Investigations into the Phylogeny of the Lycosoid Spiders and Their Kin (Arachnida: Araneae: Lycosoidea)

CHARLES E. GRISWOLD

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 539

SERIES PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

Emphasis upon publication as a means of "diffusing knowledge" was expressed by the first Secretary of the Smithsonian. In his formal plan for the institution, Joseph Henry outlined a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge." This theme of basic research has been adhered to through the years by thousands of titles issued in series publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

Smithsonian Contributions to Anthropology
Smithsonian Contributions to Botany
Smithsonian Contributions to the Earth Sciences
Smithsonian Contributions to the Marine Sciences
Smithsonian Contributions to Paleobiology
Smithsonian Contributions to Zoology
Smithsonian Folklife Studies
Smithsonian Studies in Air and Space
Smithsonian Studies in History and Technology

In these series, the Institution publishes small papers and full-scale monographs that report the research and collections of its various museums and bureaux or of professional colleagues in the world of science and scholarship. The publications are distributed by mailing lists to libraries, universities, and similar institutions throughout the world.

Papers or monographs submitted for series publication are received by the Smithsonian Institution Press, subject to its own review for format and style, only through departments of the various Smithsonian museums or bureaux, where the manuscripts are given substantive review. Press requirements for manuscript and art preparation are outlined on the inside back cover.

Robert McC. Adams
Secretary
Smithsonian Institution

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 539

Investigations into the Phylogeny of the Lycosoid Spiders and Their Kin (Arachnida: Araneae: Lycosoidea)

Charles E. Griswold

SMITHSONIAN INSTITUTION PRESS
Washington, D.C.
1993

ABSTRACT

Griswold, Charles E. Investigations into the Phylogeny of the Lycosoid Spiders and Their Kin (Arachnida: Araneae: Lycosoidea). *Smithsonian Contributions to Zoology*, 539, 39 pages, 87 figures, 4 tables, 1993.—The phylogenetic relationships of spider families classically placed in the superfamily Lycosoidea, which possess a grate-shaped tapetum in some or all of the indirect eyes, are examined through exemplar taxa scored for 68 classical or newly elaborated characters. A derived calamistrum, which forms an oval to rectangular patch, is considered a synapomorphy uniting the Lycosoidea and several other genera formerly placed in the Tengellidae and Miturgidae. In the resulting analysis the Lycosoidea are shown to be monophyletic and the Tengellidae and Miturgidae polyphyletic. The Senoculidae, Oxyopidae, Stiphidiidae, and Psechridae form a monophyletic group. The monophyly of the Lycosidae, Trechaleidae (including Rhoicininae), Pisauridae plus Dolomedidae, and Zoropsidae are confirmed, whereas monophyly of the Ctenidae, Machadoniinae, and Uliodoninae are called into question.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging-in-Publication Data
Griswold, Charles E.
Investigations into the phylogeny of the Lycosoid spiders and their kin (Arachnida: Araneae, Lycosoidea) / Charles E. Griswold.
p. cm. - (Smithsonian contributions to zoology ; no. 539)
Includes bibliographical references.
1. Spiders—Phylogeny. I. Title. II. Title: Lycosoid spiders and their kin (Arachnida: Araneae: Lycosoidea). III. Series.
QL1.S54 no. 539 [QL458.4] 591 s-dc20 93-733 [595.4'4] CIP

Contents

Investigations into the Phylogeny of the Lycosoid Spiders and Their Kin (Arachnida: Araneae: Lycosoidea)

Charles E. Griswold

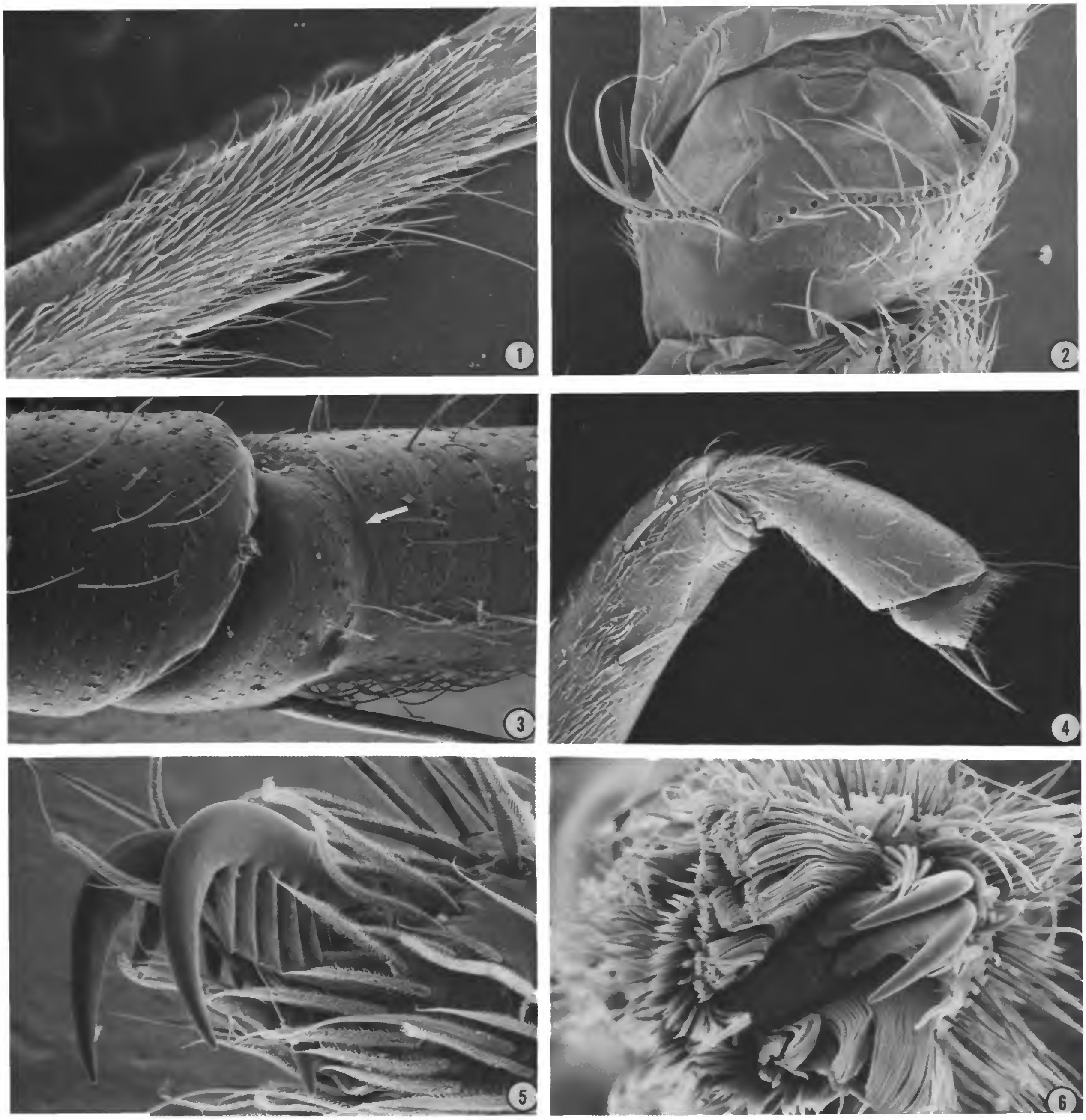
Introduction

This higher classification study had as its impetus a revisionary and phylogenetic analysis of the genera *Machadonia* and *Phanotea,* diverse but poorly known cursorial spiders from the cool-temperate forests of southern Africa. The taxonomic placement of these genera has never been stable. Most recently Lehtinen (1967) considered them (along with the genera *Campostichomma* and *Devendra* from Sri Lanka) to comprise his subfamily Machadoniinae of the Miturgidae, but the reasoning behind the association with the miturgids was not clear, and recent efforts to define the Miturgidae on the basis of synapomorphies (Platnick, 1990) suggested that the inclusion of the Machadoniinae was without basis. A possible key to the affinities of the Machadoniinae came in the discovery of a hitherto unreported leg character: a subbasal suture in the leg tibiae of males (Figures 3, 4) along which the legs of preserved specimens were frequently broken. Survey of the literature (Roth and Roth, 1984) and a large number of spider families revealed that this feature has a very restricted distribution: in the four machadoniine genera as well as a few obscure taxa placed by Lehtinen in his Miturgidae Uliodoninae (i.e., *Raecius, Uduba,* and *Zorodictyna*). Discovery of an apparently identical structure on the tibiae of male *Zoropsis* suggested that this "tibial crack" might be a synapomorphy for the family Zoropsidae. On the basis of a grate-shaped tapetum in the indirect eyes, *Zoropsis* was placed by Homann (1971) in a monophyletic group including the Lycosidae (Lycosoidea, sensu Levi, 1982b), and discovery of a similar grate-shaped tapetum in *Machadonia* appeared to corroborate the group characterized by the tibial crack. Subsequent discovery that *Uduba* has the more primitive canoe-shaped tapetum, and that *Takeoa,* which is arguably the closest relative of *Zoropsis,* lacks the tibial crack, revealed that the situation was not so simple. Once again understanding spider phylogeny was seen to be, as succinctly put by Coddington and Levi (1991:575), "not so much a question of finding characters as it is of allocating homoplasy."

Understanding the relationships of *Zoropsis,* the Machadoniinae, and other taxa (i.e., *Raecius, Uduba,* and *Zorodictyna*) with the tibial crack required consideration of other higher taxa potentially linked to these by synapomorphies. The occurrence of a grate-shaped tapetum in *Zoropsis* and *Machadonia* necessitated inclusion of all families for which a grate-shaped tapetum had been unambiguously recorded: Acanthoctenidae, Ctenidae, Dolomedidae, Lycosidae, Oxyopidae, Pisauridae, Psechridae, Senoculidae, Stiphidiidae, and Zoropsidae (Homann, 1971). A third potential synapomorphy was the nature of the calamistrum. A narrow, linear calamistrum, consisting of one or two rows of curved, laterally serrate setae (Foelix and Jung, 1978) occurs at all levels of the Araneomorphae. A calamistrum consisting of an oval to rectangular patch of typical calamistral setae (Figure 1) exhibits a restricted distribution in, and is potentially a synapomorphy for, a small group of entelegyne Araneoclada (for Araneoclada see Platnick, 1977). Such a calamistrum is found in most cribellate lycosoids (Acanthoctenidae; Zoropsidae; Psechridae (the rectangular psechrid calamistrum, described as having several rows, is not significantly different from those of acanthoctenids and zoropsids: e.g., Courtois, 1911, figs. 9a,b, 10a–c)), but not in stiphidiids; cribellate members of Lehtinen's "Miturgidae Uliodoninae" (*Raecius, Uduba,* and *Zorodictyna*), and the genera *Tengella* and *Zorocrates.* In sum, possession by a higher taxon of a male tibial crack, grate-shaped tapetum, oval calamistrum, or any combination thereof, mandated inclusion in the study. Finally, of potential significance is a new character described herein: a set of interlocking lobes on the tegulum and subtegulum. The tegulum has a promarginal lobe on its dorsolateral surface which interlocks with a corresponding lobe on the subtegulum

---

Charles E. Griswold, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118.



FIGURES 1–6.—1, 6: *Zoropsis spinimana*, Vernet-les-Bains, France; 2: *Machadonia punctata*, Karkloof, South Africa; 3, 4: *Phanotea* new species 1, Stormsrivier, South Africa; 5: *Campostichomma manicatum*, Matruata and Kandy, Sri Lanka (1, calamistrum; 2, trochanter of leg IV; 3, male leg tibia, showing depressed area of weakness corresponding to tibial suture (arrow); 4, male leg femur, patella and tibia: tibia broken at tibial suture; 5, tarsus I, showing pretarsal claw; 6, tarsus II, showing lateral tufts).

(Figures 9, 19, 25) in the unexpanded bulb. Such lobes are found in *Tengella*, *Raecius*, *Zorodictyna*, the Zoropsidae and Ctenidae, *Devendra*, *Machadonia*, and most *Phanotea*, and at least in *Psechrus* in the Psechridae. The distribution of this character has not been widely surveyed, in part because expansion of the bulb may be necessary to reveal the presence of lobes. In some (but not all) species of *Agroeca* (Liocranidae) there is a promarginal lobe on the subtegulum (without a corresponding lobe on the tegulum). This mechanism has not been observed in the Amaurobiidae. This character, occurring in both taxa with canoe-shaped and grate-shaped tapeta, is another potential synapomorphy uniting the Lycosoidea and their near relatives.

TAXA

The terminal taxa are exemplars, embodying the actual character states exhibited by a given species rather than a hypothetical ground-plan for the higher taxon. While it might be argued that a higher classification study should deal primarily with higher taxa summarized as ground-plans, and that consideration of exemplars instead might actually misrepresent primitive character states for those taxa, I feel that hypothesizing primitive states for a suite of taxa as little known and as poorly defined as many treated here would be premature. Hypothesizing the ancestral states of characters for a higher taxon amounts to optimizing those characters to the basal node of a cladogram for that higher taxon, the results of which are often ambiguous and are highly dependent on the distribution of character states among terminals and their interrelationships. As Maddison, Donoghue, and Maddison (1984) pointed out, the primitive state of a character for a higher taxon (i.e., that state optimized at the "ingroup node") is also highly dependent on the cladistic structure of the outgroup. Explicit phylogenetic hypotheses regarding the ingroup structure of higher taxa treated here are available only for the Lycosidae (Dondale, 1986), and therefore suggestion of primitive states for characters in the other higher taxa amounts to little more than guesswork or worse, wishful thinking. The use of exemplar species, on the other hand, uses only real data, and at least serves to frame hypotheses of homology and character evolution to be tested as the higher taxa become better understood. In those cases in which the limits of higher taxa are as yet dubious, the relationships suggested for exemplars should hold at least for monophyletic groups including the exemplar. Insofar as the exemplars truly represent their higher taxa, the set of interrelationships suggested should ultimately hold for those taxa. Choice of exemplars to reflect the basonyms of higher taxa insures that conclusions based on exemplars will be relevant to those higher taxa, regardless of subsequent relimitation. The probability of erroneously misrepresenting a poorly known higher taxon through an exemplar seems less than the probability of hypothesizing an erroneous ground plan. In short, judicious choice of exemplars in phylogenetic studies of poorly understood higher taxa effects the best compromise between observation and hypothesis.

Included Taxa

Except for Zoropsidae, familial placement follows Platnick, 1989.

AMAUROBIIDAE.—*Rhoicinus* was placed in the new subfamily Rhoicininae of the Amaurobiidae by Lehtinen (1967), but is almost certainly misplaced in that family (see definition of Amaurobiidae in Griswold, 1990). *Rhoicinus* has long been known to resemble the lycosids in carrying the egg sac attached to the spinnerets (Simon, 1898). The grate-shaped tapetum (Homann, 1971; pers. obs.) mandates inclusion.

CTENIDAE.—Except for a core of genera characterized by 2 claws, claw tufts, and the 2-4-2 arrangement of the eyes, the limits of this family have been fluid. The grate-shaped tapetum occurs in at least two pairs of eyes (Homann, 1971; pers. obs.), and in cribellate representatives (e.g., *Acanthoctenus*) there is an oval calamistrum. I have included a cribellate *Acanthoctenus* and a doublet of classical, ecribellate ctenid genera: *Ctenus* and *Phoneutria*.

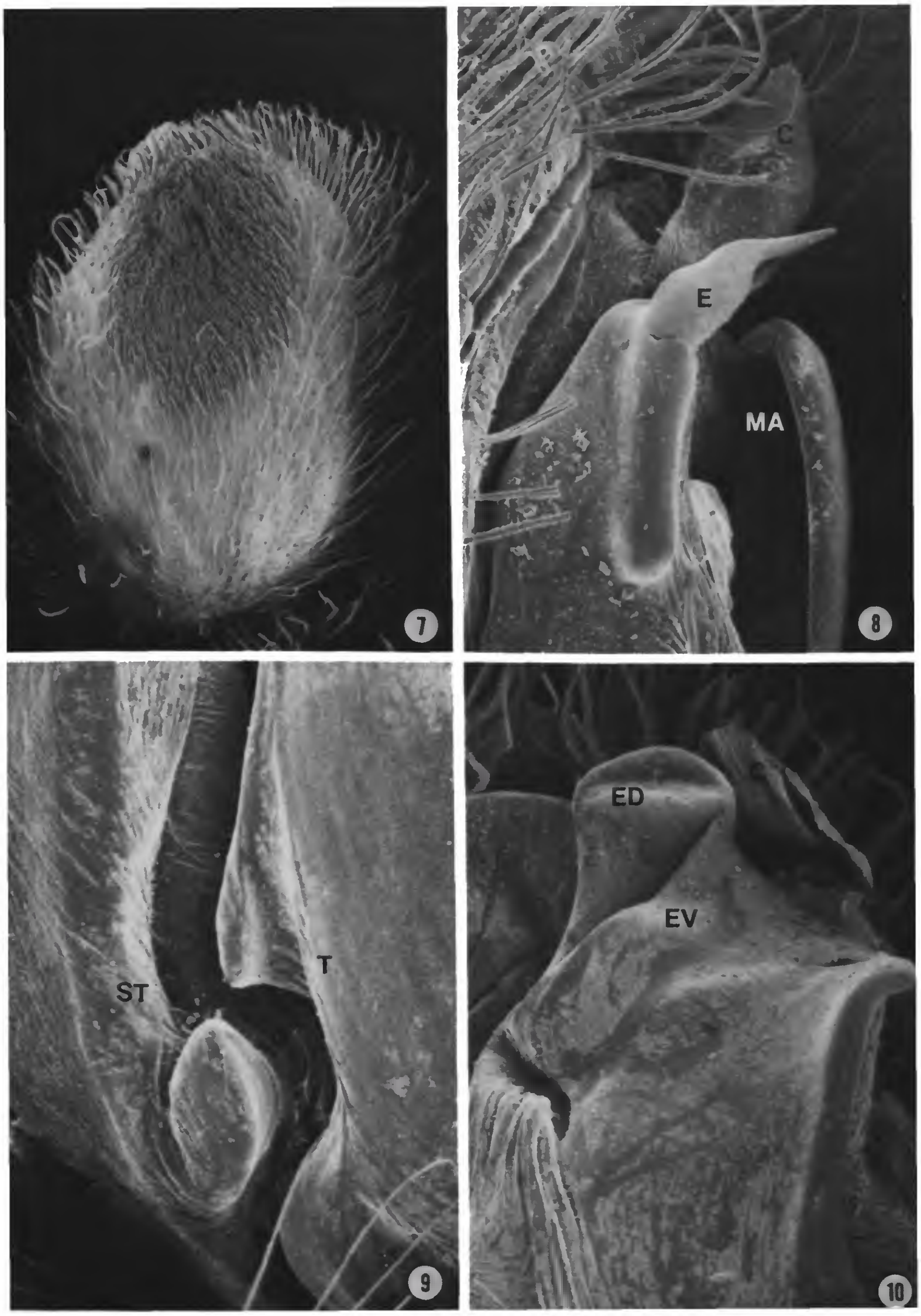
DOLOMEDIDAE.—This family, proposed by Lehtinen (1967) for some members of the traditional Pisauridae, has never been clearly defined and is of dubious validity (Brignoli, 1983:465). Sierwald (1989, 1990) has studied the male and female genitalia of several representatives of the classic Pisauridae, including *Dolomedes*. At least *Dolomedes* has a grate-shaped tapetum (pers. obs.). A representative of the type genus, *Dolomedes*, was chosen.

LYCOSIDAE.—This family, nominate taxon of the Lycosoidea, comprises ecribellate spiders with grate-shaped tapeta (Homann, 1971; pers. obs.) and highly modified ocular regions. Uniquely among the families considered here, a cladogram for the major subgroups has been proposed (Dondale, 1986). In an effort to encompass the diversity of the family, I have chosen exemplars from the most plesiomorphic (*Sosippus placidus*, Sosippinae) and one of the most derived (*Lycosa helluo*, Lycosinae) subfamilies.

MITURGIDAE.—Proposed by Lehtinen (1967) without clear argumentation, the limits of this family may change greatly after careful phylogenetic consideration of included taxa. Taxa treated herein were placed by Lehtinen in his subfamilies Machadoniinae and Uliodoninae. The ecribellate Machadoniinae (*Campostichomma, Devendra, Machadonia,* and *Phanotea*) all have the male tibial crack, and at least *Machadonia* has the grate-shaped tapetum (tapeta were not observed in *Campostichomma* and *Devendra,* and the tapetum of *Phanotea* appears to be derived from the grate-shaped type). Among the Uliodoninae the cribellate *Raecius, Uduba,* and *Zorodictyna* have the male tibial crack and oval calamistrum (at least *Uduba* retains the canoe-shaped tapetum). The ecribellate *Uliodon* lacks the male tibial crack, but at least *Uliodon tarantulinus* has a grate-shaped tapetum, more elaborately folded than that of *Stiphidion,* in the ALE and PER, and accordingly is included in the study.

OXYOPIDAE.—This ecribellate family is recorded as having a grate-shaped tapetum (Homann, 1971), although the reflecting structure of the tapetum is lost. The neotropical genus *Tapinillus,* which is known to build webs for prey capture (Griswold, 1983; Mora, 1986) and may therefore be a primitive representative of the family, was chosen as exemplar.

PISAURIDAE.—The grate-shaped tapetum (Homann, 1971) mandates inclusion of *Pisaura,* the type genus of the family. Sierwald (1989, 1990) has studied the male and female



FIGURES 7-10.—7, 9, 10: *Phanotea* new species 1, Stormsrivier, South Africa; 8: *Machadonia robusta*, Table Mountain, South Africa (7, male cymbium, dorsal, showing scopulate patch; 8, prolateral view of embolus; 9, prolateral view of bulb showing interlocking lobes; 10, embolic apex, prolateral view). (Abbreviations: C = conductor, E = embolus, ED = dorsal division, EV = ventral division, MA = median apophysis, ST = subtegulum, T = tegulum.)

genitalia of several representatives of the classic Pisauridae. *Trechalea* was discussed by Sierwald (1990) as a member of the *Trechalea*-genus group of the classical Pisauridae. Like other members of the *Trechalea*-genus group, *Trechalea* has a well-developed grate-shaped tapetum (pers. obs.) and carries the egg sac attached to the spinnerets (Sierwald, 1990; pers.

obs.). Carico (1986:305) suggested that *Trechalea* and some related genera might comprise a separate family.

PSECHRIDAE.—This family exhibits both the grate-shaped tapetum (Homann, 1971) and oval calamistrum. Representatives of both classical genera, *Psechrus* and *Fecenia*, were included.

SENOCULIDAE.—This monogeneric ecribellate family is reported by Homann (1971) to have the most elaborately folded, grate-shaped tapetum. A representative of *Senoculus* is included.

STIPHIDIIDAE.—Homann (1971) considered the tapetum of the PME of *Stiphidion* grate shaped, although the lateral folds of the tapetum are very shallow (Homann, 1971, fig. 32D). A calamistrum consisting of a single row of setae is anomalous among the cribellate taxa treated herein.

TENGELLIDAE.—An oval calamistrum mandates inclusion of the two cribellate members this family, *Tengella* and *Zorocrates*, which otherwise have the primitive canoe-shaped tapetum (Homann, 1971; pers. obs.) and lack the tibial crack.

ZOROPSIDAE.—Lehtinen (1967) synonymized the classic Zoropsidae with the Zoridae (but inappropriately used the latter, younger name). Levy (1990) reestablished the Zoropsidae as a separate family. *Zoropsis* has the grate-shaped tapetum (Homann, 1971; pers. obs.), oval calamistrum (Figure 1), and male tibial crack. *Takeoa* has the grate-shaped tapetum (pers. obs.) and oval calamistrum, but lacks the male tibial crack.

Taxa Excluded or Not Considered

A number of taxa have previously been considered to be related to one or more of the taxa listed above. These have not been considered here because critical examination revealed that they share no putative synapomorphies with the included taxa, they are too little known to provide the full suite of character data, or because investigation of the controversy regarding their placement would have greatly increased the scope of the study. Lehtinen (1967) placed the Homalonychidae in his Pisauroidea (along with Oxyopidae, Pisauridae, and Senoculidae). The ecribellate *Homalonychus* lacks the male tibial crack and has only canoe-shaped tapeta (Homann, 1971). Lehtinen (1967) placed the Cycloctenidae, Selenopidae, and Zoridae in his Lycosoidea (along with Ctenidae, Dolomedidae, and Lycosidae). Homann (1971) rejected these conclusions, placing *Cycloctenus* with *Selenops* in the Selenopidae, and suggesting that these taxa were not related to the Lycosoidea. Placement of *Zoropsis* and *Takeoa* in the Zoridae by Lehtinen (1967) implies that *Zora*, type genus of that family, should be considered in this study. But the ecribellate *Zora* has neither the male tibial crack (pers. obs.) nor the grate-shaped tapetum (Homann, 1971), suggesting that the classic zoropsids are misplaced in the Zoridae. *Zora* possesses none of the provisional synapomorphies necessary for inclusion in this analysis, and will not be considered further. Levi (1982b) included the Toxopidae in his Lycosoidea. The eyes have a typical canoe-shaped tapetum covering rhabdoms folded in a grate-shaped manner. The tapetum is not truly grate shaped, and therefore I do not consider the toxopids further. *Phanotea natalensis* Lawrence, *P. latebricola* Lawrence, and *P. simoni* Lawrence have long been unique among species assigned to *Phanotea* in lacking teeth on the female epigynum (Lawrence, 1951, fig. 1a,d; 1952, fig. 72) and having a convex, hook-like median apophysis on the male palp (Lawrence, 1951, fig. 1b). These species do not appear to have the grate-shaped tapetum, and the male of *P. natalensis* and newly discovered male of *P. latebricola* both lack the male tibial crack. *Phanotea natalensis, P. latebricola,* and *P. simoni* are hereby excluded from *Phanotea* and not considered further. Gray (1973) described the genus *Janusia* from a cave in southern Australia and noted its resemblance to *Phanotea*. As this interesting ecribellate taxon is eyeless and known only from the female, it is currently impossible to consider eye, calamistrum, or male characters that might suggest affinities. The only taxon reported to have a grate-shaped tapetum that is not represented in the matrix is the Thomisidae, considered by Homann (1975) to be the sister-group of Lycosoidea (comprising Lycosidae, Senoculidae, and Oxyopidae). Other than possible homology in tapetal form, there is little to suggest inclusion of the thomisids. They are ecribellate (therefore the form of the calamistrum in their cribellate ancestors is unknown), and they lack the male tibial crack, deep trochanteral notch, and interlocking lobes on the tegulum and subtegulum characteristic of a large (and presumably monophyletic) group including families with and without the grate-shaped tapetum. To consider Thomisidae to be the sister-group of the Lycosoidea, which includes cribellate members, is to require yet another independent loss of the cribellum. Evidence from palp structure (Loerbroks, 1984) suggests that thomisids are related to Salticidae. Levi (1982b) placed the thomisids in their own superfamily (along with the aphantochilids), and Coddington and Levi (1991) placed the Thomisidae in the Dionycha on the basis of claw tufts. The indications regarding the affinities of the Thomisidae are conflicting: comprehension of their potential relationship to the Lycosoidea will require investigation of the several other families placed in the Dionycha, a task far beyond the scope of this study.

ACKNOWLEDGMENTS

Support was provided by grant BSR-9020439 from the National Science Foundation. A postdoctoral fellowship from the Smithsonian Institution and warm hospitality and encouragement from Jonathan Coddington helped make this work possible. Fieldwork in Africa was made possible through the generous support of the Natal Museum, Pietermaritzburg, and by permits from the Natal Parks Board and Directorate of Forestry, Knysna; fieldwork in Australia was made possible by the National Museum of Natural History, Smithsonian Institution, and by permits from the New South Wales National Parks and Wildlife Service, Australian Capital Territory National Parks and Wildlife Service, and Commonwealth Scientific and

Industrial and Research Organization (CSIRO); fieldwork in Bolivia was supported by the Smithsonian Biological Diversity in Latin America (BIOLAT) program. P.M.C. Croeser, J. Doyen, T. Meikle, R. Moran, E. Peñaranda, and E.J. Wright assisted in the field. Susan Breyden, Vicki Godwin, and Walt Brown helped with SEM work; Scott Larcher assisted in ways too numerous to recount. Jon Coddington, Nikolaj Scharff, Petra Sierwald, and Diana Silva Dávila offered continuing advice; in particular I must thank Dr. Sierwald for generously sharing her ideas and unpublished data on the pisaurids and their relatives. Vince Roth discussed mechanisms of autospasy in spiders, and was the first to remark on the relative rarity of the male tibial crack. Drs. J. Coddington, C. Dondale, N. Platnick, N. Scharff, and P. Sierwald read and commented on a draft of the manuscript.

The following individuals and institutions are gratefully acknowledged for loan of material:

J.A. Coddington, Entomology, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM)
P.M.C. Croeser, Department of Arachnology, Natal Museum, Pietermaritzburg, South Africa (NMSA)
J. Gruber, Naturhistorisches Museum, Zoologisches Abteilung, Vienna, Austria (NHMV)
J. Heurtault and C. Rollard, Muséum National d'Histoire Naturelle, Laboratoire des Arthropodes, Paris, France (MNHN)
P. Hillyard, Arachnida and Myriapoda Section, Department of Zoology, The Natural History Museum, London, England (BMNH)
R. Jocqué, Musée Royal de L'Afrique Centrale, Tervuren, Belgium (MRAC)
H.W. Levi, Department of Invertebrates, Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ)
M. Moritz, Museum für Naturkunde, Zoologisches Institut der Humboldt Universität, Berlin, Germany (ZMB)
Y. Nishikawa, Arachnological Society of Japan, Otemon G. University, Osaka, Japan (ACJ)
N. Penny, Department of Entomology, California Academy of Sciences, San Francisco, USA (CAS)
N.I. Platnick, Department of Entomology, American Museum of Natural History, New York, USA (AMNH)
G. Rack, Zoolgisches Institut und Zoologisches Museum, Universitat Hamburg, Hamburg, Germany (ZMH)
N. Scharff, Zoologisk Museum, Copenhagen, Denmark (ZMC)

Materials and Methods

SPECIMEN CHOICE.—Exemplar species were chosen primarily for the ready availability of specimens for dissection and SEM preparation. Whenever possible, the type species of the type genus of the higher taxon was chosen, but completeness of the data set was paramount in each case. Doublets of several higher taxa (e.g., Ctenidae, Lycosidae, Psechridae, Zoropsidae, *Devendra, Machadonia, Phanotea, Uduba*) were included to allow an assessment of both the monophyly of these taxa and the behavior of the characters traditionally serving for their diagnosis. Exemplar taxa, their voucher specimens (with collection data and deposition), and higher categories that they represent (following Platnick, 1989) are listed in Table 1. Terminology for parts of the vulva follows Sierwald (1989). Abbreviations for morphological terms used in text and figures are explained in Table 2. Throughout the text references to figures from other papers are noted in lower case (fig.), whereas references to figures accompanying this paper are capitalized (Figure).

SPECIMEN PREPARATION.—Male palpi were expanded for all taxa except those represented by unique types. Palpi were expanded by immersing them overnight in a weak, watery solution of potassium hydroxide (KOH) and transferring them to distilled water where expansion continued. Palpi were transferred back and forth between KOH and distilled water until expansion stopped. Female genitalia were excised from the abdomen, cleaned in a solution of trypsin and water, and illustrated. Palpi and vulvae were examined in alcohol and in lactic acid. Subsequently, to allow examination of internal structures, vulvae were bleached through brief immersion at room temperature in a 5.25% Sodium Hypochlorite solution (regular CLOROX® household bleach; this does not constitute Institutional endorsement of this product). Bleaching provided rapid, excellent clearing of even the most heavily sclerotized genitalia with no apparent distortion of features. Vulvae were then stained lightly with Chlorazol Black, temporarily mounted in lactic acid, and examined with a compound microscope. Prior to SEM (scanning electron microscope) examination structures were cleaned in an ultrasonic cleaner: palpi and female genitalia were critical point dried, other structures were air dried. The preferred method of examining the tapetum was by microscopic examination of live or freshly dead specimens. The tapetum, a shiny reflective surface, remains clearly visible for 24–48 hours after a spider's death (after this time the retina becomes cloudy, obscuring the details of the tapetum). When live material was not available, preserved specimens were prepared by removing the chelicerae and most of the musculature from the anterior part of the cephalothorax. The cephalothorax was immersed in lactic acid for 1–5 hours. Frequently the retina cleared and details of the tapetum became visible, though, for unknown reasons, this was not always successful. If a tapetum was oval bisected by a straight dark line it was considered canoe-shaped (Homann, 1971, figs. 10A, 27B, 32A). The grate-shaped tapetum is a complex structure in which the rhabdoms are bilaterally arranged in a folded row that penetrates the tapetum (Homann, 1971), giving the shiny tapetum an appearance like that of a fireplace grate or barbecue grill. It is this complexly folded structure that causes the "sparkling" eyeshine of lycosids, pisaurids, and other Lycosoidea. I have not been able to examine the morphology of the retina: if the tapetum had the appearance of a folded grate,

TABLE 1.—Exemplars.

Exemplar taxa, their voucher specimens (with collection data and deposition), and higher categories that they represent (following Platnick, 1989):

Acanthoctenus spiniger Keyserling, 1877: male from Ecuador, collected on bananas in New York, USNM; female from Tegucigalpa, Honduras, 1953, B.H. Gilbert, USNM (Ctenidae).

Campostichomma manicatum Karsch, 1891: males and females from Maturata and Kandy, Sri Lanka, MNHN (Miturgidae, Machadoniinae).

Devendra pardale (Simon, 1898): male and female from Kandy or Maturata, Sri Lanka, MNHN (Miturgidae, Machadoniinae).

Devendra seriata (Simon, 1898: male and female from Nuwara Eliya, Sri Lanka, MNHN (Miturgidae, Machadoniinae).

Ctenus ca. *transvaalensis* Benoit, 1981: males and females from Dlinza Forest, Eshowe, Natal, South Africa, 17 Jan 1984, C.E. Griswold, NMSA (Ctenidae).

Dolomedes tenebrosus Hentz, 1844: male from Cabin John, Maryland, USA, 12 May 1912, USNM; female from Oakwood, Texas, 28 Jul 1968, J.E. Carico, USNM (Dolomedidae).

Fecenia ocracea (Doleschall, 1859): male and female from Mount Kaindi, Wau, Morobe Prov., Papua New Guinea, 3 Mar 1979, H.W. Levi, Y. Lubin, and M. Robinson, MCZ (Psechridae).

Lycosa helluo (Walckenaer, 1837): male from Keene Valley, New York, USA, 25 May 1975, USNM; female from Blacksburg, Virginia, USA, 11 Oct 1962, USNM (Lycosidae).

Machadonia robusta (Simon, 1898): male from Kirstenbosch, Skeleton Gorge Forest, Table Mountain, Cape Town, Cape. Prov., South Africa, Nov 1960, N. Leleup, MRAC; female from same locality, 29 Oct 1985, C.E. Griswold, NMSA (Miturgidae, Machadoniinae).

Machadonia urbense (Lawrence, 1942); male from Pietermaritzburg, Natal, South Africa, 25 Aug 1984, C.E. Griswold, NMSA; female holotype from Pietermaritzburg, Natal, Dec 1939, R.F. Lawrence, NMSA (Miturgidae, Machadoniinae).

Phanotea peringueyi Simon, 1896: males and females from Cango Caves, near Oudtshoorn, Cape Prov., South Africa, 2 Oct 1949, B. Malkin, CAS (Miturgidae, Machadoniinae).

Phanotea species 1: males from Skuinsbos, Stormsrivier, Cape Province, South Africa, 6–9 Dec 1981, S. and J. Peck, AMNH; females from Storms River, Cape Prov., South Africa, 20 Apr 1958, E.S. Ross and R.E. Leech, CAS (Miturgidae, Machadoniinae).

Phanotea species 2: males from Diepwalle, Cape Province, South Africa, 12–30 Dec 1981, S. and J. Peck, AMNH; female from Diepwalle Forest Station, 22 km NE Knysna, 10–13 Jan 1985, C.E. Griswold, NMSA (Miturgidae, Machadoniinae).

Phoneutria nr. *boliviensis* (F. Cambridge, 1897): male and female from San Jose, Pearl Island, Panama, 23 May 1944, J. Morrison, USNM (Ctenidae).

Pisaura mirabilis (Clerck, 1758): male from Hettenleidelheim, Reinland-Pfalz, Germany, USNM; female from Homburg, Saarland, Germany, R. Nitzsche, USNM (Pisauridae).

Psechrus himalayanus Simon, 1906: male from Kooloo Valley, India, 1870's, M.M. Carlton, MCZ; female from forest W. of Landrung, Gandaki Zone, Nepal, 21 Oct 1985, J.A. Coddington, USNM (Psechridae).

Raecius spp.: male type of *Mnesitheus zoropsides* Strand, 1915, Buea, Cameroon, NHMV; female, *Raecius* undetermined species, from Lulimbia, Zaire, Jul–Aug 1876, M. Lejeune, MRAC (Miturgidae, Uliodoninae).

Rhoicinus undetermined species: male and female from Estacion Biologico Beni, Beni Prov., Bolivia, 8–14 Nov 1989, J.A. Coddington, C.E. Griswold, E. Peñaranda, S. Larcher, and D. Silva, USNM (Amaurobiidae).

Senoculus canaliculatus F. Cambridge, 1902: male and female from Finca La Selva, 4 km SE Puerto Viejo, Sarapiqui Prov., Costa Rica, Oct 1981, C.E. Griswold, USNM (Senoculidae).

Sosippus placidus Brady, 1972: male and female from Archbold Biological Station, Florida, USA, Apr–May 1987, M. Deyrup, USNM (Lycosidae).

Stiphidion facetum Simon, 1902: male from New Zealand, AMNH; females from Waitetoko, New Zealand, AMNH, and Royal N.P., NSW, Australia, 12 Aug 1990, C.E. Griswold and T.C. Meikle, USNM (Stiphidiidae).

Takeoa nishimurai (Yaginuma, 1963): holotype female from Murozumi-cho, Hikari City, Japan, 7 Jul 1962, K.Nakagawa; allotype male from Momoyama, Fushimi-ku, Kyoto City, Japan, 22 Mar 1962, T. Nishimura, ACJ (Zoridae).

Tapinillus undetermined species: males and females from Estacion Biologico Beni, Beni Prov., Bolivia, 7 Nov 1989, C.E. Griswold, USNM (Oxyopidae).

Tengella radiata (Kulczynski, 1909): male and female from Finca La Selva, 4 km SE Puerto Viejo, Sarapiqui Prov., Costa Rica, 8–12 Jan 1986, J.A. Coddington, USNM (Tengellidae).

Trechalea undetermined species: males and females from Estacion Biologico Beni, Beni Prov., Bolivia, 7 Nov 1989, C.E. Griswold, USNM (Pisauridae).

Uduba dahli Simon, 1903 (*Marussenca madagascariensis* F. Dahl, 1901): male and female syntypes, Madagascar, Braun, ZMB (Miturgidae, Uliodoninae).

Uduba undetermined species 1: male and female from Madagascar, Forsyth Major, BMNH; males from 7 km W Ranomafana, Fianarantsoa Prov., Madagascar, 22–31 Oct 1988, W. Steiner, USNM (Miturgidae, Uliodoninae).

TABLE 1.—*Continued.*

Uliodon tarantulinus (L. Koch, 1873): males from Bundeena, Royal N. P., NSW, Australia, 11-13 Aug 1990, C. E. Griswold and T. C. Meikle, USNM; female from 9 km S Bateman's Bay, NSW, Australia, 8 Aug 1990, C. E. Griswold and T. C. Meikle, USNM (Miturgidae, Uliodoninae).

Zorocrates undetermined species: males and females from Sierra Laguna, Baja California Sur, Mexico, 12-18 Dec 1979, C. E. Griswold, USNM (Tengellidae).

Zorodictyna oswaldi (Lenz, 1891): male and female syntypes from Nossi-Be, Madagascar, 2 Jul 1888, Oswald, ZMH (Miturgidae, Uliodoninae).

Zoropsis spinimana (Dufour, 1820): male from Vernet-les-Bains, Pyrenees-Orientales, France, 22 Aug 1989, J. A. Coddington, USNM; females from Grottes des Canaletes, Pyrenees-Orientales, France, 21 Aug 1909, J. A. Coddington, USNM (Zoridae).

Zoropsis rufipes (Lucas, 1838): males and females from Tenerife, Canary Islands, Nov 1975, P. Oromi, AMNH (Zoridae).

resembling that figured by Homann (1971, figs. 28a-d, 32d,e) it was scored as grate-shaped. I did not feel that lactic acid preparation was sufficiently reliable to resolve the tapetum in all cases: if no tapetum was resolved the character was scored as unknown rather than lost.

Cladistics

DATA MATRIX.—A data matrix was assembled for 32 exemplar taxa and 68 characters (Table 3). Representatives of all families reported to have grate-shaped tapeta except Thomisidae, and all families comprising Levi's (1982b) Lycosoidea except Toxopidae, were included. Characters were scored only through direct observation on the exemplars in all cases except for behavior and tapetal morphology; for the latter characters assumptions were sometimes made for the exemplars based upon published reports regarding their higher taxa. Initial homology hypotheses were broad, considering comparable morphologies as potential homologs without regard to their distribution among terminal taxa. I believe that the truest test of homology is congruence, and that the characters should be allowed initially to weight themselves (Patterson, 1982). The 68 characters, along with their state codings, are arranged by body region as follows:

TABLE 2.—Abbreviations for morphological terms used in text and figures.

ALE = anterior lateral eyes
C = conductor
BS = base of spermatheca
CD = copulatory duct
CO = copulatory opening of epigynum
DTP = distal tegular protuberance
E = embolus
ED = dorsal division of embolic apex
EF = epigynal fold
EG = inner margin of external epigynal groove
EL = basal lobe of embolus
ELP = process on basal lobe of embolus
EM = basal membranous connection of embolus to tegulum
EV = ventral division of embolic apex
FD = fertilization duct
HS = head of spermatheca
ITC = inferior tarsal claw
LL = lateral lobes of epigynum
MA = median apophysis of tegulum
ML = median lobe of epigynum
MS = median sector of epigynum
MTP = membranous tegular process
OQP = ocular quadrangle, posterior
PER = posterior eye row
PC = paracymbium
PME = posterior median eyes
PT = palpal tibia
RLA = retrolateral apophysis of tibia
ST = subtegulum
STP = sclerotized tegular process
T = tegulum
VA = ventral apophysis of tibia

Character 1.—Male palpal tibia with retrolateral apophysis (RLA).

0 = present. A sclerotized retrolateral apophysis (Figures 20, 26, 34, 38) is present on the palpal tibia of males of most species studied. The retrolateral tibial apophysis occurs widely in the higher Araneoclada (Griswold, 1990:14-15) and is probably a synapomorphy for a large group of superfamilies and other higher taxa including Dionycha, Lycosoidea, Amaurobioidea, and Dictynoidea (the "RTA clade" of Coddington and Levi, 1991).

1 = absent. The apophysis is entirely absent in *Psechrus* (Levi, 1982a, figs. 7, 8) and the Lycosidae (Figure 57; Brady, 1962, figs. 33-39; Dondale, 1986, figs. 5, 8, 9). In *Rhoicinus* (Exline, 1960, fig. 2) there is a membranous pit in this position (see character 2); the surrounding tibial apophysis is lost.

Character 2.—Male palpal tibia with retroapical cuticle unsclerotized.

0 = absent. In most species studied the cuticle at the retrolateral apical margin of the tibia is sclerotized and setose.

1 = present. The retroapical cuticle is asetose, membranous and concave in *Trechalea* (where it is surrounded by a complex retrolateral tibial apophysis: Figure 53; see also Sierwald, 1990, fig. 31, and Carico and Minch, 1981, fig. 2 for *Rhoicinus*, where it is a simple pit (Exline, 1960, fig. 2). Sierwald (1990:35) noted the similarity between the

TABLE 3.—Character by taxon matrix. Rows represent characters. First state listed is coded as "0," second state as "1," etc; "?" = unknown; "-" = not applicable. Term abbreviations: PT = male palpal tibia, mt = metatarsus, t = tarsus, prs = present, abs = absent, others follow Table 2. Columns represent taxa. Taxon abbreviations: AC = *Acanthoctenus spiniger*, CA = *Campostichomma manicatum*, CT = *Ctenus* ca. *transvaalensis*, DO = *Dolomedes tenebrosus*, Dp = *Devendra pardale*, Ds = *Devendra seriata*, FE = *Fecenia ocracea*, LY = *Lycosa helluo*, Mr = *Machadonia robusta*, Mu = *Machadonia urbense*, PH = *Phoenutria* nr. *boliviensis*, PI = *Pisaura mirabilis*, Pp = *Phanotea peringueyi*, P1 = *Phanotea* species 1, P2 = *Phanotea* species 2, PS = *Psechrus himalayanus*, RA = *Raecius* spp., RH = *Rhoicinus* sp., SE = *Senoculus canaliculatus*, SO = *Sosippus placidus*, ST = *Stiphidion facetum*, TA = *Takeoa nishimurai*, TE = *Tengella radiata*, TP = *Tapinillus* sp., TR = *Trechalea* sp., Ud = *Uduba dahli*, U1 = *Uduba* sp., UL = *Uliodon tarantulinus*, ZD = *Zorodictyna oswaldi*, Zr = *Zoropsis rufipes*, Zs = *Zoropsis spinimana*, ZT = *Zorocrates* sp.

Character	TZRZCUUATZZDDPPPMMPCSTSPFUDPTRLS EDATAd1CAsrspp12ruHTEPTSELOIRHYO
1. PT retrolateral apophysis: prs; abs;	00000000000000000000000100000111
2. PT retrolateral pit: abs; prs;	00000000000000000000000000001100
3. PT ventral apophysis: abs; prs;	01101110000110000000001000000000
4. Cymbium dor. scopula: abs; prs;	01100111111001110100000110000011
5. Cymbium dorbasal projection: abs; prs;	01000000000000000001000000000000
6. ST/T lobes: prs; abs;	00011110000001000000111011111111
7. C: articulate; abs; tegulum;	00000110000000000000000000021020
8. C: membranous; convex;	00000--00000000000001111011--0-1
9. Membranous C: opposed to E; grooved;	00000--0100000001110----0----0--
10. Fleshy C: grooved; opposed to E;	--------------------0001-00----1
11. Fleshy C: simple; flexible lobe;	--------------------1110-00----0
12. MA: pres; abs;	00000000000000000000001100000000
13. MA: median; retrobasal;	0000000000000011000000--00000000
14. MA: convex; concave;	0010100100011111111100--00000000
15. Cup shaped MA: simple; bimarginate;	--0-0--0---001111111------------
16. Convex MA: hook; bilobed; triangular;	00-0-22-000---------00--00001122
17. Hooked MA: simple; bifid;	00-0----011---------00--0000----
18. MA: longitudinal; transverse;	0000011000000000000000--00000011
19. T: oval; bifid; with ST notch;	00000110000000000000000000002222
20. DTP: abs; pres;	00000000000000000000000000111111
21. STP: abs; prs;	00110000000000000001000010010000
22. MTP: simple; projecting;	01000000111000000000000000000000
23. E base: fixed; flexibly attached;	00000110000000000000000001111111
24. E base lobe: abs; prs;	00011110000000000000000001111111
25. E lobate base: with process; simple;	---0000------------------1000001
26. E curve: clockwise; counterclockwise;	00000110000000000000000000111111
27. E: stout; slender; ED+EV; flange;	00011111230002230002111111111111
28. Epigynum: LL+MS; undivided;	00000110000000000000011000000000
29. LL: unmodified; pocket; tooth;	02000--0011222222222--0000000200
30. LL tooth: short; long; post. margin;	-0---------000110000---------2--
31. MS: convex; unmodified;	00000--1000100001000--1101110100
32. Convex MS: scape; long; median;	00021---200-0000-011----0---1-11
33. ML scape: simple; erect;	000------11-0111-0------0-------
34. ML scape divot: prs; abs;	100------00-1000-0------0-------
35. EG: abs; seperate; to CD; to FD;	20000000000022233220000000010022
36. CD: short; long; loop;	00002220000000001100102000100000
37. HS: small; large; abs;	11002220000000001111111110000000
38. BS, internal: simple; chambered;	00001111000000000000000000000000
39. BS, shape: simple; lobe; sinuate;	00022220100000000001000002201111
40. FD: posterior; median;	00010000100000000000000000110000
41. Crib: divided; contiguous; entire;	0220-110000-----------000-------
42. Cribellum: linear; oval; abs;	00012111000222222222220002222222
43. PER: straight; recurved;	00001001111110001111101001111111
44. Sternum length/width: <1.2; > 1.2;	01110110000000110000100000000011
45. Sternum between coxae 4: no; yes;	00000000100000000000111110111101
46. ALE, PME in line: no; yes;	00000001000000000011100000000000
47. PER/OQP <1.6: no; yes;	00000000000000000001000000000011
48. Labium length/width: >1.2; <0.08;	00000001111000001101001001111111
49. Retromarginal teeth: 3; 4; 2; 0;	10001000000110000011032112100000
50. Tapetum: canoe; grate; derived;	00?0?001111??2??1111111111111111
51. Tib. I length/car. width: <2.7; >3;	00000000000000000000000110000000
52. Male tibial crack: abs; prs;	01101110011111111100000000000000
53. Tarsal trichobothrial rows: 2+; 1;	00000000000000000000011110000000
54. Claw tufts: abs; prs;	00000001111000000011000111000000

TABLE 3.—*Continued.*

Character	TZRZCUUATZZDDPPPMMPCSTSPFUDPHRLS EDATAd1CAsrspp12ruHTEPTSELOIEHYO
55. Troc. notch: deep; shallow; abs;	01200110111000000000111110000000
56. Tarsal organ: simp.; keyh.; stellate;	01002?2001??210?1?000000?1000000
57. Tric. base: trns. ridges; smooth;	000000000000000?00001110?0111111
58. Feathery hairs: abs; prs;	00001000000110000000101000010000
59. Tib. I vent. spines: 4; 4+; 5; 7+; 3;	0001000333300000112204-0-4003044
60. Female Tib. I, lat. spines: prs; abs;	01111110000110111111000001001001
61. Male Tib. I, dor. spines: 0; 1; 2+;	02100102011000001122020000122000
62. Female Tib. I, dor. spines: abs; prs;	00000000000000000000110000110000
63. Male mt, lateroap. spines: abs; prs;	01111000000000000000000000100110
64. Calamistrum: prs; abs;	00001000000111111111110001111111
65. Calamistrum: broad; linear;	0000-000000-----------100-------
66. Scopula I: beneath mt+t; t; abs;	10102000000220000000222220022200
67. Nursery web: no; yes;	0????????00??0??000?0000?0110000
68. Eggsac on spinnerets: no; yes;	0????????00??0??000?0000?0001111

Trechalea genus-group and *Rhoicinus* in this feature and suggested a possible relationship (Sierwald, 1990:41) between these taxa.

Character 3.— Male palpal tibia with ventral apophysis (VA) in addition to retrolateral.

0 = absent (Figures 11, 47, 57).

1 = present. A ventral apophysis at the tibial apex (Figures 19, 25–27, 34, 37) occurs sporadically in the Araneoclada (Griswold, 1990:15).

Character 4.—Cymbial dorsal scopulate patch.

0 = absent. Setae on cymbial dorsum undifferentiated, similar to those on other segments.

1 = present, with a dense dorsal patch of erect, scopulate setae of equal length (Figure 7; Levi, 1982a, fig. 8; Levy, 1990, fig. 7).

Character 5.—Cymbial dorsobasal projection.

0 = absent. The cymbium gradually tapers dorsobasally to tibial apex (Figures 27, 37).

1 = present. A proximad-directed, dorsobasal projection on the cymbium occurs in *Ctenus* (Benoit, 1981, fig. 4) and *Zorodictyna* (Figure 21).

Character 6.—Subtegulum/tegulum locking lobes.

0 = present. The tegulum has a promarginal lobe on its dorsolateral surface which interlocks with a corresponding lobe on the subtegulum (Figures 9, 19, 25) in the unexpanded bulb.

1 = absent. The margins of tegulum and subtegulum are without interlocking lobes.

Character 7.—Conductor, form.

0 = articulated, differing from tegulum in texture. It may be hyaline (Figures 21, 31, 44) or fleshy (Figure 47) (see character 8).

1 = absent. No part of palpal bulb serves to guide or protect embolus.

2 = tegular outgrowth of the same texture and color as tegulum (Figure 59).

Character 8.—Conductor type.

0 = hyaline. Conductor transparent and very thin (Figures 19–21, 31, 44) (see character 9).

1 = convex, fleshy, either translucent or opaque (Figure 47) (see characters 10, 11).

Character 9.—Shape of hyaline conductor.

0 = opposite embolus tip. Embolus not surrounded or obscured by conductor for any part of its length (Figures 21, 26, 34).

1 = embracing embolus apex. Conductor surrounds and hides apical part of embolus (Figures 43, 44).

Character 10.—Fleshy conductor.

0 = grooved, embracing embolus. An elongate groove guides or covers the embolus for part of its length (Figure 47).

1 = convex, swollen, without well-defined groove to receive embolus. In *Psechrus* the fleshy conductor arises from the apex of the tegulum and is closely associated with the embolus (Levi, 1982a, fig. 7), while in *Sosippus* the structure considered a conductor by Brady (1962, figs. 34, 36) is an erect, digitiform structure arising from the middle of the tegulum.

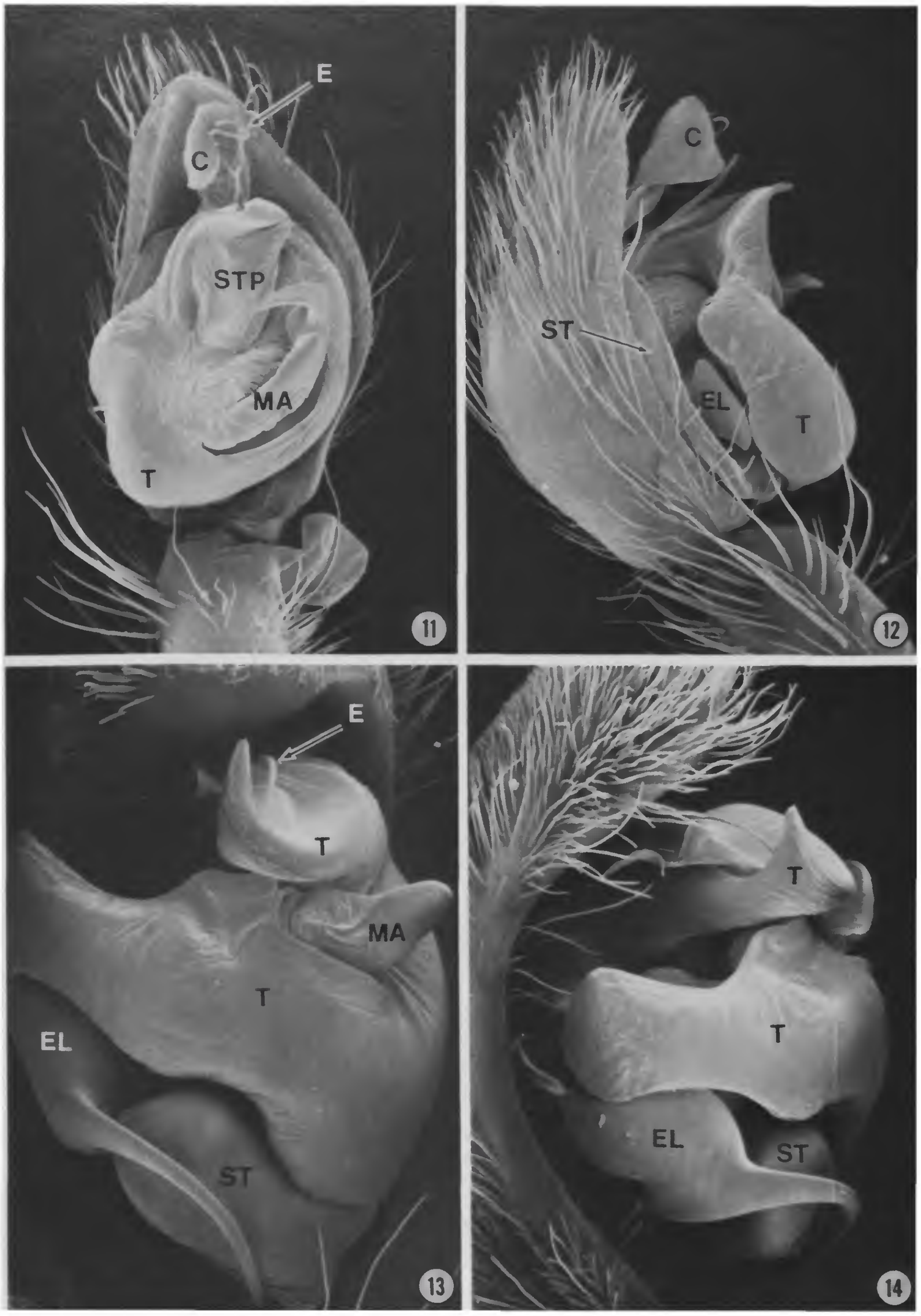
Character 11.—Fleshy conductor.

0 = simply attached.

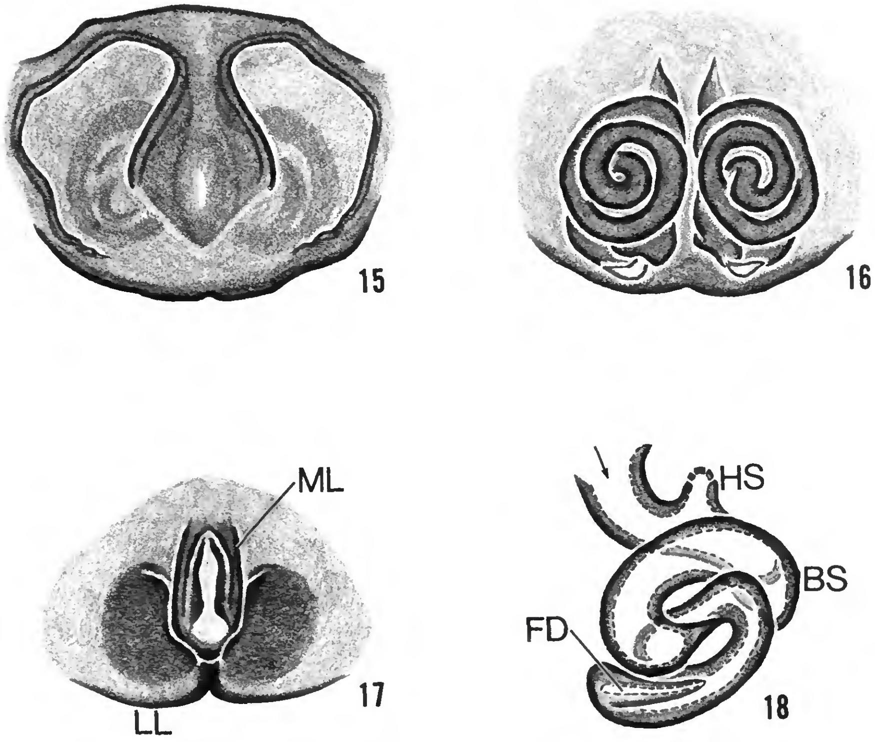
1 = flexibly attached lobe, broadest distally. The conductors of *Stiphidion* (Davies, 1988, figs. 20, 21) and *Senoculus* (Pickard-Cambridge, 1902, pl. 33: fig. 3 "a"; Chickering, 1941, fig. 7) are remarkably similar, being narrowly attached to the tegulum and becoming broad distally with a deep transverse groove embracing the embolus for much of its length; the conductor is sclerotized distally and pointed retroapically. The conductor of *Tapinillus,* while smaller than those of the previous taxa, has a fleshy, flexible base and sclerotized tip (Figures 56, 58).

Character 12.—Median apophysis.

0 = present. A sclerotized, flexibly attached apophysis arises



FIGURES 11–14.—11, 12: *Zorocrates* sp., Baja California Sur, Mexico; 13, 14: *Uduba* species 1, Ranomafana, Madagascar (the position of the embolus against the tegulum is artifactual; ordinarily it rests against the apex of the cymbium) (11, palpus, ventral; 12, palpus, prolateral view; 13, palpus, ventral; 14, palpus, prolateral). (Abbreviations: C = conductor, E = embolus, EL = basal lobe of embolus, MA = median apophysis, ST = subtegulum, STP = sclerotized tegular process, T = tegulum.)



FIGURES 15-18.—15, 16: *Uduba* species 1, Madagascar; 17, 18: *Zorocrates* sp., Baja California Sur (15, 17, epigynum, ventral; 16, vulva, dorsal; 18, left vulva, dorsal). (Abbreviations: BS = base of spermatheca, FD = fertilization duct, HS = head of spermatheca, LL = lateral lobes, ML = median lobe (arrow represents copulatory opening).)

from the central, retrolateral, or basal region of the tegulum (Figures 11, 13, 20).

1 = absent. No such apophysis arises from this part of tegulum.

Character 13.—Median apophysis, position on tegulum.

0 = median, insertion near middle of tegulum (Figures 11, 38).

1 = retrobasal, insertion near proximal margin of tegulum.

Character 14.—Median apophysis, shape.

0 = convex, club- or hook-shaped, narrow, convex on all surfaces or with concavities forming only narrow grooves (Figures 13, 20, 54) (see characters 16, 17).

1 = cup-shaped, prolateral surface a deep, oval concavity that is closed distally, retrolateral surface arched, convex (Figures 8, 25, 31). Although *Dolomedes tenebrosus* has a flattened, strap-like median apophysis, other species have hook-like median apophyses with a narrow prolateral groove (Carico, 1973); accordingly *Dolomedes* is coded as 0 for this character (see character 15).

Character 15.—Cup-shaped median apophysis.

0 = simple, concavity with single rim (Figures 25, 31).

1 = bimarginate, concavity with inner and outer rims, these separated at apex of apophysis (Figure 8).

Character 16.—Convex median apophysis.

0 = hooked or bent distally (Figures 11, 20; Wolff, 1978, figs. 3, 7).

1 = large, swollen, with 2 apical lobes. This form is found in *Rhoicinus* (Exline, 1960, fig. 14) and *Trechalea* genus-group (Figures 52, 54; Sierwald, 1990, figs. 32, 36).

2 = triangular in cross section, simple. This form occurs in *Uduba* (Figure 13) and Lycosidae (Figure 59).

Character 17.—Hooked median apophysis.

0 = simple (Figures 20, 21).

1 = apex bifid, typical of *Zoropsis* (Levy, 1990, figs. 9, 11, 19).

Character 18.—Median apophysis, angle.

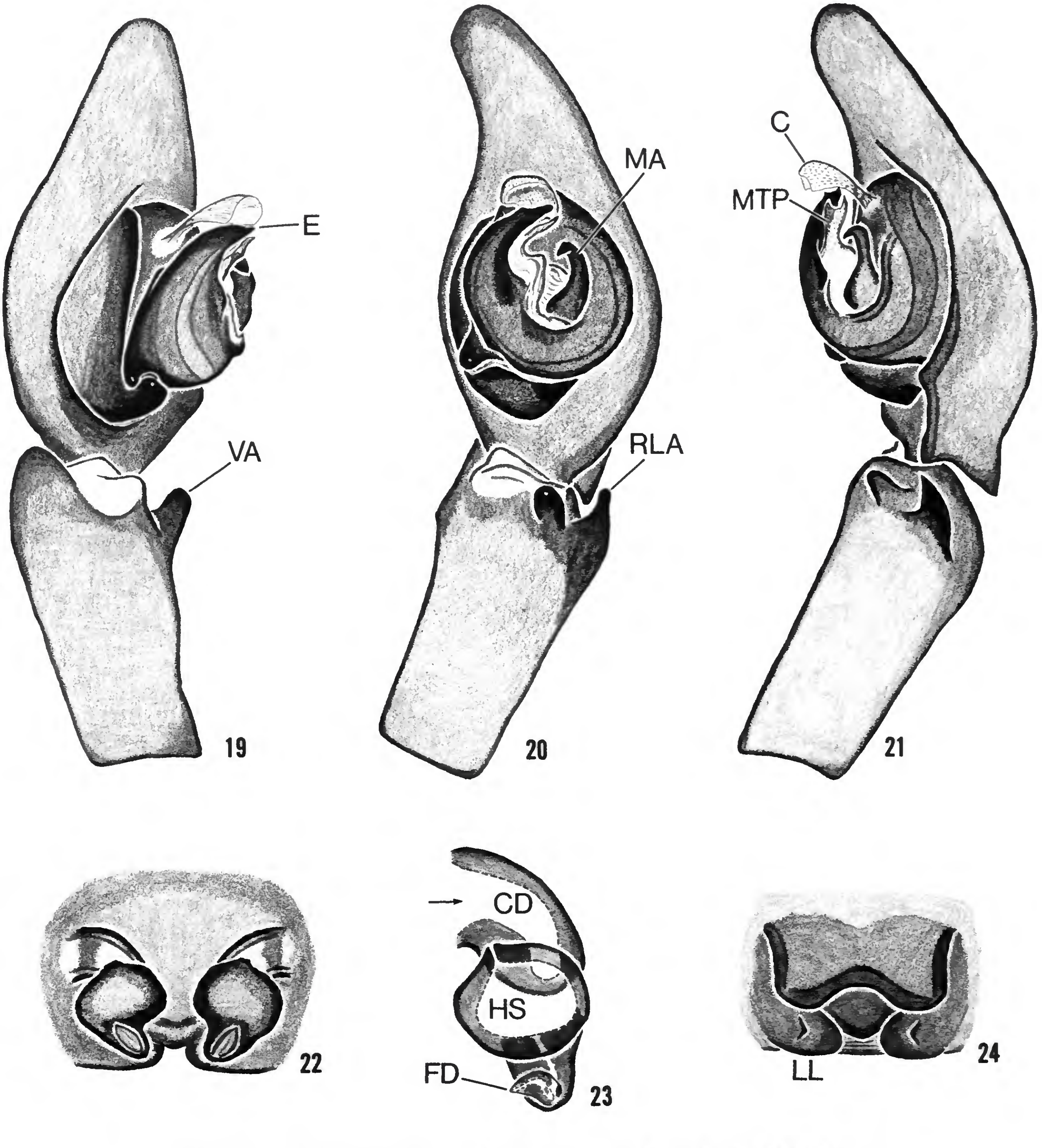
0 = longitudinal (Figures 11, 20, 38), typical of the majority of taxa treated here.

1 = transverse (Figures 13, 59), typical of *Uduba* and Lycosidae.

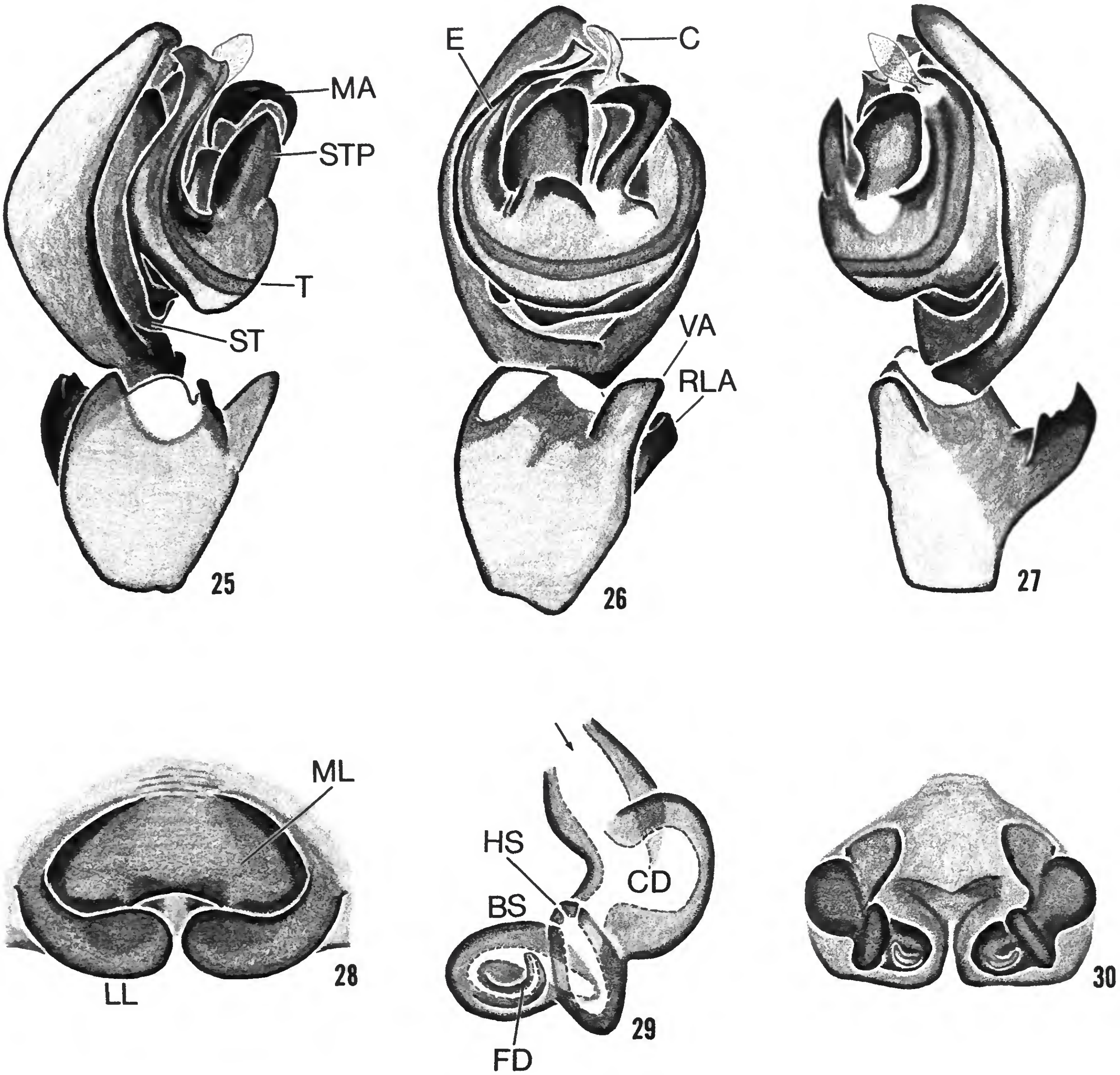
Character 19.—Tegulum, shape.

0 = oval (Figures 11, 20).

1 = apex divided into separate proapical and retroapical processes (*Uduba*: Figure 13; Lehtinen, 1967, fig. 81).



FIGURES 19–24.—*Zorodictyna oswaldi* (syntypes of *Agroeca oswaldi* Lenz), Nossi-Be, Madagascar (19–21, male palpus: 19, prolateral; 20, ventral; 21, retrolateral; 22, vulva, dorsal; 23, left vulva, dorsal; 24, epigynum, ventral). (Abbreviations: C = conductor, CD = copulatory duct (arrow represents copulatory opening), E = embolus, FD = fertilization duct, HS = head of spermatheca, MA = median apophysis, MTP = membranous tegular process, RLA = retrolateral apophysis, VA = ventral apophysis.)



FIGURES 25-30.—*Raecius* spp. 25-27: *Raecius zoropsides* (male type of *Mnesitheus zoropsides* Strand), Buea, Cameroon; 28-30: *Raecius* sp., Lulimbia, Zaire (25-27, male palpus: 25, prolateral; 26, ventral; 27, retrolateral; 28, epigynum, ventral; 29, left vulva, dorsal; 30, vulva, dorsal). (Abbreviations: BS = base of spermatheca, C = conductor, CD = copulatory duct (arrow represents copulatory opening), E = embolus, FD = fertilization duct, HS = head of spermatheca, MA = median apophysis, ML = median lobe, LL = lateral lobes, RLA = retrolateral apophysis, ST = subtegulum, STP = sclerotized tegular process, T = tegulum, VA = ventral apophysis.)

2 = notched probasally so that subtegulum is visible in ventral view. This is typical of *Rhoicinus* (Exline, 1960, fig. 2); the *Trechalea* genus-group (Sierwald, 1990, figs. 31, 34; *Trechalea*: Figure 52), and the Lycosidae (Figure 59; Sierwald, 1990, fig. 48; Brady, 1962, figs. 33, 37; Dondale and Redner, 1983, figs. 10, 35, 47).

Character 20.—Distal tegular protuberance (DTP).

0 = absent.

1 = present. Sierwald (1990) described a tegular form in pisaurids and dolomedids in which the proapical margin of the tegulum is produced into a protuberance (DTP) that subtends the flexible attachment of the embolic division

(Sierwald, 1990, figs. 2-5, 7, 8, 35). Similar morphology occurs in *Rhoicinus* (Exline, 1960, fig. 14) and the lycosids (Figure 59). Although Sierwald (1990:37) considered the DTP to be absent in the *Trechalea* genus-group, I score it as present for *Trechalea* because in this taxon the proapical tegulum at the base of flexible attachment of the embolic division is weakly projecting and truncate. In contrast, the proapical tegulum beneath the flexible attachment of the embolic division in *Uliodon, Campostichomma*, and *Uduba* is evenly convex.

Character 21.—Sclerotized tegular projection (STP) arising near embolic base.

0 = absent, with the tegulum near embolic base convex, simple (Figures 37, 38).

1 = present. Middle of tegulum has a sclerotized projection of various forms; may be small (*Ctenus*; *Fecenia*) or large (*Zorocrates*: Figure 11; *Raecius*: Figures 25-27; *Pisaura*: Sierwald, 1990, fig. 7 "da").

Character 22.—Median membranous region of tegulum.

0 = simple, convex. The region of the tegulum between the base of the median apophysis and base of the embolus is usually not sclerotized. Typically this region is flat or bulging slightly (Figure 37).

1 = with projection (MTP) arising near embolic base. The median membranous region of the tegulum may be produced in various ways. In *Zoropsis* the membrane is produced into a short apical process (Levy, 1990, fig. 9 'p'); in *Takeoa* this process is very narrow, elongate, and largely hidden behind the embolus (Yaginuma, 1963, fig. 10). In *Zorodictyna* the process has an apical groove which embraces the proximal margin of the embolic apex (Figures 19-21).

Character 23.—Embolus base.

0 = fixed, with sclerotized attachment to main body of tegulum (Figures 19, 33, 37, 38).

1 = flexibly attached to tegulum by membranous cuticle. In *Uliodon* membranous cuticle (EM) joins the bases of embolus and median apophysis, and joins both of these as a unit to the tegulum (Figure 47). In the pisaurids and dolomedids the embolic division is attached to the tegulum via the "basal membranous tube of apical division" (bmt) of Sierwald (1990, figs. 2, 4, 30). Similar (and I believe homologous) membranous connections of the embolic division to the tegulum are found in *Trechalea, Rhoicinus*, and the lycosids (Brady, 1962, fig. 36; Exline, 1960, figs. 2a, 14).

Character 24.—Embolus arising from basal lobe (EL).

0 = absent, with embolus origin gradually tapering from tegular surface (Figures 19, 37, 38).

1 = present, with base of embolus bulbous or lobate (Figures 12, 14, 33, 47, 59), whether or not firmly or flexibly attached to the tegulum.

Character 25.—Basal lobe of embolus with process (ELP).

0 = present, with lobe or protuberance (e.g., *Uduba*: Figure 14; *Campostichomma*: Figures 31, 34). The terminal apophysis (ta) of the *Trechalea* genus-group (Sierwald, 1990, figs. 32, 33), *Rhoicinus* (Exline, 1960, fig. 2a) and many lycosids (Figure 59; Dondale, 1986, figs. 5, 7, 11 "term."; Sierwald, 1990, fig. 48) and an apophysis of the apical division of pisaurids and dolomedids (e.g., the lateral subterminal apophysis (la) of *Dolomedes* (Sierwald, 1990, figs. 4, 5) and the sclerotized, bulbous basal process of the apical division (ad) in *Pisaura* (Sierwald, 1990, fig. 7) may be homologs.

1 = absent, basal lobe smoothly curved (e.g., *Uliodon*: Figure 47; *Sosippus*, Brady, 1962, fig. 36).

Character 26.—Embolus, direction of curve (left bulb, ventral view).

0 = clockwise, typical for most included taxa (Figures 20, 34, 47).

1 = counterclockwise. In *Uduba* the long, slender embolus is directed proximad and behind the subtegulum, extending distad behind the tegulum to emerge from behind the retroapical margin of the tegulum and rest against the ventroapical face of the cymbium (Figures 13, 14). In the lycosid group of higher lycosoids (pisaurids and dolomedids, lycosids, *Trechalea* genus-group, and *Rhoicinus*) the embolus arises from the apical division and curves back across the middle of the bulb (e.g., *Lycosa*: Figures 57, 59; *Dolomedes* (Sierwald, 1990, fig. 5).

Character 27.—Embolus, shape.

0 = stout, tapering to apex, convex (Figures 8, 20) or flattened (Figures 25, 26).

1 = slender, curved spine (Figures 13, 31, 47).

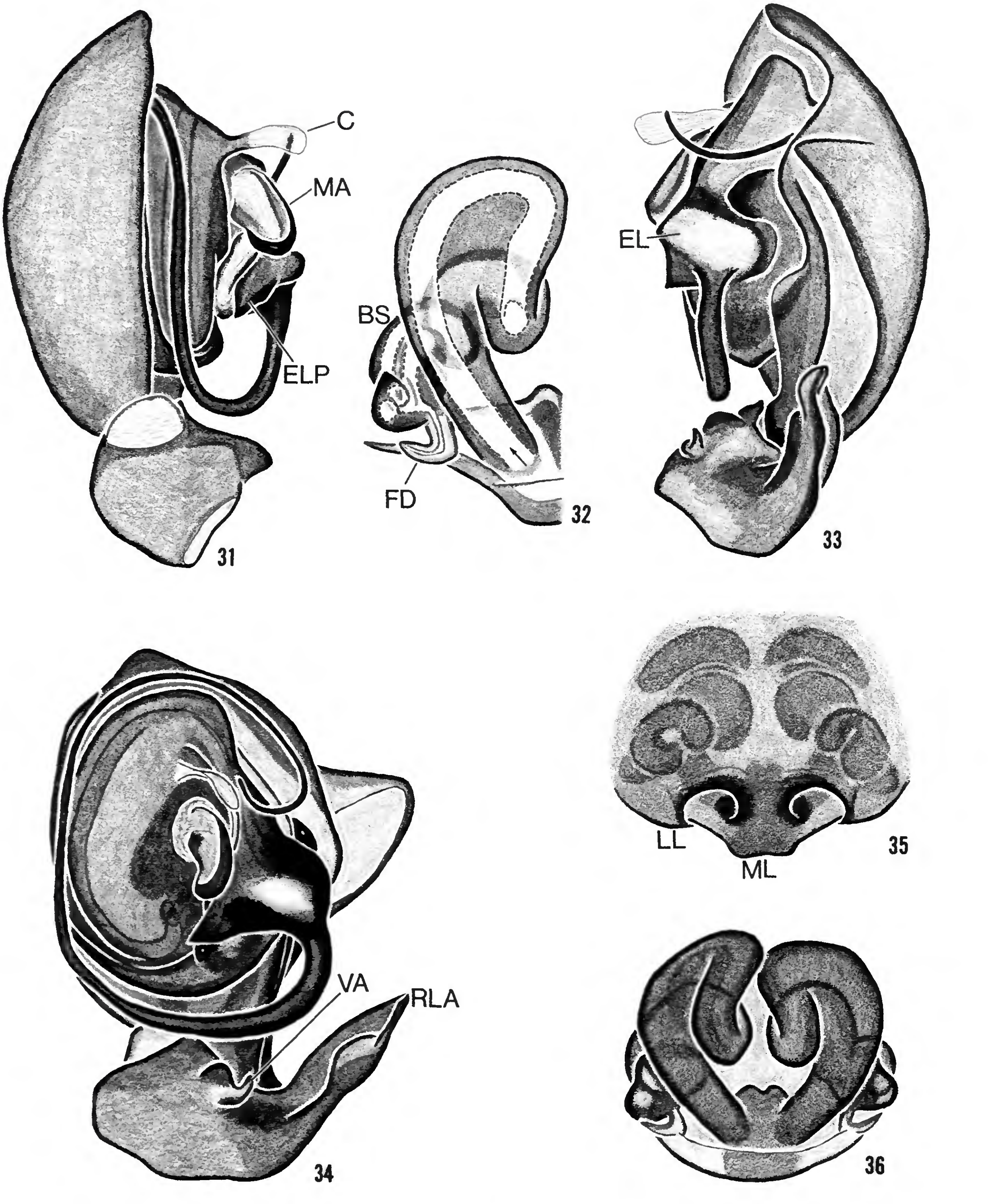
2 = broad, concave, apex divided into dorsal (ED) and ventral (EV) lobes (Figure 10). This form is typical of *Phanotea*, and similar embolic forms may be found in *Takeoa* (Yaginuma, 1963, fig. 10) and *Ctenus*.

3 = a broad, thin flange.

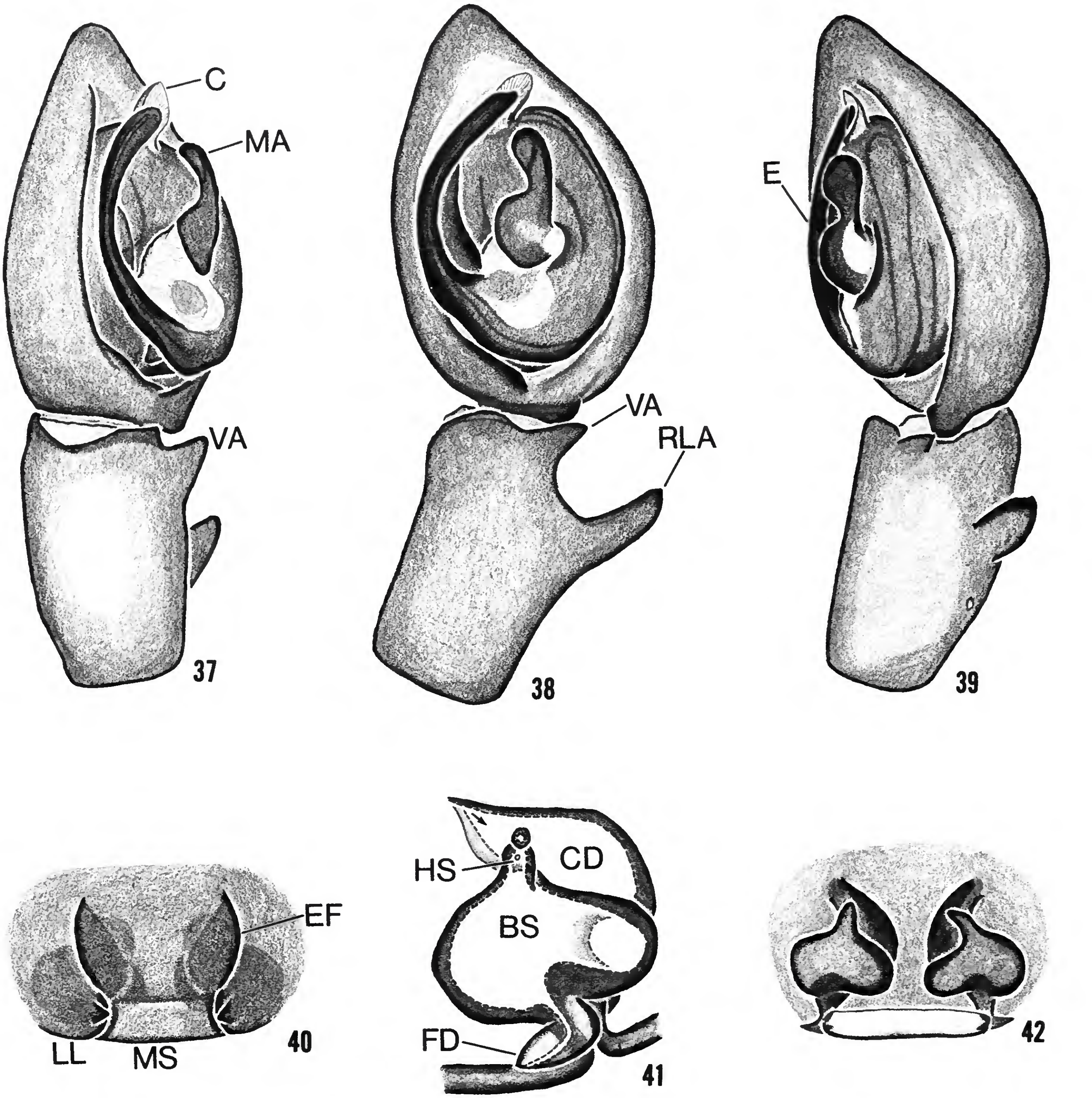
Character 28.—Epigynal configuration.

0 = clearly divided by longitudinal epigynal folds (EF; Sierwald, 1989 "epf") into a median sector (MS; Sierwald, 1989 "mf"; Jarvi, 1905 "septum") and paired lateral lobes (LL; Sierwald, 1989 "ll") (Figures 17, 28, 35, 40, 45, 46, 48; Sierwald, 1989, figs. 1, 3). The median sector is commonly enlarged and forms a median lobe (ML; see characters 31-33). Although *Dolomedes tenebrosus* has transversely inclined epigynal folds that do not reach the posterior margin of the epigynum, other species have typical folds (Carico and Holt, 1964); accordingly, *Dolomedes* is scored as 0.

1 = MS and LL fused, not divided longitudinally into three parts. The epigynum of *Uduba* consists of a median longitudinal lobe with depressed atria on each side; the copulatory openings may be beneath the median lobe or beneath the lateral lip of the atrium. In *Senoculus* the

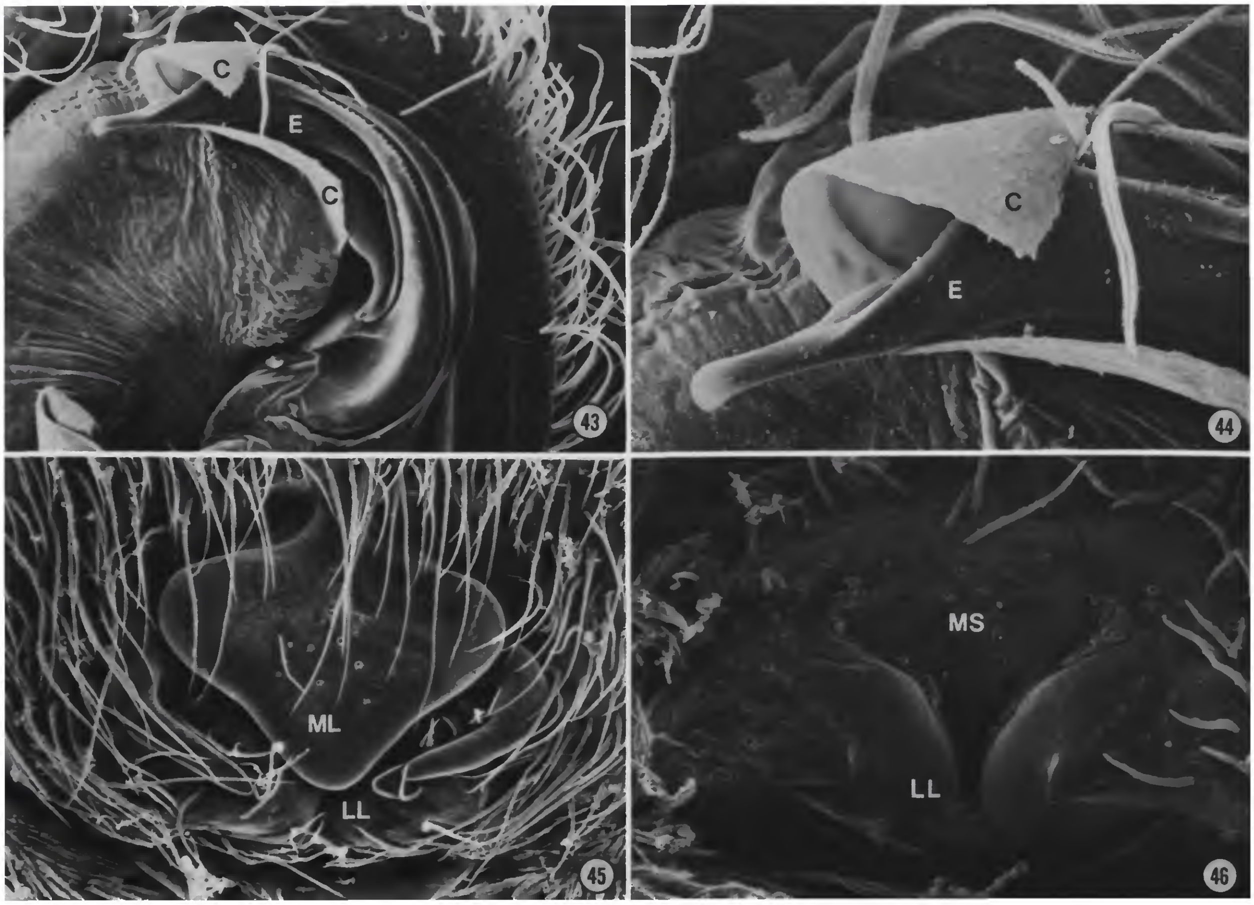


FIGURES 31–36.—*Campostichomma manicatum*, Maturata and Kandy, Sri Lanka: 31, 33, 34, male palpus (31, prolateral; 33, retrolateral; 34, ventral); 32, left vulva, dorsal; 35, epigynum, ventral; 36, vulva, dorsal. (Abbreviations: BS = base of spermatheca, C = conductor, EL = basal lobe of embolus, ELP = process on basal lobe of embolus, FD = fertilization duct (arrow represents copulatory opening), LL = lateral lobes, MA = median apophysis, ML = median lobe, RLA = retrolateral apophysis, VA = ventral apophysis.)



FIGURES 37–42.—*Devendra seriata*, Nuwara Eliya, Sri Lanka: 37–39, male palpus (37, prolateral; 38, ventral; 39, retrolateral); 40, epigynum, ventral; 41, left vulva, dorsal; 42, vulva, dorsal. (Abbreviations: BS = base of spermatheca, C = conductor, CD = copulatory duct (arrow represents copulatory opening), E = embolus, EF = epigynal fold, FD = fertilization duct, HS = head of spermatheca, LL = lateral lobes, MA = median apophysis, MS = median sector, RLA = retrolateral apophysis, VA = ventral apophysis.)

epigynum has an anteriad-directed horn-like projection on each side, behind which a depression leads into the copulatory opening (Chickering, 1941, figs. 9, 10). The posterior margin of the epigynal plate preserves no vestige of former separation into MS and LL in either *Uduba* (Figure 15) or *Senoculus*.



FIGURES 43–46.—*Machadonia punctata*, Karkloof, South Africa: 43, 44, male palpus, ventral; 45, *Phanotea* sp., Diepwalle, South Africa; 46, *Machadonia robusta*, Table Mt, South Africa (45, 46, epigynum, ventral). (Abbreviations: C = conductor, E = embolus, LL = lateral lobes, ML = median lobe, MS = median sector.

Character 29.—Lateral lobes (LL), modifications.

0 = convex, unmodified (Figures 28, 48; Sierwald, 1989, figs. 3, 9).
1 = concavity or pocket. Lateral, longitudinal pockets are characteristic of *Zoropsis* (Levy, 1990, figs. 13, 14).
2 = tooth (Figures 24, 40, 45, 46; Lehtinen, 1967, fig. 91; Benoit, 1974, fig. 10; 1979, figs. 1–12).

Character 30.—Lateral lobes with teeth.

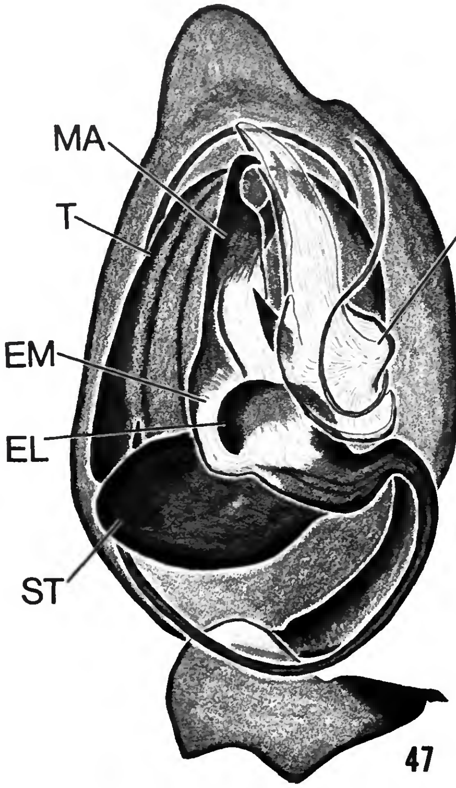
0 = short, median, typical of *Machadonia* (Figure 46; Lawrence, 1942, figs. 25, 26a), *Devendra* (Figure 40), *Zorodictyna* (Figure 24), some *Phanotea* (Lawrence, 1964, fig. 24), and ctenids (Benoit, 1974, fig. 10).
1 = long, median (some *Phanotea*: Figure 45).
2 = on posterior margin (*Rhoicinus*: Exline, 1960, figs. 6, 11).

Character 31.—Median sector of epigynum (MS), form.

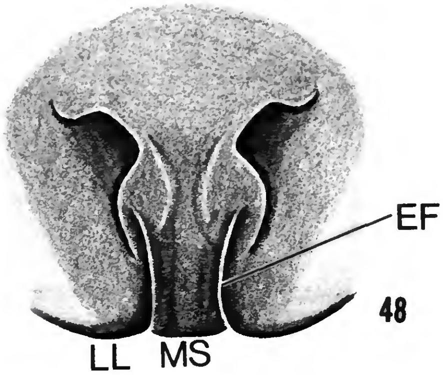
0 = median lobe (ML); swollen, with a lobe or protuberance (see char. 33).
1 = unmodified, flat or gently convex, e.g., *Psechrus* (Levi, 1982a, fig. 11), some *Machadonia* (Figure 46; Lawrence, 1942, fig. 26a), *Uliodon* (Figure 48), and *Dolomedes* (Carico, 1973, figs. 56, 58).

Character 32.—Median lobe, form.

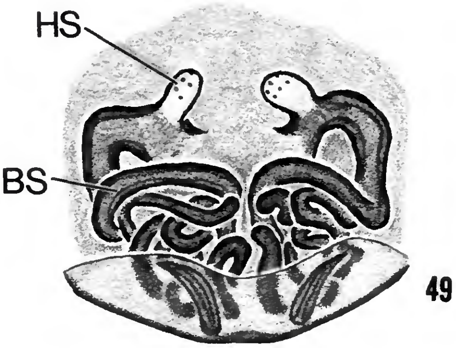
0 = scape, projecting ventrad with abrupt posterior margin; can be small, e.g., some *Machadonia* (Lawrence, 1942, fig. 25) and *Devendra*, to large and beak-like (e.g., Figures 24, 28; also *Tengella*: Wolff, 1978, fig. 5; *Fecenia*: Levi, 1982a, fig. 78).
1 = a swollen lobe extending to posterior margin of epigynum is typical of ctenids (e.g., Benoit, 1979, figs.



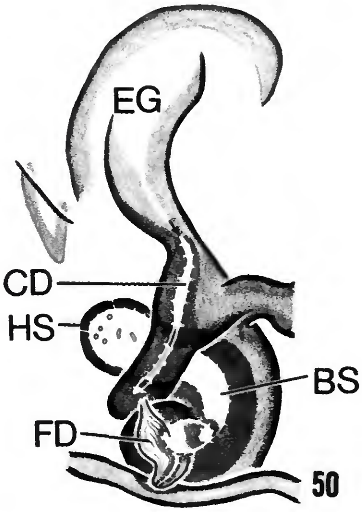
47



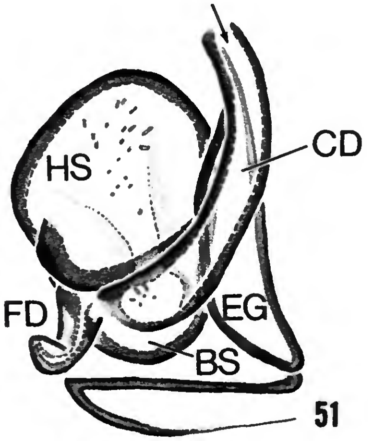
48



49

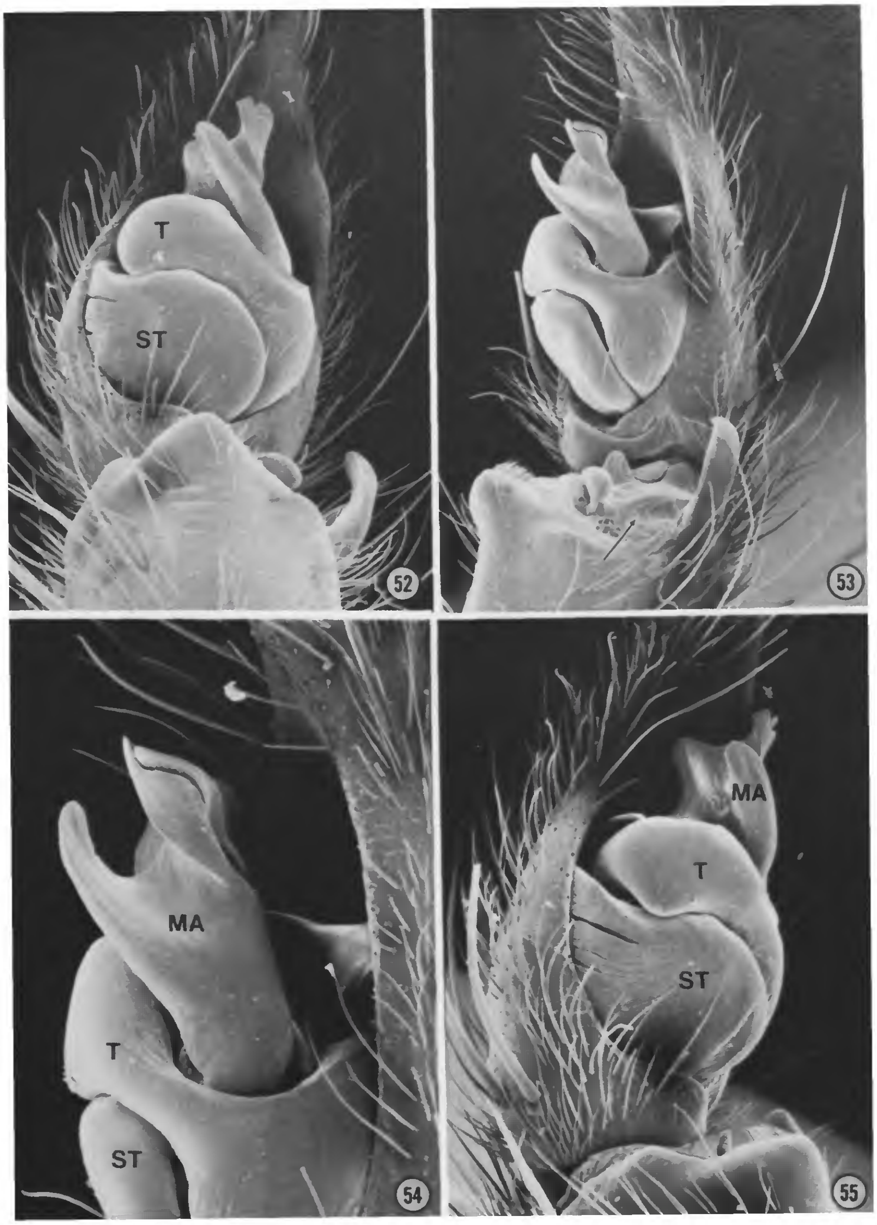


50



51

FIGURES 47–51.—47–49, *Uliodon tarantulinus*, New South Wales, Australia; 50, *Phanotea peringueyi*, Cango Caves, South Africa; 51, *Machadonia punctata*, Karkloof, South Africa. 47, male palpus, ventral; 48, epigynum, ventral; 49–51, vulva, dorsal. (Abbreviations: BS = base of spermatheca, C = conductor, CD = copulatory duct (arrows represent copulatory openings), EF = epigynal fold, EG = inner margin of external epigynal groove, EL = basal lobe of embolus, EM = basal membranous connection of embolus, FD = fertilization duct, HS = head of spermatheca, LL = lateral lobes, MA = median apophysis, MS = median sector, ST = subtegulum, T = tegulum.)



FIGURES 52–55.—*Trechalea* sp., Beni Prov., Bolivia, male palpus: 52, ventral; 53, 54, retrolateral; 55, prolateral. Arrow points to unsclerotized cuticle. (Abbreviations: MA = median apophysis, ST = subtegulum, T = tegulum.)

1–12) and lycosids (e.g., Dondale, 1986, fig. 6; Brady, 1962, figs. 14, 16, 19, 22), where it is usually broadest posteriorly, whereas a posteriorly narrowed ML occurs in *Campostichomma* (Figure 35).

2 = median longitudinal swellings. *Zorocrates* has a narrow median ridge with a deep central pit (Figure 17) and *Takeoa* has a median longitudinal lobe extending anteriad of the lateral lobes (Lehtinen, 1967, fig. 403).

Character 33.—Scape.

0 = simple, broadly attached anteriorly (e.g., *Tengella*: Wolff, 1978, fig. 5; *Fecenia*: Levi, 1982a, fig. 78; *Raecius*: Figure 28, *Zorodictyna*: Figure 24).

1 = an erectile scape, narrowly attached anteriorly, is typical of *Zoropsis* (Levy, 1990, figs. 13, 15, 17, 20) and

Phanotea (Figure 45; Lawrence, 1964, fig. 24).

Character 34.—Posterior divot or fossa on scape.
0 = present.
1 = absent.

Character 35.—Internal margin of epigynal groove (EG).
0 = not apparent on dorsal surface of epigynal plate (Figures 22, 30).
1 = internal bulge, separate from vulva.
2 = broad bulge, leading to copulatory duct (CD) (e.g., *Phanotea*: Figure 50).
3 = narrow, approximately parallel to copulatory duct, extending posteriad to near level of fertilization duct (FD) (*Machadonia*: Figure 51).

Character 36.—Shape of copulatory duct (CD).
0 = short, broad, length less than vulva (e.g., *Zorocrates*: Figure 18; *Zorodictyna*: Figure 23).
1 = long, length greater than or equal to vulva (e.g., *Machadonia*: Figure 51; *Dolomedes*: Carico, 1973; fig. 52 "BC").
2 = very long, length greater than vulva and looped back on itself (e.g., *Uduba*: Figure 16; *Campostichomma*: Figure 32; *Stiphidion*: Davies, 1988, fig. 6). Although the head of the spermathecae (HS) is lost in *Uduba* and *Campostichomma*, the elongate vulval ducts of these taxa suggest that both the copulatory ducts (CD) and spermathecal base (BS) are elongate: they are coded accordingly for characters 36 and 39.

Character 37.—HS (head of spermatheca-that area of vulva with pores; see Sierwald, 1989, figs. 17, 18, 24-26).
0 = small, narrow, smaller than BS (e.g., *Zorocrates*: Figure 18; *Devendra*: Figure 41; *Raecius*: Figure 29; *Phanotea*: Figure 50; *Uliodon*: Figure 49; *Dolomedes*: Carico, 1973, figs. 51, 52, "AB"; *Rhoicinus*: Exline, 1960, figs. 13, 15, "3"; *Sosippus*: Brady, 1962, fig. 20, "s").
1 = large, spherical, larger than BS (e.g., *Psechrus*: Levi, 1982a, fig. 10; *Fecenia*: Levi, 1982a, fig. 77; *Zorodictyna*: Figure 23; *Machadonia*: Figure 51; *Stiphidion*: Davies, 1988, figs. 5, 6).
2 = absent, no porose area (*Uduba* and *Campostichomma*: Figure 32).

Character 38.—BS (base of spermatheca; that area just before fertilization duct; see Sierwald, 1989, for complete definition), internal structure.
0 = simple, spherical or tubular (e.g., *Zorocrates*: Figure 18; *Raecius*: Figure 29; *Machadonia*: Figure 51; *Phanotea*: Figure 50).
1 = chambered (e.g., *Campostichomma*: Figure 32).

Character 39.—BS (base of spermatheca), external form.
0 = simple (e.g., *Raecius*: Figure 29; *Devendra*: Figure 41; *Phanotea*: Figure 50; *Stiphidion*: Davies, 1988, fig. 6).
1 = pronounced lobe (e.g., *Rhoicinus*: Exline, 1960, figs. 13, 15 "4"; lycosids (Brady, 1962, fig. 20 "B").
2 = long, sinuate (*Zorocrates*: Figure 18; *Uliodon*: Figure 49; *Dolomedes*: Carico, 1973, fig. 52 "FT"). See character 36.

Character 40.—Fertilization duct (FD), position.
0 = posterior (e.g., *Zorodictyna*: Figure 23; *Phanotea*: Figure 50; *Machadonia*: Figure 51).
1 = median (e.g., *Dolomedes*: Carico, 1973, fig. 53, Sierwald, 1989, fig. 6).

Character 41.—Cribellum, division (Coddington, 1990:7, and Griswold, 1990:14, discussed the polarity and significance of an entire and divided cribellum. Within the Araneomorphae an entire cribellum is primitive and the divided state is derived. Among the taxa treated here it appears that reversion to the entire state has occurred).
0 = well-divided.
1 = contiguous, each half touching.
2 = entire, though spinning field may be divided.

Character 42.—Cribellum, form.
0 = each half transversely linear (e.g., *Fecenia*: Levi, 1982a, fig. 71; *Takeoa*: Yaginuma, 1963, fig. 11; Levy, 1990, fig. 1).
1 = oval to triangular, longitudinal diameter equal to transverse (e.g., *Acanthoctenus*: Pickard-Cambridge, 1902, pl. 33: fig. 13b; Courtois, 1911, fig. 11c).
2 = absent, cribellum transformed to colulus.

Character 43.—PER, shape.
0 = nearly straight, ratio of OAL to OQL less than 1.20 (e.g., Wolff, 1978, figs. 1, 2, 6; Levi, 1982a, fig. 12).
1 = recurved, ratio of OAL to OQL greater than 1.20 (e.g., Benoit, 1978, fig. 2a; Davies, 1988, fig. 2; Yaginuma, 1963, fig. 3; Levy, 1990, fig. 3; Brady, 1962, figs. 1-9).

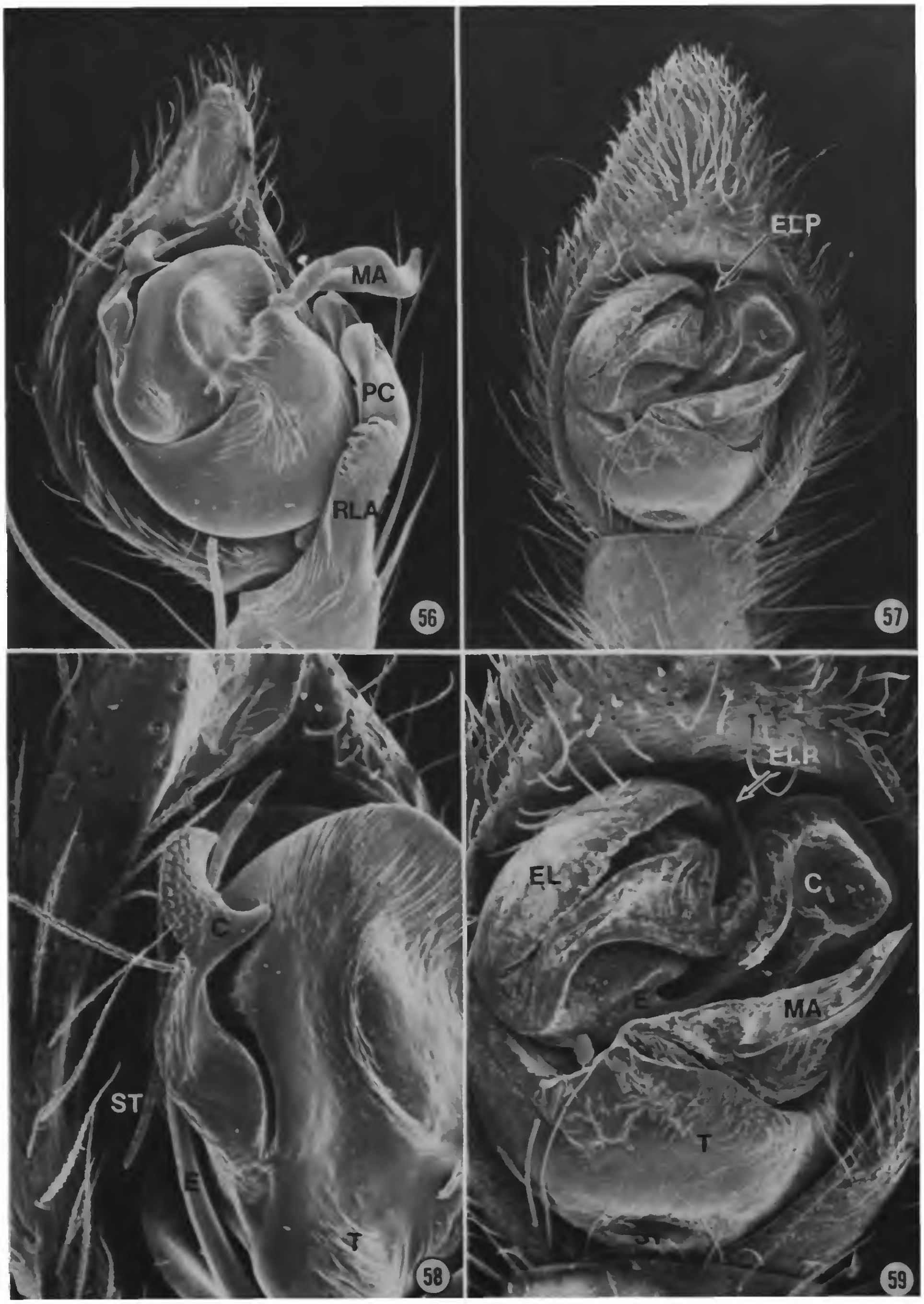
Character 44.—Sternum, ratio of length to width.
0 = greater than 1.20.
1 = less than 1.20.

Character 45.—Sternum with point extending between coxae IV.
0 = absent.
1 = present (e.g., Levi, 1982a, figs. 2, 69; *Rhoicinus*: Exline, 1960, fig. 4).

Character 46.—ALE and PME in transverse line (typical "ctenid" eye pattern).
0 = no.
1 = yes, as in *Acanthoctenus* (Pickard-Cambridge, 1902, pl. 33: fig. 13a); ctenids (Benoit, 1974, fig. 1; 1978, fig. 1a; 1979, fig. 15), and *Senoculus*.

Character 47.—PLE behind PME, ratio of PER to OQP less than 1.6 (typical of Lycosidae).
0 = no.
1 = yes (Brady, 1962, figs. 5-9).

Character 48.—Labium, ratio of length to width.
0 = greater than 1.20.



FIGURES 56–59.—Male palpus, ventral 56, 58, *Tapinillus* sp., Beni Prov., Bolivia: 57, 59, *Lycosa helluo*, New York, USA (ST sunken into alveolus; more prominent in fresh specimens). (Abbreviations: C = conductor, E = embolus, EL = basal lobe of embolus, ELP = process on basal lobe of embolus, MA = median apophysis, PC = paracymbium, RLA = retrolateral apophysis, VA = ventral apophysis, ST = subtegulum, T = tegulum.)

1 = less than 1.18.

Character 49.—Cheliceral retromargin, number of teeth.
0 = three.
1 = four.
2 = two.
3 = none.

Character 50.—Tapetum.

0 = with only a canoe-shaped tapetum, having two shiny oval parts bisected by a longitudinal dark line (Homann, 1971, figs. 10A, 27B, 32A). This kind only occurs in *Tengella* (pers. obs.), *Zorocrates* (Homann, 1971:218), *Uduba* (pers. obs.), and *Zorodictyna* (pers. obs.).

1 = tapeta in at least some eyes grate-shaped, each half of tapetum weakly (e.g., *Stiphidion*: Homann, 1971, fig. 32D) to strongly (e.g., Homann, 1971, figs. 12C, 32E) folded. This occurs in psechrids (Homann, 1971:224, 261; Levi, 1982a, figs. 73, 74, 88), *Takeoa* (pers. obs.), *Acanthoctenus* (Homann, 1971:224, 261), *Zoropsis* (Homann, 1971:261; pers. obs.), *Machadonia* (pers. obs.), Oxyopidae (in spite of the loss of the reflecting tapetum, Homann (1971:262) places the oxyopids among those spiders with the grate-shaped tapetum; accordingly this is coded here as 1 for *Tapinillus*), *Senoculus* (Homann, 1971:261, fig. 32E), *Uliodon* (pers. obs.), *Dolomedes* (pers. obs.), Pisauridae (Homann, 1971:261), *Trechalea* (pers. obs.), *Rhoicinus* (Homann, 1971:261; pers. obs.), Lycosidae (Homann, 1971:261; pers. obs.), Ctenidae (Homann, 1971:261) and *Stiphidion* (Homann, 1971, fig. 32D).

2 = diffuse. In *Phanotea peringueyi* the greater part of the tapetum is diffuse and splotchy, with a group of regularly arranged splotches along the outer lateral margin. I failed to resolve a tapetum in *Campostichomma, Devendra, Raecius,* and *Phanotea* species 1 and 2; accordingly these are scored "?" for this character.

Character 51.—Ratio of male tibia I length to carapace width.
0 = less than 2.7.
1 = greater than 3.0 (typical of psechrids).

Character 52.—Male tibial crack; a conspicuous suture line visible through the cuticle at the base of the leg tibiae of males just distal to the basal pair of ventral spines; it is visible on the surface as a shallow, depressed ring (Figures 3, 4). Autospasy at this point apparently does not occur.
0 = absent.
1 = present.

Character 53.—Tarsus, dorsal trichobothria.
0 = 2 or 3 irregular rows.
1 = 1 row (psechrids: Levi, 1982a, fig. 72; Lehtinen, 1980, fig. 6 "Psechridae"; *Stiphidion,* and Oxyopidae).

Character 54.—Dense claw tufts in pretarsal region, obscuring pretarsus and ITC (if present).
0 = absent (Figure 5).
1 = present (Figure 6).

Character 55.—Trochanter notch.
0 = deep (e.g., Roth, 1964, figs. 4, 19, 21).
1 = broad, very shallow (e.g., Roth, 1964, figs. 5, 27).
2 = absent (e.g., Roth, 1964, figs. 6, 11).

Character 56.—Tarsal organ, form.
0 = aperture simple, oval to round (Figures 64, 65, 71, 78, 80, 82).
1 = keyhole-shaped (oval to round, but with longitudinal seam extending proximad of aperture) (Figures 63, 66).
2 = stellate, margin forming several inward-pointing lobes (Figures 72, 76, 77). Tarsal organs of *Fecenia, Uduba dahli, Devendra seriata, Zoropsis rufipes, Machadonia urbense,* and *Phanotea* sp. 2 were not scanned, and are therefore coded as "?"

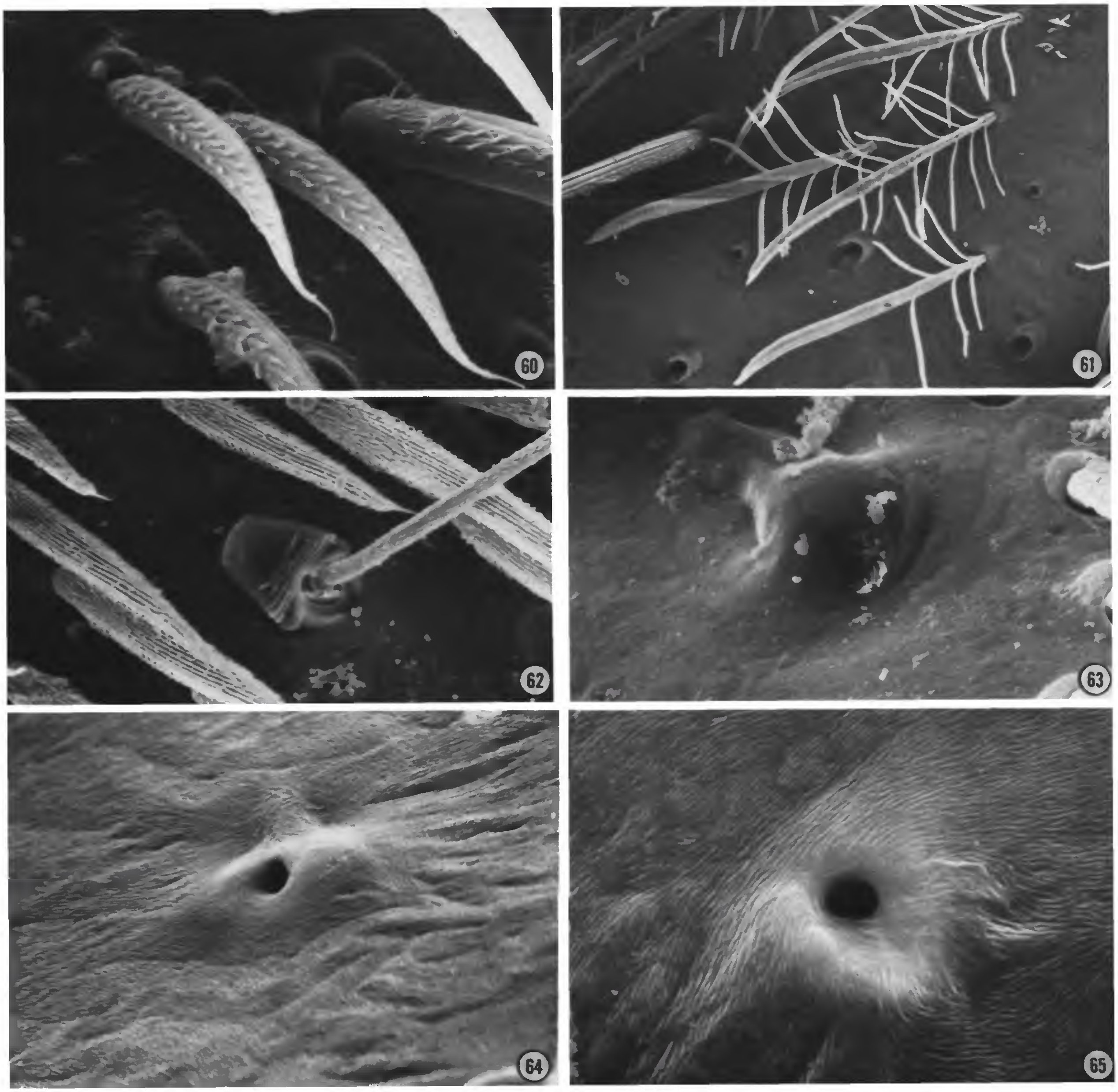
Character 57.—Trichobothrial base, texture of hood.
0 = transversely striate (Figures 62, 67, 69–71, 73, 77).
1 = with fine longitudinal striations (e.g., *Rhoicinus*: Figure 81; *Tapinillus*: Figure 83) to smooth (e.g., *Dolomedes:* Figure 79). Trichobothrial bases of *Fecenia* and *Phanotea* sp. 2 were not scanned and are therefore coded as "?"

Character 58.—Flattened feathery hairs on legs.
0 = absent, all hairs of normal, plumose-laminar form (sensu Lehtinen, 1975), with many fine, short to long barbs arranged in spiral whorls around the shaft (Figures 60, 62, 71).
1 = present, setae flattened with long lateral barbs (Figures 61, 74, 75, 77).

Character 59.—Pairs of ventral spines on tibia I of both sexes.
0 = four pairs occur in the majority of taxa.
1 = universally in *Machadonia* there is an extra anteroventral spine just behind the apical pair (4+1). A similar pattern occurs in *Zorocrates.*
2 = five pairs occur in the ecribellate ctenids.
3 = seven or more pairs occur in *Acanthoctenus, Takeoa,* and *Zoropsis.*
4 = three pairs occur in lycosids and in *Uliodon.* The single pair in *Fecenia* and 2 pairs *Stiphidion* are autapomorphic and are scored "?" for not applicable.

Character 60.—Female tibia I, lateral spines.
0 = present.
1 = absent.

Character 61.—Male tibia I, dorsal spines.
0 = absent.
1 = one.
2 = two or more. *Tapinillus, Pisaura,* and *Trechalea* have a



FIGURES 60–65.—Legs: 60, *Machadonia robusta*, female, Table Mt, South Africa, plumose setae; 61, *Senoculus canaliculatus*, female, Finca La Selva, Costa Rica, feathery setae; 62, 63, *Zorodictyna oswaldi*, female, Nossi-Be, Madagascar; 64, *Tengella radiata*, female, Finca La Selva, Costa Rica; 65, *Psechrus himalayanus*, female, Gandaki Zone, Nepal (62, trichobothrium and plumose setae; 63–65, tarsal organs).

basal and a subapical spine, and *Zorodictyna*, *Acanthoctenus*, *Phoneutria*, and *Ctenus* have a row of 3 median spines.

Character 62.—Female tibia I, dorsal spines.

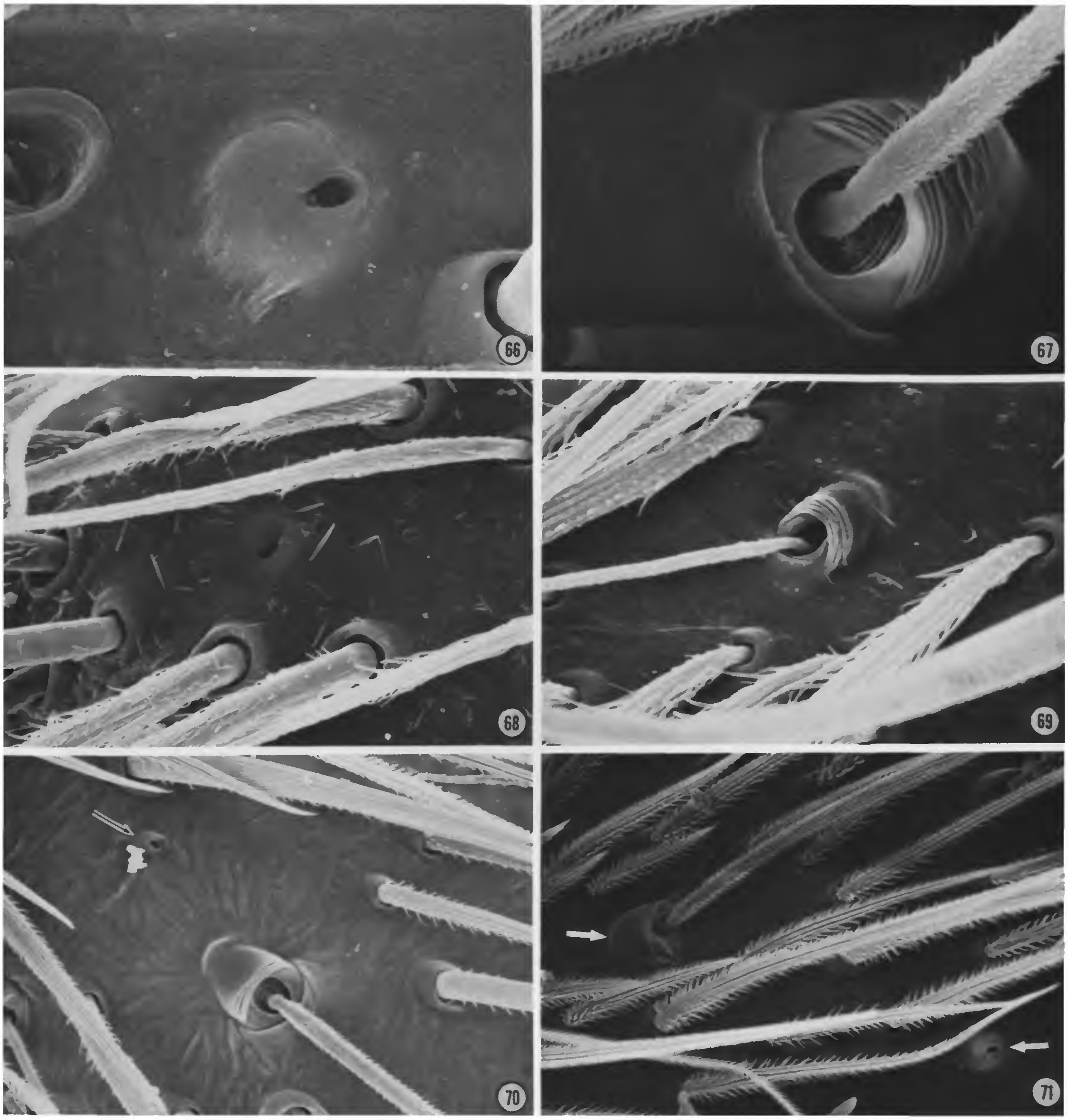
0 = absent.

1 = present. *Tapinillus*, *Senoculus*, *Pisaura*, and *Dolomedes* have a basal and a subapical.

Character 63.—Male metatarsus I or II, lateroapical pairs of spines.

0 = absent.

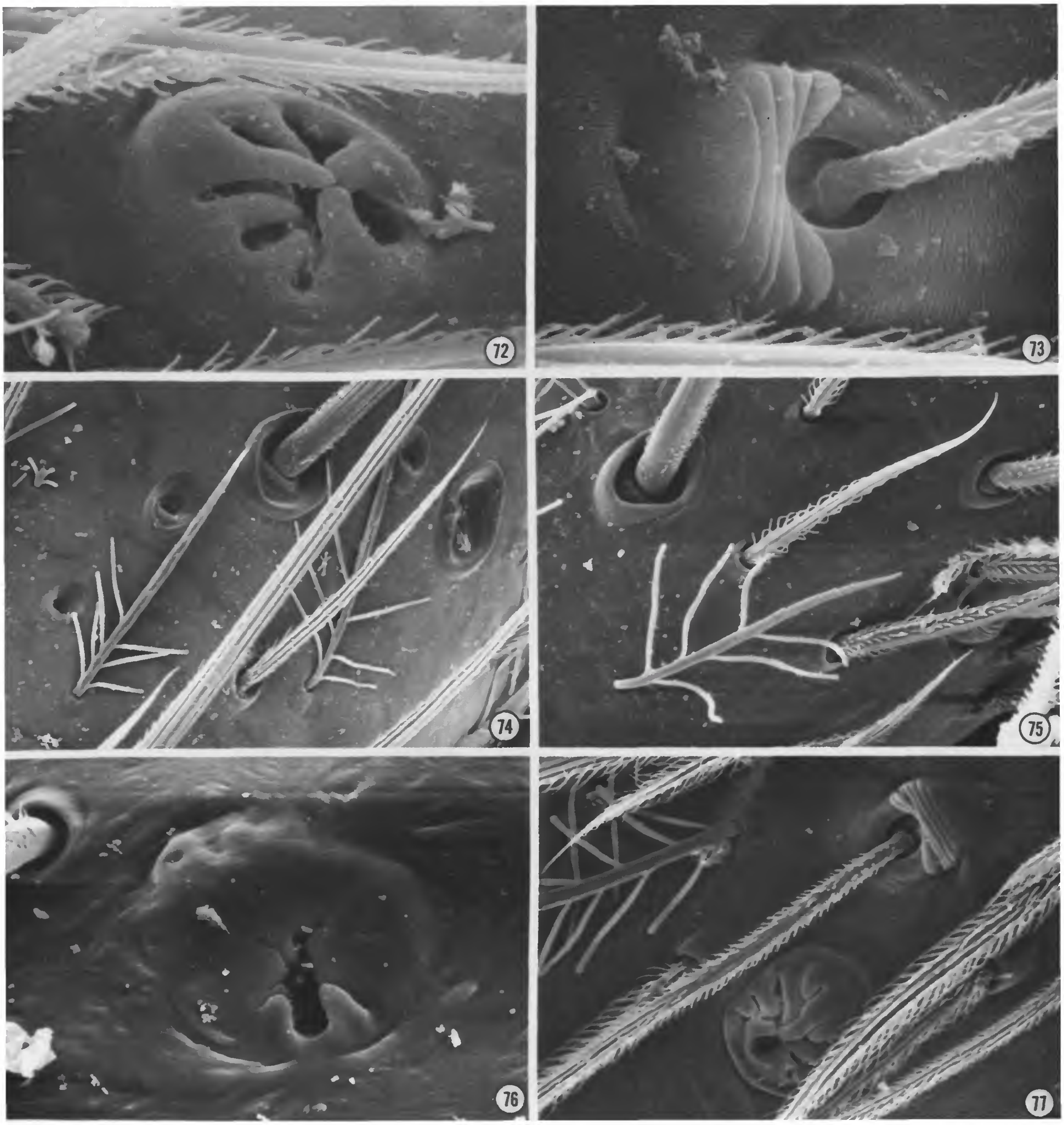
1 = present in *Zorocrates*, *Campostichomma*, *Raecius*, *Zorodictyna*, *Dolomedes*, *Rhoicinus*, and *Lycosa*.



FIGURES 66–71.—Legs: 66, 67, *Zoropsis spinimana*, female, Barcelona, Spain; 68, 69, *Takeoa nishimurai*, allotype male, Kyoto City, Japan; 70, *Acanthoctenus spiniger*, female, Tegucigalpa, Honduras; 71, *Zorocrates* sp., female, Baja California Sur, Mexico (66, 68, tarsal organ; 67, 69, trichobothrium; 70, 71, tarsal organ, trichobothrium, and plumose setae (arrows to tarsal organs and trichobothrial base)).

Character 64.—Calamistrum.
0 = present.
1 = absent.

Character 65.—Calamistrum shape.
0 = broad, oval (Figure 1; Courtois, 1911, figs. 11a, 12a) to rectangular (Courtois, 1911, figs. 9a,b, 10a–c).
1 = linear, with a single row of calamistral setae (*Stiphidion*).



FIGURES 72–77.—Legs: 72–74, *Devendra pardale*, female, Kandy, Sri Lanka; 75, 77, *Campostichomma manicatum*, female, Kandy, Sri Lanka; 76, *Uduba* species 1, male, Ranomafana, Madagascar (72, 76, tarsal organ; 73, trichobothrial base; 74, 75, feathery setae; 77, tarsal organ, trichobothrial base, and plumose and feathery setae).

Character 66.—Scopula, leg I.

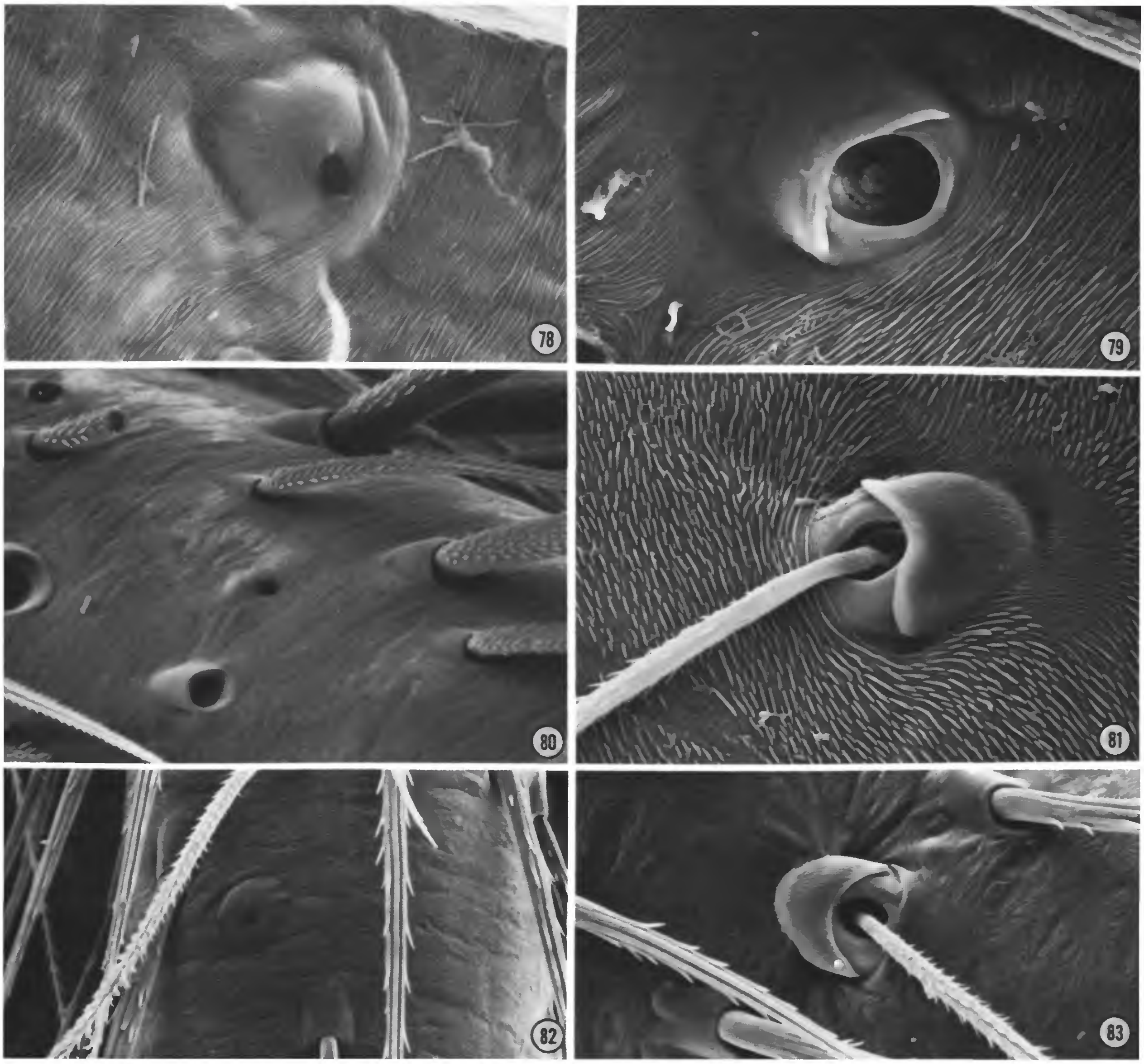
0 = beneath tarsus and metatarsus.

1 = beneath tarsus only in *Tengella* and *Raecius*.

2 = absent in the psechrids, *Campostichomma* and *Devendra*, *Tapinillus*, *Senoculus*, *Pisaura*, *Trechalea*, *Rhoicinus*, and *Stiphidion*.

Character 67.—Nursery web.

0 = absent.



FIGURES 78-83.—Legs: 78, 79, *Dolomedes tenebrosus*, male, Maryland, USA; 80, 81, *Rhoicinus* sp., female, Beni Prov., Bolivia; 82, 83, *Tapinillus* sp., female, Beni Prov., Bolivia (78, 80, 82, tarsal organ;. 79, 81, 83, trichobothrial base).

1 = present in *Dolomedes* and *Pisaura*. Reproductive biologies of *Zorocrates, Fecenia, Uduba, Campostichomma, Devendra, Raecius, Zorodictyna, Takeoa, Acanthoctenus, Phanotea* spp. 1 and 2, and *Ctenus* are unknown, and are scored as "?" for this character.

Character 68.—Egg sac carried on spinnerets.

0 = no.

1 = yes, as in lycosids, *Rhoicinus* (Exline, 1960:579; Simon, 1898:321), *Trechalea* (Sierwald, 1990, pers. obs.). Reproductive biologies of *Zorocrates, Fecenia, Uduba, Campostichomma, Devendra, Raecius, Zorodictyna, Takeoa, Acanthoctenus, Phanotea* spp. 1 and 2, and *Ctenus* are unknown, and are scored as "?" for this character.

Quantitative Analysis

CALCULATION OF MOST PARSIMONIOUS TREES.—The matrix was analyzed to produce a heuristic solution using Hennig86, version 1.5 (Farris, 1988). Characters were considered unordered. *Tengella* was chosen as the working outgroup because all other taxa had presumably derived characters (e.g., grate-shaped tapetum, male tibial crack, lobate embolic base) in common with some subset of the taxa. Data were analyzed using the the h; bb;, h*; bb*;, m; bb;, m; bb*;, m*; bb*; and t; bb*; options. The m*; bb*; and t; bb*; options each gave the same 9 equally parsimonious cladograms of 244 steps; all other options failed to find as short a solution. Variation in the order of taxon input occasionally had an effect on the result. Input order was shuffled five times and analyzed with m*; bb*;. The same 9 equally parsimonious cladograms of 244 steps were found in 4 out of the 5 runs; the fifth failed to find any cladograms as short. The nelson consensus of the 9 cladograms is equivalent to that shown in Figures 84–87 except for the lack of components H, V, and AA.

CHOICE OF TREES.—To choose among these alternatives, this suite of 9 cladograms was subjected to successive character weighting (Farris, 1969; Carpenter, 1988). Characters were re-weighted based upon their relative agreement with the cladograms obtained: characters agreeing well with the initial cladograms are given greater weight than those requiring more homoplasy. Three rounds of successive weighting, implemented through the xs w; m*; bb*; commands of Hennig86 produced a stable solution of three equally parsimonious cladograms (character weights assigned through this routine are listed in Table 4). As these three were among the original suite of 9, they are preferred. Each of the three most parsimonious cladograms chosen through successive approximations weighting differed only in alternative pairings of components V, S, and K on Figure 85, but in each case the pairing is problematical. Pairing of components S and K is supported by the loss of cribellum and calamistrum, which subsequently re-evolves in *Stiphidion* and the psechrids. Parallel evolution of such a complex character system is unlikely. Pairings of clade V with either S or K are based on characters shared between *Acanthoctenus* in clade V and the other components: in each case immediate reversal is required at node U (*Takeoa* plus *Zoropsis*). For these reasons I prefer the Nelson (strict) consensus of these three cladograms, which also requires 244 steps, as the most realistic reflection of the possible phylogenetic relationships among the taxa treated in this study (Figures 84–87). This cladogram, which has a basal trichotomy and a trichotomy arising from node AA, has a consistency index of 0.38 and a retention index of 0.63. The consistency index may be considered low: this reflects my liberal a priori coding of homologies, many of which prove to be parallelisms in terminals. One could recode these independent transformations as new (frequently autapomorphic) states, thereby increasing the consistency index, but as this would serve to hide variability and de-emphasize the role of quantitative phylogenetics in interpreting homoplasy, I prefer to retain the codings and accept the low consistency.

TRACING CHARACTER EVOLUTION.—The "Dos equis" (xx) routine of Hennig86 was used to assess the length of alternative trees and to trace character changes. Ambiguous optimizations were resolved by hand. Character changes at nodes and in terminal taxa are listed in Table 4, and all character changes are mapped on Figures 84–87. In the "Discussion" certain characters are cited as synapomorphies supporting monophyletic groups. In many cases there are additional instances of homoplasy for these same characters that are not explicitly discussed: for a full account of homoplasy refer to Figures 84–87 and Table 4. In this paper the use of the term "unique" to refer to character states is relevant only to the taxa included in the data set.

TESTS OF TAXON AND CHARACTER HYPOTHESES.—Hypotheses concerning the monophyly of taxa or the homology of characters were evaluated quantitatively by determining the cost in parsimony (i.e., extra steps required over this data set) if a given taxon or character were to be considered uniquely derived. The unique derivation of a taxon or character was forced by including an artificial character in the data set supporting that hypothesis. This character was then incrementally weighted using the command cc /weight character; through a series of Hennig86 runs using the t; bb*; routine. At the end of each test run the length of the resulting trees was noted. A strict consensus tree was then found using nel; tp; and this tree was examined for a component representing the hypothetical group. When this group was found, the extra length required by it was calculated as follows (length of tree for which group found - weight of artificial character necessary to force monophyly of that group - minimum length of tree for original data set). For example, the monophyly of the Ctenidae was tested by including an artificial character grouping *Acanthoctenus, Ctenus,* and *Phoneutria.* This character was incrementally weighted through a series of runs until these three taxa formed a monophyletic group. The length of the trees on which this occurred was 253 steps and the weight of the artificial character necessary to force this was 5. The extra steps required by the hypothesis of ctenid monophyly was calculated (253-5-244=4): this hypothesis requires four additional steps on this data set. It might be considered simpler to use a tree manipulation routine such as xx of Hennig86 to arrange the taxa of interest in a monophyletic group and count the extra steps required by this arrangement. This will not necessarily give the shortest tree possible, though, as there might be arrangements of the other taxa that would reduce the length of the tree. It is preferable to force the monophyly of a hypothetical group through character weighting and allow a powerful tree-finding routine to arrange the other taxa in the most parsimonious way possible.

Discussion

RESULTS: TAXA.—The Lycosoidea (Levi, 1982b) emerge as monophyletic on the cladogram (Figure 84), supported at node

TABLE 4.—Behavior of Characters on Figures 84–87. Columns are Character (Char.), Steps, Consistency (Con.), Retention Index (Ret.), Weight accorded through successive weighting (Wt.), and Changes at nodes and in terminal taxa (abbreviations as in data matrix, Table 3). Reversals are noted: -r (node or taxon).

Char.	Steps	Con.	Ret.	Wt.	Nodes and terminals with changes
1	3	0.33	0.33	1	A, PS, RH
2	1	1.00	1.00	10	B
3	4	0.25	0.57	1	mult. optimizations possible
4	7	0.14	0.60	0	A, P, 1, W, V, Z, Mu
5	2	0.50	0	0	ZD, CT
6	4	0.25	0.80	2	Pp, Y, K-rPS
7	4	0.50	0.33	1	W, HE, Pl, LY
8	3	0.33	0.66	2	K-rFE-rRH
9	3	0.33	0.33	1	mult. optimizations possible
10	2	0.50	0	0	PS, SO
11	1	1.00	1.00	10	H
12	2	0.50	0	0	PS, ST
13	1	1.00	1.00	10	O
14	4	0.25	0.72	1	RA, CA, AC, S
15	1	1.00	1.00	10	Q
16	3	0.66	0.75	5	B, A, W
17	1	1.00	1.00	10	T
18	2	0.50	0.66	3	A, W
19	2	1.00	1.00	10	C, W
20	1	1.00	1.00	10	E
21	5	0.20	0	0	RA, ZT, PI, FE, CT
22	2	0.50	0.66	3	U, ZD
23	2	0.50	0.87	4	W, F
24	2	0.50	0.90	4	F, Y
25	2	0.50	0	0	UL, SO
26	2	0.50	0.85	4	E, W
27	8	0.37	0.58	2	P-rP1, K, Y, AC, TA, Zs, CT
28	2	0.50	0.66	3	G, W
29	4	0.50	0.81	4	T, S, RH, ZD
30	2	1.00	1.00	10	O, RH
31	7	0.14	0.25	0	AC, Ds, Mr, K-rFE-rC, RH
32	5	0.40	0.50	2	L, C, CA, TA, ZT
33	2	0.50	0.75	3	T, P
34	2	0.50	0	0	TE, Dp
35	5	0.60	0.75	4	TE, A, Pl, Q, M
36	5	0.40	0.50	2	M, SE, DO, X, ST
37	5	0.40	0.75	3	TE, ZD, P, J, X
38	2	0.50	0.66	3	X, AC
39	6	0.33	0.60	2	mult. optimizations possible
40	3	0.33	0.33	1	D, ZT, TA
41	2	1.00	1.00	10	W, Z
42	6	0.33	0.63	2	Y, AC, CA, G, F, S
43	5	0.20	0.63	1	CA, A A-rP -r1 -rTP
44	5	0.20	0.55	1	A, O, SE, BB-rCA
45	4	0.25	0.70	1	mult. optimizations possible
46	3	0.33	0.33	1	L, AC, SE
47	2	0.50	0.50	2	A, CT
48	5	0.20	0.71	1	F, V, ST, N-rPH
49	9	0.33	0.33	1	TE, CA, DO, L, 1, R, UL, ST, TP
50	2	1.00	1.00	10	A A, P
51	1	1.00	1.00	10	1
52	5	0.20	0.69	1	T, Q-rL, BB-rZT
53	2	0.50	0.66	3	J-rSE
54	4	0.25	0.62	1	L, I, V, UL
55	5	0.40	0.70	2	U, J, W, ZD, RA
56	7	0.28	0.16	0	T, ZD, Pp, Mr, UL, R, X
57	2	0.50	0.87	4	H, E

TABLE 4.—*Continued.*

Char.	Steps	Con.	Ret.	Wt.	Nodes and terminals with changes
58	5	0.20	0.20	0	mult. optimizations possible
59	8	0.50	0.60	3	M, ZT, L, V, HE, A, TP, UL
60	6	0.16	0.64	1	L, HE, SO, BB, S-rPp
61	11	0.18	0.25	0	mult. optimizations possible
62	2	0.50	0.66	3	G, D
63	5	0.20	0.33	0	DO, HE, LY, BB-rW
64	4	0.25	0.75	1	G, F, S, CA
65	1	1.00	1.00	10	ST
66	7	0.28	0.54	1	TE, RA, B, R, J, CA, Pl
67	1	1.00	1.00	10	D
68	1	1.00	1.00	10	C

AA by the unique derivation of the grate-shaped tapetum (character 50) as well as the recurved posterior eye row (character 43, subsequently reversed in *Phanotea,* the psechrids, and *Tapinillus*). A second monophyletic group, retaining the primitive canoe-shaped tapetum, is supported at node BB by appearance of a ventral apophysis on the male palpal tibia (character 3; subsequently lost in *Zorocrates*), a long, narrow sternum (character 44), a parallel origin of the male tibial crack (character 52; subsequently reversed in *Zorocrates*), and loss of lateral spines on the female tibia I (character 60). The cladogram has a basal trichotomy: no characters unite the monophyletic groups at nodes AA and BB with each other nor do any characters unite either of these with *Tengella.*

The highly distinctive genus *Uduba* is supported at node W by a large suite of derived characters, including loss of the palpal conductor (character 7), a triangular median apophysis (character 16) transversely inserted (character 18), the unique apically bifid tegulum (character 19), a flexibly attached embolus (character 23) curved in a counterclockwise direction (character 26), and fusion of the lateral and median sectors of the epigynum (character 28). The looped copulatory duct (character 36), loss of spermathecal heads (character 37), chambered spermathecal base (character 38), and stellate tarsal organ (character 56) unite *Uduba* with *Campostichomma* at node X, and these genera are united with *Zorocrates* at node Y by the loss of the tegular and subtegular locking lobes (character 6), presence of a basal lobe (character 24) on the long, slender embolus (character 27), and the long, sinuate spermathecal base (character 39). Finally, the African and Malagasy genera *Raecius* and *Zorodictyna* are united at node Z by the unique entire cribellum (character 41).

Within the Lycosoidea (Figure 85) three well-defined monophyletic groups are united at nodes V, S, and K. Claw tufts (character 54) and highly spinose first and second legs (character 59) unite *Acanthoctenus* with the zoropsids at node V to form the "zoropsoid complex." The two species of *Zoropsis* (node T) share a hooked median apophysis with a unique bifid apex (character 17), an epigynum with pockets on the lateral lobes (character 29) and a flexibly attached, erectile scape (character 33), and a parallel derivation of the male tibial crack (character 52); these are in turn united with *Takeoa* at node U by the MTP (character 22) and shallow trochanteral notch (character 55).

A cup-shaped median apophysis (character 14), teeth on the lateral lobes of the epigynum (character 29), male tibial crack (character 52), and loss of the cribellum and calamistrum (characters 42 and 64) support a monophyletic group at node S (Figure 85). Within this "ctenoid complex" (Figure 86) the ctenids *Phoneutria* and *Ctenus* are united at node L by a swollen median lobe extending to the posterior margin of epigynum (character 32), the 2-4-2 arrangement of eyes (character 46), 4 retromarginal teeth (character 49), and claw tufts (character 54). The male tibial crack (character 52) is lost in the ctenids. *Machadonia* is supported at node M by the membranous conductor embracing the embolic apex (character 9), a unique external epigynal groove that extends posteriad to the fertilization ducts (character 35:3) and long copulatory duct (character 36), and a pattern of ventral spination on tibia I of both sexes in which there is an extra anteroventral spine just behind the apical pair (character 59:1). Characters uniting the three species of *Phanotea* at node P are the embolus with a broad, concave, apex divided into dorsal (ED) and ventral (EV) lobes (character 27:2), an erectile scape on the epigynum similar to that of *Zoropsis* (character 33), a straightened PER (character 43), and a unique derived tapetum (character 50:2). *Devendra* is supported at node R by a ventral apophysis on the male palpal tibia (character 3), 4 teeth on the cheliceral retromargin (character 49), a stellate tarsal organ (character 56), feathery hairs (character 58), and loss of scopulae on the legs (character 66). *Machadonia* and the ctenids are united at node N by a broad labium (character 48) and dorsal spines on male tibia I (character 61), and these taxa are in turn united with *Phanotea* at node Q by the unique bimarginate median apophysis (character 15).

Finally, a large group of classic lycosoid families are united at node K (Figure 85) by the loss of the tegular and subtegular locking lobes (character 6), a convex, fleshy conductor on the male palp (character 8; subsequently reversed in *Fecenia* and *Rhoicinus*), and a slender embolus (character 27).

Within the "higher lycosoids" (Figure 87) are two clades at

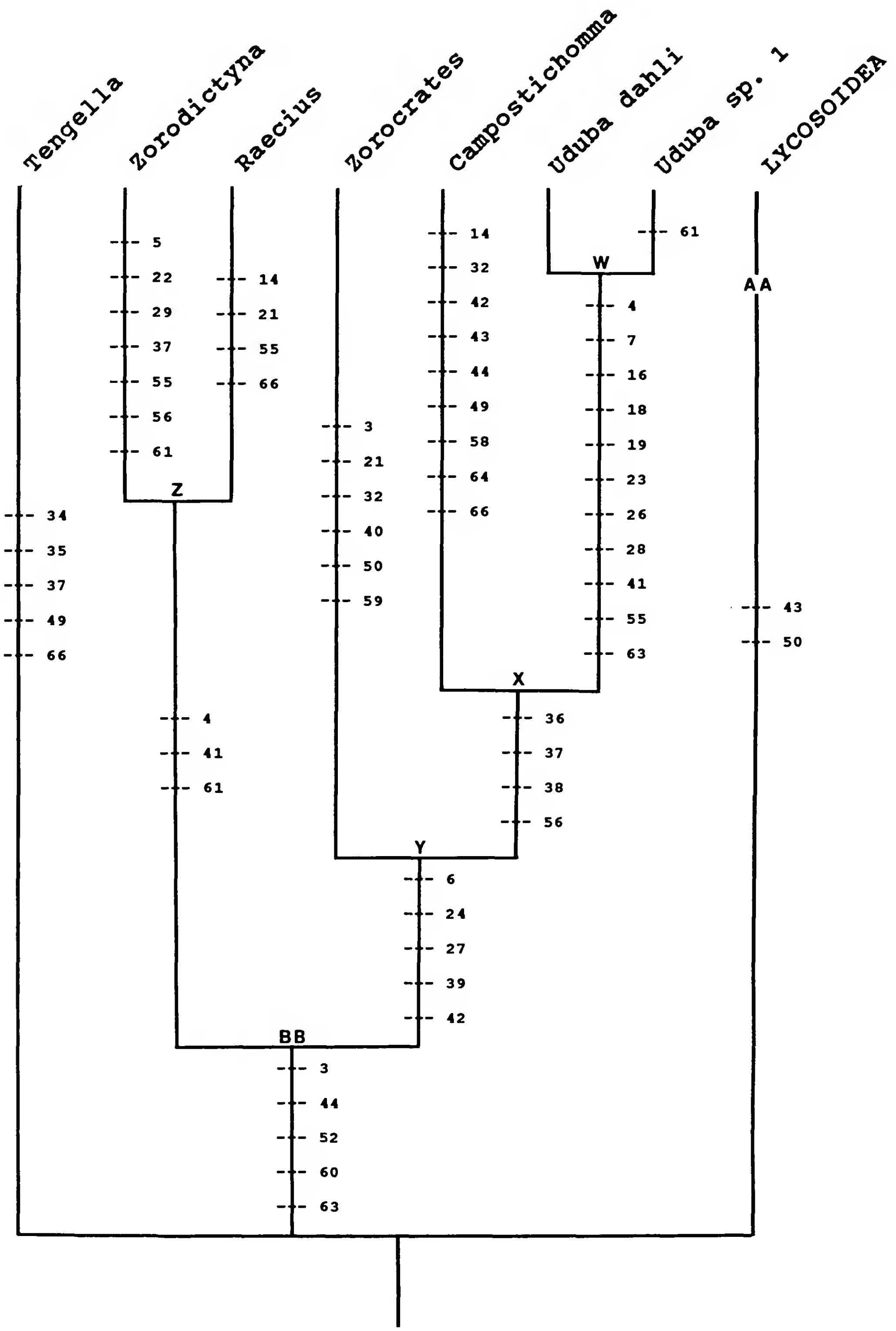


FIGURE 84.—Cladogram for Lycosoidea, Tengellidae, and related taxa. Character state changes noted on branches.

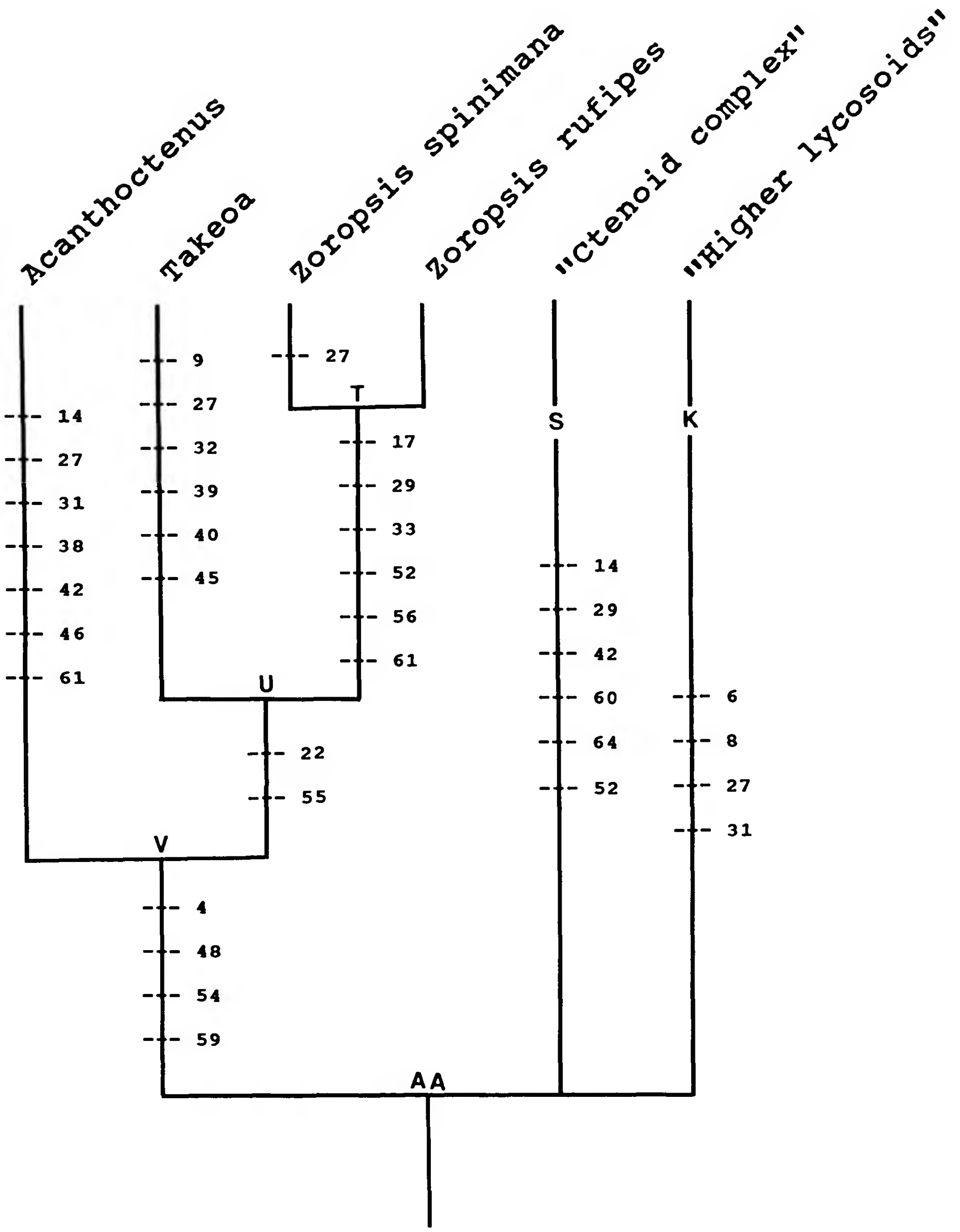


FIGURE 85.—Cladogram for Lycosoidea showing "Zoropsoid complex" (node V), "Ctenoid complex" and "Higher lycosoids." Character state changes noted on branches.

nodes J and F. Node J (the "stiphidiid group") is supported by large spermathecal heads (character 37), the unique restriction of tarsal trichobothria to a single row (character 53), and loss of scopulae (character 66). *Senoculus* and the oxyopid *Tapinillus* are united at node G by loss of the distinction between median and lateral sectors on the epigynum (character 28), loss of the cribellum and calamistrum (characters 42 and 64), and presence of dorsal spines on female tibia I (character 62). A unique grooved, flexibly attached lobate conductor (character 11), smooth hood on the trichobothrial bases (character 57), and

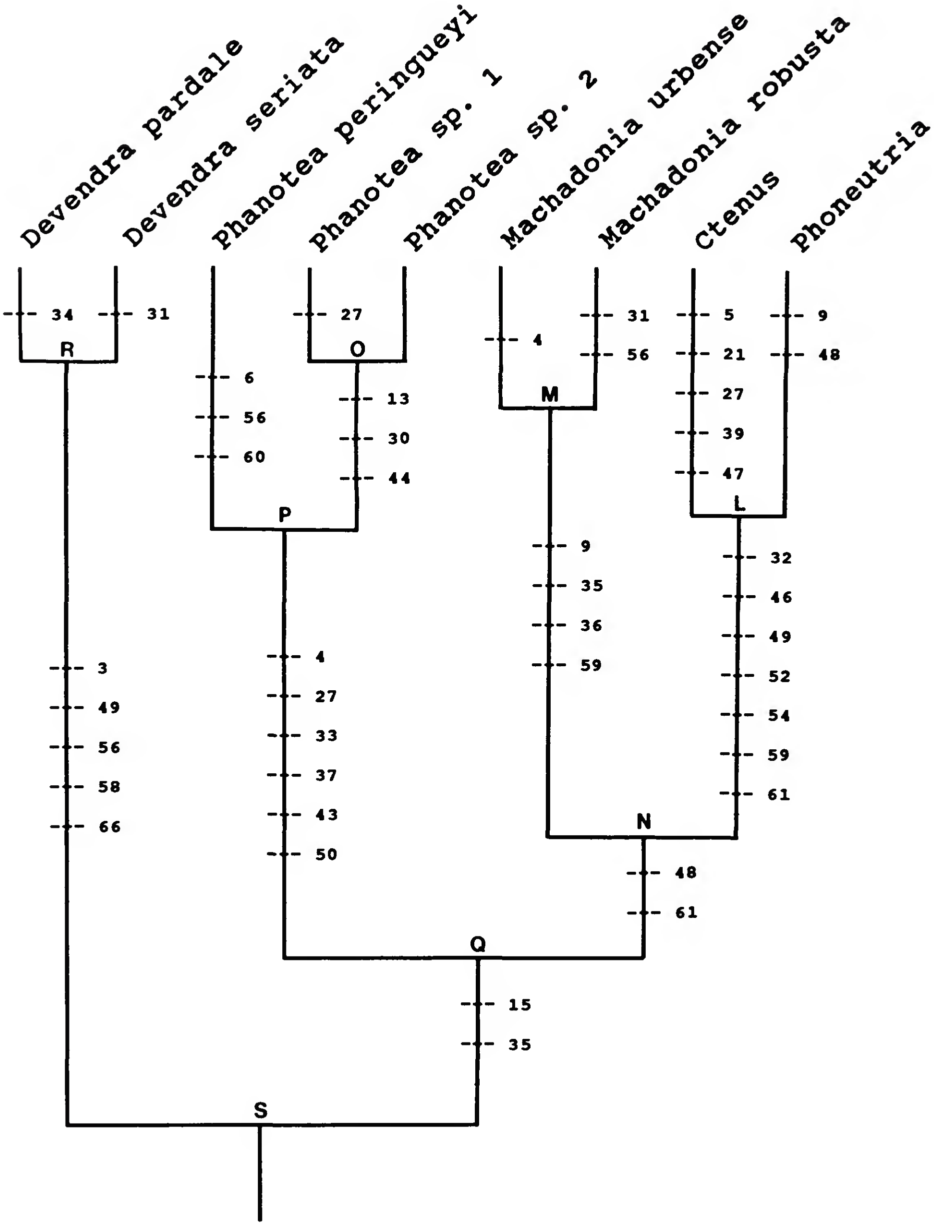


FIGURE 86.—Cladogram for "Ctenoid complex." Character state changes noted on branches.

feathery setae (character 58) unite these genera with *Stiphidon* at node H. Feathery setae were not observed in *Tapinillus*, necessitating loss in this instance. The psechrids (*Psechrus* and *Fecenia*: node I) share a straight PER (character 43), 4 teeth on the cheliceral retromargin (character 49), the unique very long tibia I (character 51), and claw tufts (character 54).

Node F (the "lycosid group") is supported by having the lobate embolic base (character 24) flexibly attached to the tegulum by membranous cuticle (character 23), and loss of the cribellum and calamistrum (characters 42 and 64). The highly distinct Lycosidae (*Lycosa* and *Sosippus*) are united at node A by loss of apophyses on the male palpal tibia (character 1; with parallel losses in *Rhoicinus* and *Psechrus*), a triangular median apophysis (character 16:2) transversely attached (character 18), strongly recurved PER (character 47), and reduction to three the ventral spine pairs beneath tibia I (character 59). Their sister group comprises the Trechaleidae (represented by *Rhoicinus* and *Trechalea*), supported at node B by the unique region of unsclerotized retroapical cuticle on the male palpal tibia (character 2), a unique large, swollen, median apophysis with 2

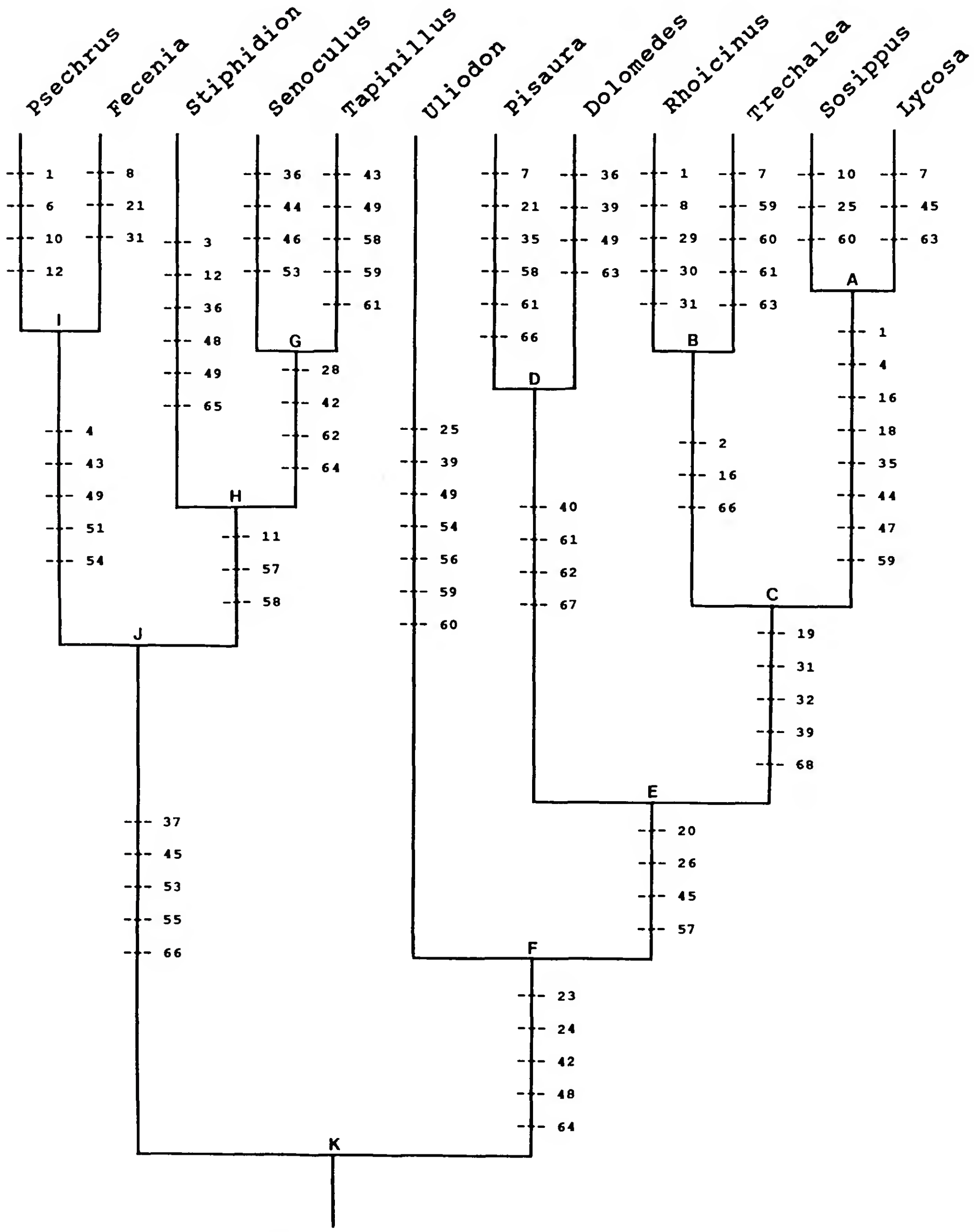


FIGURE 87.—Cladogram for "Higher lycosoids." Character state changes noted on branches.

apical lobes (character 16:1), and loss of scopulae (character 66). The sister group relationship of the lycosids and trechaleids is supported at node C by a unique palpal bulb having the tegulum notched probasally so that the subtegulum is visible in ventral view (character 19), a lobate spermathecal base (character 39), and the behavior of carrying the eggsac on the spinnerets (character 68; unique within this data set). Median fertilization ducts (character 40), dorsal spines on tibiae I of males (character 61) and females (character 62), and the unique nursery web (character 67) unite the classic pisaurids *Pisaura* and *Dolomedes* at node D; these are united with the Lycosidae and Trechaleidae at node E by having the proapical margin of the tegulum produced into a protuberance (DTP) which subtends the flexible attachment of the embolic division (character 20), a counter-clockwise curving embolus (character 26), and a smooth hood on the trichobothrial bases (character 57).

RESULTS: CHARACTERS.—Given the optimizations of character states on the cladogram, it is justifiable to suggest a hypothetical ground-plan for the basic tengelloid-lycosoid stock. A number of character systems deserve attention. Character numbers are noted in parentheses.

The primitive form of male palpus for this whole assemblage appears to have been one with a single retrolateral tibial apophysis, U-shaped subtegulum and oval tegulum (each with an interlocking lobe on the prolateral side), stout, fixed embolus curving in a clockwise direction (left palpus, ventral view), hook-like median apophysis, and apical hyaline conductor. Principal modifications of the basic form of palpal tibia include the evolution of an additional ventral tibial apophysis (3) at node BB, in *Devendra*, and in *Stiphidion*, and complete loss of the retrolateral apophysis (1) in parallel in *Psechrus*, *Rhoicinus*, and the Lycosidae. The conductor is lost (7:1) in *Uduba*, *Trechalea*, *Pisaura*, and *Lycosa* (concave tegular processes function as conductors in the latter two taxa), and modified into a convex, grooved structure (8) for the higher lycosoids at node K (a reversal to the primitive, hyaline form is subsequently required in *Fecenia*). A membranous tegular projection in *Rhoicinus*, also coded as a conductor, requires a second case of reversal. The homology of this reduced, digitate structure with the fan-shaped primitive conductor is dubious, though, and perhaps the conductor of *Rhoicinus* is truly lost as in its sister group, *Trechalea*. A cup-shaped median apophysis (14) has apparently arisen four times: in *Raecius*, *Campostichomma*, *Acanthoctenus*, and in the ctenoid complex at node S; the median apophysis has been lost (12) in parallel in *Psechrus* and *Stiphidion* (though the presence of median apophyses in other psechrids and stiphidiids demonstrates that it is clearly part of the ground plan for each family). The transversely attached (18), triangular (16:2) median apophysis is clearly a parallelism in *Uduba* and the lycosids (directed ventrad in the former and retrolaterad in the latter), while the enlarged, bilobate median apophysis (16:1) is a unique synapomorphy for the Trechaleidae (node B: including Sierwald's (1990) "*Trechalea* genus-group" and *Rhoicinus*). Slender emboli (27:1) appear in parallel 3 times: in *Acanthoctenus*, at node Y for *Zorocrates*, *Campostichomma*, and *Uduba*, and at node K for the higher lycosoids. Development of a distinct terminal division (23) of the bulb (embolus flexibly attached to tegulum) occurs in parallel in *Uduba* and at node F; and in the pisaurids plus dolomedids, trechaleids, and lycosids (node E) the flexible attachment is subtended by the distal tegular protuberance (20). It appears that the lobate embolic base primitively has a process, and the smooth embolic lobes (25) found in *Uliodon* and *Sosippus* appear to be derived. This lends support to Dondale's (1986) suggestion that loss of the terminal apophysis on the embolic base is a synapomorphy for the lycosid subfamily Sosippinae. The lobate embolic base is not fully correlated with development of a terminal division: *Zorocrates* and *Campostichomma* have lobate embolic bases that are fixed on the tegulum.

The primitive form of epigynum appears to be one with a swollen median sector and unmodified lateral lobes clearly demarcated by epigynal folds; the median sector is produced into a small, transverse scape with a posterior divot. An erectile scape (33) has evolved in parallel in *Zoropsis* and *Phanotea*; whereas a flat, unmodified median sector has been derived in parallel several times. Fusion of the median sector and lateral lobes (28) has occurred in parallel in *Uduba* and in *Tapinillus* plus *Senoculus*. Teeth on the lateral lobes (29:2) have evolved in parallel three times: in *Rhoicinus* (where they are posterior), in *Zorodictyna*, and in the ctenoid complex (node S). Virtually all characters for the vulva are highly homoplasious, with parallel derivations of similar morphologies in terminal taxa.

The cribellum and calamistrum have been scored as separate characters because they are not always perfectly correlated. In fact, loss of the cribellum and calamistrum are correlated on the cladogram. The primitive condition appears to be an oval calamistrum and transversely linear, divided cribellum. The halves of the cribellum have become oval (42:1) in *Acanthoctenus* and *Zorocrates* plus *Uduba*, and the cribellar division has disappeared (41:2) in *Zorodictyna* plus *Raecius*. The calamistrum has reverted to the linear form (65) in *Stiphidion* (the primitive form in the Neocribellatae). Four independent losses of the cribellum (42) and calamistrum (64) are required: in *Campostichomma*, in the ctenoid complex (node S), at node G for *Tapinillus* plus *Senoculus*, and at node F for *Uliodon* plus the pisaurids plus dolomedids, trechaleids, and lycosids. Since the pioneering work of Lehtinen (1967), Forster (1970), and Baum (1972) demonstrated that cribellate and ecribellate taxa could be sister groups, few studies have quantitatively examined the evolutionary implications of homoplasy in the cribellate condition, and none have included as wide a mix of cribellate and ecribellate taxa as this one. Independent losses of the cribellum and calamistrum are not unequivocal optimizations in all cases, and in some of the original nine most parsimonious trees loss and subsequent regain of the cribellum and calamistrum was required. It is worthy of note that for an earlier version of this data set including mostly cribellate taxa, loss and subsequent regain of the cribellum and calamistrum was unambiguously required. Parallel evolution of so complex a suite of structures and behaviors as that involved in the cribellate condition is unlikely to receive much support from arachnologists, and is difficult to accept even when preferred by parsimony. It is still too soon to tell if a complete range of taxa, rather than an admittedly incomplete data set made up of exemplars, will allow preference for independent losses of the cribellum and calamistrum in each case.

The primitive condition for the ocular region appears to be an eye arrangement in two straight to weakly curved rows, with each indirect eye having a canoe-shaped tapetum. A recurved posterior eye row (43) has been derived in parallel in *Campostichomma* and for the Lycosoidea (node AA): reversals to a straight PER have occurred in *Phanotea, Tapinillus* and the psechrids. The classic 2-4-2 "ctenid" eye pattern (46) appears to have evolved in parallel three times: in the true ctenids (node L), in *Acanthoctenus,* and in *Senoculus.* The grate-shaped tapetum (Homann, 1971) was uniquely derived (50:1) for the Lycosoidea (node AA), though it is necessary to assume that the form found in *Phanotea* is a modification (50:2) of the grate-shaped form, and that *Devendra* will be found to have a grate-shaped form or some modification thereof (e.g., loss).

The primitive form of legs appears to have deeply notched trochanters, entire tibiae in males, four pairs of ventral spines beneath the first and second tibiae in both sexes and no dorsal spines, well-developed scopulae on the tarsi and metatarsi (but no claw tufts), plumose setae, two or three irregular rows of tarsal trichobothria with transversely ridged basal hoods, and a capsulate tarsal organ with a simple round to oval orifice. Modification of the ventral spination of leg tibiae has occurred in parallel several times with the loss of spines or gain of an additional spine or pair of spines. Highly spinose tibiae with seven or more pairs of ventral spines (59:3) have evolved in parallel in the zoropsoid complex (*Acanthoctenus* plus the zoropsids) and in *Trechalea.* Dorsal spines on male tibiae (61) have evolved in parallel several times; those on female tibiae (62) have evolved in parallel in Pisauridae and Dolomedidae (node D) and for *Tapinillus* plus *Senoculus.* Claw tufts (54) evolved four times: in the zoropsoid complex (node V), in the true ctenids (node L), in the psechrids (node I), and in *Uliodon*; reduction or loss of scopulae occurred in parallel several times. The tarsal trichobothria were reduced to a single row (53) at node J; although homoplasy is required in *Senoculus,* the distally widened trichobothrial row in this taxon is unlike the two or three irregular rows found elsewhere. Loss of the transverse ridges on the basal hood (57) occurred in parallel at nodes H (stiphidiids, oxyopids, and senoculids) and E (pisaurids plus dolomedids, trechaleids, and lycosids); feathery setae (58) evolved in parallel and/or were lost several times.

Two striking modifications of the legs deserve special consideration because they have never been reported before: the basal crack on male leg tibiae (52), and the stellate tarsal organ (56:2). Could these not be clear synapomorphies the influence of which has been "swamped" by random homoplasy in the data set? Although homoplasy is required for these characters even on the cladogram chosen through successive approximations weighting (i.e., in which the influence of random homoplasy should have been minimized), it is instructive to assess the cost in extra steps to consider these characters uniquely derived. To do this I forced the monophyly of groups defined by each character by weighting that character through a series of Hennig86 runs (see *Tests of taxon and character hypotheses* above). Three additional steps (247-244) were necessary to make the stellate tarsal organ define a monophyletic group, a small cost considering the total number of steps required for the data, and it is possible that additional data will tip the balance toward that character. The cost of making the male tibial crack define a monophyletic group is much higher: seven steps (251-244), including the addition of homoplasy in the grate-shaped tapetum, recurved posterior eye row, cup-shaped median apophysis, and enhanced tibial spination. It seems unlikely that additional data could tip the balance in favor of this character, and I must conclude that the male tibial crack is an apparently "great" character that fails in light of the distributions of other characters.

Conclusions

My approach to investigating the higher classification of taxa spread across 12 families has involved scoring the maximum number of characters for the minimum number of taxa: the maximum number of characters because I did not want to accept a priori hypotheses based upon one or another "one-character" system; the minimum number of taxa because taxon number greatly affects the speed with which the data can be analyzed and the ease with which the influence of a single taxon or character can be isolated and interpreted. Because of the rather thin representation of the exemplars, all conclusions must be considered as provisional, but some conclusions may be considered stronger than others. One result from this quantitative analysis mirrors conventional taxonomic wisdom: that there are "solid" groups and "difficult" groups. The numerous preliminary analyses of provisional versions of the data set revealed that some groupings were stable, whereas others could be dramatically affected by the inclusion or exclusion of a single taxon or character. Due to this instability, no formal reclassification is presented. In particular, the relationships of *Zorodictyna* plus *Raecius, Acanthoctenus, Devendra,* and the Psechridae were subject to alteration through small changes in the data set. On the other hand, some groupings (e.g., of the ctenids, *Phanotea* and *Machadonia*; of *Uliodon* with the pisaurids plus dolomedids, trechaleids, and lycosids; of *Stiphidion, Tapinillus,* and *Senoculus*) were very stable.

I feel that the relationships suggested here are the most thoroughly documented available, and it is worthwhile to consider some implications for previous classifications and suggestions of relationships. Among the more intriguing possibilities are that several classical or previously established groups may not be monophyletic. In particular, separation of *Acanthoctenus* from *Ctenus* plus *Phoneutria* suggests that the classical Ctenidae may not be monophyletic. This is not too surprising, as the limits of the Ctenidae have never been stable, with groups retaining three claws (e.g., *Cupiennius*) sometimes being excluded (Lehtinen, 1967). In addition, several taxa proposed by Lehtinen (1967) and represented in the data set (i.e., Miturgidae, and the miturgid subfamilies Tengellinae, Uliodoninae, and Machadoniinae) appear not to be monophyletic. Could these results be an artifact of random homoplasy? As with the male tibial crack and stellate tarsal organ (see *Tests of taxon and character hypotheses* above), I calculated the additional cost in steps required by the monophyly of each of the previously proposed taxa. Monophyly of the classic Ctenidae (*Acanthoctenus, Ctenus,* and *Phoneutria*) required four additional steps (248–244), that of Lehtinen's Tengellinae (*Tengella* and *Zorocrates*: the ecribellate *Titiotus* was not included) required three additional steps (247–244), and that of Lehtinen's Machadoniinae (*Campostichomma, Devendra, Machadonia,* and *Phanotea*) required only two additional steps (246–244). To make Lehtinen's Uliodoninae (*Raecius, Uduba, Uliodon,* and *Zorodictyna*: the fossil *Adamator* and poorly known ecribellate *Calamistrula* were not included) monophyletic required seven steps (251–244), and to group members of all subfamilies into a monophyletic Miturgidae required eight additional steps (256–244). None of these groups are well supported by the data, though the monophyly of the Machadoniinae deserves further consideration.

What then of the positive results? The Lycosoidea, Psechridae, and Lycosidae emerge as monophyletic. The association of *Machadonia* and Ctenidae on the basis of detailed character data reflects the strong "gestalt" similarity between these groups in appearance and lifestyle. Carico (1986) suggested that a group of genera (including *Trechalea*) traditionally placed in the Pisauridae and Dolomedidae should be recognized as a distinct family Trechaleidae. Sierwald (1990) offered strong morphological evidence for a distinct "*Trechalea* genus group" (corresponding to Carico's Trechaleidae) and suggested that *Rhoicinus* was related. She also suggested (pers. comm.) that these together might be the sister group of the Lycosidae. My results support the suggestion of a monophyletic Trechaleidae (including *Rhoicinus*) as sister group of the Lycosidae. *Pisaura* and *Dolomedes* are clearly sister groups, underscoring the close relationship suggested by Sierwald (1990). I cannot comment on the validity of the family Dolomedidae, except to note that *Dolomedes* differs from *Pisaura* largely in the retention of plesiomorphic characters. The relationship of *Uliodon* to the pisaurids plus dolomedids, trechaleids, and lycosids is surprising, albeit well supported. Although *Uliodon* had previously been considered related to ctenids (Simon, 1897; Roewer, 1954), it had never been considered close to wolf spiders. The tapetum of *Uliodon* appears to be typically grate-shaped, and the fleshy conductor and flexibly attached embolic division suggest placement here. Placement of the Miturgidae within the Lycosoidea is uncertain. Although *Uliodon* shares with *Miturga* a lengthened apical segment of the posterior lateral spinnerets (in addition to the deeply notched trochanters and strong leg scopulae widespread among the taxa considered here), I could not confirm a grate-shaped tapetum in *Miturga* (though the lateral loops of the tapetum are not classically canoe-shaped either). At least *Eutichurus,* which also shares the spinneret characters with *Uliodon* and *Miturga,* has a classic canoe-shaped tapetum. The limitation and placement of the Miturgidae requires further study. A final surprise is the close association of the oxyopids and senoculids with the cribellate stiphidiids and psechrids. It may be significant that *Tapinillus, Stiphidion,* and the psechrids are unique among the web-building taxa considered here in hanging beneath the sheet web rather than running on the upper surface (*Senoculus* builds no web for prey capture (Coville and Griswold, 1983)).

The significance of genitalic characters in the higher classification of spiders deserves discussion. Genitalic characters (characters 1–40) predominate in the data set, outnumbering somatic and behavioral characters (characters 41–68) by 40 to 28, and accordingly play an important role in generating the hypothesis outlined here. The average consistency index of the genitalic characters (0.530) is slightly higher than that for the somatic and behavioral characters (0.455). Genitalic characters are frequently considered by taxonomists to be "species characters," and their use at higher taxonomic levels is often met with skepticism. Indeed, greater sampling density in the taxa represented for this study by exemplars might reveal additional genitalic homoplasy and render the value of these characters dubious. On the other hand, I have sought basic genitalic similarities across families. The striking similarity of palpal structure among such disparate taxa as *Tengella, Zorodictyna, Zoropsis, Devendra, Machadonia,* and *Ctenus,* which otherwise differ among one another in eye arrangement, tapetal form, spination, and the nature of tarsal claws and claw tufts, suggests that some aspects of genitalic morphology may be extremely conservative. The apparent conservatism of some genitalic characters, as illustrated by the relative equivalence in genitalic and somatic consistency, might be considered to run counter to the frequently recognized phenomenon of "rapid genitalic evolution" most recently discussed by Eberhard (1985). This is not the case: genitalic characters still provide the best means of distinguishing species within taxa treated here, as, for example, in *Machadonia* (Griswold, 1991) and *Phanotea* (Griswold, in press). Genitalic differences between species are built upon broad similarites among families. It appears that genitalia simultaneously provide conservative characters of value in higher classification and rapidly evolved characters that serve to distinguish closely related taxa.

Finally, if a single lesson emerges from this study, it is that reliance on a single character or character system in classification is likely to mislead with regard to the true phylogeny. The poor performance of several striking characters, both classic and newly discovered, and the weak support for some classic taxa by this data set suggests that meticulous studies of the comparative morphology of a character system are not truly complete until the implications of those new discoveries for other character systems are made clear.

Literature Cited

Baum, S.

1972. Zum "Cribellaten-Problem": die Genitalstrukturen der Oecobiinae und Urocteinae (Arachnida: Araneidae: Oecobiidae). *Abhandlungen und Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, new series, 16:101–153.

Benoit, P.L.G.

1974. Contribution à l'étude du genre *Africactenus* avec une clé des espèces (Araneae, Ctenidae). *Revue de Zoologie Africaine*, 88: 131–142.

1978. Espèces est-africaines du genre *Ctenus* Walckenaer (Araneae—Ctenidae). *Revue de Zoologie Africaine*, 92(2):525–532.

1979. Études sur les Ctenidae africains (Araneae), VIII: Gen. *Ctenus* Walck.—groupe *abditus*. *Revue de Zoologie Africaine*, 93(2): 425–444.

1981. Études sur les Ctenidae africains (Araneae), XI: Étude des mâles isolés. *Revue de Zoologie Africaine*, 95(1):29–44.

Brady, A.R.

1962. The Spider Genus *Sosippus* in North America, Mexico, and Central America (Araneae, Lycosidae). *Psyche*, 69(3):129–164.

Brignoli, P.M.

1983. *A Catalogue of the Araneae Described between 1940 and 1981*. Manchester: Manchester University Press.

Carico, J.E.

1973. The Nearctic Species of the Genus *Dolomedes* (Araneae, Pisauridae). *Bulletin of the Museum of Comparative Zoology*, 144: 435–488.

1986. Trechaleidae: A 'New' American Spider Family. *In* W. G. Eberhard, Y.D. Lubin, and B.C. Robinson, editors, *Proceedings of the Ninth International Congress of Arachnology, Panama 1983*, page 305. Washington, D.C.: Smithsonian Institution Press.

Carico, J.E., and P.C. Holt

1964. A Comparative Study of the Female Copulatory Apparatus of Certain Species in the Spider Genus *Dolomedes*. *Technical Bulletin, Agricultural Experiment Station, Blacksburg, Virginia*, 172:5–27.

Carico, J.E., and E.W. Minch

1981. A New Species of *Trechalea* (Pisauridae) from North America. *Bulletin of the American Museum of Natural History*, 170(1): 154–156.

Carpenter, J.M.

1988. Choosing among Equally Parsimonious Cladograms. *Cladistics*, 4:291–296.

Chickering, A.M.

1941. The Senoculidae of Panama. *Papers of the Michigan Academy of Sciences, Arts, and Letters*, 26:195–218.

Coddington, J.A.

1990. Ontogeny and Homology in the Male Palpus of Orb-weaving Spiders and Their Relatives, with Comments on Phylogeny (Araneoclada: Araneoidea, Deinopoidea). *Smithsonian Contributions to Zoology*, 496:1–52.

Coddington, J.A., and H.W. Levi

1991. Systematics and Evolution of Spiders (Araneae). *Annual Review of Ecology and Systematics*, 22:565–592.

Courtois, J.

1911. Sur le cribellum et le calamistrum des Araignées cribellates. *Diplôme Etudes Supérieur, Faculté des Sciences de L'Université de Paris*, 107:1–54.

Coville, R.E., and C.E. Griswold

1983. The Nesting Biology of *Trypoxylon xanthandrum* (Hymenoptera: Sphecidae) in Central America, a Hunting Wasp Specializing on Spiders of the Family Senoculidae. *Journal of the Kansas Entomological Society*, 56(2):205–216.

Davies, V.T.

1988. Three New Species of the Spider Genus *Stiphidion* (Araneae: Amaurobioidea: Stiphidiidae) from Australia. *Memoirs of the Queensland Museum*, 25(2):265–271.

Dondale, C.D.

1986. The Subfamilies of Wolf Spiders (Araneae: Lycosidae). *Actas X Congreso de Arachnología, Jaca, España, 1986*, 1:327–332. Barcelona: Imprenta Juvenil.

Dondale, C.D., and J.H. Redner

1983. Revision of the Wolf Spiders of the Genus *Arctosa* C.L. Koch in North and Central America (Araneae: Lycosidae). *Journal of Arachnology*, 11:1–30.

Eberhard, W.G.

1985. *Sexual Selection and Animal Genitalia*. Cambridge and London: Harvard University Press.

Exline, H.

1960. Rhoicinine Spiders (Pisauridae) of Western South America. *Proceedings of the California Academy of Sciences*, series 4, 29 (17):577–620.

Farris, J.S.

1969. A Successive Approximations Approach to Character Weighting. *Systematic Zoology*, 18:374–385.

1988. Hennig86, version 1.5. [Computer Program Distributed by Its Author, 41 Admiral Street, Port Jefferson Station, NY 11776, USA.]

Foelix, R.F., and H. Jung

1978. Some Anatomical Aspects of *Hypochilus thorelli* with Special Reference to the Calamistrum and Cribellum. *Symposia of the Zoological Society of London*, 42:417–422.

Forster, R.F.

1970. The Spiders of New Zealand, III. *Otago Museum Bulletin*, 3:1–184.

Gray, M.R.

1973. Cavernicolous Spiders from the Nullarbor Plain and South West Australia. *Journal of the Entomological Society of Australia*, 12:207–221.

Griswold, C.E.

1983. *Tapinillus longipes* (Taczanowski), a Web-building Lynx Spider from the American tropics. *Journal of Natural History*, 17: 979–985.

1990. A Revision and Phylogenetic Analysis of the Spider Subfamily Phyxelidinae (Araneae, Amaurobiidae). *Bulletin of the American Museum of Natural History*, 196:1–206.

1991. A Revision and Phylogenetic Analysis of the African Spider Genus *Machadonia* Lehtinen (Araneae: Lycosoidea). *Entomologica Scandanavica*, 22:305–351.

In press. A Revision and Phylogenetic Analysis of the African Spider Genus *Phanotea* Simon (Araneae: Lycosoidea). *Annales, Sciences Zoologiques, Musée Royal de L'Afrique Centrale*.

Homann, H.

1971. Die Augen der Araneae: Anatomie, Ontogenie und Bedeutung für die Systematik (Chelicerata, Arachnida). *Zeitschrift für Morphologie der Tiere*, 69:201–272.

1975. Die Stellung der Thomisidae und der Philodromidae im System der Araneae (Chelicerata, Arachnida). *Zeitschrift für Morphologie der Tiere*, 80:181-202.

Järvi, T.H.

1905. Zur Morphologie der Vaginalorgane einiger Lycosiden. *Festschrift für Palmen*, 6:3-36.

Lawrence, R.F.

1942. A Contribution to the Araneid Fauna of Natal and Zululand. *Annals of the Natal Museum*, 10(2):141-190.

1951. The Cave-living Spiders of the South African Genus *Phanotea* Simon (Agelenidae). *Revue de Zoologie et de Botanique Africaines*, 45:49-54.

1952. New Spiders from the Eastern Half of South Africa. *Annals of the Natal Museum*, 12:183-226.

1964. New Cavernicolous Spiders of South Africa. *Annals of the South African Museum*, 48(2):57-75.

Lehtinen, P.T.

1967. Classification of the Cribellate Spiders and Some Allied Families, with Notes on the Evolution of the Suborder Aranemorpha. *Annales Zoologici Fennici*, 4:199-468.

1975. Notes on the Phylogenetic Classification of Araneae. *Proceedings of the 6th International Arachnological Congress, Amsterdam, 1974*, pages 26-29.

1980. Trichobothrial Patterns in High-Level Taxonomy of Spiders. *In* J. Gruber, editor, *Verhandlungen der 8: Internationaler Arachnologen-Kongress, Wien*, pages 493-498. Vienna: Verlag H. Engermann.

Levi, H.W.

1982a. The Spider Genera *Psechrus* and *Fecenia* (Araneae: Psechridae). *Pacific Insects*, 24:114-138.

1982b. Araneae. *In* S.P. Parker, editor, *Synopsis and Classification of Living Organisms*, 2:77-95. New York: McGraw Hill.

Levy, G.

1990. On the Cribellate Spider *Zoropsis lutea* in Isreal (Araneae, Zoropsidae). *Bulletin of the British Arachnological Society*, 8: 139-143.

Loerbroks, A.

1984. Mechanik der Kopulationsorgane von *Misumena vatia* (Clerck, 1757) (Arachnida: Araneae: Thomisinae). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, new series, 27: 383-403.

Maddison, W.P., M.J. Donoghue, and D.R. Maddison

1984. Outgroup Analysis and Parsimony. *Systematic Zoology*, 33:83-103.

Mora, G.

1986. Use of Web by *Tapinillus longipes* (Araneae: Oxyopidae). *In* W.G. Eberhard, Y.D. Lubin, and B.C. Robinson, editors, *Proceedings of the Ninth International Congress of Arachnology, Panama 1983*, pages 173-175. Washington, D.C.: Smithsonian Institution Press.

Patterson, C.

1982. Morphological Characters and Homology. *In* K.A. Joysey and A.E. Friday, editors, Problems of Phylogenetic Reconstruction. *Systematics Association Special Volume*, 21:21-74. London and New York: Academic Press.

Pickard-Cambridge, F.O.

1902. Arachnida: Araneida and Opiliones. *Biologia Centrali Americana; Zoology*, 2:313-424.

Platnick, N.I.

1977. The Hypochiloid Spiders: A Cladistic Analysis, with Notes on the Atypoidea (Arachnida, Araneae). *American Museum Novitates*, 2627:1-23.

1989. *Advances in Spider Taxonomy, 1981-1987; A Supplement to Brignoli's A Catalogue of the Araneae described between 1940 and 1981*. Manchester: Manchester University Press.

1990. A Review of the Spider Genus *Teminius* (Araneae, Miturgidae). *American Museum Novitates*, 2963:1-12.

Roewer, C.F.

1954. *Katalog der Araneae von 1758 bis 1940*. Volume 2a, pages 1-923. Bruxelles.

Roth, V.D.

1964. The Taxonomic Significance of the Spider Trochanter. *Annals of the Entomological Society of America*, 57(6):759-766.

Roth, V.D., and B.M. Roth

1984. A Review of Appendotomy in Spiders and Other Arachnids. *Bulletin of the British Arachnological Society*, 6(4):137-146.

Sierwald, P.

1989. Morphology and Ontogeny of Female Copulatory Organs in American Pisauridae, with Special Reference to Homologous Features (Arachnida: Araneae). *Smithsonian Contributions to Zoology*, 484:1-24.

1990. Morphology and Homologous Features in the Male Palpal Organ in Pisauridae and Other Spider Families, with Notes on the Taxonomy of Pisauridae (Arachnida: Araneae). *Nemouria*, 35:1-59.

Simon, E.

1897. *Histoire naturelle des Araignées*, 2, Part 1. Pages 1-192. Paris: Roret.

1898. *Histoire naturelle des Araignées*, 2, Part 2. Pages 193-380. Paris: Roret.

Wolff, R.J.

1978. The Cribellate Genus *Tengella* (Araneae: Tengellidae?). *Journal of Arachnology*, 5:39-144.

Yaginuma, T.

1963. A New Zoropsid Spider from Japan. *Acta Arachnologica*, 18:1-6.

REQUIREMENTS FOR SMITHSONIAN SERIES PUBLICATION

Manuscripts intended for series publication receive substantive review (conducted by their originating Smithsonian museums or offices) and are submitted to the Smithsonian Institution Press with Form SI-36, which must show the approval of the appropriate authority designated by the sponsoring organizational unit. Requests for special treatment—use of color, foldouts, case-bound covers, etc.—require, on the same form, the added approval of the sponsoring authority.

Review of manuscripts and art by the Press for requirements of series format and style, completeness and clarity of copy, and arrangement of all material, as outlined below, will govern, within the judgment of the Press, acceptance or rejection of manuscripts and art.

Copy must be prepared on typewriter or word processor, double-spaced, on one side of standard white bond paper (not erasable), with 1¼" margins, submitted as ribbon copy (not carbon or xerox), in loose sheets (not stapled or bound), and accompanied by original art. Minimum acceptable length is 30 pages.

Front matter (preceding the text) should include: **title** page with only title and author and no other information; **abstract** page with author, title, series, etc., following the established format; **table of contents** with indents reflecting the hierarchy of heads in the paper; also, **foreword** and/or **preface**, if appropriate.

First page of text should carry the title and author at the top of the page; **second page** should have only the author's name and professional mailing address, to be used as an unnumbered footnote on the first page of printed text.

Center heads of whatever level should be typed with initial caps of major words, with extra space above and below the head, but no other preparation (such as all caps or underline, except for the underline necessary for generic and specific epithets). Run-in paragraph heads should use period/dashes or colons as necessary.

Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

Formal tables (numbered, with captions, boxheads, stubs, rules) should be submitted as carefully typed, double-spaced copy separate from the text; they will be typeset unless otherwise requested. If camera-copy use is anticipated, do not draw rules on manuscript copy.

Taxonomic keys in natural history papers should use the aligned-couplet form for zoology and may use the multi-level indent form for botany. If cross referencing is required between key and text, do not include page references within the key, but number the keyed-out taxa, using the same numbers with their corresponding heads in the text.

Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or "...Jones (1910:122)." If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

Footnotes, when few in number, whether annotative or bibliographic, should be typed on separate sheets and inserted immediately after the text pages on which the references occur. Extensive notes must be gathered together and placed at the end of the text in a notes section.

Bibliography, depending upon use, is termed "Literature Cited," "References," or "Bibliography." Spell out titles of books, articles, journals, and monographic series. For book and article titles use sentence-style capitalization according to the rules of the language employed (exception: capitalize all major words in English). For journal and series titles, capitalize the initial word and all subsequent words except articles, conjunctions, and prepositions. Transliterate languages that use a non-Roman alphabet according to the Library of Congress system. Underline (for italics) titles of journals and series and titles of books that are not part of a series. Use the parentheses/colon system for volume (number):pagination: "10(2):5-9." For alignment and arrangement of elements, follow the format of recent publications in the series for which the manuscript is intended. Guidelines for preparing bibliography may be secured from Series Section, SI Press.

Legends for illustrations must be submitted at the end of the manuscript, with as many legends typed, double-spaced, to a page as convenient.

Illustrations must be submitted as original art (not copies) accompanying, but separate from, the manuscript. Guidelines for preparing art may be secured from the Series Section, SI Press. All types of illustrations (photographs, line drawings, maps, etc.) may be intermixed throughout the printed text. They should be termed **Figures** and should be numbered consecutively as they will appear in the monograph. If several illustrations are treated as components of a single composite figure, they should be designated by lowercase italic letters on the illustration; also, in the legend and in text references the italic letters (underlined in copy) should be used: "Figure 9b." Illustrations that are intended to follow the printed text may be termed **Plates**, and any components should be similarly lettered and referenced: "Plate 9b." Keys to any symbols within an illustation should appear on the art rather than in the legend.

Some points of style: Do not use periods after such abbreviations as "mm, ft, USNM, NNE." Spell out numbers "one" through "nine" in expository text, but use digits in all other cases if possible. Use of the metric system of measurement is preferable; where use of the English system is unavoidable, supply metric equivalents in parentheses. Use the decimal system for precise measurements and relationships, common fractions for approximations. Use day/month/year sequence for dates: "9 April 1976." For months in tabular listings or data sections, use three-letter abbreviations with no periods: "Jan, Mar, Jun," etc. Omit space between initials of a personal name: "J.B. Jones."

Arrange and paginate sequentially every sheet of manuscript in the following order: (1) title page, (2) abstract, (3) contents, (4) foreword and/or preface, (5) text, (6) appendices, (7) notes section, (8) glossary, (9) bibliography, (10) legends, (11) tables. Index copy may be submitted at page proof stage, but plans for an index should be indicated when the manuscript is submitted.