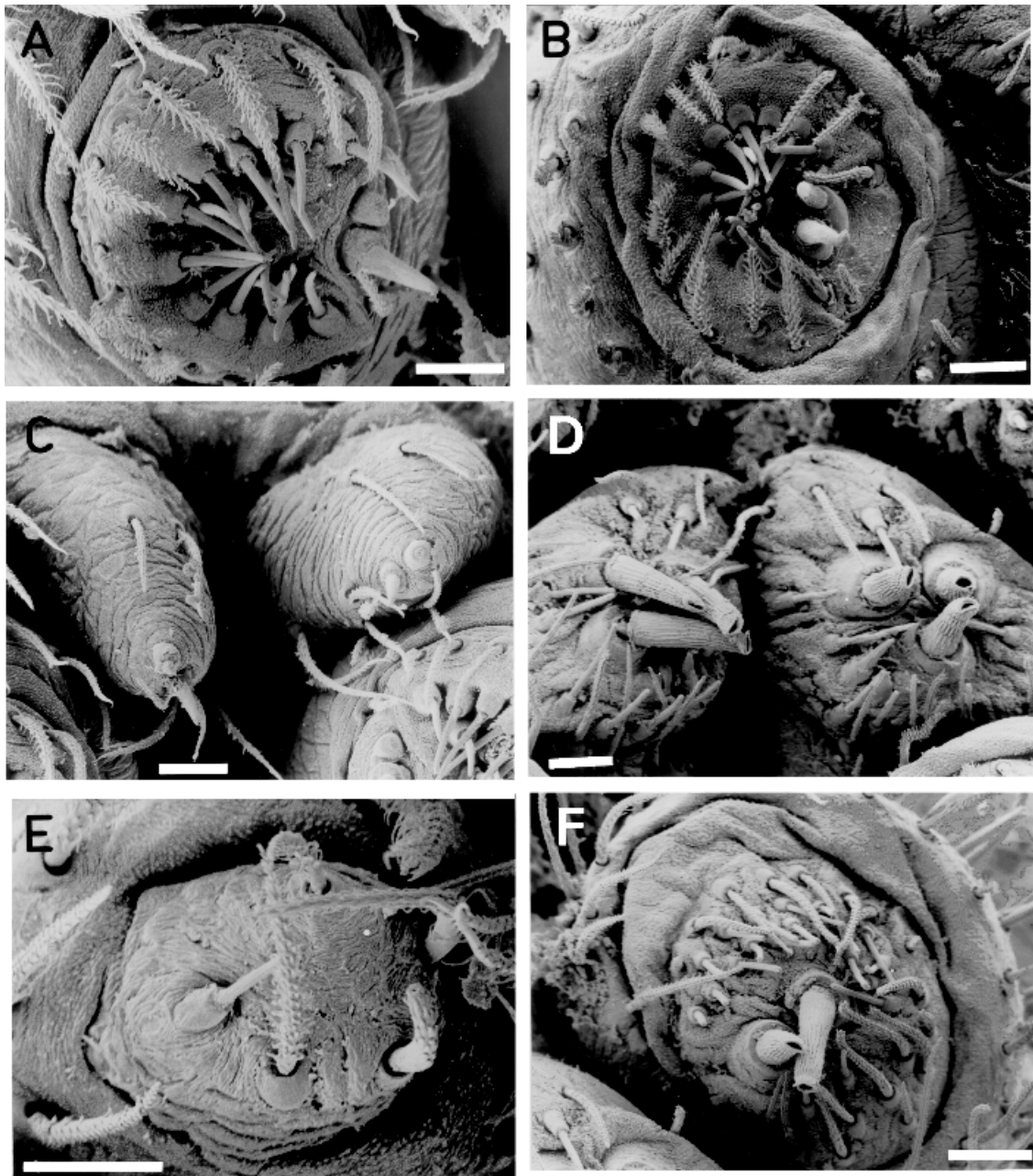
Fig. 9 A–F. *Cambalida coriacea*. —A. Male ALS. —B. Female ALS. —C. Male PMS. —D. Female PMS. —E. Male PLS. —F. Female PLS. Scale bars, 20 µm.

Clade 20 includes 21 genera and is supported by the absence of spines on male cymbium pl edge (character 49:0, reversed in five taxa), the presence of terminal ve preening brushes on mt III and IV (character 58:1), the absence of curved strong hairs frontally on the abdomen (character 101:1, reversed in *Sphingius*) and the presence of a male epigastric sclerite (character 105:1, reversed in six terminal taxa).

Clade 20 is further characterized by the almost universal absence of an MA (character 138:0) and by reduction of leg spination, starting at node 23 for fe median and apical do spines (characters 15, 18, 19, 21 and 22), at node 25 for fe I basal do spine (character 14), ti III (character 32) and mt (characters 40, 41 and 42) and at node 34 for ti IV (characters 33 and 36). Clade 21 holds a basal position in clade 20 and

differs from the other component taxa of the clade by the presence of rows of bristles with modified tips (character 4:0), the presence of pl spines on male and female palpal fe (characters 44:0 and 50:1), the presence of ventral scopulae on mt and ta (characters 61:1 and 62:1), a small male do scutum (character 103:1), a coiled sperm duct (character 134:1), additional apophyses at embolus base (character 141:1, paralleled in *Pseudocorinna*) and a pro- and retrolaterally protruding subtegulum (character 142:2). Clade 34 is a large subclade of clade 20: it encompasses seven phrurolithine genera and *Hortipes*, the large tropical African genus tentatively placed in Liocranidae by Bosselaers & Ledoux (1998) and Bosselaers & Jocqué (2000b). Clade 34 is supported by the absence of plv and rlv spines on ti IV (character 33:0), the absence of rl spines on male ti IV (character 36:0), the absence of intercoxal sclerites in males (character 67:0), a simple sternal border (character 73:0), the absence of a chilum (character 81:1, reversed in *Phruronellus*), the absence of an apical maxillar hair tuft (character 86:0), a slanting carapace (character 87:0, transformed to bulging, 87:2, in *Orthobula* Simon, 1896) and the presence of a ve apophysis on male palpal fe (character 122:1). Clade 31, the sister group of clade 34, can be considered to encompass the Trachelinae, to which the peculiar South African genus *Lessertina* Lawrence, 1942, considered to be Corinnidae *incertae sedis* by Bosselaers & Jocqué (2000a), can now be added. Clade 31 is characterized by the presence of leg cusps (character 10:1).

Although it must be admitted that Bremer support for clades 8 and 20 is not very high, it is striking how these clades are also recovered, in only slightly altered form, by the other parsimony approaches that were explored. The strict consensus of the equally weighted analysis (Fig. 6A) comprises clade 8, albeit with a different internal structure and without *Cybaeodes*, and clade 20, although the latter clade has a more pectinate structure in the equally weighted solution and has *Drassinella* and *Sphingius* branching in basal position. The ci-based successive weighting tree (Fig. 6B) is quite similar to the preferred implied weighting tree, but includes *Rhaeboctesis* in clade 8 and has a more pectinate structure within clade 20. The similarities observed between trees found with different methods lend extra support to the reliability of clades 8 and 20.

Seven smaller clades belonging to the three large clades discussed above have high Bremer support, larger than 3.0: clade 2, *Clubiona*; clade 3, *Liocranum*, *Mesiotelus* and *Hesperocranum*; clade 10, the genera belonging to Castianeirinae; clade 12, *Castianeira* and *Cambalida*; clade 21, *Corinna* and *Creugas*, two closely related genera and the only taxa included in the present analysis that belong to the subfamily Corinninae with a reasonable degree of certainty (Bonaldo 2000); clade 23, encompassing *Andromma*, *Brachyphaea*, five armoured corinnid genera with longitudinally fused pleural

bars and the tracheline and phrurolithine genera; and clade 28, grouping three heavily armoured genera. These seven clades can be considered to be monophyletic groups that are strongly supported by the data available.

It is tempting to draw far-reaching taxonomic conclusions from the cladogram obtained, because the latter strongly suggests that Liocranidae and Corinnidae are polyphyletic. However, after careful consideration and discussion, we have judged it prudent to refrain from radical rearrangements within Clubionidae *sensu lato*. A profound rearrangement of the family assignment of so many genera belonging to Clubionidae *sensu lato* can only be justified after a larger scale analysis has been performed including many more dionychan genera. Three possibilities that have been considered, but rejected, are discussed below.

1 Transfer of *Liocranum* L. Koch, 1896, *Mesiotelus* Simon, 1897 and *Hesperocranum* Ubick & Platnick, 1991 to Clubionidae. The grouping of these genera with *Clubiona* in clade 1 and the absence of cylindrical gland spigots in all clade 1 genera except *Hesperocranum* is not sufficient evidence on which to base such a transfer, which would make the family Liocranidae cease to exist. First of all, branch support for clade 1 is low. Furthermore, clade 1 is not retained in the equally weighted trees found (Fig. 6A). In addition, it might well be that some genera currently placed in Anyphaenidae or Salticidae are more closely related to *Clubiona* than the genera included in clade 3.

2 Restriction of Liocranidae to the taxa of clade 3. The somewhat anomalous placing of *Hesperocranum*, a genus possessing cylindrical gland spigots, in clade 3 renders such an action questionable at this moment. Moreover, such a move would of course raise the issue of a proper placing of the remaining Liocranid genera. It is difficult to give an indisputable answer to this question based on the present cladogram, because of the somewhat uncertain position of genera like *Rhaeboctesis*. Given the gaps in our present knowledge of the phylogeny of Dionycha in general and Clubionidae *sensu lato* in particular, it seems better not to alter the scope of Liocranidae so drastically.

3 Establishment of a new family, corresponding to the genera in clade 8 and their known close relatives. This drastic intervention would remove Castianeirinae from Corinnidae and group them with the bulk of Liocranidae, with the exception of the genera in clade 3. Such a new family would include the genera presently grouped in Castianeirinae, e.g. *Aetius* O. Pickard-Cambridge, 1896; *Apochinomma* Pavesi, 1881; *Cambalida* Simon, 1910; *Castanilla* di Caporiacco, 1936; *Castianeira* Keyserling, 1879; *Castoponera* Deeleman-Reinhold, 2001; *Coenoptychus* Simon, 1885; *Copa* Simon, 1885; *Corinnomma* Karsch, 1880; *Echinax* Deeleman-Reinhold, 2001; *Graptartia* Simon, 1896; *Humua* Ono, 1987; *Mazax* O. Pickard-Cambridge, 1898; *Medmassa* Simon, 1887

(the Asian species); *Merenius* Simon, 1909; *Messapus* Simon, 1898; *Myrmecium* Latreille, 1824; *Myrmecotypus* O. Pickard-Cambridge, 1894; *Poecilepta* Simon 1896; *Pranburia* Deeleman-Reinhold, 1993; *Psellocoptus* Simon, 1896; *Serendib* Deeleman-Reinhold, 2001; *Sphecotypus* O. Pickard-Cambridge, 1895; and at least the following genera not belonging to Castianeirinae: *Agraecina* Simon, 1932; *Agroeca* Westring, 1861; *Apostenus* Westring, 1851; *Brachyanillus* Simon, 1913; *Coryssiphus* Simon, 1903; *Cybaeodes* Simon, 1878; *Itatsina* Kishida, 1930; *Macedoniella* Drensky, 1935; *Neoanagraphis* Gertsch & Mulaik, 1936; *Paratus* Simon, 1898; and *Scotina* Menge, 1873. A rearrangement of this magnitude is felt to be too drastic based on the present results alone. Moreover, *Rhaeboctesis* is placed outside clade 8 in our preferred tree (as stated above) and would have to be considered *incertae sedis* under such a scheme. *Rhaeboctesis* has many characters in common with the genera belonging to clade 13, and future work might allow it to be placed inside that clade, as the successive weighting tree (Fig. 6B) already suggests. But the anomalous position of *Rhaeboctesis* in the present cladogram suggests that a hurried formal recognition of clade 8 might result in considerable taxonomic instability.

Considering the arguments given above, a formal large-scale rearrangement of the families constituting Clubionidae *sensu lato* is not proposed here. However, we do propose to transfer the subfamily Phrurolithinae to Corinnidae. Such a transfer has been defended before by Penniman (1985) and Wunderlich (1986, 1995), and it is considered a far less destabilizing and more plausible rearrangement than the three scenarios discussed above. Phrurolithinae (clade 34) is placed as the sister group of Trachelinae (clade 31) in our preferred tree, based on the absence of plv and rlv spines on mt III and IV (characters 40:0 and 41:0) and large ST2 (character 154:2), where applicable. The same sister group relationship, *Lessertina* not included, is seen in the equally weighted and ci-based successive weighting solutions (Fig. 6A,B). Moreover, there is good branch support in the preferred implied weighting tree for clades 23 and 25, which encompass both subfamilies. Platnick (1975: 3) has already stated that 'It seems unlikely then that either the castianeirines or the corinnines are the sister group of the trachelines', a view which is confirmed here. *Drassinella* is not placed within Phrurolithinae in our preferred tree because the genus differs from the genera placed in that subfamily by its extensive leg and palpal spination (characters 14:1, 15:1, 17:1, 18:1, 19:1, 20:1, 21:1, 22:1, 32:0, 33:1, 36:1, 40:[12], 41:1, 42:1, 45:2, 51:2, 53:3, 54:2 and 55:1). Nevertheless, *Drassinella* is placed in clade 20 in the preferred tree, the clade that also contains *Corinna*, the type genus of Corinnidae. In the equally weighted and successively weighted solutions, *Drassinella* is similarly placed in the large clade containing *Corinna*. Penniman (1985) placed *Drassinella* as the sister group of Phrurolithinae and Platnick

& Ubick (1989: 2) considered the genus 'a close relative, if not a member, of the Phrurolithinae'. We propose to transfer the following genera from Liocranidae to Corinnidae: *Drassinella* Banks, 1904; *Hortipes* Bosselaers & Ledoux, 1998; *Liophrurillus* Wunderlich, 1992; *Orthobula* Simon, 1896; *Phonotimpus* Gertsch & Davis, 1940; *Piabuna* Chamberlin & Ivie, 1933; *Phrurolinillus* Wunderlich, 1995; *Phrurolithus* C. L. Koch, 1839; *Phruronellus* Chamberlin, 1921; *Phrurotimpus* Gertsch & Davis, 1940; and *Scotinella* Banks, 1911.

Some interesting additional remarks can be made about the placing and composition of a few genera in the preferred cladogram (Fig. 5).

Andromma does not turn out to be the sister genus of *Hortipes*, as was supposed earlier (Bosselaers & Jocqué 2000b). Instead, *Andromma* is placed as the sister genus of *Brachyphaea* in the present tree. Both genera share the presence of a retrocoxal hymen in males and females (characters 1:1 and 2:1), AME which are larger than PME (character 96:2), the absence of a dorsal scutum in males (character 102:0) and, as opposed to *Hortipes*, two plv and rlv spines on mt IV (character 41:2), a bilateral chilum (character 82:0), a reduced serrula (character 85:1), closely spaced female PLS (character 121:0) and a complex, bifid tibial apophysis (character 127:4). Moreover, *Andromma*, considered by Simon (1893) to be closely related to *Cybaeodes*, turned out to be unrelated to that genus in our analysis. *Hortipes*, on the other hand, is grouped among genera traditionally placed in the subfamily Phrurolithinae (clade 34), based on a range of character states which are not present in *Andromma*: the presence of a short indentation on pa I and II (character 7:1), fe I plv spines (character 12:1), a long, bent, shaggy hair at the fang base (character 79:1) and a simple sternal border (character 73:0), and the absence of fe I, III and IV basal do spines (characters 14:0, 17:0 and 20:0), ti IV plv, rlv and rl spines (characters 33:0 and 36:0), a chilum (character 81:0) and an apical maxillary hair tuft (character 86:0). However, *Hortipes* differs from other Phrurolithine genera by the absence of both a ve femoral apophysis (character 122:0) and an inflated tegulum (character 132:0).

Orthobula is placed in Phrurolithinae as the most parsimonious solution in our cladograms, but the taxon also has some characters reminiscent of Trachelinae: the presence of tarsal spines (character 11:1), the absence of fe I plv spines (character 12:0), a tuberculate sternum and carapace (character 74:1), a bulging carapace (character 87:2) and five large spigots in two rows on female PMS (character 120:4). *Orthobula* is badly in need of revision and future work will decide whether or not its present place in Phrurolithinae will stand.

It should also be mentioned that *Medmassa* Simon, 1877 is not a monophyletic group: the African species *Medmassa proxima* de Lessert, 1923, used as one of the exemplar taxa in our matrix, and *Medmassa nitida* Lawrence, 1937 are certainly not congeneric with the type species *Medmassa frenata*

Simon, 1877, which is a castianeirine (Deeleman-Reinhold 2001). After revision, the African species presently attributed to *Medmassa* should be placed in a new genus, an intervention which is outside the scope of the present work.

Conclusions

The results of this cladistic analysis seriously challenge the presently prevailing classification of the former Clubionidae *sensu lato*. This comes as no surprise, as the current affiliation of genera to Liocranidae and Corinnidae is generally considered to be unsatisfactory. The results of the present analysis strongly suggest that at least Liocranidae, and probably also Corinnidae, are polyphyletic. In the interest of taxonomic stability, no rearrangements beyond the transfer of Phrurolithinae to Corinnidae are proposed here. Undoubtedly, the cladogram obtained is only a single step forward in a continuing process of phylogenetic reconstruction, and many improvements to it will be proposed in the future. In order to gain a more detailed insight into the phylogeny of the former Clubionidae *sensu lato*, a much larger data matrix will have to be studied, encompassing a very broad selection of dionychan spider genera. Preferably, this enormous task should be executed as a group effort by several arachnologists.

Acknowledgements

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Appendix

Taxa examined to provide exemplar data, with collection data and deposition. Asterisk indicates type species of genus. Families in which taxa are placed according to prevailing views are added between square brackets (Gn, Gnaphosidae; Cl, Clubionidae; Li, Liocranidae; Co, Corinnidae); modified from Platnick (1997) as explained in the text.

*Agraecina lineata** (Simon, 1878) [Li]; 5m: France, Corsica and Menton (MNHN 2095); 1f: France, Les Saintes Maries, 'Collection Berland, entrée n°4.25.9.62' (MNHN).

*Agroeca brunnea** (Blackwall, 1833) [Li]; 1m: Belgium, Beerse, 'De Schrieken', pitfall trap in pine wood with bracken, 20 February 1995, J. Bosselaers leg. (CJB 1003); 1f: same locality, pitfall trap in alder marsh, 2 December 1994, J. Bosselaers leg. (CJB 882).

Andromma sp. [Li]; 7m, 17f: Congo, Rutshuru, December 1939, J. Ghesquière leg. (MRAC 22.878/22.901).

*Apostenus fuscus** Westring, 1851 [Li]; 3m, 1f: Yugoslavia, Slavonski Pozega, among oak litter, 26 March 1972, C. Deeleman-Reinhold leg. (CCD).

Brachyphaea proxima de Lessert, 1921 [Co]; 1m, 1f: Kenya, coastal scrub, J. Murphy leg. (CJM 4096).

Cambalida coriacea Simon, 1910 [Co]; 1m: Ivory Coast, Apouesso, Bossematié classified forest, pitfall trap, 23 April 1995, R. Jocqué & M. Tanoh leg. (MRAC 204.302); 2m: same

data, 2 July 1995 (MRAC 204.285); 1f: same data, 20 May 1995 (MRAC 204.299); 1f: same data (MRAC 204.301).

Castianeira occidens Reiskind, 1969 [Co]; 1m: USA, California, San Diego County, Marine Corps Base Camp Pendleton, coastal sage scrub, 18 March 1999, T. Prentice leg. (UCR); 1f: San Diego County, Miramar Naval Air Station, coastal sage scrub, pitfall trap, May 1996, T. Prentice leg. (UCR) (Prentice *et al.* 1998).

Cetonana martini (Simon, 1896) [Co]; 2m, 2f: South Africa, Natal, Durban, G. Gravell leg. (MRAC 144.702).

*Clubiona pallidula** (Clerck, 1757) [Cl]; 1m: Belgium, St. Martens Latem, 10 May 1981, P. Grootaert leg. (RBINS); 1f: Netherlands, Texel, Oosterend, in kitchen garden, 15 July 1988, J. Bosselaers leg. (CJB 614).

Clubiona phragmitis C. L. Koch, 1843 [Cl]; 1m: Belgium, Zonhoven, 'Ter Kolveren', under bark of dead poplar in meadow-land, 29 August 1983, J. Bosselaers leg. (CJB 63); 1 m: Belgium, Westmeerbeek, in moist *Erica* heath, 21 July 1988, J. Bosselaers leg. (CJB 618); 1f: Belgium, Diepenbeek, under loose bark of poplar, 21 December 1983, J. Bosselaers leg. (CJB 63); 1f: Belgium, Heverlee, meadow, 17 June 1984, J. Bosselaers leg. (CJB 275).

Copa benina Strand, 1915 [Co]; 1m, 3f: Tanzania, Arusha, 1500 m, 4 September 1972, P. Benoit leg. (MRAC 145.973).

Corinna nitens (Keyserling, 1891) [Co]; 2m, 1f: Brazil, Rio Grande do Sul, Novo Hamburgo, 27 February 1979, T. de Lema leg. (MCN 8558); 1m: Rio Grande do Sul, São Leopoldo, 27 June 1987, L. de A. Moura leg. (MCN 16884); 1f: Rio Grande do Sul, São Francisco de Paula, Barragem dos Bugres, 25 November 1998, L. de A. Moura leg. (MCN 30653).

*Coryssiphus praeusta** Simon, 1903 [Li]; 1m: (holotypus) South Africa, Cape Province, Cape of Good Hope (MNHN 18807); 1m: Cape Province, Houtbaai, Tierbos, December 1960, N. Leleup leg. (MRAC 131.824); 1f: same data (MRAC 131.824); 3f: Cape Province, East slope of Table Mountain, Kirstenbosch, November 1960, N. Leleup leg. (MRAC 131.898).

Creugas bajulus (Gertsch, 1942) [Co]; 1m: USA, California, San Diego County, Miramar Naval Air Station, coastal sage scrub, pitfall trap, May–June 1996, T. Prentice leg. (UCR); 1f: same data, August 1996 (UCR) (Prentice *et al.* 1998).

Cybaeodes marinae Di Franco, 1989 [Li]; 1m: Italy, Sicily, Nebrodi, east slope of Monte Pagano, 550m, mixed shrub with *Quercus suber* and *Q. gussonei*, September 1988 (AMNH); 1m, 1f: Italy, Lazio, Rome, Castelporziano, oakwood, 13 October 1986, Bonavita leg. (AMNH).

*Drassinella modesta** Banks, 1904 [Li]; 1m: USA, California, Santa Barbara, 12 April 1948, H. L. Shantz leg. (AMNH); 1f: California, San Gabriel Mountains, Big Tujunga Canyon, January 1953, R. Schick leg. (AMNH).

*Gnaphosa lucifuga** (Walckenaer, 1802) [G]; 1m, 2f: Rumania, Brosteni (RBINS).

Hesperocranum rothi* Ubick & Platnick, 1991 [Li]; 1m: USA, California, Tulare County, 2.5 miles east of Cal. Hot Springs, 15 September 1959, V. Roth & W. Gertsch leg. (AMNH); 1f: California, Fresno County, Kings Cyn. Nat. Park, Cedar Grove, 13 September 1959, V. Roth & W. Gertsch leg. (AMNH).

Hortipes luytenae* Bosselaers & Ledoux, 1998; 2m, 2f (paratypi) [Li]: South Africa, Natal, Ngome State Forest, 27°49′ S 31°26′ E, pitfall trap in dense forest, April 1992, M. v. d. Merwe leg. (NCA 93/791).

Lessertina mutica* Lawrence, 1942 [Co]; 1m, 1f: South Africa, Eastern Cape Province, East London, Pineapple Research Station, 33°1′ S 27°58′ E, hand captured, 2 December 1977, G. Petty leg. (NCA 77/1113); 2m, 2f: same data (MRAC 206.567).

Liocranoeca striata* (Kulczynski, 1882) [Li]; 1m: France, Southern France, coastal area (MNHN 6147); 1f: France, Corsica and Menton (MNHN 2095).

Liocranum giersbergi Kraus, 1955 [Li]; 1m, 2f: Italy, Sardinia, Villanova Strisaili, pitfall trap at lakeside in wood, 23 May 1997, J. van Keer leg. (CJK 1757).

Liocranum rupicola* (Walckenaer, 1825) [Li]; 1m: France, Corbières, vallée de l'Haute Aude, Quillan, 350 m, stony slope, 15 June 1995, B. Vercammen leg. (CJK 1526): 2f: France, Corsica, Gorges de la Restonica, 1300 m, under stones in pinewood, 26 May 1995, J. van Keer leg. (CJK 1504); 1f: France, Corsica, Calacuccia, evergreen forest, 16 November 1981, P. R. Deeleman leg. (CCD).

Liophrurillus flavitarsis* (Lucas, 1846) [Li]; 1m, 1f: Spain, Malaga, L. Lund leg. (ZMUC 163); 1m: Italy, Gennazano, Bergsøe leg. (ZMUC 93); 1f: Algeria, Bona, 36°54′ N 7°46′ E, Meinert leg. (ZMUC 210).

Medmassa proxima de Lessert, 1923 [Co]; 1m, 1f: South Africa, Eastern Cape Province, East London, 33°01′ S 27°58′ E, Pineapple Research Station, pitfall traps in natural bush, December 1981, G. Petty leg. (NCA 92/111).

Meriola decepta* Banks, 1895 [Co]; 2m: USA, Ohio, Franklin County, Sharon Woods Metropolitan Park, 9 October 1973, A. J. Penniman leg. (AMNH); 1f: same data, 23 October 1973 (AMNH); 1f: same data, 3 July 1973 (AMNH).

Mesiotelus cyprius Kulczynski, 1908 [Li]; 1m, 8f: Cyprus, Troodos Mountain, 1600 m, under stones in pine forest, 28 October 1981, P. R. Deeleman leg. (CCD); 7f: Crete, Zoniana, outside Sventoni Cave, 700 m, under stones, 6 April 1996, J. Bosselaers leg. (CJB 1047).

Messapus martini* Simon, 1898 [Co]; 1m (holotypus), 1f (paratypus): South Africa, Natal, C. Martin leg. (MNHN 19680).

Neoanagraphis chamberlini* Gertsch & Mulaik, 1936 [Li]; 2m: USA, New Mexico, Socorro County, Sevilleta 20 miles north Socorro, 1500–2200 m 1989–1992, S Brantley leg. (UCR, now in CJB); 1f: same data (UCR).

Oedignatha scrobiculata* Thorell, 1881 [Co]; 1m, 2f: Seychelles, Little Sister, pitfall traps, 17 September 1975, M. Mühlenberg leg. (MRAC 177.050 and MRAC 177.060).

Orthobula calceata Simon, 1896 [Li]; 1m, 1f: Rwanda, Pindura, dry forest with *Sansevieria*, 3 December 1985, Jocqué, Nsengimana & Michiels leg. (MRAC 164.797).

Phrurolithus festivus* (C. L. Koch, 1835) [Li]; 1m, 1f: Belgium, Mol, 'Ginderbuiten', *Calluna* heath, near ants nest, 5 May 1997, H. Henderickx leg. (CJB); 2m, 4f: Belgium, Beerse, *Calluna* heath, in litter near ants nest, 3 May 1997, J. Bosselaers leg. (CJB).

Phruronellus formica* (Banks, 1895) [Li]; 3m, 1f: USA, Arizona, 20 miles south Flagstaff (Oak Cr.), 4 December 1935, W. Ivie leg. (AMNH).

Phrurotimpus alarius* (Hentz, 1847) [Li]; 1m: USA, Ohio, Franklin County, Sharon Woods Metropolitan Park, 29 May 1973, A. J. Penniman leg. (AMNH); 1f: same data, 17 July 1973 (AMNH); 1m: Indiana, Evansville, 28 June 1943, H. Dybas leg. (FMNH); 1f: Illinois, Chicago, Swallow Cliff Woods, northwest of Palos, 215 m, among litter in mixed *Quercus* woodland with shrubs, 30 June 1998, J. Bosselaers leg. (CJB 1378).

Piabuna nanna* Chamberlin & Ivie, 1933 [Li]; 2m: USA, Utah, west side of Utha Lake (middle), 40°15′ N 111°52′ W, 2 September 1941, W. Ivie leg. (AMNH); 1f (paratypus): Utah, Raft River Mountains, Dove Cr., 41° N 113° W, 9 September 1932, R. V. Chamberlin leg. (AMNH).

Pseudocorinna sp. [Co]; 1m, 1f: Ivory Coast, Appouesso, Bossematié Classified Forest, modified Malaise trap, 1 December 1994, R. Jocqué leg. (MRAC 200.936, MRAC 200.984).

Rhaeboctesis secundus Tucker, 1920 [Li]; 2m, 2f: South Africa, Northern Transvaal, Dendron, pitfall traps, 12 June 1969, A. S. Dippenaar leg. (MRAC 203.035).

Scotina celans (Blackwall, 1841) [Li]; 1m, 4f: France, Banyuls (MNHN); 2f: France, Saint Gilles (MNHN); 1f: Yugoslavia, Island Cres, Jama, Lipici Cave, 1 April 1972, C. L. & P. R. Deeleman leg. (CCD).

Scotina gracilipes (Blackwall, 1859) [Li]; 1m, 2f: Denmark, Anholt, plantation, 11 August 1946, Ø. Christensen leg. (ZMUC 14); 2m: Belgium, Kalmthout, willow scrub and *Calluna* heath, 15 and 29 November 1976, P. Baert leg. (CJK 862).

Scotinella minnetonka (Chamberlin & Gertsch, 1930) [Li]; 1m, 1f: USA, Minnesota, Hennepin County, Minneapolis, federal land near Fr. Snelling St. Park, under debris in old field, B. Cutler leg. 9 May 1986 (AMNH); 1f: Wisconsin, Kewaunee County, Kewaunee, in leaf litter under maple, A. Ziemer leg. (FMNH).

Sphingius gothicus Deeleman-Reinhold, 2001 [Li]; 1m: Thailand, Mae Hia, pitfall trap, 5 February 1988, P. J. Schwendinger leg. (CCD); 1f: Thailand, Doi Suthep, 1180 m, 30 March 1987, C. Deeleman-Reinhold leg. (CCD).

Teutamus fertilis Deeleman-Reinhold 2001 [Li]; 1m, 2f: N. Sumatra, Gunung Leuser Nat. Park at Ketambe, 4 May 1986, S. Djojosudharmo leg. (CCD); 1f: same data, 3 June 1986; 2f: same data, 4 June 1986 (CCD).

Trachelas schenkeli de Lessert, 1923 [Co]; 1m, 1f: Congo, Katanga, Elisabethville, C. Seydel leg. (MRAC 137.457).

Specimens of genera mentioned in the text that were studied but not included in the data matrix:

Brachyanillus liocraninus* Simon, 1913 [Li]; 1 subad. f (holotypus): Algeria, Oran Department, Misserghin, cave of the fourth spring in the Misserghin ravine, 17 November 1909 (MNHN 499).

Itatsina praticola (Bösenberg & Strand, 1906) [Li]; 1f: Japan, Osaka Prefecture, 14 November 1954 (AMNH).

Otacilia luzonica (Simon, 1898) [Li]; 1m (holotypus): Philippines, Luzon, Antipolo (MNHN 13697).

Paratus reticulatus* Simon, 1898 [Li]; 1 subad. f (holotypus): Sri Lanka, Kandy (MNHN 18261).

Thysanina serica* Simon, 1910 [Co]; 1m (holotypus): Namibia, Lüderitzbucht, L. Schultze leg. (MNHN).