

PHYLOGENETIC, HOST AND BIOGEOGRAPHIC ANALYSES OF THE PILOPHORINI (HETEROPTERA: MIRIDAE: PHYLINAE)

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Abstract—A cladistic analysis is performed for 114 species of Pilophorini, using 73 characters with 190 states. Illustrations or figure references to the literature are provided for most characters. The resultant Nelson (strict) consensus cladogram is used as a justification for the recognition of the following genera: *Alepidiella* Poppius, *Aloea* Linnavuori, *Druthmarus* Distant, *Hypseloecus* Reuter, *Neoambonea* Schuh, *Parambonea* Schuh, *Parasthenaridea* Miller, *Pherolepis* Kulik (paraphyletic), *Pilophorus* Hahn, and *Sitenaridea* Reuter (paraphyletic). *Pilophorus indonesicus* is proposed as a replacement name for *Bilirania sumatrana* Schuh (= *Pilophorus*), a secondary homonym of *Pilophorus sumatranus* Poppius. A list of currently recognized genera and species with summary distributions and host plant associations, and a key to genera are included.

Host associations are plotted on the cladogram to reveal the pattern of host shifts. At the generic level and above, a pattern of colonization, rather than co-evolution, is strongly indicated; at the species level, genera of Pilophorini often show restricted plant-group associations, but no clear pattern of coevolution emerges. Major distributional patterns in the Pilophorini are mapped, discussed and compared with historical biogeographic schemes for some other groups. The Pilophorini appear to be of tropical Gondwanan origin with subsequent spread into, and differentiation in, the temperate Northern Hemisphere.

Introduction

The plant bug tribe Pilophorini is known from approximately 155 species placed in 10 genera. Species belonging to the group are usually associated with a single plant species or group of plants, with some taxa being at least partly predatory on other insects. Many members of the phylogenetically more advanced lineages are weakly to strongly myrmecomorphic.

The Pilophorini, as presented here, has been documented in regional studies as monophyletic by Wagner (1952), Odhiambo (1960) and Schuh (1974, 1976, 1984). On the basis of synapomorphies in the male and female genitalia and the possession of lanceolate, silvery, scalelike setae. The Pilophorini of Carvalho (1958) was a heterogeneous grouping of genera brought together on the basis of myrmecomorphic appearance, an ill-defined attribute that shows little congruence with other morphological characteristics, and which occurs in many more phyletic lines of the Miridae than reflected in Carvalho's classification (Schuh, 1986).

The Pilophorini was a cosmopolitan group in the classification of Carvalho (1958), with a number of genera occurring on all continental land areas except Antarctica; no clades were restricted to any particular land area. In the present classification there is a much more obvious relationship between diversity and distribution, with the eight basal species on the cladogram—and only those—restricted to the New World tropics, virtual absence of the group from Australia and temperate South America, and the Northern Hemisphere fauna (with limited exceptions) comprising members of the relatively most apomorphic clade. Leston (1961) concluded that geographical distribution was of no utility in understanding the evolution of Miridae. The present analysis suggests that

Leston's perception was influenced by the fact that many higher taxa with which he was dealing were not monophyletic.

Through the use of cladistic analysis, I provide a more consistent classification of the Pilophorini in which most genera are based on synapomorphies, analyse the evolution of host associations in the group, and relate pilophorine distributions to those of other groups of Miridae as well as some other groups of animals and plants, and to large-scale events in earth history.

Phylogenetics

TAXA EXAMINED

The present analysis treats 114 of the approximately 155 species currently placed in the Pilophorini. The remaining 40 or so species were not included because: males were not available for examination of genital characters important to the analysis, or because they were members of species groups all of which are very similar to one another and for which at least one species was already included. A revised generic classification of the Pilophorini is presented in the form of a cladogram (Fig. 7) and as an alphabetical list in Appendix 1. Explanations of some nomenclatural and taxonomic changes made to accommodate this classification were made by Schuh (1989).

CHARACTERS, CHARACTER CODING AND DATA ANALYSIS

Much of the character information used in this analysis was developed during previous studies (Schuh, 1974, 1984, 1989; Schuh and Schwartz, 1988) with additional information derived from the works of Linnavuori (1975, 1986) and Josifov (1977, 1987). Specimens of all included taxa were examined in order to assure accurate and consistent character coding. Appendix 2 presents a list of 73 characters with 190 states, the distributions of which are listed in Table 1 for 114 pilophorine taxa and an outgroup. Figs 1–5 illustrate many of those characters, including male vesicae for several species which previously had not been documented in the literature (*Pilophorus confusus*, *P. disjunctus*, *P. mongolicus*, *P. niger*, *P. pusillus*, *P. setulosus*, and *P. sinuaticollis*), or if illustrated, inaccurately (*Pilophorus cinnamopterus*), or which show previously undescribed variation (*Pilophorus choii*). The outgroup condition is coded as that generally found in the non-pilophorine Phylinae (the putative sister group of the Pilophorini; Schuh, 1974, 1976, 1984). In many cases (excluding characters of the genitalia) the same outgroup condition is also found in the Orthotylinae, the sister group of the Phylinae (Schuh, 1984). Experimentation with outgroup coding produced no change in cladogram rooting, attesting to the monophyly of the Pilophorini.

Characters and character states for which homologous structures could not be identified were assigned a missing data code (-); characters for which information was not available are shown as "?". Examples of the former situation are characters 60 and 61, where I treated data concerning ornamentation of the mesial spine as missing for those taxa which possess no mesial spine. This approach should satisfy the conditions for proper coding of absences set forth by Pimentel and Riggins (1987). In the case of characters 46–51, variation was not easily homologized, and indeed, it was not obvious that what I refer to as the "posterior band of scalelike setae" was homologous in all cases. Thus, I treated different conditions as different characters.

Table 1
Data on 73 characters for 114 species of Pilophorini.

Character No.	111111111	222222222	333333333	444444444	555555555	666666666	777
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	012
outgroup	111111112	111111121	11112--1-	112111111	111121111	111111111	--1---111- 11-
araguaiana	121111111	111112121	111121211	112111111	111121111	111111211	--1---2122 111
carmelitana	121111111	111112121	111121212	112112212	222221111	111112211	--1---2122 111
carvalho	121111111	111112121	111121212	112111112	221121111	111112211	--1---2122 111
hansonii	121111111	111112121	111121211	112112222	222221111	112112211	--1---2122 111
maldonadoi	121111111	111112121	111121212	112112222	221221111	112112211	--1---2122 111
rondonia	121111111	111112121	111121212	112111112	222121111	111112211	--1---2122 111
vulgaris	121111111	111112121	111121212	112112212	222221111	112112211	--1---2122 111
australis	121111111	111113121	111121213	112112222	222221111	112112211	--1---2122 112
liberiensis	121111111	111112121	11112??11	11211????	??1??1111	11??12211	--1---2122 111
nigra	121111111	111112121	111121213	112112222	222221111	112112211	--1---21?? 112
pacifica	121111111	111112121	111122112	112112222	222221111	112112211	--1---2122 112
papuensis	121111111	111112121	111121213	112112222	222221111	112112211	--1---2121 111
piceoniger	121111111	111112121	111121213	112112222	222221111	112112211	--1---2121 112
rufescens	121111111	111112121	111122113	112112222	222221111	112112211	--1---2121 111
suturalis	121111111	111112121	111122112	112112222	222221111	112112211	--1---2122 112
arecae	121111111	111112121	111122112	112112222	222221111	112111211	--1---2122 213
australis	121111221	221121112	111122112	112112222	222221111	111113311	--1---2143 233
cunealis	121111221	221121112	111122112	112112222	222221111	111113311	--1---2143 233
nairobi	121111221	221121112	111122112	114332222	222321111	122113311	--1---2143 233
nigritula	121111221	221121112	111122?12	112112222	232221111	122113311	--1---21?? 233
transvaalensis	121111221	221113321	11112??11	112112222	221221111	112111?11	--1---21?? 233
cynanchi	121111221	2211123312	121122212	212112222	222221111	1121115421	--1---2133 233
uniformis	121111221	2211123312	121122212	212112222	222221111	1121115421	--1---2133 233
russeola	121111221	2211123322	111122212	212112222	222221111	1121115421	--1---2133 233
samaru	121111221	2211123321	111122212	112112222	222221111	1121124411	--1---2233 223
yotvata	121111221	2211123321	111122212	212112222	222221111	1121124411	--1---2233 223
deemingi	121111111	111112121	1111123211	212112222	222221111	1121123321	--1---2133 213
ifugao	121111111	111112121	1111123213	212112222	222221111	1121123322	2111112133 213
koroba	121111111	111112121	1111123213	212112222	222221111	1121123322	2113-2133 213
maesta	121111111	111112121	1111123213	212112222	222221111	1121121311	--1---2133 213
morobe	121111111	111112121	1111121213	212112222	222221111	1121123321	--1---2133 213
munroi	121111111	111112121	1111123213	212112222	222221111	1121123321	--1---2133 213
opima	121111111	111112121	1111123213	212112222	222221111	1121123321	--1---2133 213
rustenbergens	121111111	111112121	1111121212	212112222	222221111	1121123321	--1---2143 213
visci	121111111	111112121	1111123213	212112222	222221111	1121123322	2111112133 213
heidemanni	221121212	111112132	1111112131	312112222	222221111	1122113322	2121112133 213
Druthmarus	221121212	1111112122	1111113311	112112222	222221111	1121113322	2112122133 213
aenescens	121111212	1111113232	1111121211	1121121221	332221111	1131113322	3111113133 213
amplus	121111212	1111113232	1111121211	1121123221	331221111	1131113322	3111113133 213
fasciatus	121111212	1111112232	2111121211	1121111221	332321111	1111113322	3111113133 213
kiritschenkoii	121111212	1111112232	1111121211	1121122221	332221111	1121113322	1111113133 213
linnavuorii	2211111221	2211112122	2211122221	1121111312	332312111	1231211321	--1---2133 213
lestoni	2211111221	2211112122	2211113?21	1121111?12	??3?3?111	12?1211321	--1---2133 213
samoanus	2222111211	1111112322	2211121221	2121111?21	??3?2?111	11?1213321	--1---2133 113
alstoni	2222222212	1111112132	2213123311	1121111331	3333322211	1112213322	2112112133 213
arborescens	2222122212	1111113132	2224123211	3132211131	4133221111	1232313322	2111112133 213
dailanh	2222122212	1111113132	2223123211	1122111331	3333222211	11?2313321	--2---2133 213
daradae	2211221212	1121111332	2213123311	1121111331	3333121111	112121332?	--1---2133 213
formosanus	2212222212	1111113132	2213123211	1121111331	4333221111	1121213321	--2---2133 213
fyau	2211212212	1111111332	2213123221	1112111331	3333222211	1112213322	2121122133 213
kockensis	2222122212	1111111332	2213123221	1143111331	3333222211	1112213321	--1---2133 113
pilosus	2211222212	1111112132	2213123311	1121111331	4133221111	1121213322	2121112133 213
torrevillasii	2222222212	1111112132	2213121121	2121111331	3333222211	1112213322	2112112133 213
typicus	2212222212	1111112132	2213123211	1121111331	3133222211	1112213322	2111122133 213
sundae	221121212	112121132	2213123311	1121111111	3333222211	1112213311	2111112133 213
culion	2311422212	1131312132	2213123?21	1223111311	3313222211	1112213321	2111112133 213

continued

Table 1—*contd.*

myrmecoides	2211422212	1131212132	2213123731	1223111111	3333222211	1112213322	2111112133	213
prolixus	2211312212	1131212132	2213123221	1223311331	4333222211	113221????	??1???????	???
furvus	3211211212	1111112142	2213123311	1121111331	3313221111	2132213321	2111112133	213
Pheidemannii	3211211212	1111112142	2213123321	1121111331	3313221111	2132213321	2111112133	213
juniperi	2222211212	1111112132	2213133321	2121111331	3333222311	1132213322	2121122133	213
americanus	2211211212	1111112232	2213123321	1111111331	3333222211	1132213322	2121112133	213
amoenus	2211211212	1111112332	2213122321	2121111331	3333222211	1132213322	2121112133	213
cinnamopteris	2211211212	1111111332	2213123321	1121111331	3333222211	1132313322	2121112133	213
concolor	2212211212	1111111332	2213123331	3121111331	3333222211	1132213322	2121112133	213
crassipes	2212211212	1111112332	2213121331	2111111331	3333222211	1132213322	2221122133	213
diffusus	2211211212	1111112232	2213123321	1111111331	3333222211	1132213322	2121112133	213
henryi	2211211212	1111112232	2213121221	2111111331	3333222211	1132213322	2221122133	213
lucidus	2211211212	1111113132	2213123311	2121111331	3333222311	1112213322	3111112133	213
piceicola	2211211212	1111112332	2213132331	2121111331	3333222211	1132213322	2121112133	213
strobilicola	2211211212	1111112332	2213132321	2121111331	3333222211	1132213322	2121112133	213
taxodii	2211211212	1111112232	2213121121	2121111331	3333222211	1112213322	2221122133	213
tibialis	2211211212	1111112332	2213121131	3121111331	3333222211	1132213322	2221122133	213
uhleri	2211211212	1111112332	2213123321	2111111331	3333222211	1132213322	2121112133	213
crembroides	2211211212	1112111232	2212123311	1121111331	3333222211	1132213322	2121112133	213
clavicornis	2211211212	1121111232	2212123221	1121111331	3333222211	1132213322	2121112133	213
dislocatus	2211211212	1111112232	2212123311	1121111331	3333222211	1132213322	2121112133	213
exiguus	2211211212	1112111232	2212123311	1121111331	3333222211	1132213322	2121112133	213
floridanus	2211111212	1111112232	2212121211	1121111331	3333222222	1132213322	2121122133	213
fuscipennis	2211211212	1112111232	2212123211	1121111331	3333222211	1132213322	2121112133	213
geminus	2211111212	1111112132	2212121211	1121111331	3333222221	1132213322	2121112133	213
gracilis	2211111212	1111112332	2211121212	1121111331	3333222222	1132213322	2121122133	213
schaffneri	2211111212	1111112232	2212123311	2121111331	3333222211	1132213322	2121112133	213
stonedahl	2211311212	1112111232	2212123321	1121111331	3333222221	1132213322	2121112133	213
yungansenis	2211111212	1111112232	1112121221	1121111331	3332211111	1122113322	2121131333	213
clavatus	2211211212	1111112332	2212123311	2111111331	3333222212	1132213322	3111113133	213
confusus	2211211212	1111112232	2212123221	1143311331	3333222211	1132213322	3111113133	213
disjunctus	2211211212	1111113132	2212123221	1143311331	3333222311	1132213322	3111113133	213
erraticus	2211211212	1111111232	2212122111	2121111331	3333222211	1132213322	1111113133	213
miyamotoi	2211211212	1111112232	2212123321	2121111331	3333222211	1132213322	1111122133	213
mongolicus	2211211212	1111111332	2212123311	1121111331	3333222211	1132213322	1111113133	213
niger	2211211212	1111112132	2212123321	1111111311	3333222211	1132213322	3111113133	213
okamotoi	2211211212	1111111232	2212123211	1121111331	3333222211	1132213322	3111113133	213
perplexus	2211211212	1111111332	2212123321	2121111331	3333222211	1132213322	3111113133	213
pusillus	2211211212	1111111232	2212123311	1121111331	3333222211	1132213322	1111122133	213
setulosus	2211211212	1111112232	2212123311	1143311331	3333222211	1132213322	3111113133	213
sinuaticollis	2211211212	1111111332	2212123331	3111111331	3333222211	1132213322	3111113133	213
choii	2211211212	1111113232	2212123311	2121111311	3333222211	1132213322	1111113133	213
koreanus	2211211212	1111112232	2212123321	2143311331	3333222211	1132213322	3111113133	213
balli	2211211212	1111112132	2212121321	2132211331	3333222211	1132213322	3111113133	213
brunneus	2211211212	1111112332	2212123311	1121111331	3333222212	1132213322	3111113133	213
chiricahuae	2211211212	1111112332	2212123311	1121111331	3333222211	1132213322	3111113133	213
discretus	2211211212	1111112232	2212121311	2121111331	3333222211	1132213322	3111113133	213
explanatus	1211211212	1111112232	1112121321	1121111331	3333222211	1132213322	3111113133	213
longisetosus	2211211212	1111112232	2212123311	2143311331	3333222212	1132213322	3111113133	213
neoclavatus	2211211212	1111112332	2212123321	2121111331	3333222212	1132213322	3111113133	213
nevadensis	2211211212	1111111332	2212123321	1132211331	3333222211	1132213322	3111113133	213
salicis	2211211212	1111112332	2212123321	2132211331	3333222211	1132213322	3111113133	213
schwarzi	2211211212	1111111332	2212123321	2143311331	3333222211	1132213322	3111113133	213
setiger	2211211212	1111111232	2212123321	2143311331	3333222212	1132213322	3111113133	213
tomentosus	2211211212	1111112332	2212121321	1143311331	3333222211	1132213322	3111113133	213
vicarius	2211211212	1111112332	2212123321	1133311331	3333222211	1132213322	3111113133	213
walshii	2211211212	1111112332	2212123311	1121111331	3333222212	1132213322	3111113133	213

Character state trees for all multistate characters are shown in Fig. 6, indicating graphically the root and branching pattern for each. Multistate characters were coded initially as "morphoclines". Those characters whose coding did not conform to the cladogram topology were recoded, except as noted below. The procedure was repeated until a stable solution was achieved. This approach (transformation series analysis) was originally described by Mickevich (1982) and later amplified by Mickevich and Weller (1990) and Mickevich and Lipscomb (1991). Characters 12 and 71 were not recoded

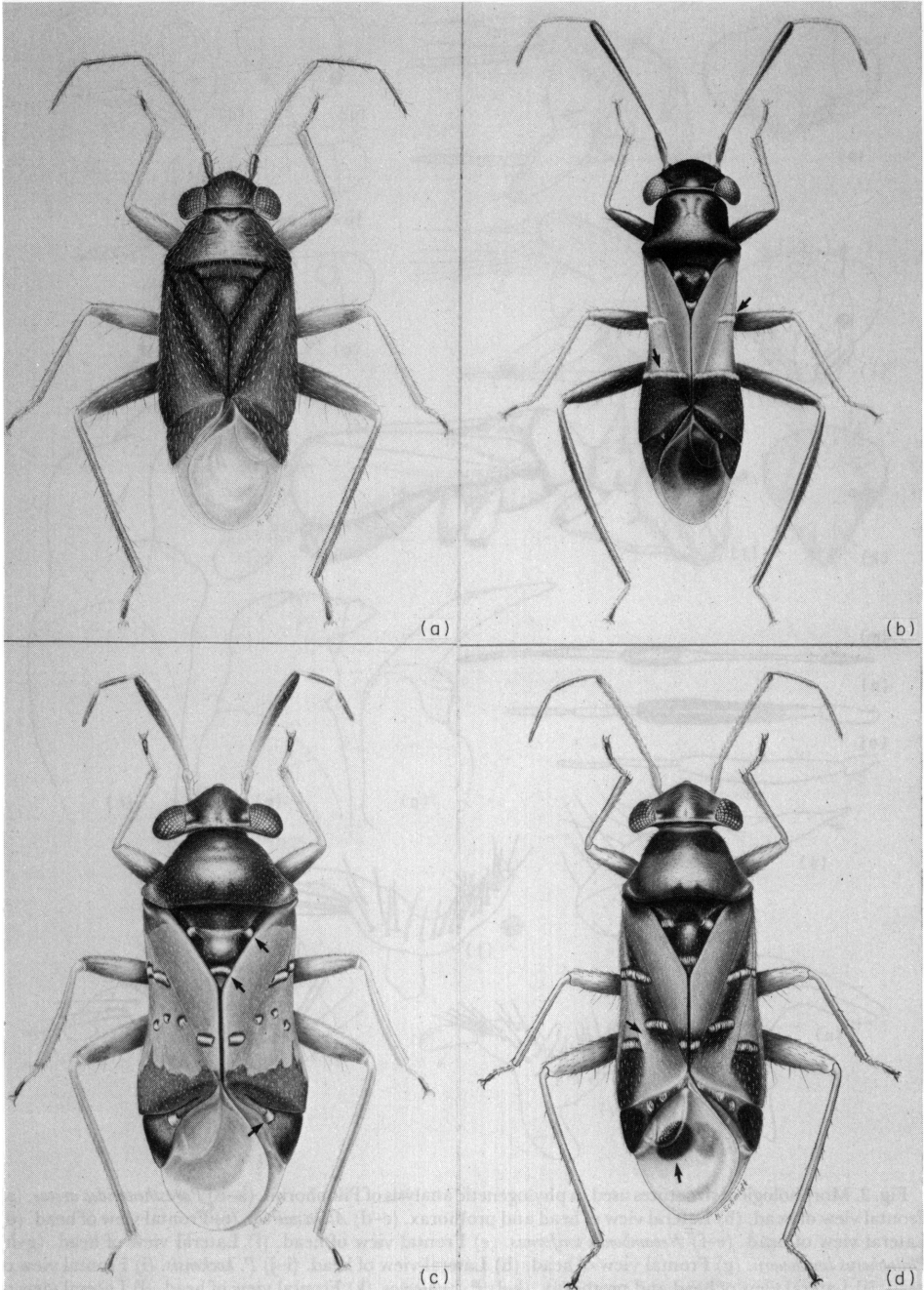


Fig. 1. Habitus views of four Pilophorini species. (a) *Sthenaridea maldonadoi*. (b) *Pilophorus amoenus*. (c) *P. heidemanni*. (d) *P. floridanus*.

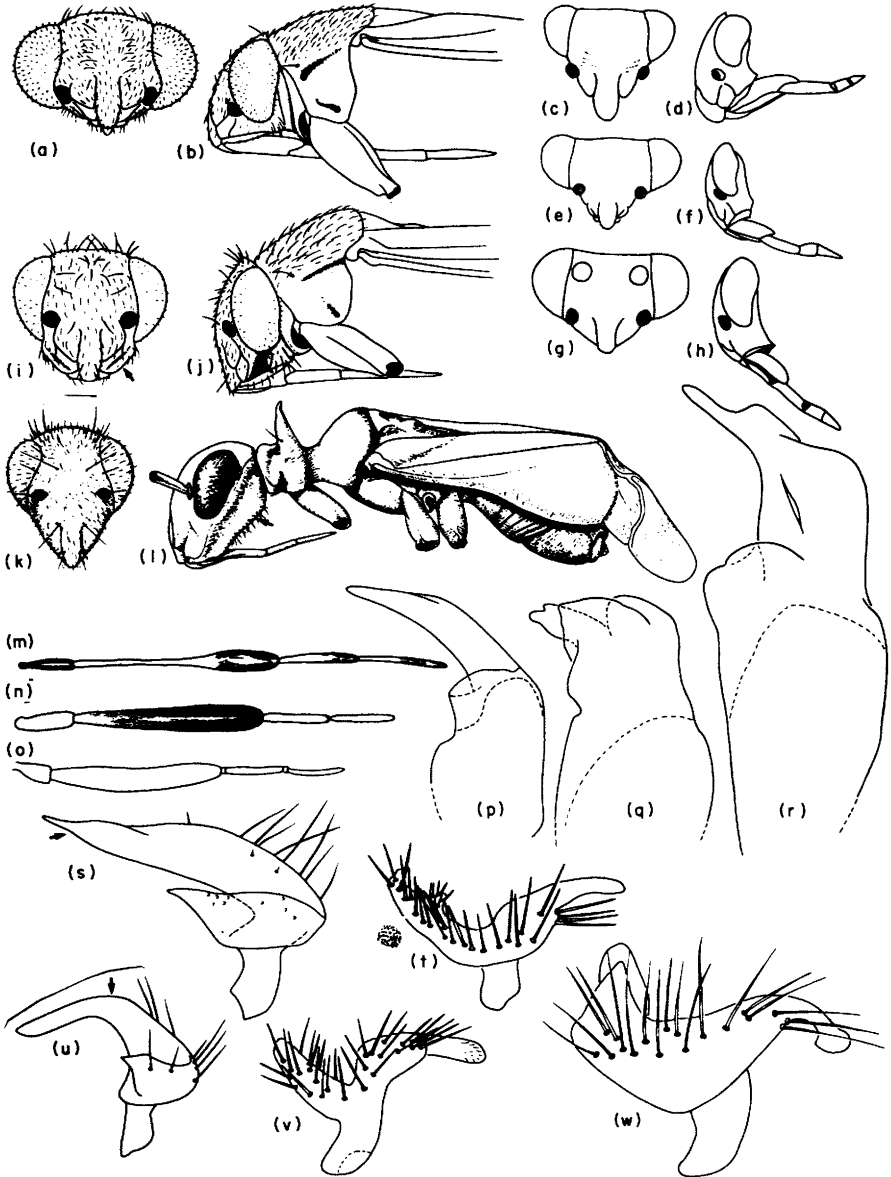


Fig. 2. Morphological structures used in phylogenetic analysis of Pilophorini. (a-b) *Parasthenaridea arecae*. (a) Frontal view of head. (b) Lateral view of head and prothorax. (c-d) *Aloea nairobi*. (c) Frontal view of head. (d) Lateral view of head. (e-f) *Neoambonea uniformis*. (e) Frontal view of head. (f) Lateral view of head. (g-h) *Philophorus linnavuorii*. (g) Frontal view of head. (h) Lateral view of head. (i-j) *P. kockensis*. (i) Frontal view of head. (j) Lateral view of head and prothorax. (k-l) *P. kathleenae*. (k) Frontal view of head. (l) Lateral view of thorax and abdomen. (m-o) Antennae. (p) *P. laetus*. (n) *Alepidiella heidemanni*. (o) *Druthmarus philippinensis*. (p-r) Phallothecae. (p) *Sthenaridea pacifica*. (q) *Pherolepsis aenescens*. (r) *Pilophorus pilosus*. (s-w) Left parametres. (s) *Sthenaridea pacifica*. (t) *S. papuensis*. (u) *Neoambonea samaru*. (v) *N. uniformis*. (w) *Pilophorus tibialis*.

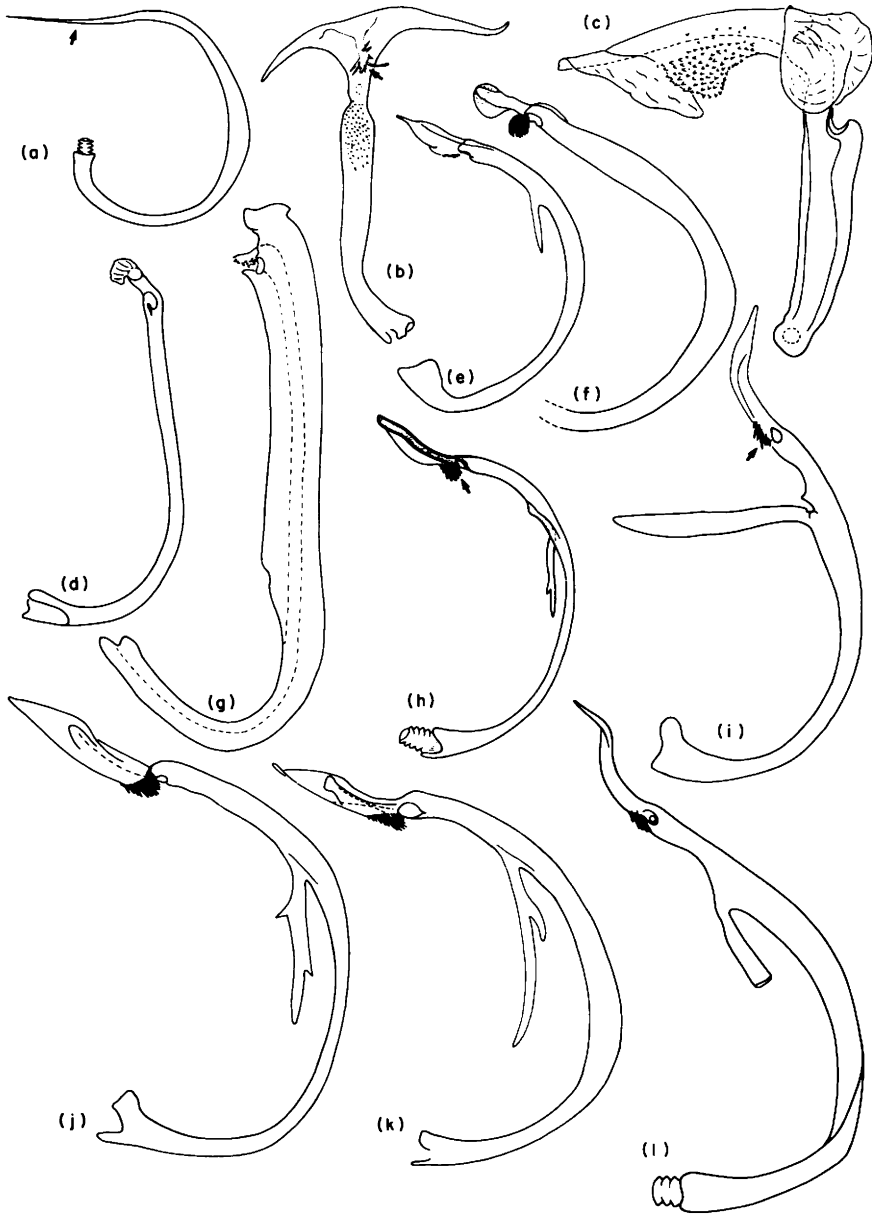


Fig. 3. Male vesicae illustrating structures used in phylogenetic analysis of Philophorini. (a) *Sthenaridea pacifica*. (b) *Neoambonea uniformis*. (c) *N. samaru*. (d) *Aloea samueli*. (e) *Hypseloecus visci*. (f) *H. munroi*. (g) *H. maesta*. (h) *Druthmarus philippinensis*. (i) *Alepidiella heidemanni*. (j) *Pherolepis amplus*. (k) *P. aenescens*. (l) *Pilophorus yunganensis*.

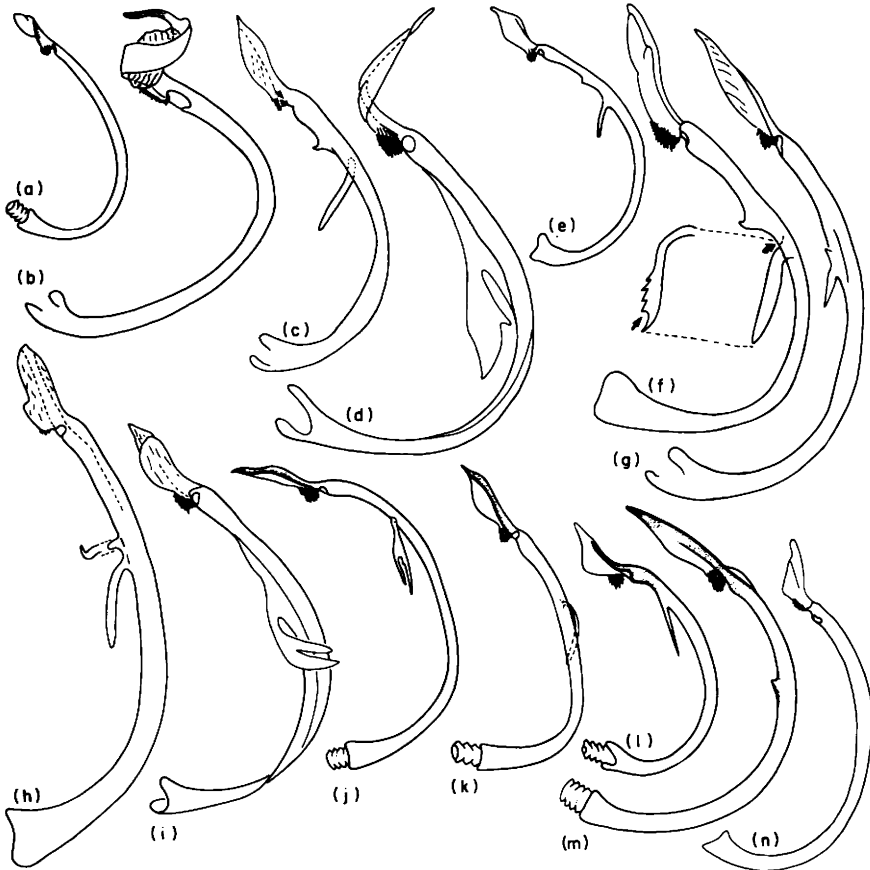


Fig. 4. Male vesicae of 14 *Pilophorus* species, illustrating structures used in phylogenetic analysis of Pilophorini. (a) *samoanus*. (b) *linnaevuorii*. (c) *juniperi*. (d) *miyamotoi* (figured as *setulosus* Horvath by Schuh, 1984). (e) *schaffneri*. (f) *tibialis*. (g) *cinnamopteris*. (h) *pilosus*. (i) *lucidus*. (j) *alstoni*. (k) *typicus*. (l) *myrmecoides*. (m) *formosanus*. (n) *furvus*.

to conform to the final cladogram; because of their position recoding would have had no effect on the final topology, and the coding presented was to be preferred on the basis of morphocline analysis. Although polarity and transformation hypotheses have traditionally been based purely on "biological" knowledge, Mickevich and her co-authors have argued persuasively that character transformation considered outside of a phylogenetic context is premature and often times indefensible, a conclusion that I found inescapable in this study and elsewhere (Schuh and Stys, in press).

A preliminary cladistic analysis of the data was conducted using the mainframe package PHYSYS (Farris and Mickevich, 1985). This provided a general concept of relationships within the Pilophorini and offered some help with character interpretation, but I lacked long-term access to the program. The final analyses were performed using Hennig86 (Farris, 1988), a program with most of the functionality of PHYSYS, but which operates on a personal computer.

All runs used the mh* and bb* options in Hennig86 version 1.51 with 320 k bytes of memory available for tree storage. Both algorithms use branch swapping to achieve a solution, bb* applying the technique in a more exhaustive fashion. The exact-solution

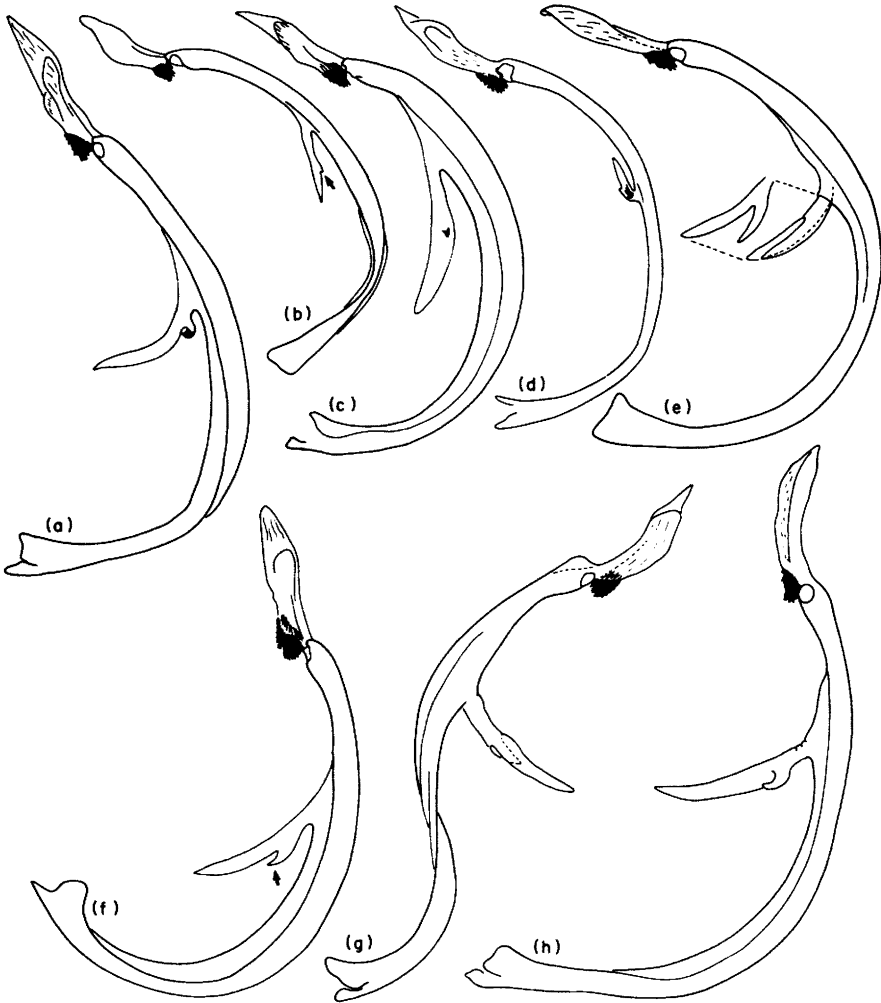


Fig. 5. Male vesicae of eight *Pilophorus* species, illustrating structures used in phylogenetic analysis of Pilophorini. (a) *sinuaticollis*. (b) *mongolicus*. (c) *pusillus*. (d) *choii*. (e) *niger*. (f) *setulosus*. (g) *disjunctus*. (h) *confusus*.

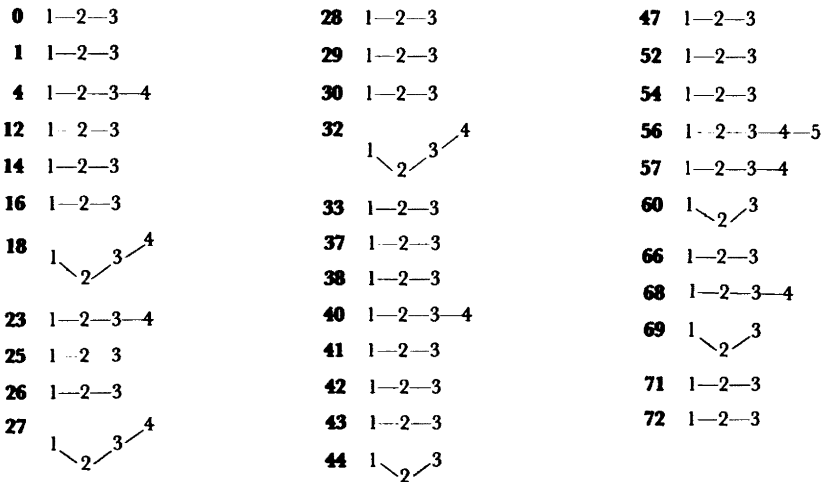


Fig. 6. Character state trees for multistate characters.

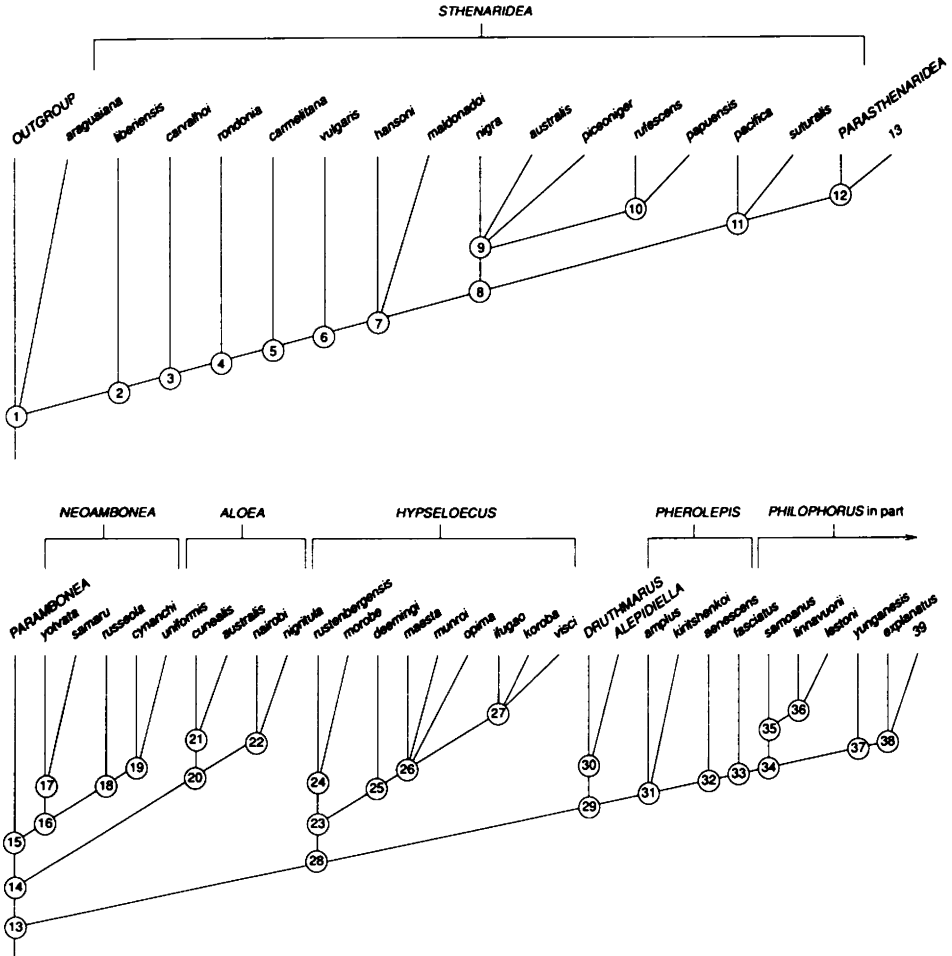


Fig. 7 (Parts 1 and 2 of 4). Cladogram of 114 species of Pilophorini [Nelson (strict) consensus of 1408 cladograms; length = 454, consistency index = 0.26, retention index = 0.83].

tree-building algorithms in Hennig86 function effectively up to a limit of about 28 taxa (Platnick, 1989) and therefore could not be applied. One would anticipate from Platnick's (1989) results that the cladograms found using *bb** are of minimum length, but it is certain that they do not represent all possible topologies, because the memory limit of 1408 cladograms was always attained. Platnick (1989) analysed a data set called SCHU; those data represented an early version of my data, but his results cannot be directly compared with those presented here because I re-interpreted some characters and discovered several errors in the original matrix.

Fig. 7 presents a Nelson (strict) consensus of 1408 cladograms. The input cladograms used in computing the consensus tree had a length of 419 steps, a consistency index of 0.28, and a retention index of 0.85 (see Fitzhugh, 1989; Farris, 1989); the consensus has a length of 454, a consistency index of 0.26 and a retention index of 0.83. Lengths, consistency indices, and retention indices for characters in Table 1 used to compute the cladogram in Fig. 7 are presented in Appendix 2.

With such large numbers of cladograms, it would seem desirable to select a preferred

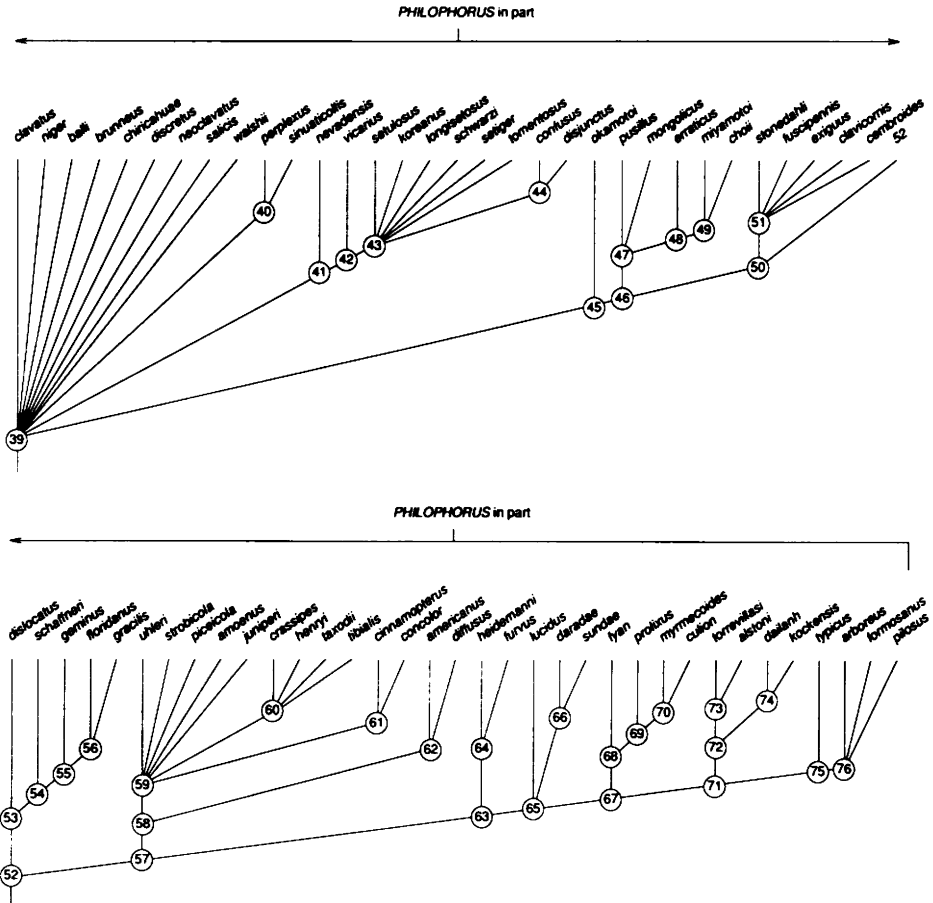


Fig. 7 (Parts 3 and 4 of 4). Cladogram of 114 species of Pilophorini.

subset for more detailed consideration. The successive approximations approach to character weighting, originally described by Farris (1969) and more recently applied by Carpenter (1988), could not be implemented because the numbers of cladograms always exceeded available memory space. It was therefore certain that successive approximations weighting would be applied to only a subset of all possible cladograms and would produce a potentially spurious result.

Synapomorphies for all nodes in Fig. 7 are listed in Table 2. Characters for which alternative optimizations exist at a node are indicated as a range, e.g., *x,y*. No states of characters 22 and 64 represent synapomorphies on the consensus cladogram in Fig. 7, as is also the case with some states of certain multistate characters. Autapomorphies for all terminal taxa can be determined from the original character matrix (Table 1).

Systematic Conclusions

The present phylogenetic analysis provides the detailed diagnoses of the genera recognized by Schuh (1989). No formal categories are recognized between the level of tribe and genus. The most consistent characters supporting the major nodes on the

Table 2

List of synapomorphies for Fig. 7 (listed by node, character number and state; states listed as a range, e.g. 1-2, indicate alternative equally parsimonious resolutions on the cladogram, often as a result of missing data; numbers in parentheses indicate at which subsequent node the alternative optimization is resolved). Characters 22 and 64 are autapomorphic.

1	1-2, 16-2, 57-2, 66-2, 68-2	39-17-3, 26-3
2	39-1.2 (3-2), 40-1.2 (3-2), 41-1.2 (3-2), 56-2	40-16-1
3	29-2	41 32-3, 33-2, 34-2
4	42-2	42 33-3, 34-3
5	35-2, 36-2, 43-2	43-17-2, 30-1.2 (142-1), 32.4
6	52-2	44-30-2
7	37-2, 38-2	45-16-1, 17-2, 28-1
8	72-2	46 60-2
9	29-3, 69-1.2 (10-1)	47 60-1
10	72-1	48 30-1
11	26-2, 27-1	49-16-2
12	70-2, 72-3	50-62-2, 66-2
13	7-1.2 (14-2; 29-2), 56-3, 57-3, 68-3, 69-3	51 13-2
14	8-2, 10-2, 11-2, 71-3	52 16-2
15	17-3, 57-3.4 (16-4)	53-48-2
16	15-2, 24-2, 30-1.2 (18-2), 56-4	54-4-1
17	30-1.2, 55-2, 67-2, 71-2	55-27-2
18	19-2, 56-5, 58-2	56-49-2, 65-2
19	18-1, 21-2	57 23-3
20	14-2, 68-4	58 28-2
21	52-1	59-17-3, 30-2
22	51-2	60-61-2, 65-2
23	30-2, 55-2	61 16-1, 26-3
24	26-1	62 32-1
25	26-3	63-17-1, 62-1
26	29-3	64-0-3, 42-1, 46-1, 47-1, 50-2, 59-1
27	59-2	65-52-1
28	27-2, 58-2	66-12-2, 16-1, 37-1
29	18-2.3 (31-3), 19-2, 29-1, 59-2	67 6-2, 27-2
30	0-2, 4-2, 9-2, 25-1	68 28-2, 33-2
31	17-2, 26-1, 39-1, 40-3, 41-3, 52-2.3 (38-3), 66-3	69-4-3, 12-3, 14-2, 31-2, 33-3
32	36-1, 60-3	70-4-4, 5-2, 38-1
33	20-1.2 (39-2), 35-1, 43-3	71-3-2, 5-2
34	0-2, 28-2, 37-3, 45-1.2 (38-2), 54-1.2 (38-2)	72-2-2, 63-1.2
35	18-2, 38-1.2 (36-1), 59-1, 66-2	73-44-3
36	8-2, 17-1, 26-2, 39-2	74-4-1, 33-2, 59-1
37	9-2, 23-2, 38-3, 42-3, 53-2	75-41-1
38	4-2, 27-3, 46-2, 47-2	76-16-2.3, 40-4, 46-1, 47-1, 51-2

cladogram are discussed in the text below. The key in Appendix 3 will facilitate generic identifications. Two paraphyletic genera, *Sthenaridea* Reuter and *Pherolepis* Kulik, are recognized until such a time as additional character data become available (see additional discussion below).

Node 1. A number of characters are indicated as potential synapomorphies for the Piloophorini, in addition to those previously recognized.

Nodes 1 to 12. *Sthenaridea* Reuter: Beginning at the base of the cladogram (Fig. 7), note that most of the species currently placed in the genus *Sthenaridea* do not form a monophyletic group, a result contrary to that presented by Schuh (1984) and Schuh and Schwartz (1988), in which *Sthenaridea* Reuter was treated as monophyletic, based on the structure of the vesica in the male. As was pointed out by Schuh and Schwartz

(1988), this grouping has long suffered from flawed diagnoses. In view of the fact that most of the nodes involving *Sthenaridea* species are supported by limited character information—in particular, some judgments concerning the presence of scalelike setae in this group are subject to interpretation depending on the condition of available specimens—I have maintained the paraphyletic *Sthenaridea* until such time as more specimens and character information become available. All included species can be recognized by the simple unornamented vesica lacking a visible secondary gonopore (57-2), a symplesiomorphy relative to all non-*Sthenaridea* pilophorine species.

Node 12. As hypothesized by Schuh (1984), *Parasthenaridea arecae* Miller, is the sister group of all Pilophorini other than *Sthenaridea*.

Node 13. The male genitalia, including the structure of the apex of the vesica (56-3), the secondary gonopore (57-3), and the phallosome (68-3; 69-3) support the remaining Pilophorini as a monophyletic group.

Node 14. The monophyly of this group is supported by the structure of the labium (8-2; 10-2), buccal cavity (11-2) and left paramere (71-3).

Node 15. This node is most consistently supported by the strongly rugose pronotal surface (17-3).

Node 16. *Neoambonea* Schuh: Species placed at this node have vesicae which are distinctive among the Pilophorini [character 56-4; Fig. 3(b and c)] but which vary dramatically from the unique form found in *Parambonea transvaalensis*. I have chosen to name only a single monophyletic group for the species at nodes 17 and 18, because even though the vesicae differ in the species arising at the two nodes, there is greater similarity among them with any other pilophorines.

Node 20. *Aloea* Linnavuori: This node is supported by the presence of distinctly elevated calli (14-2) and an erect and more or less straight phallosome (68-4).

Node 28. This node is consistently diagnosed by the distinctive form of the glassy spicules subtending the secondary gonopore [58-2; e.g. Fig. 3(f, h)].

Node 23. *Hypseloecus Reuter* (see Schuh [1989] for synonymy and re-assignment of species): This group has a very uniform habitus, but shows substantial variation in the structure of the vesica [compare Fig. 3(e-g)]. Specimens representing undescribed species exhibit additional autapomorphic conditions, such as: the second antennal segment is enlarged and flattened, very much like antennal segment 1 in *Pilophorus lestoni*, or the scalelike setae on the dorsum are aggregated into a single, complete, broad transverse band on the hemelytra at the level of the apex of the scutellum (a condition similar to that found in *Pilophorus alstoni* and *P. torrevillasi*). *Hypseloecus* can be most easily recognized by the intense velvety black patches on the meso- and metapleura (55-2), a trait which also occurs at node 17. The metatibial spines with dark spots at their bases (30-2) are also distinctive, but this condition shows limited variation within the group and also occurs in a few other species of pilophorines.

Node 29. This node represents a transition to a more strongly myrmecomorphic habitus. It is most consistently diagnosed by the nearly universal presence of a mesial vesical spine (59-2) and by a distinctive scutellar structure (18-3).

Node 30. The present analysis clarifies the position of *Druthmarus* Distant (in this study represented by *Druthmarus philippinensis* Schuh), a group whose relationship to "*Ambonea*" (= *Hypseloecus*) was previously ambiguous (Schuh, 1984). The sister group relationship with *Alepidiella* Poppius is most obviously supported by the strongly inflated second antennal segment [25-1; Fig. 2(n and o)].

Node 31. Taxa arising at this node are distinguished by the loss of setae on the

propleuron (39-1), aggregations of setae into patches on the meso- and metathoracic pleura (40-3; 41-3) and usually on the cuneus (52-3), and the twisted vesica (66-3).

The genus *Pherolepis* Kulik (1968) as recognized here (see also Schuh, 1989) comprises four species, all of which had most recently been placed in the genus *Hypseloecus* (Kerzhner, 1970), but they have little in common with the type species of that group, *visci* (Puton), or with its other members. Rather than name new genera on the basis of limited phylogenetic evidence, I retain Kulik's concept of *Pherolepis* until such time as additional character information produces more strongly supported groupings.

Node 34. Pilophorus Hahn: I have chosen to apply the classical name *Pilophorus* at this level of the cladogram, because some of the characters traditionally used to define the group [lateral aggregations of scalelike setae on the scutellum (37-2) and an anterior band of scalelike setae on the corium (45-2)] arise here, and because the three taxa originating at node 35 are relatively poorly known and possess unusual combinations of characters relative to other Pilophorini.

Nodes 35 and 36. All characters supporting these nodes show some variation. The relationship between *Pilophorus lestoni* and *P. linnavuorii* seems relatively strong, whereas the sister group relationship between these two taxa and *P. samoanus* is more tenuous. *Pilophorus lestoni* and *P. linnavuorii* are very similar to Holarctic *Pilophorus* species in their general body conformation and many setal characters, although the structure of the buccal cavity and the labium is very similar to the condition found in taxa arising at node 14. The structure of the apex of the vesica is novel for these two species, but offers no information of help in establishing relationships with other taxa.

Pilophorus samoanus has an unusual pronotal structure and distribution of scalelike setae on the hemelytra, and also has setiform parempodia, all novel characteristics within the Pilophorini, and attributes which make it difficult to place phylogenetically. Additional specimens in better condition than those that were available to me would be most helpful in attempting to clarify its relationships.

Nodes 37 and 38. Pilophorus yunganensis and *P. explanatus* are unusual among *Pilophorus* species for having convex corial margins and the abdomen broadly joined to the thorax. *Pilophorus yunganensis* also has a diffuse placement of scalelike setae on the hemelytra, but falls within *Pilophorus* on the basis of nearly all other characters.

The following nodes represent apparently monophyletic groups of three or more species within *Pilophorus*:

Node 41. nevadensis group. This clade includes those North American *clavatus* group species of Schuh and Schwartz (1988)—as well as several Palearctic species—with long to very long setae on the dorsum (characters 32-3, 33-3, 34-3).

Node 47. This group of Palearctic species is united by the sub-basal ornamentation of the mesial vesical spine (60-1).

Node 51. [*exiguus* group in part of Schuh and Schwartz (1988)]. This group of species from the western Nearctic is held together by the presence of a campanulate pronotum (13-2).

Node 53. [*exiguus* group in part of Schuh and Schwartz (1988)]. This group of Nearctic species is recognized by having the posterior band of scalelike setae offset at the radial vein [48-2; Fig. 1(d)].

Node 57. This group is defined by the unique corial texture (23-3).

Node 59. All species at this node have flattened hind tibiae (28-2). They are all large conifer-inhabiting species (as are those of node 62), most belonging to the *americanus*, *amoenus*, and *crassipes* groups of Schuh and Schwartz (1988). Only the *crassipes* group

appears to be monophyletic (node 60), the other two groups recognized by Schuh and Schwartz being unsupported in this analysis. The group is primarily Nearctic with approximately equal numbers of species in eastern and western North America, and two species, *P. cinnamopterus* and *P. benjamin* (the latter not included in the data matrix), restricted to the western Palearctic.

Node 60. *Pilophorus crassipes* species group of Schuh and Schwartz (1988): This clade is supported by the presence of subapical denticles on the mesial vesical spine [61-2; Fig. 4(f)] and the mesial spine arising from lateral surface of vesica [65-2; Fig. 4(f)].

Node 63. This group is defined by the smooth pronotum (17-1) and the absence of a mesial barb on the vesica (62-1), both of which show some homoplasy.

Node 64. This lineage (also including *P. nasicus*) comprises the *furvus* group of Schuh and Schwartz (1988). It is distinctive in a number of features, listed in Table 2, most notably the elevated and nearly conical scutellum (18-4).

Node 65. This group, recognized by the absence of scalelike setae on the cuneus (52-1), shows more morphological variation than any other assemblage of *Pilophorus* species, particularly in head and pronotal structure, differentiation of setal patches and bands and the structure of the vesica. A number of additional species appear to belong to this group (e.g. *javanus* Poppius, *sumatranus* Poppius), but these are poorly known. Furthermore, it seems clear from material in existing collections that many more related species remain to be described.

Node 68. This grouping, recognized, among other characters, by the elongate setae on the frons and vertex (33-2), includes (node 69) most of the species originally described in the genera *Bilirania* Carvalho (see also *P. sundae*), *Biliranooides* Schuh and *Strictotergum* Zou, several species of which were not included in this analysis, because they represent only minor morphological variants and were available from very limited material. If these genera were recognized, *Pilophorus* would have to be divided into additional genera or subgenera. As can be seen from the synapomorphy list in Table 2, many other characters support their placement in *Pilophorus*, whereas those attributes diagnostic for the species arising at node 69 are autapomorphic within *Pilophorus*.

Node 71. Synapomorphies for this group include the carinate genae (3-2) and the gular roll (5-2). A number of novel characteristics are found at nodes 72 and 75. Clades formed at nodes 69 and 71 represent some of the most strongly myrmecomorphic of all species of Miridae.

Host Analysis

Most pilophorines are associated with a single plant species or with groups of closely related plants. Known hosts are listed in Appendix 1. Where life histories are better known it appears that many pilophorines (at least in the Northern Hemisphere) are partly predaceous. Kullenberg (1944) and Southwood and Leston (1959) summarized knowledge of the habits of *Pilophorus cinnamopterus*, *P. perplexus* and *P. confusus*; they are all predaceous-phytophagous (sometimes referred to as mixed feeders or oligophagous in the literature on the Miridae). *P. cinnamopterus* lives commonly on *Pinus sylvestris* where it feeds on the needles and buds, but it is also a predator of aphids. *Pilophorus perplexus* inhabits oaks and other deciduous trees and feeds on aphids as well as other small arthropods, habits similar to those of *P. confusus*. Fulton (1918) documented predation of aphids on apple in eastern North America by *Pilophorus walshii* [a misidentification of *P. perplexus* according to Wheeler and Henry (1976)]; but see host listing in Schuh and

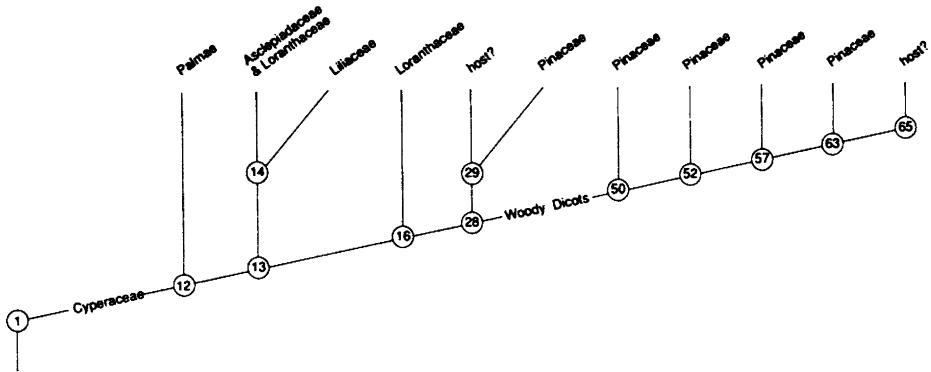


Fig. 8. Host cladogram for Pilophorini.

Schwartz, 1988]. Schuh and Schwartz (1988) suggested that pilophorine host plant associations may be strongly influenced by the presence of acceptable prey organisms, which are in many cases probably members of the Auchenorrhyncha or Sternorrhyncha (Hemiptera). This idea derives from the observation that many members of what Schuh and Schwartz referred to as the *Pilophorus clavatus* species group can often be found on a variety of plant taxa, even within a limited geographic area.

In Fig. 8 host associations of the major clades of Pilophorini are plotted on a simplified version of the cladogram in Fig. 7. I follow the practice of Andersen (1979) and Schuh and Polhemus (1980) in fitting extrinsic—in this case host—data to the phylogenetic hypothesis based on structural (intrinsic) characters. This approach allows one to estimate the number of host changes in the Pilophorini, as well as to predict habits of taxa for which no host information is currently available.

As in some other groups of Miridae [Halticini in the Orthotylinae (Schuh, 1974, 1976); Stenodemini + Mecistoscelini in the Mirinae (Schwartz, 1987)], the primitive association is with monocots. Although the host listings for *Sthenaridea* are incomplete, available evidence (Schuh, unpublished observations; T. J. Henry, pers. comm.), indicates that most—if not all—species are associated with sedges (Cyperaceae), sometimes with rushes (Juncaceae), or rarely with grasses (Gramineae). The sedge-associated species are probably strictly phytophagous, in that no obvious prey appear to be present on the hosts. The other monocot feeders include *Parasthenaridea arecae*, known from Palmae, and members of the genus *Aloea* (node 20) which are restricted to species of *Aloea* (Liliaceae).

Known hosts for node 15 include loranthaceous parasites and asclepiadaceous vines in the genus *Cynanchum*. At node 23 known hosts are in the genera *Loranthus* and *Viscum* (Loranthaceae).

Alepidiella heidemanni (node 30), although rarely collected, appears to be associated exclusively with the genus *Pinus*. Nothing is known of the habits of *Druthmarus* species, but their distribution virtually precludes association with *Pinus*.

All four species placed in *Pherolepis* (nodes 31, 32, 33) are found on *Salix* (Salicaceae) and *Ulmus* (Ulmaceae) species, but nothing is known of their habits. Similarly, hosts are unknown for the three taxa arising at node 35 or for *Pilophorus yunganensis*.

Nearly all species placed between nodes 38 and 50 are associated with woody dicots, mainly, but not exclusively, with species of *Quercus* (Fagaceae) and *Salix* (and occasionally other members of the Salicaceae). There is evidence that at least some

species are predatory on Auchenorrhyncha or Sternorrhyncha (see above). *Pilophorus miyamotoi* reported from *Pinus densiflora* (Kerzhner, 1988), offers an exception to this pattern of host specialization.

Node 50 represents a conspicuous shift to the Coniferae, primarily to species of *Pinus*. As with the dicot feeders discussed above, many species associated with the Pinaceae appear to be at least in part predatory. Many conifer-inhabiting *Pilophorus* species in North America and *Pilophorus cinnamopterus* in Europe appear to feed on aphids. These comments apply to all taxa arising from node 50 with the exception of those arising at node 65.

At node 65, a plant association is known for only one species, *P. arboreus*, which was collected by pyrethrum knockdown from *Shorea johorensis* (Dipterocarpaceae). It seems certain that all species in the clade are associated with dicots, because few—if any—gymnosperms occur in their distributional range. One might also predict an association with ants, because this clade includes the most strongly myrmecomorphic species of Pilophorini [e.g. Fig. 2(1)].

DISCUSSION

The Pilophorini appear to have shifted from a primitive association with monocots, to various groups of woody dicots, then to the Coniferae (apparently more than once if *Alepidiella* is truly an obligate associate of the Coniferae), and subsequently back to woody dicots. No later than the shift to the Coniferae, predation appears to have been acquired as an important aspect of the feeding regime.

The broadest patterns of host shifts in the Pilophorini represent apparent colonizations, because host-plant groups of major pilophorine taxa adjacent to one another on the cladogram can best be described as remote. This pattern is similar to that described by Miller (1987) for the Papilionidae (Lepidoptera), and as in the case of Miller's work, would seem to rule out parallel cladogenesis between the Pilophorini and their hosts. Nonetheless, at a finer level of resolution, certain clades, such as *Aloea* and some of the conifer feeding lineages, obviously have specialized on certain plant groups and appear to be restricted to them, possibly even at the species group level in the case of the clade containing *Pilophorus exiguus*, most of whose members feed on *Pinus edulis* and its close relatives, the piñon pines.

Even in those groups where closely related species feed on closely related plants, the bugs are often not tied to a single host species (e.g. node 58, where a single bug species may breed on several *Pinus* species, or occasionally on species in other genera of Coniferae). Species of *Pilophorus* feeding on woody dicots in the Holarctic may be strongly influenced in their host associations by the presence of suitable insect prey species.

Too little information is available to speculate on whether those lineages feeding on groups such as the Asclepidaceae and Pinaceae derive some protective advantages from the toxic compounds often produced by these plants. Therefore, mechanistic theories which might explain the radiation of pilophorines on certain plant taxa (viz., Ehrlich and Raven, 1964) are beyond the reach of available data. Furthermore, in the case of the Pilophorini, theories of strict parallel cladogenesis are largely outside the realm of serious testing either because plant phylogenies are unavailable or because phylogenetic information for the Pilophorini is too imprecise to make meaningful comparisons.

The study of pilophorine host associations would benefit greatly from additional

information on habits, particularly regarding host preferences of the tropical lineages, and the degree to which predation plays a role in nutrition.

Biogeographic Analysis

The development and application of analytical methods occupy a prominent place in the modern biogeographic literature (e.g. Nelson and Platnick, 1981; Page, 1990; etc.). Unfortunately, for the Pilophorini, the complexity of the data and the widespread distributions of many taxa largely preclude application to techniques such as component analysis. Nonetheless, certain aspects of pilophorine distributions do appear to be congruent with information derived from other groups. Figs 9–11 show the distributional outlines of the major groupings recognized in the classification presented above.

Five broad patterns of pilophorine distribution in particular invite scrutiny: (1) a paraphyletic basal component (below node 8) which with the exception of one species is confined to the New World tropics; (2) an African component, including the Arabian Peninsula (node 14); (3) an Indo-Pacific (Paleotropical) component, ranging from West Africa east to New Guinea (node 23); (4) two sets of relationships suggesting sister area relationships between Southeast Asia and the southeastern United States (nodes 35 and 65); and (5) a terminal lineage nearly all of whose members are restricted to the northern land masses (but also including Southeast Asia), whereas all other species of Pilophorini occur on the southern continents or land areas derived therefrom.

Pattern 1 can be investigated only on the broadest scale, because most of the included species are widespread and their distributions greatly overlap. Nonetheless, those species of Pilophorini occurring in the New World tropics (as well as *Sthenaridea liberiensis* from West Africa) are basal on the cladogram to remaining members of the tribe. Furthermore, the distribution of those species (Fig. 9) has an outline similar to that of other insect groups, for example *Rhinacloa* Reuter (see Schuh and Schwartz, 1985), and a number of taxa listed in Liebherr (1988). A notable aspect of this distributional pattern is the occurrence of species in the Greater Antilles, but the almost complete absence from continental North America. As with *Rhinacloa basalis* (Reuter) (Schuh and Schwartz, 1985), the occurrence of *Sthenaridea vulgaris* in the southern Florida (Henry and Wheeler, 1982; Schuh and Schwartz, 1988) is part of an already widespread distribution. All indications are that this represents a range extension through introduction or other recent means, rather than fragmentation of a pre-existing range.

The remaining species in *Sthenaridea*, which do not form a monophyletic group, range across the paleotropics (Fig. 9 and as shown by Schuh, 1974, 1984), many of them having broadly overlapping distributions.

Pattern 2 (*Parambonea* + *Neoambonea*; *Aloea*) comprises species restricted primarily to the African continent (Fig. 9), and usually to the Afrotropical Region. The diversity of the tropical West African fauna is greater than the number of described taxa, as determined from examination of unworked collections.

Pattern 3 (node 23; *Hypseloecus*) invites comparison with distributional theories recently propounded for the Paleotropics (Schuh and Stonedahl, 1986), in which a close relationship is evident between Africa and the Indo-West Pacific (Fig. 10), but in which the African taxa are always basal to those occurring further east. The presence of *Hypseloecus visci* in the southern Palearctic (Fig. 10) adds an additional element to the pattern, however.

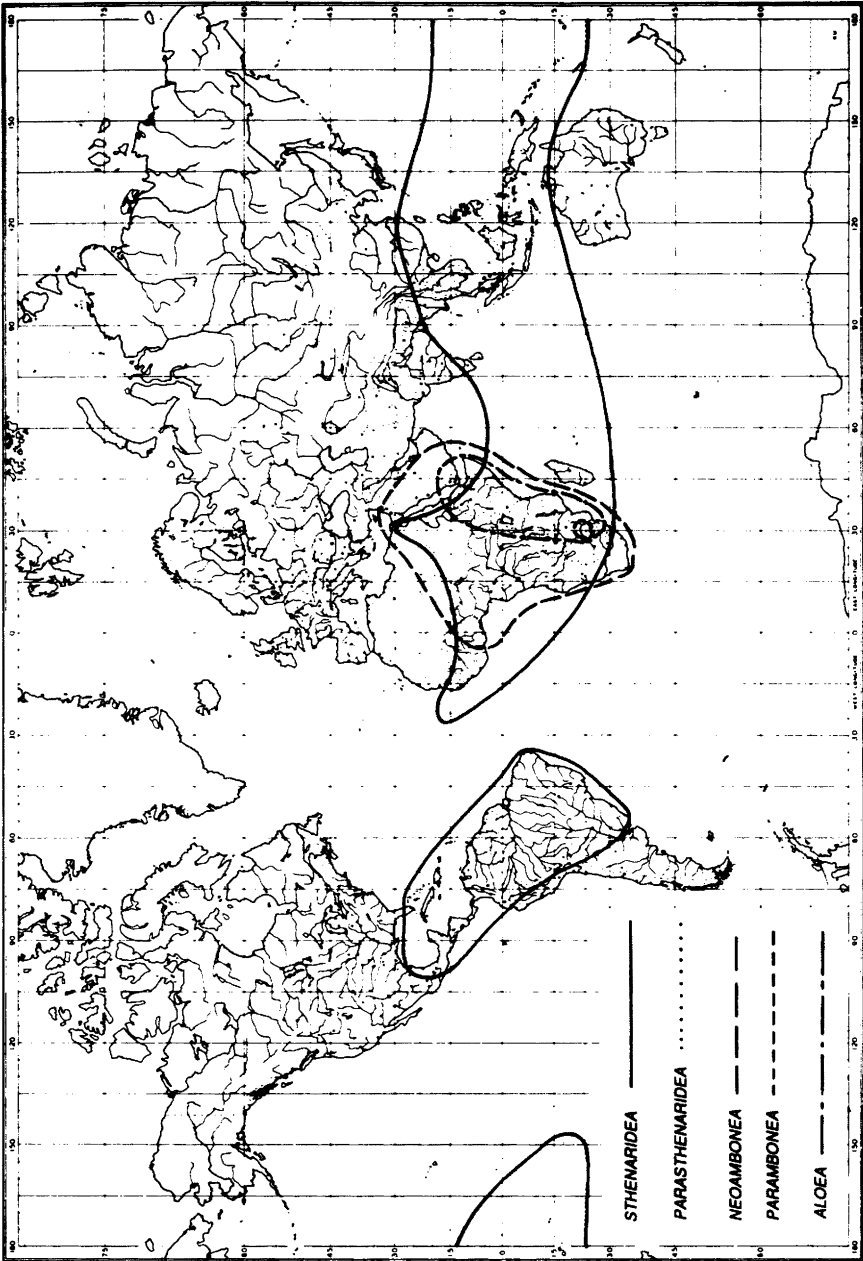


Fig. 9. Distributions of *Sthenaridea*, *Parasthenaridea*, *Neoambonea*, *Parambonea* and *Aloea*.

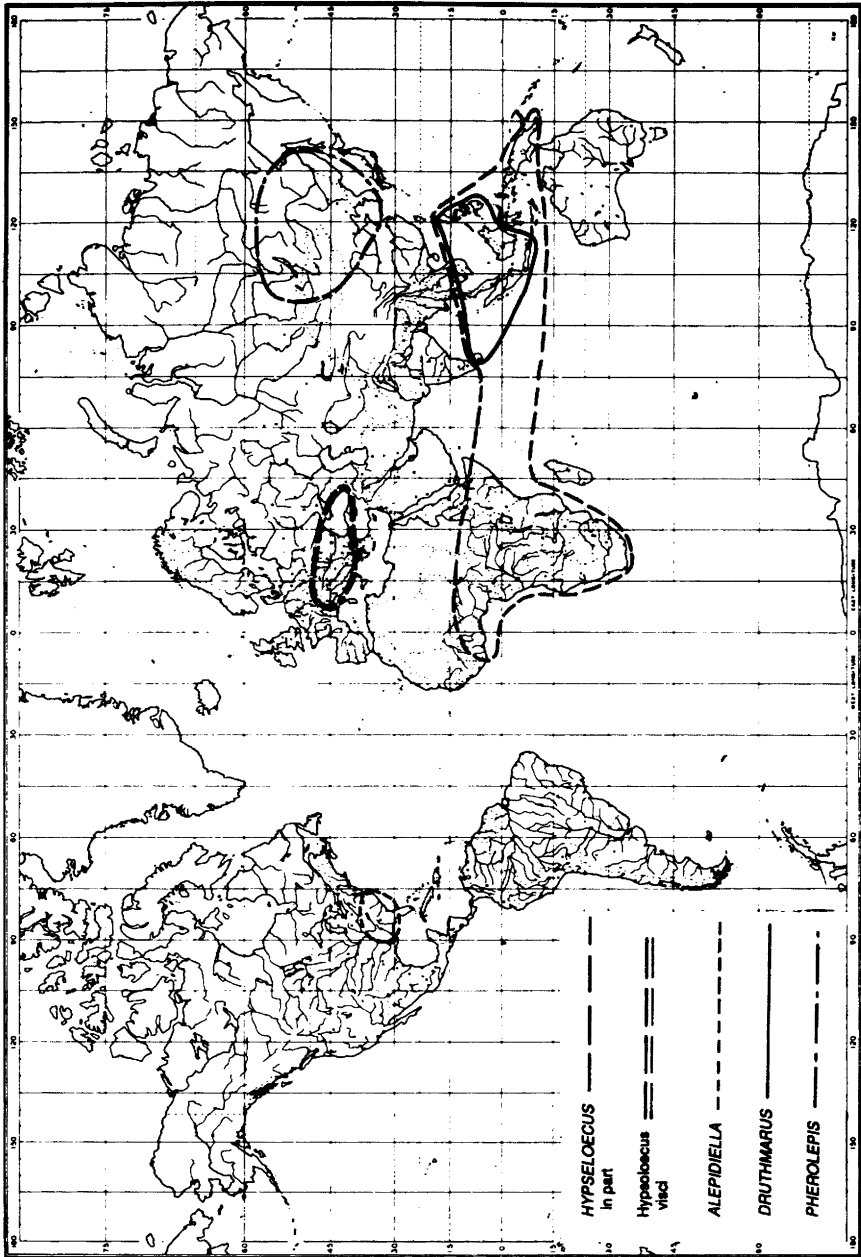


Fig. 10. Distributions of *Hypseloecus*, *Alepidiella*, *Druthmarus* and *Pherolepis*.

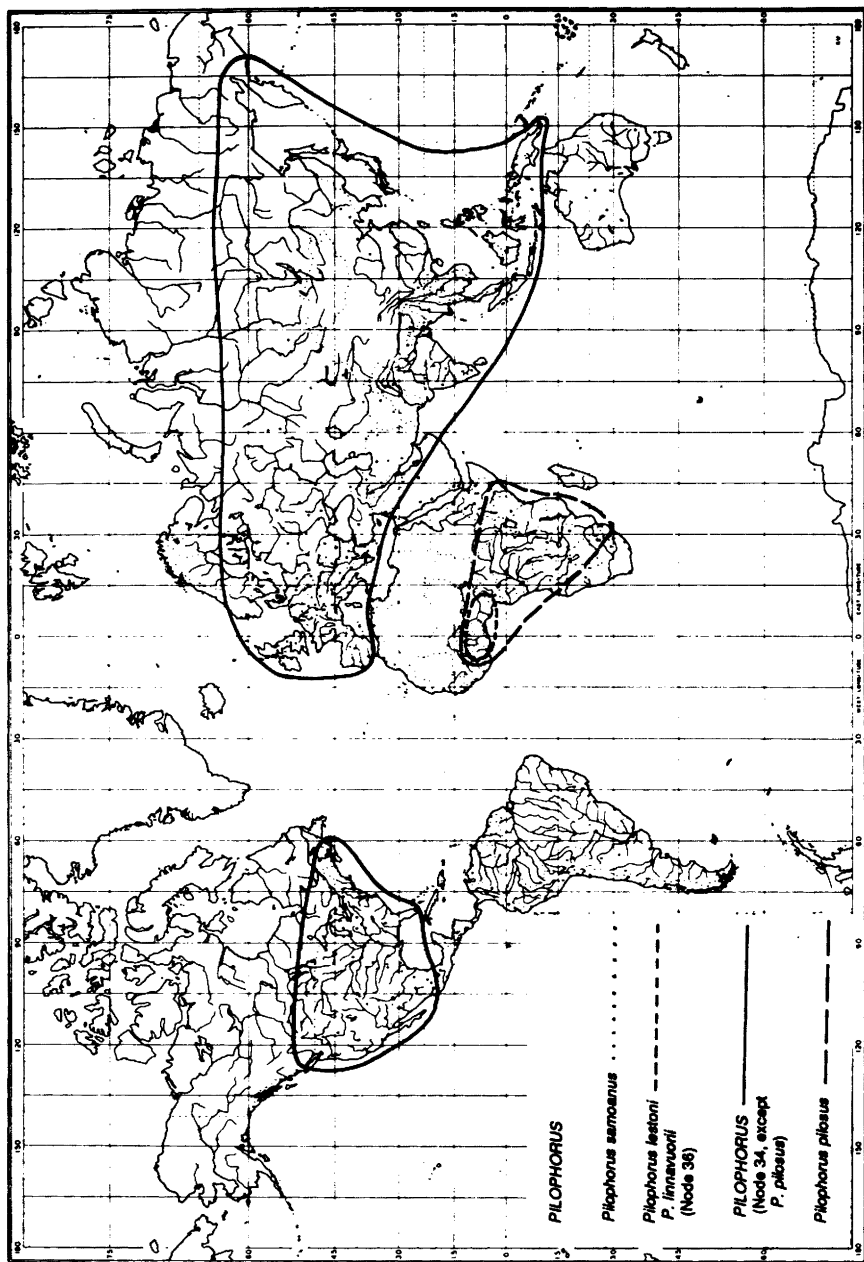


Fig. 11. Distribution of *Pilophorus*.

Pattern 4 includes two pairs of taxa indicating a relationship between Southeast Asia and the southeastern United States. A similar, if not identical pattern, has been described for many other insect groups occupying parts of southern China and the southeastern United States (e.g. Linsley, 1963). The literature contains little or no documentation as to what third area might be most closely related to this pair, although data from the Pilophorini suggest that some portion of the remaining Northern Hemisphere fauna is involved. There is a clear indication that the fauna of the southeastern United States has a complex history, and that the region may be composed of elements of quite different ages.

Pattern 5 suggests that nearly all Pilophorini on the northern land masses are more recent in origin than nearly all of those in the south (possibly excepting those at node 35). Node 31 demarcates a clade, the most primitive members of which are restricted to temperate east Asia.

Although pattern 5 contains a large number of taxa, and many of those taxa are relatively well studied, this phylogenetic analysis yields limited information on restricted areas of endemism within the Northern Hemisphere and the Asian Tropics or the interrelationships of such areas. Nonetheless, a few points are worth mentioning.

First, the eastern and western Palearctic and the eastern and western Nearctic are strictly delimited, and virtually no species cross those boundaries. Within these areas, however, the demarcation of areas of endemism is much less clear cut.

For the Palearctic, only the clade arising at node 47 is informative, with the far eastern U.S.S.R. + Korea + Japan (node 48) related to Mongolia + Transbaikal and western Europe.

For the Nearctic, only clade 53 is informative, with the following pattern: (southern Rocky Mountains (northeastern Mexico (northcentral North America (eastern United States + southeastern United States)))).

Information on taxa from Southeast Asia (as well as the widespread *Pilophorus pilosus* from Africa) involves too few taxa in too few areas to produce any definitive hypotheses.

DISCUSSION

In summary, the Pilophorini appear to be of tropical Gondwanian origin with subsequent spread into, and differentiation in, the temperate Northern Hemisphere. This scenario is compatible with the hypothesis of Schuh and Stonedahl (1986), in which taxa occurring in Africa were portrayed as primitive relative to those from tropical Asia. However, it adds an additional basal element indicating that the New World tropics (pattern 1) is basal to the Old World Tropics (patterns 2 and 3); it further suggests that parts of Southeast Asia have a relationship with the southeastern United States, and that those areas in turn are related to the remainder of the Northern Hemisphere; and, the fauna of the northern land masses is more recent in origin than that of the southern continents. Temperate South America and Australia appear to have played no part in the biogeographic history of the Pilophorini.

One does not have to search far, even within the Miridae, to find additional groups with distributions similar to those of the Pilophorini: the phyline tribe Hallodapini sensu Wagner (1973) and Schuh (1974, 1984) has an Indo-Pacific distribution with a few species in the southern Palearctic and one genus, *Cyrtopeltocoris* Reuter, in North America (Schuh, 1974); however, it is completely absent from the New World tropics. Liebherr's (1986) analysis of the subtribe Caelostomina and Ball's analysis (1985) of the Galeritini (Coleoptera: Carabidae) indicate distributions similar to those of the Pilophorini,

although with some differences in intragroup area relationships, and in the former case there are no representatives in North America.

Papers in Liebherr (1988) cite a number of distributions linking the Caribbean to West Africa, which may be part of the pattern observed in the Pilophorini. Unfortunately, none of those works contains analyses which allow for direct comparison with mine for the Pilophorini, either because they lack information on cladistic relationships or because the cladistic relationships and distributions are too broadly defined to be comparable.

Bremer (1987) advanced the hypothesis that the large Indo-Pacific biotic element on the Asian land mass could be explained through tectonic accretion of a portion of Gondwanaland to Laurasia. Certainly, this thesis finds support in the data presented here, as well as in that published by Schuh and Stonedahl (1986), and generally conforms to the distributions of untold numbers of insect and plant groups. Bremer's theory has the additional appeal of explaining—in a vicariance perspective—how a group of Gondwanan origin achieved a distribution including the Holarctic. The occurrence of the four *Pherolepsis* species and *Pilophorus yunganensis* in the eastern Palearctic and southern China respectively suggests that suturing Gondwana fragments could offer entry for the Pilophorini onto that portion of the Laurasian landmass.

A relationship between Southeast Asia and the southeastern United States is less readily explained mechanistically, unless by isolation as the result of extinction, as has apparently occurred in many plant groups.

As noted above, *Pilophorus lestoni* and *P. linnavuorii* (node 36) from tropical West Africa possess characters of the head and labium that would seem to ally them with node 14, a strictly African group. Additional inquiry might indicate that the relationships of the species at node 36 are improperly understood, and that they should assume a more basal position in the cladogram.

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**Appendix 1. List of Valid Names, Distributions, and Hosts for the Pilophorini
(names marked with an * not included in phylogenetic analysis)**

ALEPIDIELLA POPPIUS, 1914

heidemanni Poppius, 1914 /S.E. U.S.A./ [Pinaceae: *Pinus virginiana*, *P. taeda* (Schuh and Schwartz. 1988)]

ALOEA LINNAUORI, 1975

- australis** Schuh, 1974 /S. Africa: Transvaal/ [Liliaceae: *Aloe* sp. (Schuh, 1974)]
***callosa** Linnavuori, 1975 /Sudan/ [Liliaceae: *Aloe* sp. (Linnavuori, 1975)]
cunealis cunealis Linnavuori, 1975 /Somalia/ [Liliaceae: *Aloe* sp. (Linnavuori, 1975)]
***cunealis persimilis** Linnavuori, 1975 /Sudan/ [Liliaceae: *Aloe* sp. (Linnavuori, 1975)]
***iadom** Linnavuori, 1973 /Zaire/ [Liliaceae: *Aloe* sp. (Linnavuori, 1973)]
nairobi Schuh, 1989 /Kenya/
nigritula Linnavuori, 1975 /Yemen/ [Liliaceae: *Aloe* sp. (Linnavuori, 1975)]
***planiceps** Linnavuori, 1975 /Somalia/ [Liliaceae: *Aloe* sp. (Linnavuori, 1975)]
¹*samueli Schuh, 1974 /S. Africa: Transvaal/ [Liliaceae: *Aloe* sp. (Linnavuori, 1975)]

DRUTHMAREUS DISTANT, 1909

- *coxalis** (Reuter, 1891) /Java/
***magnicornis** Distant, 1909 /Sri Lanka/
philippinensis Schuh, 1984 /Philippine Islands/

HYPSELOECUS REUTER, 1891

- deemingi** (Schuh, 1989) /Chad; N. Nigeria/
ifugao (Schuh, 1984) /Philippine Islands: Luzon/
koroba (Schuh, 1984) /Papua New Guinea/
maesta (Odhiambo, 1960) /E. and W. Africa/
morobe (Schuh, 1984) /Papua New Guinea/
munroi (Schuh, 1974) /S. Africa: Transvaal/ [Loranthaceae: *Loranthus zeyheri*, L. sp. (Schuh, 1974)]
opima (Odhiambo, 1960) /E. Africa/
rustenbergensis (Schuh, 1974) /S. Africa: Transvaal/
²***squamata** (Carvalho, 1987) /Papua New Guinea/
***tamaricis** (Linnavuori, 1975) /Ethiopia/ [Loranthaceae: on a parasite of *Tamarix*]
visci (Piton, 1888) /W. Europe/ [Loranthaceae: *Viscum album*]
***v-rubra** (Linnavuori, 1975) /Sudan/

NEOAMBONEA SCHUH, 1974

- cynanchi** Schuh, 1974 /S. Africa: Cape Prov., Transvaal/ [Asclepiadaceae: *Cynanchum africanum* (Schuh, 1974)]
***russeola** (Linnavuori, 1975) /Sudan/ [prob. Loranthaceae: on parasites of *Acacia* and *Tamarix* (Linnavuori, 1975)]
samaru Schuh, 1989 /Chad; N. Nigeria/
***scutellaris** Linnavuori, 1986 /Saudi Arabia/ [Loranthaceae (Linnavuori, 1986)]
***slateri** Schuh, 1974 /S. Africa: Cape Prov./ [Asclepiadaceae: *Cynanchum obtusifolium* (Schuh, 1974)]
uniformis (Linnavuori, 1975) /Ethiopia; Kenya/ [Loranthaceae: unident. parasite of *Tamarix* (Linnavuori, 1986)]
yotvata Schuh, 1989 /Chad; S. Israel/

PARAMBONEA SCHUH, 1974

- transvaalensis** Schuh, 1974 /S. Africa: Transvaal/

PARASTHENARIDEA MILLER, 1937

- arecae** Miller, 1937 /Malaya/ [Palmae: *Areca catechu* (Miller, 1937)]

PHEROLEPIS KULIK, 1968

- aenescens** (Reuter, 1901) /U.S.S.R.: Transbaikal, Far East; Mongolia; N.E. China/ [Ulmaceae: *Ulmus pumila* (Kerzhner, 1970)]
amplus Kulik, 1968 /U.S.S.R.: Amur Prov., Maritime Territory; Korea/ [Salicaceae: *Salix rorida*, *Salix* sp. (Kerzhner, 1970)]
fasciatus (Kerzhner, 1970) /U.S.S.R.: Maritime Territory/ [Ulmaceae: *Ulmus japonica* (Kerzhner, 1988)]
kiritschenkoi (Kerzhner, 1970) /U.S.S.R.: Maritime Territory/ [Salicaceae: *Salix rorida* (Kerzhner, 1970)]

PILOPHORUS HAHN, 1826

- *alstoni** Schuh, 1984 /India, Java, Malaya, Philippine Islands/
americanus Poppus, 1914 /Western United States and Canada/ [Pinaceae: *Abies amabilis*, *Picea* sp., *Pinus albicaulis*, *P. contorta*, *P. flexilis*, *P. monophylla*, *P. monticola*, *P. ponderosa*, *P. strobiformis*, *Pseudotsuga menziesii* (Schuh and Schwartz, 1988)]

¹ Sister group of *Aloe australis*.

² Sister group of *Hypseloecus ifugao*.

- amoenus** Uhler, 1887 /Eastern North America/ [Cupressaceae: *Chamaecyparis* sp.; Pinaceae: *Picea abies*, *Pinus banksiana*, *P. clausa*, *P. rigida*, *P. strobus*, *P. sylvestris*, *P. virginiana* (Schuh and Schwartz, 1988)]
- ***angustulus** Reuter, 1888 /Mediterranean Europe/ [Fagaceae: *Quercus* spp. (Wagner, 1973)]
- arboreus** Schuh, 1989 /Borneo/ [Dipterocarpaceae: *Shorea johorensis* (Schuh, 1990)]
- ***aureus** Zou, 1983 /China: Beijing, Hebei, Henan, Shandong/
- ***bakeri** Schuh, 1984 /Philippine Islands/
- balli** Knight, 1968 /N. Mexico; S.W. United States/
- ***benjamin** Rieger, 1984 /Greece/ [Pinaceae: *Pinus* (Rieger, 1984)]
- ***bistriatus** (Zou, 1987) /China: Yunnan/
- ***borneoensis** Carvalho, 1986, /Borneo/
- brunneus** Poppus, 1914 /E. North America/ [Salicaceae: *Salix* spp.; other woody dicots (Schuh and Schwartz, 1988)]
- ***buenoi** Poppus, 1914 /S.E. United States/
- ***castaneus** (Zou, 1983) /China: Yunnan/
- cembroides** Schuh and Schwartz, 1988 /Mexico: Zacatecas; U.S.A.: W. Texas/ [Pinaceae: *Pinus cembroides*, *P. sp.* (Schuh and Schwartz, 1988)]
- chiricahuae** Knight, 1968 /U.S.A.: Arizona/ [Salicaceae: *Salix* sp. (Schuh and Schwartz, 1988)]
- choii** Josifov, 1977 /North Korea; Far Eastern U.S.S.R./ [Fagaceae: *Quercus dentata*, *Q. sp.* (Josifov, 1977; Kerzhner, 1988)]
- cinnamopteris** Kirschbaum, 1855 /Palearctic/ [Pinaceae: *Pinus sylvestris* (Kerzhner, 1988)]
- clavatus** (Linnaeus, 1767) /Palearctic; N. America: introduced/ [Cornaceae: *Cornus* sp.; Fagaceae: *Quercus* spp.; Salicaceae: *Salix* spp., *Populus* sp.; Tiliaceae: *Tilia* sp. (Wagner, 1973; Kerzhner, 1988; Schuh and Schwartz, 1988)]
- clavicornis** Poppus, 1914 /U.S.A.: Nevada, Arizona/ [Pinaceae: *Pinus monophylla* (Schuh and Schwartz, 1988)]
- concolor** Schuh and Schwartz, 1988 /U.S.A.: California, Nevada, Oregon/ [Pinaceae: *Abies concolor*, *Pinus contorta* (Schuh and Schwartz, 1988)]
- confusus** Kirschbaum, 1855 /Palearctic/ [Salicaceae: *Salix* (Wagner, 1973)]
- crassipes** Heidemann, 1892 /E. North America/ [Pinaceae: *Pinus banksiana*, *P. echinata*, *P. mugo*, *P. ponderosa*, *P. resinosa*, *P. rigida*, *P. strobus*, *P. sylvestris*, *P. taeda*, *P. virginiana*, *Tsuga canadensis* (Schuh and Schwartz, 1988)]
- culion** Schuh, 1984 /Philippine Islands/
- dailanh** Schuh, 1984 /Viet Nam; Java; Sumatra; Borneo/
- daradae** Schuh, 1984 /New Guinea/
- ***decimaculatus** Zou, 1983 /China: Yunnan/
- diffusus** Knight, 1968 /W. North America: Rocky Mountains/ [Pinaceae: *Abies* sp., *Picea engelmanni*, *Pinus albicaulis*, *P. aristata*, *P. contorta*, *P. edulis*, *P. monticola*, *P. ponderosa*, *P. flexilis* (Schuh and Schwartz, 1988)]
- discretus** Van Duzee, 1918 /S.W. U.S.A.: Mexico: Baja California/ [Compositae, Leguminosae: various woody species (Schuh and Schwartz, 1988)]
- disjunctus** Kerzhner, 1969 /U.S.S.R.: Turkmenia, Tadzhikistan and Kazakhstan (Kerzhner, in litt.); Iran/ [Salicaceae: *Salix* sp., Leguminosae: *Halimodendron halodendron*; Anacardiaceae: *Pistacea vera*; also on introduced *Catalpa* in botanical garden (Kerzhner, 1968 and in litt.)]
- dislocatus** Knight, 1968 /United States: S. Rocky Mountains/ [Pinaceae: *Pinus edulis*, *P. ponderosa* (Schuh and Schwartz, 1988)]
- erraticus** Linnavuori, 1962 /Japan: Honshu; North Korea; Far Eastern U.S.S.R./ [Betulaceae: *Alnus* sp. and other woody dicots (Josifov, 1987; Kerzhner, 1988)]
- exiguus** Poppus, 1914 /S.W. United States/ [Pinaceae: *Pinus edulis*, *P. monophylla* (Schuh and Schwartz, 1988)]
- explanatus** Schuh and Schwartz, 1988 /U.S.A.: S. Arizona/
- floridanus** Knight, 1973 /U.S.A.: Florida/ [Pinaceae: *Pinus clausa* (Schuh and Schwartz, 1988)]
- formosanus** Poppus, 1914 /Taiwan/
- furvus** Knight, 1923 /E. U.S.A./ [Pinaceae: *Pinus virginiana* (Schuh and Schwartz, 1988)]
- fuscipennis** Knight, 1926 /U.S.A.: S. Rocky Mountains/ [Pinaceae: *Pinus edulis*, *P. monophylla* (Schuh and Schwartz, 1988)]
- fyan** Schuh, 1984 /Viet Nam/
- ***gallicus** Remane, 1954 /S. France/ [Salicaceae: *Populus alba*, *Salix* spp. (Wagner, 1973)]
- geminus** Knight, 1926 /Northcentral U.S.A. and adjacent Canada/ [Pinaceae: *Pinus banksiana* (Schuh and Schwartz, 1988)]
- gracilis** Uhler, 1895 /E. U.S.A./ [Pinaceae: *Pinus banksiana*, *P. clausa*, *P. ellioti*, *P. glabra*, *P. resinosa*, *P. rigida*, *P. taeda*, *P. virginiana* (Schuh and Schwartz, 1988)]
- heidemanni** Poppus, 1914 /S.E. U.S.A./ [Pinaceae: *Pinus clausa*, *P. taeda* (Schuh and Schwartz, 1988)]
- henryi** Schuh and Schwartz, 1988 /S.E. U.S.A./
- ***indonesicus** new name for *Pilophorus sumatranus* (Schuh, 1984), a secondary homonym of *Pilophorus sumatranus* Poppus, 1914 /Sumatra/
- ***javanus** Poppus, 1914 /Java/

- juniperi** Knight, 1923 /E. North America/ [Cupressaceae: *Chamaecyparis lawsoniana glauca*, *Juniperus chinensis sargentii*, *J. C. pfutzeriana hetzi*, *J. virginiana*, *J. communis*; Pinaceae: *Thuja orientalis* (Schuh and Schwartz, 1988)]
- ***kathleena** Schuh, 1984 /S.E. Asia: "Carat"/
- kockensis** Schuh, 1984 /Sumatra/
- koreanus** Josifov, 1977 /North Korea/ [on various woody dicots including: *Castanea* sp., *Quercus* sp., *Salix* dp., *Ulmus* sp. (Josifov, 1977)]
- laetus** Heidemann, 1892 /E. North America/ [Cupressaceae: *Juniperus virginiana*; Pinaceae: *Picea abies*, *Pinus banksiana*, *P. echinata*, *P. eliottii*, *P. resinosa*, *P. rigida*, *P. strobus*, *P. sylvestris*, *P. taeda*, *P. virginiana*, *Thuja orientalis* (Schuh and Schwartz, 1988)]
- lestoni** Schuh, 1989 /Ghana/
- linnavuorii** Schuh, 1989 /W. Africa/
- longisetosus** Knight, 1968 /U.S.A.: Rocky Mountains/ [Fagaceae: *Quercus gambelli*, *Q.* sp. (Schuh and Schwartz, 1988)]
- lucidus** Linnavuori, 1962 /Japan: Kyushu; Far Eastern U.S.S.R./
- ***maculata** (Schuh, 1984) /Thailand/
- ³***minutissimus** Linnavuori, 1975 /Africa/ Incertae Sedis (see Schuh, 1989)
- ***minutus** Knight, 1973 /S.W. U.S.A./
- miyamotoi** Linnavuori, 1961 (incorrectly recorded and figured as *setulosus* by Schuh, 1984) /Japan: Kyushu; Far Eastern U.S.S.R./ [Pinaceae: *Pinus densiflora* (Kerzhner, 1988)]
- mongolicus** Kerzhnev, 1984 /Mongolia; U.S.S.R.: Transbaikal/ [Rosaceae: *Amygdalus pedunculata*; Ulmaceae: *Ulmus pumila* (Kerzhner, 1984)]
- myrmecoides** (Carvalho, 1956) /Philippine Islands/
- ***nasicus** Knight, 1926 /S.E. U.S.A./
- neoclavatus** Schuh and Schwartz, 1988 /E. North America/ [Betulaceae: *Alnus* sp.; Fagaceae: *Quercus ilicifolia*, *Q. stellata*; Salicaceae: *Salix longifolia* (Schuh and Schwartz, 1988)]
- nevadensis** Knight, 1968 /Interior W. U.S.A./ [Compositae: *Artemisia tridentata*, *Chrysothamnus viscidiflorus*; Saxifragaceae: *Ribes* sp. (Schuh and Schwartz, 1988)]
- niger** Poppius, 1914 /China: W. Hupeh; Japan: Honshu; E. Mongolia (unpublished); Far Eastern U.S.S.R./ [woody dicots (Kerzhner, 1988); Salicaceae: *Salix* (Josifov, 1987); Aceraceae: *Acer mono*; Caprifoliaceae: *Lonicera* sp., Fagaceae: *Quercus dentata*; Ulmaceae: *Ulmus pumila* (Kerzhner, in litt.)]
- okamotoi** Miyamoto and Lee, 1966 /Korea; Far Eastern U.S.S.R./
- ***palawana** (Schuh, 1984) /Philippine Islands: Palawan/
- perplexus** Douglas and Scott, 1865 /Europe; North America (introduced)/ [Various woody dicots (Schuh and Schwartz, 1988)]
- piceicola** Knight, 1926 /N.E. North America/ [Pinaceae: *Picea abies*, *P. glauca*, *P. g. albertiana*, *P. polita*, *P. pungens*, *P. rubens*, *Pinus sylvestris*, *Pseudotsuga mensziesii* (Schuh and Schwartz, 1988)]
- pilosus** Odhiambo, 1958 /Africa/
- ***pilosus brevicollis** Linnavuori, 1975 /Sudan/
- ***pleiku** (Schuh, 1984) /Viet Nam/
- prolixus** Schuh, 1989 /Philippine Islands: Negros Island/
- ***pseudoperplexus** Josifov, 1987 /Japan: Honshu; North Korea; U.S.S.R.: Maritime Territory/ [on various woody dicots, including *Quercus mongolica*, *Acer mono*, *Fraxinus rhynchophylla*, *Phellodendron amurense* (Josifov, 1987; Kerzhner, 1987)]
- ***pulcher** (Henry, 1931) /Sri Lanka/
- pusillus** Reuter, 1878 /Europe/ [on various woody dicots including: *Quercus*, *Sarothamnus*, *Ulmus* (Wagner, 1973)]
- salicis** Knight /U.S.A.: Rocky Mountains/ [Salicaceae: *Salix interior*, *S.* sp. (Schuh and Schwartz, 1988)]
- samoanus** Knight, 1935 /Samoa/
- schaffneri** Schuh and Schwartz, 1988 /N.E. Mexico/ [Pinaceae: piñon pine (Schuh and Schwartz, 1988)]
- scharzi** Reuter, 1909 /W. North America/ [various woody dicots (Schuh and Schwartz, 1988)]
- ***scutellaris** Reuter, 1902 /Tunisia/
- setiger** Knight, 1941 /N.E. North America/ [Betulaceae: *Corylus* sp.; Fagaceae: *Quercus ilicifolia* (Schuh and Schwartz, 1988)]
- setulosus** Horvath, 1905 /Japan: Honshu, Kyushu; Far Eastern U.S.S.R./ [Salicaceae: *Salix*, rarely other woody dicots (Kerzhner, 1988)]
- sinuaticollis** Reuter, 1879 /U.S.S.R.: Middle Asia and Transcaucasus (Kerzhner, in litt.)/ [Salicaceae: *Populus diversifolia* (Kerzhner, in litt.), *Salix* spp. (Kiritshenko, 1964); Eleagnaceae: *Hippophae rhamnoides* (Kiritshenko, 1964)]
- stonedahli** Schuh and Schwartz, 1988 /W. U.S.A./ [Pinaceae: *Pinus ponderosa* (Schuh and Schwartz, 1988)]
- strobicicola** Knight, 1922 /N.E. North America/ [Pinaceae: *Picea abies*, *Pinus strobus*, *P. sylvestris*, *P. banksiana*, *Larix decidua* (Schuh and Schwartz 1988)]

³ Material of this species was inadequate to determine with certainty whether or not the taxon is actually a member of the Pilophorini (see discussion in Schuh, 1989: 15).

- ***sumatranus** Poppius, 1914 /Sumatra/
 * *sumatranus* (Schuh, 1984) see *Pilophorus indonesicus*
sundae (Schuh, 1984) /Northern Australia; Lesser Sunda Islands/
taxodii Knight, 1941 /S.E. U.S.A./ [Cupressaceae: *Taxodium distichum* (Schuh and Schwartz, 1988)]
tibialis Van Duzee, 1918 /W. U.S.A.; N. Mexico/ [Cupressaceae: *Juniperus monophylla*, *J. occidentalis*, *J. scopulorum*; Pinaceae: *Abies lasiocarpa*, *Pinus aristata*, *P. attenuata*, *P. chihuahuana*, *P. contorta*, *P. edulis*, *P. flexilis*, *P. monophylla*, *P. monticola*, *P. ponderosa*, *P. sabiniana*, *Pseudotsuga menziesii* (Schuh and Schwartz, 1988)]
tomentosus Van Duzee, 1918 /U.S.A.: S. California/ [Compositae: *Baccharis pilularis*, *Chrysothamnus* sp.; Salicaceae: *Salix lasiolepis*, *S. nigra* (Schuh and Schwartz, 1988)]
torrevillasi Schuh, 1984 /Borneo; Malaya; Philippine Islands/
typicus (Distant, 1909) /Tropical and subtropical Asia; Greater Sundas; New Guinea/
uhleri Knight, 1923 /N.E. North America/ [Pinaceae: *Larix decidua*, *Picea abies*, *P. glauca*, *P. pungens*, *Pinus banksiana*, *P. mugo*, *P. strobus*, *P. sylvestris*, *Tsuga canadensis* (Schuh and Schwartz, 1988)]
 ***validicornis** Kerzhner, 1977 /Far Eastern U.S.S.R./ [Pinaceae: *Picea glennii* (Kerzhner, 1988)]
vicarius Poppius, 1914 /U.S.A.: Rocky Mountains/ [various woody dicots (Schuh and Schwartz, 1988)]
walshii Uhler, 1887 /E. North America/ [Leguminosae: *Gleditsia triacanthos* (Schuh and Schwartz, 1988)]
yunganensis Schuh, 1984 /China: Yung An/

STHENARIDEA REUTER, 1891

- araguaiana** (Carvalho, 1948) /C. Mexico south to Peru, incl. Greater and Lesser Antilles/
australis (Schuh, 1974) /Madagascar; S. Africa/ [Cyperaceae: *Cyperus distans*, *C. latifolius*, *C. rotundis*, *Scirpus costatus*, *S. dioecus* (Schuh, 1974)]
 ***bergrothi** (Poppius, 1914) /Madagascar/
carmelitana (Carvalho, 1948) /C. America south to S. Brazil/
carvalhoi Schuh and Schwartz, 1988 /C. Mexico south to S. Brazil, incl. Greater and Lesser Antilles/ [Cyperaceae: *Fimbristylus spadicea* (Schuh and Schwartz, 1988)]
 ***clypealis** (Poppius, 1914) /Malawi/
 ***femoralis** (Poppius, 1914) /Malawi/
hansoni Schuh and Schwartz, 1988 /C. America south to Ecuador; Lesser Antilles/
 ***howanus** (Poppius, 1914) /Madagascar/
liberiensis Schuh, 1989 /Liberia/
 ***mahensis** (Distant, 1913) /Seychelle Islands/
maldonadoi Schuh and Schwartz, 1988 /C. America south to C. Brazil; Greater Antilles/
nigra (Poppius, 1914) /Tropical Africa/ [Cyperaceae spp. (Linnavuori, 1975)]
 ***nigra pallidicornis** (Linnavuori, 1975) /Sudan/ [in alpine meadows and forest undergrowth (Linnavuori, 1975)]
pacifica (Schuh, 1984) /Indo-West Pacific/
 ***paludicola** (Linnavuori, 1975) /Sudan/ [in swamps (Linnavuori, 1975)]
papuensis (Schuh, 1984) /Papua New Guinea/
piceonigra (Motschulsky, 1863) /Indo-West Pacific/ [Cyperaceae: *Scleria margaritifera* (Usinger, 1946)]
rondonia Schuh and Schwartz, 1988 /Brazil: Rondonia/
rufescens (Poppius, 1915) /Indo-West Pacific/ [Cyperaceae: *Rhynchospora corymbosa* (Usinger, 1946)]
suturalis (Reuter, 1900) /Africa/ [Cyperaceae: *Cyperus latifolius*, *Scirpus costatus*; Gramineae: *Cynodon dactylon*; Junacaceae: *Juncus kraussii* (Linnavuori, 1975; Lindberg, 1958)]
vulgaris (Distant, 1893) /New World Tropics/ [Cyperaceae: *Cyperus lazulae* (Schuh and Schwartz, 1988)]

Appendix 2. Character Descriptions for the Pilophorini (Left margin: character number, length on tree, consistency index, retention index)

GENERAL STRUCTURE

- 0 5 0.40 0.93 body form: (1) ovoid [Fig. 1(a)]; (2) elongate [Figs. 1(b,d)]; (3) short and stout [Fig. 1(c)].

STRUCTURE OF HEAD AND LABIUM

- 1 2 1.00 1.00 head: (1) convex behind; (2) concave behind [Figs 1(a-d)]; (3) concave behind but exerted [Fig. 2(l)].
 2 4 0.25 0.50 genae straight or rounded in frontal view: (1) straight in frontal view [Fig. 2(k)]; (2) distinctly convexly rounded in frontal view [Fig. 2(i)].
 3 6 0.16 0.50 genae flat or carinate: (1) flat or very broadly rounded or weakly to moderately carinate [Fig. 2(b)]; (2) conspicuously elevated and strongly carinate [Fig. 2(j)].
 4 8 0.37 0.90 gula: (1) obsolete; (2) short to moderately long [Figs 2(a,j)]; (3) long without carina; (4) long and with a carina [Fig. 2(l)].

- 5 3 0.33 0.80 gular ridge or roll: (a) absent; (2) present.
- 6 1 1.00 1.00 mandibular plate protruding above maxillary plate: (a) absent; (2) present [Figs 2(k, l)].
- 7 2 0.50 0.96 head below eyes in males: (1) obsolete [Fig. 2(b)]; (2) not obsolete and often approaching half the height of an eye [Figs 2(k, l)].
- 8 2 0.50 0.90 labial shape: (1) segments 3 and 4 elongate and slender with a combined length usually nearly 2 times length of segment 2 [Figs 2(b, j)]; (2) segments 3 and 4 enlarged, combined length at most slightly greater than length of segment 2 [Figs 2(d, f)].
- 9 4 0.25 0.92 labial segment one: (1) surpassing posterior margin of head and reaching to about midpoint of prosternal xyphus [Figs 2(b, d, f, h)]; (2) same length as buccal cavity or only slightly longer but never reaching to midpoint of prosternal xyphus [Figs 2(j, l)].
- 10 2 0.50 0.90 labial segment one: (1) slender (Fig. 2(b)); (2) very heavy [Figs 2(d, f, h)].
- 11 2 0.50 0.90 buccal cavity: (1) ovoid and directed more or less ventrally and serving as a receptacle for at least 1/2 the length of labial segment 1 [Figs 2(b, j, l)]; (2) usually round and like the apex of the clypeus strongly oriented posteroventrally and receiving only the extreme basal portion of labial segment 1 (Figs 2(d, f, h)).

STRUCTURE OF PRONOTUM, SCUTELLUM AND MESOS CUTUM

- 12 3 0.66 0.83 pronotal shape: (1) pronotum not constricted between anterior and posterior lobes [Figs 1(a, d)]; (2) pronotum weakly constricted between anterior and posterior lobes; (3) pronotum strongly constricted between anterior and posterior lobes and necklike or more or less hourglass shaped [Fig. 2(l)].
- 13 1 1.00 1.00 pronotum campanulate or not: (1) pronotum not campanulate; (2) pronotum campanulate.
- 14 4 0.50 0.71 calli: (1) obsolete [Fig. 1(a-d)]; (2) distinct but not conical; (3) in the form of long conical projections [Fig. 2(l)].
- 15 1 1.00 1.00 pronotal punctures: (1) absent; (2) present.
- 16 24 0.08 0.37 pronotal surface (1): (1) dull; (2) moderately shining; (3) highly polished and shining.
- 17 25 0.08 0.72 pronotal surface (2): (1) smooth and sometimes granulose or otherwise roughened but never punctured or rugose; (2) weakly to moderately rugulose; (3) strongly rugose.
- 18 5 0.60 0.95 Scutellar development: (1) bulbous; (2) flat or weakly transversely rounded [Fig. 1(a)]; (3) elevated anteromesially and flattened laterally and apically [Figs 1(b, d)]; (4) strongly elevated mesially and nearly conical and flattened laterally and apically [Fig. 1(c)].
- 19 2 0.50 0.96 mesoscutum elevation: (1) flat and only slightly elevated anteriorly [Fig. 1(a)]; (2) moderately to highly elevated anteriorly [Figs 1(b-d)].

STRUCTURE OF HEMELYTRA

- 20 3 0.33 0.95 corial margin: (1) convex [Fig. 1(a)]; (2) weakly to strongly sinuous [Figs 1(b-d)].
- 21 3 0.33 0.95 hemelytra: (1) at most weakly declining laterally and entire length of costa always visible from above [Fig. 1(a)]; (2) strongly declining laterally and coastal margin usually at least partially obscured in dorsal view (Figs 1(b-d)).
- 22 2 0.50 0.00 hemelytral conformation: (1) not conforming to abdomen; (2) conforming to abdomen.
- 23 4 0.75 0.98 corial texture: (1) uniform; (2) weakly polished posterolaterally, dull and matte-like posteromesially [Fig. 1(d)]; (3) weakly polished posteriorly, dull and matte-like anteriorly [Fig. 1(b)]; (4) strongly polished and highly shining anteriorly and posteriorly with remainder tomentose.
- 24 1 1.00 1.00 hemelytral punctuation: (1) absent; (2) punctate.

ANTENNAL STRUCTURE AND COLORATION

- 25 6 0.33 0.20 antennal segment 2: (1) terete or boxlike [Figs 2(n, o)]; (2) elongate, slender, and nearly cylindrical; (3) weakly to strongly clavate [Fig. 2(m)].
- 26 26 0.7 0.69 coloration of antennal segment 3: (1) dark; (2) light; (3) light proximally and dark distally [Fig. 2(m)].
- 27 21 0.9 0.69 coloration of antennal segment 4: (1) dark; (2) light; (3) light proximally and dark distally [Fig. 2(m)].

STRUCTURE AND COLORATION OF TIBIAE

- 28 25 0.08 0.52 metatibia in cross section: (1) nearly cylindrical [Fig. 1(a)]; (2) weakly to moderately flattened [Fig. 1(b)]; (3) strongly flattened.
- 29 27 0.07 0.45 metatibia in lateral view: (1) nearly straight [Fig. 1(a)]; (2) weakly to moderately curved [Fig. 1(b)]; (3) strongly curved.
- 30 9 0.22 0.82 metatibial coloration: (1) unicolorous dark; (2) unicolorous light; (3) spotted at bases of tibial spines.

VESITURE

- 31 1 1.00 1.00 genal setae: (a) a few erect setae, sometimes rather heavy and bristle like [Fig. 2(j)]; (2) numerous long erect setae [Fig. 2(l)].
- 32 17 0.17 0.54 common setae on hemelytra: (1) bristlelike; (2) when present, of moderate length and reclining; (3) moderate length and nearly erect; (4) long to very long and nearly erect.
- 33 11 0.18 0.71 common setae on frons and vertex: (1) when present, of moderate length and reclining; (2) moderately long and erect; (3) very long and erect.
- 34 9 0.22 0.70 common setae on pronotum: (1) when present, of moderate length and reclining; (2) moderately long and erect; (3) very long and erect.
- 35 2 0.50 0.97 scalelike setae on head: (1) absent; (2) present.
- 36 7 0.28 0.86 scalelike setae on pronotum: (1) absent; (2) widely distributed; (3) present on anterior margin only.
- 37 8 0.25 0.88 lateral scalelike scutellar setae: (a) absent; (2) scattered; (3) weakly to strongly aggregated [Figs 1(b-d)].
- 38 11 0.18 0.84 apical scalelike scutellar setae: (1) absent; (2) scattered; (3) weakly to strongly aggregated [Figs 1(b-d)].
- 39 3 0.33 0.94 scalelike setae on propleuron: (1) absent; (2) scattered individual setae or in small scattered patches.
- 40 4 0.75 0.97 scalelike setae on mesopleuron: (1) absent; (2) scattered individual setae or in small scattered patches; (3) weakly to strongly aggregated on posterior margin of mesepimeron and directed posteroventrally; (4) aggregated and directed anteroventrally.
- 41 7 0.28 0.88 scalelike setae on metapleuron: (1) absent; (2) scattered individual setae or in small scattered patches; (3) weakly to strongly aggregated on posterior margin of metepisternum or sometimes absent if also aggregated on mesopleuron.
- 42 9 0.22 0.87 scalelike setae on abdomen: (a) absent; (2) scattered individual setae or in small scattered patches; (3) aggregated in a patch anterolaterally.
- 43 4 0.50 0.95 scalelike setae on hemelytra: (1) absent; (2) scattered [Fig. 1(a)]; (3) aggregated in patches or bands [Figs 1(b-d)].
- 44 4 0.50 0.33 Anterior band of scalelike setae on clavus: (1) present across width of clavus but offset from portion of band on corium; (2) absent; (3) present across entire clavus and contiguous with band on corium.
- 45 2 0.50 0.97 anterior band of scalelike setae on corium only: (a) absent; (2) present [Figs 2(b-d)].
- 46 4 0.25 0.94 complete posterior band of scalelike setae (1): (1) absent or sometimes consisting of scattered patches; (2) present [Figs 1(b-d)].
- 47 7 0.28 0.90 complete posterior band of scalelike setae (2): (1) absent; (2) not interrupted mesad of radial vein although sometimes offset [Fig. 1(b)]; (3) interrupted mesad of radial vein or at claval suture.
- 48 2 0.50 0.80 complete posterior band of scalelike setae offset at radial vein: (1) absent; (2) present [Fig. 1(d)].
- 49 7 0.14 0.14 complete posterior band of scalelike setae offset at claval suture: (1) absent; (2) present [Fig. 1(d)].
- 50 1 1.00 1.00 posterior band of scalelike setae in the form of four discrete patches: (1) absent; (2) present [Fig. 1(c)].
- 51 4 0.25 0.57 posterior band of scalelike setae incomplete and consisting of one or two or three patches: (1) absent; (2) present.
- 52 15 0.13 0.81 scalelike setae or cuneus: (1) absent; (2) scattered [Fig. 1(a)]; (3) more or less aggregated anteriorly or anteromesially [Figs 2(b-d)].

MEMBRANE COLORATION

- 53 2 0.50 0.97 membranal coloration: (1) unicolorous or mottled [Fig. 1(a)]; (2) with a large more or less strongly contrasting dark patch at least partially covering cells [Figs 2(b-d)].

ABDOMINAL STRUCTURE

- 54 5 0.40 0.93 abdominal shape: (1) broader basally than at any point posterior to base; (2) parallel sided or weakly to moderately constricted basally but never bulbous apically; (3) strongly constricted basally and bulbous apically.

THORACIC PLEURON

- 55 2 0.50 0.90 intense velvety black patches on meso- and metapleura: (1) absent; (2) present.

VESICAL STRUCTURE

- 56 10 0.40 0.79 apex of vesica (1): (1) variously modified but never as follows; (2) in the form of a simple attenuated sclerotized tubular structure [Fig. 3(a)]; (3) with a sclerotized "backbone"

- distad of secondary gonopore attended on one side by a membranous elaboration [Figs 5(a-h)]; (4) with a single asymmetrical winglike structure [Fig. 3(c)]; (5) with large paired winglike structures [Fig. 3(b)].
- 57 3 1.00 1.00 secondary gonopore when present (1): (1) strongly sclerotized and horse collar shaped; (2) secondary gonopore absent; (3) present as a lateral indentation on vesica [e.g., Figs 5(a-h)]; (4) present as a circular sclerotized opening but without "horsecollar" ornamentation [Fig. 3(b)].
- 58 4 0.25 0.88 glassy spicules subtending secondary gonopore: (1) absent; (2) present [e.g., Figs 3(b, h)].
- 59 8 0.12 0.83 Mesial spine of vesica: (a) absent; (2) present as a well developed elongate lanceolate or cylindrical process [Figs 3(h, i, etc.)].
- 60 7 0.28 0.83 subbasal or mesial ornamentation of mesial spine on surface of spine adjacent to vesica: (1) barb or denticle [Fig. 3(j)]; (2) none; (3) thumblike process [Figs 3(k), 5(f), etc.].
- 61 1 1.00 1.00 subapical denticles of mesial spine: (1) none; (2) one to four [Fig. 4(f)].
- 62 7 0.14 0.77 mesial barb on vesica and sometimes subtending mesial spine: (1) absent; (2) present [Figs 4(c, f, h, m)].
- 63 4 0.50 0.33 mesial spine of vesica apically: (1) not bifid; (2) bifid [Figs 3(h), 4(j)].
- 64 2 0.50 0.00 shape of mesial spine: (1) mesial spine more or less cylindrical or if flattened not distinctly broadest at midpoint; (2) mesial vesical spine flattened and broadest at about midpoint [Fig. 4(d)].
- 65 6 0.16 0.44 point of origin of mesial vesical spine: (1) mesial vesical spine arising from "inner" surface of vesica; (2) mesial vesical spine arising from lateral surface of vesica [Figs 4(f, k, etc.)].
- 66 4 0.50 0.93 shape of vesica: (1) sigmoid or otherwise not conforming to the following conditions; (2) C shaped and more or less flat at least basally; (3) C shaped and distinctly twisted [Fig. 5(g, etc.)].
- 67 1 1.00 1.00 vesica heavily scleroized with a "hooklike" formation just proximal to secondary gonopore: (1) absent; (2) present [Fig. 3(c)].

PHALLOTHECAL STRUCTURE

- 68 4 0.75 0.94 phallosome shape: (1) straight but fixed to phallobase; (2) conventional and curved [(Fig. 2(p)); (3) with a curved but short and narrow apical portion [Figs 2(q, r)]; (4) erect and more or less straight.
- 69 3 0.66 0.93 apex of phallosome: (1) strongly pointed; (2) elongate but not strongly pointed; (3) beak-like or without distinctive ornamentation [Figs 2(q, r)].

PARAMERE STRUCTURE

- 70 3 0.33 0.88 left paramere splayed out: (1) conventional phylline shape and not splayed out; (2) weakly to strongly splayed out [Figs 2(u, w)].
- 71 3 0.66 0.93 left paramere cleft: (1) not cleft; (2) weakly cleft [Fig. 2(u)]; (3) strongly cleft [Fig. 2(v)].
- 72 3 0.66 0.95 posterior arm of left paramere: (1) flattened and moderately to greatly elevated and dorsal margin angulate [Fig. 2(t)]; (2) strongly flattened and greatly elongated and usually acuminate at apex [Fig. 2(s)]; (3) not strongly flattened or elevated and dorsal margin not angulate.

Appendix 3. Key to the Genera of Pilophorini

1. Scalelike setae present on propleuron and scattered; scalelike setae of meso- and metathoracic pleura of more or less scattered distribution and not aggregated on posterior margin of sclerite (Schuh, 1984: Fig. 76) 2
- Scalelike setae absent from propleuron; scalelike setae always present on meso- and metathoracic pleura and always aggregated on posterior margin of sclerite 9
2. Antennal segment 2 distinctly swollen and enlarged over nearly entire length [Figs 2(n, o)] 3
- Antennal segment 2 never swollen over nearly entire length, although sometimes weakly to moderately clavate or otherwise modified 4
3. Coloration of dorsum in large part castaneous, never unicolorous black; S.E. United States *Alepidiella* Poppius
- Coloration of dorsum unicolorous black (Schuh, 1984: figs 74, 75); S.E. Asia, Sri Lanka *Druthmarus* Distant
4. Labium distinctly tapering toward acuminate apex, segments 3 and 4 elongate and slender, basal segment elongate but not particularly heavy [Figs 2(b, j, l)]; buccal cavity elongate-ovoid and directed more or less ventrally 5
- Labium heavy over entire length, not conspicuously tapering toward apex, segments 3 and 4 of a combined length at most slightly greater than length of segments 2; basal segment long and heavy [Figs 2(d, f, h)]; buccal cavity nearly round and strongly directed posteriorly 7

- 5. Meso- and metathoracic pleura each with an intense velvety black patch near dorsal margin; body form usually more or less rectangular or quadrate, length apex tylus-cuneal fracture usually greater than 2.00 mm; southern Palearctic, Paleotropical. *Hypseloecus* Reuter
- Meso- and metathoracic pleura rarely with intense velvety black patches; body form ovoid (Schuh and Schwartz, 1988: fig. 33), length apex tylus-cuneal fracture always less than 1.55 mm 6
- 6. Vesica in the form of a simple attenuated tube as in Fig. 3(a); found on sedges, rushes, and grasses; Pantropical *Sthenaridea* Reuter
- Vesica more complicated (Schuh, 1984: fig. 122), not in the form of a simple tube; found on Palmae; Malaya *Parasthenaridea* Miller
- 7. Pronotum dull, smooth, without rugosities (Schuh, 1974: figs 84, 85); calli pronounced; found on *Aloe*; Africa, Arabian Peninsula *Aloea* Linnavuori
- Pronotum distinctly rugose, calli never distinctly pronounced; known from Loranthaceae and Asclepiadaceae. 8
- 8. Vesica with one or two distal "horns" [Figs 3(b,c)]; body coloration varying from reddish to jet black; Africa, Arabian Peninsula *Neoambonea* Schuh
- Vesica without distal "horns" (Schuh, 1974: fig. 327); body coloration in known species always jet black; southern Africa *Parambonea* Schuh
- 9. Hemelytra with one or more distinctive, narrow, transverse bands of silvery, scalelike setae [Figs 1 (b-d)]; general body form often at least vaguely—often strongly—myrmecomorphic; Holarctic, Africa, Indo-West Pacific. *Pilophorus* Hahn
- Hemelytra without narrow transverse bands of silvery setae, although sometimes with silvery scalelike setae restricted to a limited portion of corium and clavus; general body form not myrmecomorphic; Eastern Palearctic *Pherolepis* Kulik