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The conformation of the male palpal organs of Linyphiid spiders, and its application to the taxonomic and phylogenetic analysis of the family (Araneae: Linyphiidae)

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Summary

The palpal conformations, as herein defined, of species from most of the European genera of the family Linyphiidae have been analysed. The genera, both erigonine and linyphiine, have been grouped according to their conformations, and inferences have been drawn concerning the relationships between both the groups themselves and the individual members of the groups. Based on the results of the analyses, and on the assumption that the plesiomorphous (primitive) form of the linyphiid palp was simple, and that the apomorphous (derived) forms are more complex, a partial phylogenetic classification of the Linyphiidae has been drawn up. The scheme proposed indicates that the family should not be split into the traditional subfamilies Linyphiinae and Erigoninae, but that both linyphiine and erigonine forms have arisen from more than one part of the phylogenetic tree. Provisional proposals are made for a number of taxonomic changes, and a short list of new synonyms is appended.

Contents

A. Introduction

The work described in this paper originated during a study of the erigonine spiders of Europe; most of the species and examples of all of the currently used genera have been examined. The results obtained prompted a similar study of the linyphiine spiders, but the work carried out in this area so far has been much more limited in scope. In consequence, the greater part of the paper is devoted to the erigonine spiders. The terms "erigonine" and "linyphiine" are used as convenient labels for spiders of the family Linyphiidae which have certain characteristics summarised by Locket and Millidge (1953), Wiehle (1960) and Merrett (1963); these terms are to be regarded as descriptive only, and to have no phylogenetic significance, i.e. it is not to be assumed that the erigonines and linyphiines are 2 distinct subfamilies. The object of the paper is to discuss briefly the problems inherent in any attempt to erect a phylogenetic system for this family, and to propose a new approach to the use of the male palpal organs as indicators of phylogenetic relationships.

The taxonomy of the Linyphiidae (and particularly of the erigonines) is made exceptionally difficult by the close similarity in the somatic characters of all the species. There has consequently been a strong tendency among arachnologists (the author being equally culpable!) to create many monotypic genera for the erigonines, or to include in a genus

only a few closely related (sibling) species. It would certainly be better (if it were possible) in this homogeneous group if kinship relationships could be made evident in the binomial species names by fusing together some of these multitudinous genera, within which sub-genera or species groups could be used to indicate the smaller branches of the phylogenetic tree. In order to do this, it will be essential to find better means for establishing relationships (in the phylogenetic sense) between the species. The formation and continued use of large numbers of small genera will serve merely to obscure relationships, and it should be the aim of the taxonomist to use the genus to show relationship rather than to indicate difference.

To produce a classification of the Linyphiidae which can legitimately be regarded as phylogenetic is obviously a formidable problem. Palaeontological evidence is completely lacking; virtually nothing is known at this time about their comparative ethology, physiology, embryology or genetics. The ecological preferences of these mainly ground-living species are probably of little significance for taxonomy, particularly as many species seem to be fairly adaptable and may show different habitat preferences in different parts of Europe. Hence at the present time there is no alternative but to base the taxonomy exclusively on morphological characters, and indeed almost exclusively on external morphological characters.

Numerous attempts (summarised by Merrett, 1963) have been made to classify the Linyphiidae into groups or subfamilies, on the basis of selected morphological characters, but none of these attempts makes any pretence of leading to a classification which can be regarded in any way as phylogenetic. In addition, there is no agreement amongst arachnologists on the question of the dividing line (if such exists) between the erigonines and the linyphiines, nor on the question of the position of certain transitional genera. Both Jackson (1932) and Bristowe (1938) expressed the opinion that the grouping of linyphiid species into genera and higher taxa would eventually be based on the structure of the sex organs, presumably on the basis that these organs, which do not appear until the final moult and are then used solely for copulation, should have been but little subject to selection by environmental factors.

Occasional attempts have been made by arachnologists to base erigonine taxonomy on some feature of the male palpal organs (particularly Crosby and Bishop in numerous papers on the N. American species; and Wiehle, 1960), and in recent years special emphasis has been laid on the structural forms of the "embolic division" and the "median apophysis" as seen in the expanded palp, for both erigonine and linyphiine species (Merrett, 1963). (Note: the author prefers the term "suprategulum" as proposed by Saaristo (1971) to replace the term "median apophysis", on the ground that this avoids confusion when discussing the apophysis ("suprategular apophysis") which arises from the forward end of the suprategulum). Within apparently well-defined genera (and particularly in the erigonines) the embolic division (ED) can show quite wide variations in shape, and the embolus can vary considerably in length; the variations in the suprategular apophysis (SA) are often less pronounced. In consequence of this intrageneric variability of the ED and the SA it has been difficult or impossible to infer that any particular form of these component parts, as seen in the expanded palps, is uniquely characteristic of a group of species which could rank as a taxon of generic or higher order. In practice, therefore, it has almost always been necessary when assigning an erigonine species to a genus to rely to a marked extent on somatic characters. Linyphiine genera have also been based largely on somatic characters, though attempts have been made in recent years to define some genera on the structure of the sex organs (e.g. Merrett, 1963; Saaristo, 1971, 1972, 1973(1), (2), 1974).

The use of somatic characters for genus delineation is of course in no way unusual or undesirable, but in the Linyphiidae the problem is to find somatic characters which appear to be stable enough within what experience indicates to be good (i.e. probably monophyletic) genera. In order to be able to deduce that a group is monophyletic, it is necessary (Hennig, 1966) to identify at least one apomorphous (derived) character (no matter how "trivial") which is common to all members of the group (synapomorphous character). Because of the paucity of good morphological characters available in the Linyphiidae, and in the erigonines particularly, and because of character plasticity, it has usually not been possible to pinpoint such synapomorphous characters for a genus or

a fortiori for the higher taxa.

In the past, taxonomists have relied heavily on the use of such characters as the spacing, curvature and size of the eyes, the cheliceral teeth, and the form of the male head, when dealing with the erigonines. The eyes and cheliceral teeth normally show too much individual variation, and are often too difficult to measure accurately, to be of much value, at any rate above species level. The male head seems to be a volatile character (e.g. in *Walckenaera*), and in general is of value only at the species level; it may occasionally, however, offer a confirmatory indication at a higher level. Examples of other characters which have often been employed in the taxonomy of the erigonines are abdominal scuta, tarsal claws, and the chaetotaxy. Abdominal scuta are found, usually only in the male, in a number of genera, and it seems almost certain that scuta have been developed more than once in the family; but why only in certain small erigonines (at least in Europe) is obscure. The extent of the scuta can be variable within a species and within the species of a genus (e.g. *Pelecopsis*); within *Mecopisthes* the species *silus* has a distinct scutum in the male, while its sibling *peusi* has no scutum. Nevertheless the presence of abdominal scuta may sometimes offer indications which are useful for phylogenetic analysis. Lehtinen and Saaristo (1969) have suggested that the *pattern* of sclerotisation may be important.

In several genera (e.g. *Walckenaera, Gonatium, Tapinocyba*) the tarsal claws (particularly on legs I and II) are equipped with long comb-like teeth. This character can be useful in diagnosis, but it seems probable either that it has been developed on several separate occasions in the family, or (perhaps more probably) that it is a primitive character which has been retained in some cases. It is perhaps of significance that the small theridiids *Robertus* and *Enoplognatha* have similar pectinate claws. Despite its erratic occurrence, this character may sometimes offer useful indications for phylogenetic analysis.

One of the most useful characters for erigonine and linyphiine taxonomy has been the chaetotaxy. The tibial spinal formula, the presence or absence of a trichobothrium on metatarsus IV, and the position of the metatarsal trichobothria are characters which are often reasonably reliable at the generic level; but they are not completely reliable. Even with current generic limits (which are probably set too narrowly in many cases) there appear to be occasional variations in the spinal formula (e.g. *Araeoncus praeceps* Holm 1962; *Erigone svenssoni* Holm 1975). If some of the generic limits were widened, then the spinal formula within genera could become less constant. There are a number of cases where well-defined genera (e.g. *Entelecara*) contain species both with and without the 4th metatarsal trichobothrium, and hence this character, though often useful as a practical tool, cannot be considered as reliable for genus delineation. There are even a few examples where the 4th metatarsal trichobothrium appears in a species where it is normally absent (*Erigone longipalpis:* Murgatroyd, 1954, Murphy, 1974(1); *Micrargus herbigradus:* Murphy, 1974(2)), indicating perhaps that in these species the trichobothrium has not long been lost. The position of the metatarsal trichobothria (indicated by the expression Tm I, etc. (Locket and Millidge, 1953)) within a species is somewhat variable, perhaps usually by *ca.* ± 10% (Wunderlich, 1972, Palmgren, 1976); but this variation will almost certainly follow a normal statistical distribution about a mean value, with the majority of specimens showing a variation of probably ± 5%. (Note: in this paper, the values given for TmI are for the adult ♀). Despite this inherent variability, the values of TmI are often useful, in conjunction with the tibial spinal formula, for indicating the possible generic affinities of a species; within a few genera, however (e.g. *Walckenaera*), the position of the trichobothria is far from constant from species to species (but see Section C10 p. 32). An additional chaetotaxic character which is used in Sections C and D is the number of trichobothria on the dorsal side of the male palpal tibia; this number varies from 1-5. Most of the typical erigonine species have 1 or 2, while the genera which appear to be more primitive have 3 or more; the typically linyphiine species normally have 3 or 4.

Despite the practical value of chaetotaxy in erigonine taxonomy, it has seemed to some authors (Lehtinen and Saaristo, 1970) that such meristic/numerical characters can have little value in phylogenetic analysis, because of the probability that there has been parallel development within the family of such simple characters. Nevertheless, the work reported in the present paper indicates that the position of the metatarsal trichobothria does probably

have some phylogenetic significance, when taken in conjunction with the palpal conformation.

This brief review of some of the characters commonly used by taxonomists seems to show that not one is acceptably reliable, on its own, for the delineation of genera or higher taxa; i.e. the identification of reliable synapomorphous characters for the higher taxa in the Linyphiidae seems rarely if ever to have been achieved. This is perhaps not surprising in view of the paucity of available characters on the one hand, and the large number of species involved on the other. Whether additional characters yet to be investigated, e.g. the fine structure of hairs or cuticle by electron microscopy, will improve this situation remains to be seen.

B. Palpal Conformation

It is the chief aim of this paper to draw attention to a morphological character which, though perhaps an obvious one, does not appear to have been studied in detail nor used explicitly to indicate relationships at generic and higher levels in the erigonine or linyphiine spiders. This is the "conformation" of the male palpal organ, which is defined as the spatial arrangement or organisation of the unexpanded palpal organ as a whole, i.e. the holomorphology of the palpal organ. Palpal conformation is therefore concerned as much or more with the arrangement of the individual parts of the palp as with the detailed shapes and forms of the parts. In emphasising the importance of conformation, the author does not intend in any way to underestimate the value of the earlier work carried out on the expanded palp (particularly by Merrett, 1963); but while expansion of the palp is often necessary to discern the full details of the component parts, it must be emphasised that the expanded palp may sometimes give a misleading picture of the conformation.

This concept of palpal conformation (referred to hereafter simply as conformation), though never described as such, has in fact been used intuitively to some extent by a few arachnologists in their taxonomic studies. The majority of the figures of palps so far published have not however been detailed or accurate enough to show the detailed conformations which will be discussed in this paper.

The author has observed that, despite considerable variations which may occur in the ED and (to a lesser extent) in the SA within apparently well-based erigonine genera, the conformation appears to remain essentially constant within these genera. For this and other reasons which will become clear in this paper, the author puts forward the view that comparative analysis of conformations, in conjunction with other characters, should prove to be of greater significance in exploring phylogenetic relationships than consideration of the structures of the ED and SA alone.

In this paper, the palp is considered as directed forwards from the head of the spider, and the side which is outside is described as the lateral side, while the side which is inside is described as the mesal side; the distal end of the palp is thus the anterior end. The figures of the palps are of the right palp viewed from the inside and rather below (i.e. meso-ventrally) unless otherwise stated. The palps were immersed in clove oil and examined by transmitted light under a monocular microscope to observe the route of the seminal duct.

The form of the male palp is basically similar in almost all erigonines (Merrett, 1963); this is shown semi-diagrammatically in Fig. 1. The tegulum is normally more or less vertical, i.e. the seminal duct runs approximately up and down. The suprategulum, which is always to some extent sclerotised, is located on the mesal side of the palp, and lies along the dividing line between the sub-tegulum and the tegulum; at its distal end the suprategulum carries the suprategular apophysis, which takes a variety of forms ranging from the simple to the complex. The seminal duct runs from the reservoir in the subtegulum by a circular or spiral pathway down through the tegulum on the lateral side and up on the mesal side and along the suprategulum to the embolic division. The connection to the embolic division is made via a membranous stalk (arising from the suprategulum) which carries the duct and which may have a membranous or semi-membranous extension projecting forwards; the extension may be fused to the suprategular apophysis. The embolic division is very variable in form, but consists essentially of a radical part from which arises the embolus and sometimes other apophyses; the embolus may be very long or merely a short stub, and the radical part may extend backwards as a "tail". The linyphiine palp is essen-

tially of the same form, but the embolic division is much larger and more complex, and the suprategular apophysis is usually relatively simple; the tegulum is most frequently more or less horizontal, which is also the case in a few erigonines (e.g. *Ceratinella*).

The erigonine spiders are all closely similar morphologically, the species differing from each other only in relatively minor respects; it is only in the adult males that startling morphological differences may appear. This close similarity in characters strongly predicates a common ancestry. If, as is nowadays accepted by many arachnologists, the erigonine spiders form part of the Linyphiidae (without making any assumptions on the existence within the family of the two sub-families Linyphiinae and Erigoninae), then both the erigonines and the linyphiines must have evolved from a common ancestor, the stem species of the family. Given a common ancestry, then a consideration of the (at first sight) bewildering variety of palpal forms in the family indicates, as probably the simplest logical hypothesis, that this wide matrix of palpal forms has evolved by elaborative radiation in a number of directions from one relatively simple conformation.

In modern terminology, the plesiomorphous (primitive) conformation in the Linyphiidae is inferred to have been of the simplest form, while the more complex conformations present in most of the present species are the more apomorphous (derived) forms of this character.

The reasons for the increasing complexity of the palpal organs are obscure. There seems to be no good reason to assume in this family that increasing complexity equates with increasing efficiency in copulation. It is scarcely conceivable, for example, that the palp of the common species *Pocadicnemis pumila* (Bl.), with a long whip-like embolus, can be more mechanically efficient for sperm transfer to the female vulva than the simpler palp of the even commoner *Erigone dentipalpis* (Wid.) which has a short stub-like embolus. And indeed it is perhaps meaningless to suggest, with reference to species (populations) which exist today, that any one combination of palp/vulva is more efficient than any other; only one thing can be regarded as certain, namely that the reproductive equipment of all current species has been efficient enough to ensure the survival of the species. The changes (elaborations) in the palpal conformation within the family may therefore have been an unavoidable side effect of genetic changes associated with adaptations to their environment (e.g. Levi, 1961, p.8).

The simplest conformation of the linyphiid type of palp would probably be where the suprategulum has only a rudimentary or small apophysis, and where the seminal duct runs down from the suprategulum to enter directly into the dorsal or lateral side of a small, simple ED, equipped with a short embolus. The conformation of the stem species of the family is not of course known from any direct evidence, but is assumed to be a simple form close to this type; there is no reason to think that the *completely* plesiomorphous conformation of the linyphiid palp exists in any current species. At some time, and probably fairly early during the evolution of the family, a phylogenetic branch arose in which the duct entry moved away from this probable primitive position on the lateral or dorsal side (Fig. 8) of the ED to a less direct entry on the mesal side (e.g. Fig. 43). This displacement of the duct entry subsequently went a stage further to give the conformation where the duct passes across the ED, near the base of the embolus, and then loops back into the base of the embolus (e.g. Fig. 45); this is considered to be the most apomorphous form of duct entry (in the European fauna). In species with small ED's, narrow from top to bottom, the change involved between dorsal entry and dorso-mesal entry is obviously small (and perhaps to some extent subjective, since where the stalk ends and the ED begins is not sharply defined), but the change becomes significant when the ED is larger or when the duct entry passes fully over to the mesal side (e.g. Fig. 43). With one or two doubtful exceptions, all the linyphiid species present in Europe today seem to have been derived from one or other of these basic duct conformations. One major branch of the linyphiines has arisen from the conformation with the lateral duct entry, and another major branch from the conformation with the dorsal duct entry; erigonines have arisen from both these conformations. The conformation with mesal entry has given rise almost exclusively to erigonine species, and in particular to the numerous genera with relatively long coiled emboli (Section C9, p. 19). All the palps are derivable from the basic forms by straightforward

morphological elaboration of the ED's and, to a lesser extent, of the SA's, coupled with changes to the tegulum and to the course of the duct in the tegulum.

It is put forward as a hypothesis that the various conformations present today are the results of separate phylogenetic lines of development; the basis for this postulate is the improbability that a given conformation (a relatively complex, non-adaptive character) has been evolved more than once in the family. The phylogenetic analysis carried out in this paper is on the basis of this hypothesis, and on the assumptions (i) that the primitive conformation of the palpal organs was simple, and that the derived forms are more complex; and (ii) that, in the absence of any evidence to the contrary, any regression from more complex to more simple forms has not occurred, i.e. that the evolution has been essentially in one direction only. In other words, the present-day conformations are transformation conditions of the plesiomorphous conformation, which was present in the stem species but which almost certainly no longer exists, in its entirety, in any contemporary species. Each conformation type is therefore considered to be an apomorphous character, and possession by a group of species of the same or closely similar conformations (synapomorphy) justifies the presumption of monophyly in the group (Hennig, 1966). The theory is developed in this paper by the conformational analysis of most of the European genera of erigonine and linyphiine spiders, (with fewer species studied in the latter case). The erigonine genera are split into a number of groups, on the basis of their conformations, and the possible inter-relationships of the groups are discussed. The linyphiine genera are then analysed on the basis of their conformations, and their probable relationships with some of the erigonine groups are indicated. The phylogenetic picture emerging from the comparative analysis of the conformations is shown schematically in Fig. 200 and discussed in Section E (p. 50).

C. Conformations of Erigonine Genera

1. *Leptorhoptrum/Lophomma* Group (Figs. 2-9, 12, 179)

In this group the ED is connected to the suprategulum by a clear stalk which comes down on to the dorsal side of the ED (e.g. Figs. 3, 7), and the duct enters the ED more or less on the dorsal side. The species placed in this group are postulated as having arisen, probably by several separate branchings, from ancestors which were close to the stem species. On one side of this group are the more linyphiine forms (e.g. *Leptorhoptrum*) which are close to *Hilaira* (Section C 3, p. 8) and to some linyphiine genera, and on the other side are species which are closer to the erigonine genera such as *Tapinocyba* (Section C 8, p. 15) and *Savignya* (Section C 11, p. 32).

The current genera included in this group are as follows:

Diplocentria Hull 1911
Tiso Simon 1884
Zornella Jackson 1932
"Gongylidiellum" mediocre Simon
Lophomma Menge 1867
Notioscopus Simon 1884
Troxochrus Simon 1884
Leptorhoptrum Kulcz. 1894

The genera *Diplocentria* (Fig. 2) and *Tiso* (Figs. 3, 4) have conformations fairly close to those of some *Hilaira* species, particularly to *pervicax* Hull and *nubigena* Hull (Figs. 16, 15). *Zornella* (Fig. 5) has some similarities in conformation to *Tiso*, including the fairly strongly developed SA, but it is an anomalous genus in some respects: e.g. it has 5 trichobothria on the male palpal tibia instead of the more usual 1-3.

The species *"G." mediocre* (Fig. 6) has a conformation rather like a simplified *Diplocentria* or *Hilaira*; it has tibial spines 2221, TmI 0.4, no TmIV, and is

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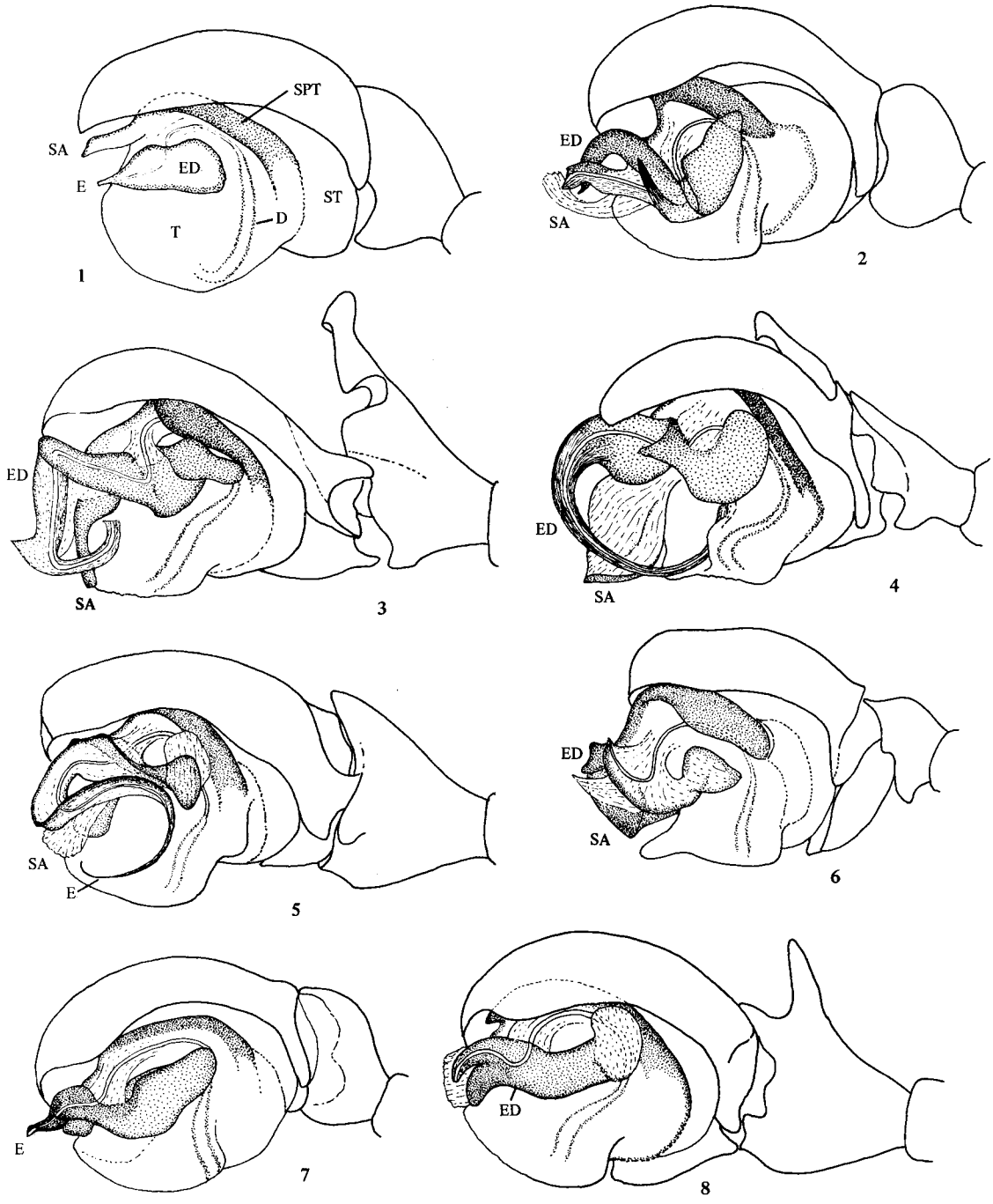
Figures

All male palps are right palps viewed from inside and rather below, unless otherwise stated. Abbreviations used: ED = embolic division; E = embolus; SA = suprategular apophysis, T = tegulum.



Figs. 1-8: Male palps. **1** Generalised erigonine palp: SPT = suprategulum, ST = subtegulum, D = duct; **2** *Diplocentria bidentata* (Emert.); **3** *Tiso vagans* (Bl.); **4** *T. aestivus* (L. Koch); **5** *Zornella cultrigera* (L. Koch); **6** *"Gongylidiellum" mediocre* Simon; **7** *Notioscopus sarcinatus* (Cambr.); **8** *Lophomma punctatum* (Bl.).

not a *Gongylidiellum.* To avoid the creation of a new genus at this stage it can perhaps be placed provisionally in *Diplocentria* until its relationships become clearer.

The genera *Lophomma, Notioscopus* and *Troxochrus* are closer to the more typically erigonine genera. *Lophomma* (Fig. 8) has a conformation which is close to that of *Tapinocyba* (Section C 8, p. 15). *Notioscopus* (Fig. 7) is similar in conformation to *Mecynargus (Rhaebothorax)* (Section C 8). *Troxochrus* (Fig. 9) could, from the form of the ED, represent a precursor of the *Savignya* group (Section C 11, p. 32).

Leptorhoptrum (Fig. 12) has a simple conformation of the same basic type, but differs from the other members of this group in having the tegulum more or less horizontal. It can be regarded as an offshoot from the *Lophomma* group, but it may have arisen from close to the stem species. The conformation of *Leptorhoptrum* is basically similar to that of some linyphiine species (Section D).

Most of the species in this group have not developed marked erigonine characters. Only *Troxochrus* has a small cephalic lobe in the male; *Notioscopus* has an elevation behind the eyes, as in some *Hilaira* species.

2. *Drepanotylus* Group (Figs. 10, 11)

The following current genera/species are included in this group:

"Tibioplus" arcuatus Tullg.
Drepanotylus Holm 1945

The three species concerned are related in conformation to the *Lophomma* group, and also probably to *Hilaira.* The species *"T." arcuatus* (Fig. 11) (which is not a *Tibioplus*) is rather similar to *Tiso,* and *Drepanotylus* (Fig. 10) can be regarded as a further extension of the *arcuatus* type. Both *arcuatus* and *Drepanotylus* have a long forward-directed membranous extension on the stalk; they differ considerably, however, in chaetotaxy. *D. borealis* Holm has a small pointed apophysis on the base of the radix of the ED which could represent a vestigial "lamella". This small group has presumably arisen by separate branchings from a phylogenetic region close to the *Lophomma* and *Hilaira* groups.

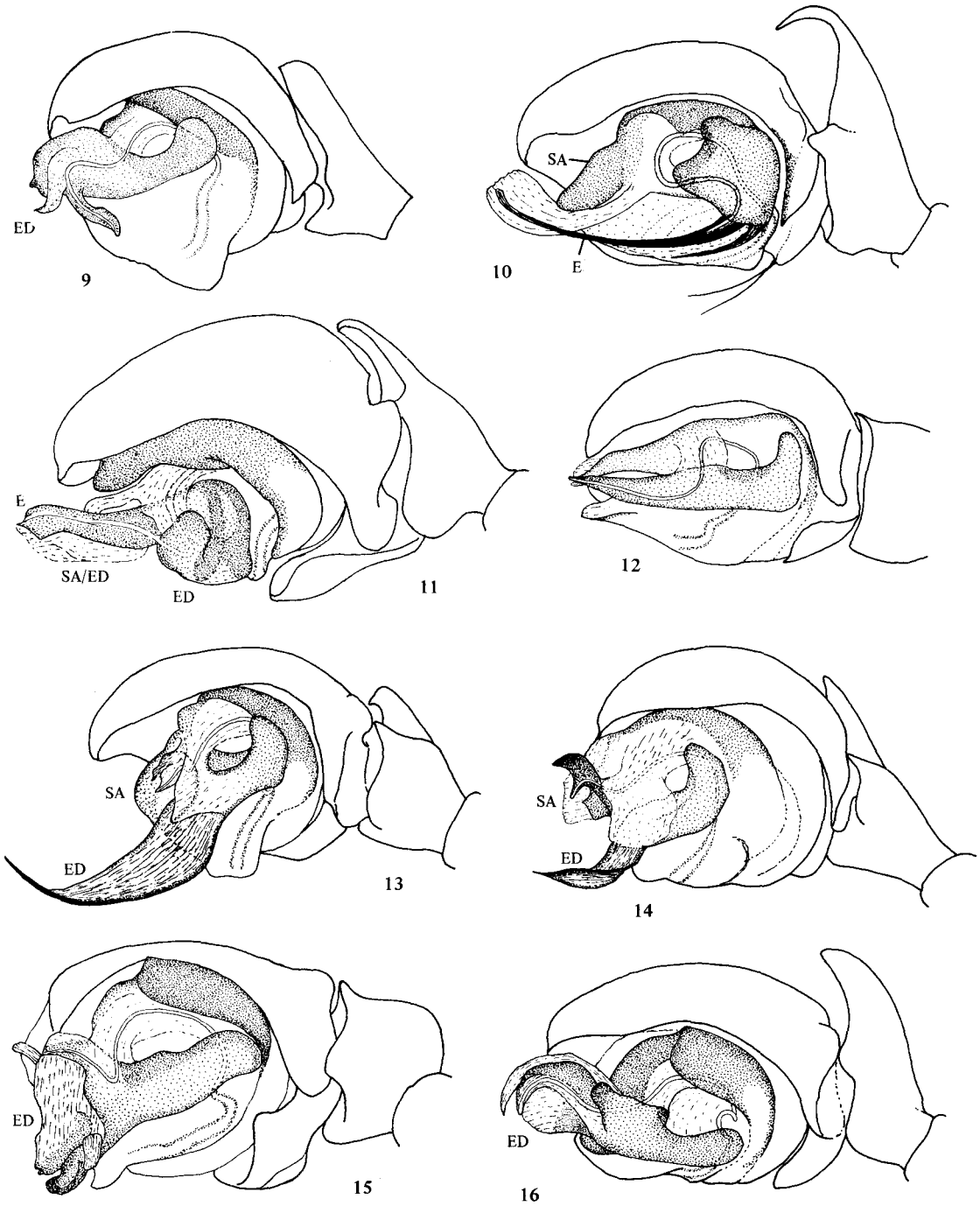
3. *Hilaira* Group (Figs. 13-20, 23, 187-188)

In this group, the duct comes down from the suprategulum in a stout stalk and enters the ED on the lateral or dorsal side; the stalk often extends, as a relatively non-sclerotised region, into the ED (e.g. Fig. 14). There is a tendency for the ED to become split into sclerotised areas joined by less sclerotised areas, as in the linyphiine type of ED. None of the species has a true cephalic lobe in the male, but the head is sometimes elevated behind the eyes. The following current genera are included in this group:

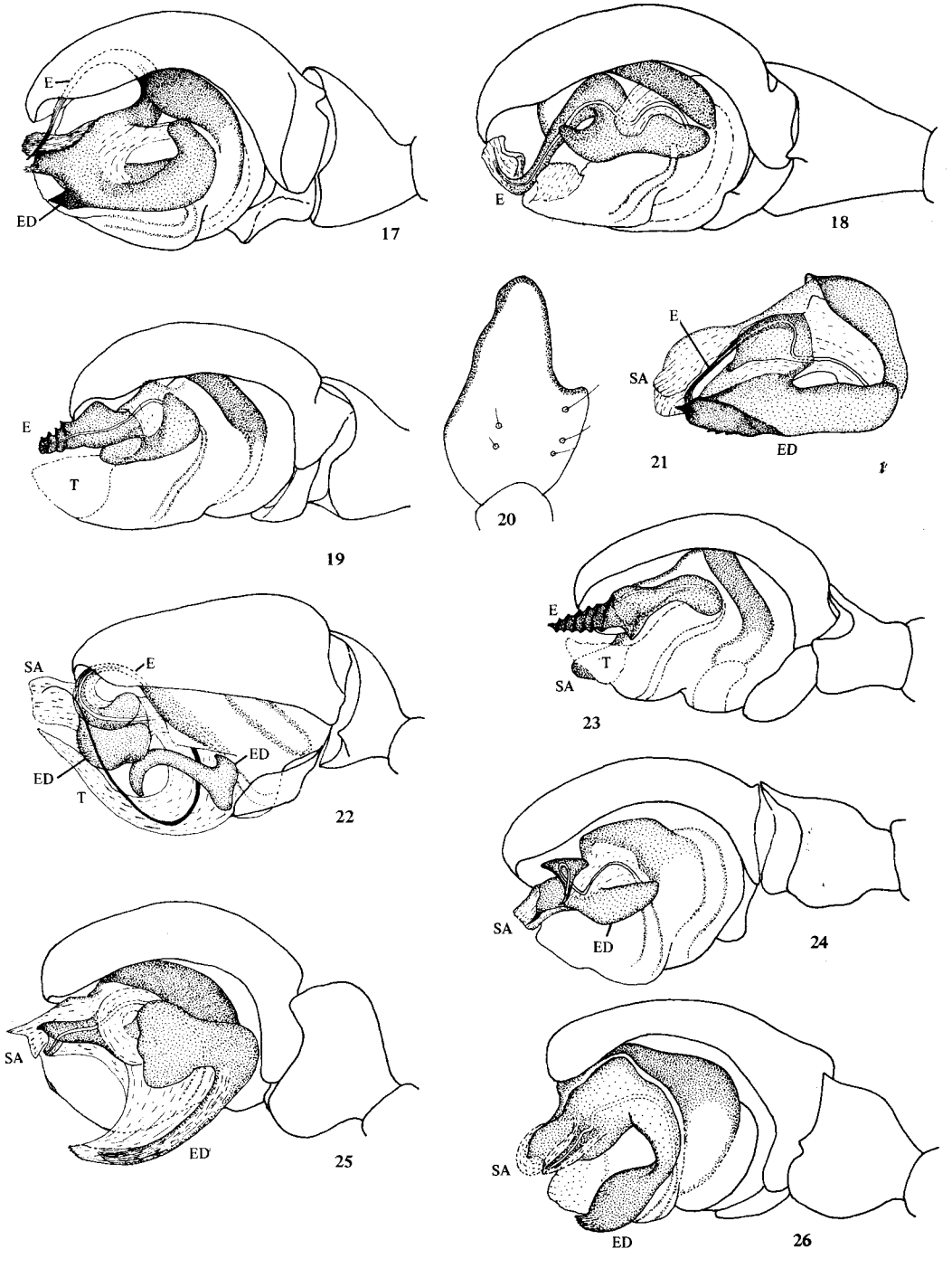
Hilaira Simon 1884
Phaulothrix Bertkau 1885
Erigonidium Smith 1904
Hylyphantes Simon 1884

All the *Hilaira* species are closely similar in chaetotaxy (tib.spines 2222, lateral spine on tib.I, TmI 0.60-0.70, TmIV present), but the male palps show fairly wide variations in the ED. *H. herniosa* (Thor.) (Fig. 13) is clearly congeneric with *H. excisa* (Cambr.) (Fig. 14) (the type species), the ED being merely an exaggerated form of the *excisa* type. In *nubigena* Hull (Fig. 15), *pervicax* Hull (Fig. 16) and the *montigena* (L.K.) group (Fig. 17) the margin of the suprategulum is folded over, a character not present in *excisa/herniosa*; a similar form of suprategulum is present in some linyphiine species. Despite the presence of the long curved embolus arising from the dorsal side of the ED in the *montigena* group, the general form of the ED is of the same type here as in *nubigena* and *pervicax.* There are 3 trichobothria on the male palpal tibia of all the species except *nubigena,* which has the unusual number of 5 (Fig. 20). Because of the differences in the ED's there must be some question whether *nubigena, pervicax* and *montigena* are congeneric with *excisa/herniosa,* but for the present they can be left in *Hilaira* as a separate species group.

P. hardyi (Bl.) (Fig. 18) has a conformation generally similar to *Hilaira,* and the embolus is to some extent intermediate between *pervicax* and *montigena.* The chaetotaxy is also similar, though the lateral spine on tib. I is absent; the male head is rather like that of *excisa.* The male palpal tibia has 4 trichobothria. It seems probable that *Phaulothrix* should be regarded as a synonym of *Hilaira* (**syn.n.**), with *hardyi*



Figs. 9-16: Male palps. **9** *Troxochrus scabriculus* (Westr.); **10** *Drepanotylus borealis* (Holm); **11** *"Tibioplus" arcuatus* (Tullg.); **12** *Leptorhoptrum robustum* (Westr.); **13** *Hilaira herniosa* (Thor.); **14** *H. excisa* (Cambr.); **15** *H. nubigena* Hull; **16** *H. pervicax* Hull.



Figs. 17-26: Male palps. **17** *Hilaira montigena* (L. Koch); **18** *Phaulothrix hardyi* (Bl.); **19** *Erigonidium graminicola* (Sund.); **20** *H. nubigena* Hull, palpal tibia (above); **21** *Gongylidium rufipes* (Sund.), ED and SA; **22** *Trematocephalus cristatus* (Wid.); **23** *Hylyphantes nigritus* (Simon); **24** *Oedothorax apicatus* (Bl.); **25** *Collinsia holmgreni* (Thor.); **26** *C. distincta* (Simon).

placed in a separate species group.

Erigonidium (Fig. 19) seems to be fairly close to *H. excisa* in conformation, but the ED has a screw-like embolus; the tibial spines have been reduced to 2211. *Hylyphantes* (Fig. 23) also probably belongs here. It has the same chaetotaxy as *Erigonidium*, but the ED is somewhat differently formed; nevertheless it seems probable that *Erigonidium* is a synonym of *Hylyphantes*, as suggested by Wunderlich (1970). Both species have 3 trichobothria on the male palpal tibia. The genus *Hylyphantes* (s.lat.) can be regarded as a small side branch from the *Hilaira* group.

This group has probably arisen from a stock with a conformation of the *Lophomma* group type, by elaboration of the ED coupled with other minor changes.

4. *Gongylidium* Group (Figs. 21, 22, 24)

The following current genera are included in this group:

Gongylidium Menge 1868
Oedothorax Bertkau 1883
Trematocephalus Dahl 1886

These genera have conformations similar in type to those of some *Hilaira* group species. The conformation of *Gongylidium* (Fig. 21) is fairly close to that of *H. (Phaulothrix) hardyi* (Fig. 18) or *H. montigena* (Fig. 17), but in *Gongylidium* the radical part is more distinctly separated from the "embolic part" by a non-sclerotised region. The *Oedothorax* species have a conformation of similar type; as in *Gongylidium*, the duct enters on the lateral side of the embolic part, which is separated from the radical part by a relatively non-sclerotised area, but in *Oedothorax* the embolus is smaller and shorter (Fig. 24). *Trematocephalus* (Fig. 22) also has a conformation of a similar basic type, though here the ED has become more complex with several distinct parts, the embolus is much longer, and the tegulum has an apophysis anteriorly. The *Oedothorax* males tend to have the cephalothorax elevated behind the eyes, as in some *Hilaira* species; the lobe in the *Trematocephalus* male is similarly placed.

All the species in this group have a similar chaetotaxy (tibial spines 2211, TmI 0.6-0.75, TmIV present), all have 3 trichobothria on the male palpal tibia, and all have a tendency to a reddish colour. Because of the similarities in conformation to *Hilaira*, as noted above, it is postulated that these genera arose from the *Hilaira* region of the phylogenetic tree.

5. *Erigone* Group (Figs. 25-33)

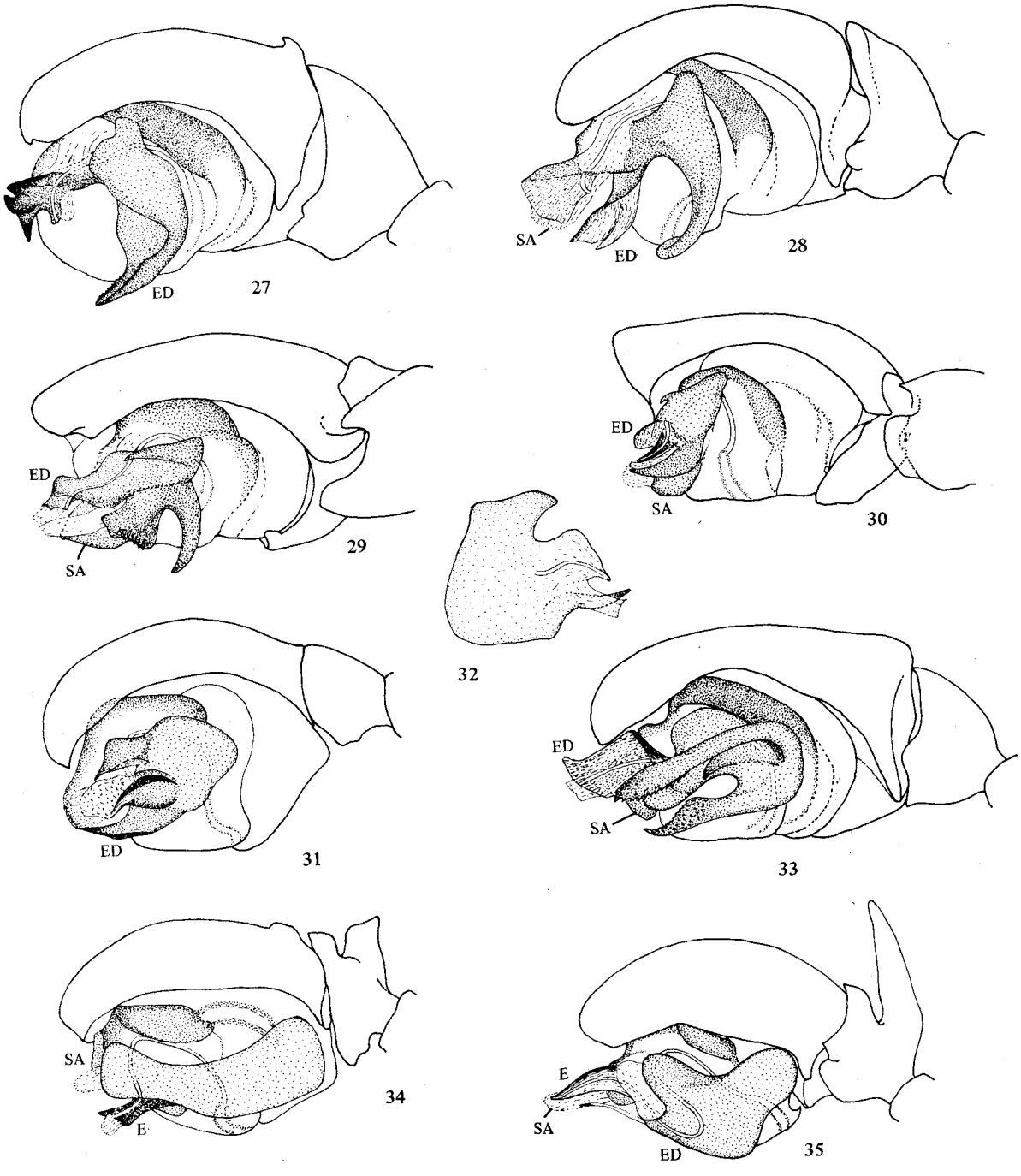
The species in this group are related to *Hilaira* (particularly *excisa*) – see below. The embolus is usually no more than a short stub on the ED, and the SA is fairly simple in form.

The following current genera/species are included in this group:

Collinsia Cambr. 1913
Halorates Hull 1911
Islandiana Braendegaard 1932
Erigone Audouin 1826
Eperigone Crosby and Bishop 1928
Anerigone Berland 1932
"Collinsia" hibernica Simon
"Centromerus" quadridentatus Wund.
Milleriana Denis 1966

The genera *Collinsia* (Figs. 25, 26) and *Halorates* (Fig. 27) are similar to one another in conformation; *C. spetsbergensis* (Thor.) and *thulensis* (Jacks.) are of the same type. *Halorates* differs from all the other European species in this group by its chaetotaxy (tibial spines 2222, TmI 0.6-0.7, TmIV present); nevertheless because of its close similarities to *Collinsia* these two genera should probably be combined (*Halorates* would have priority), with *reprobus* in a separate species group to show that it probably represents a side branch within the presumed monophyletic genus. The *Halorates/Collinsia* type of ED can have been derived from the *Hilaira excisa* type by a relatively simple transition (cf. Figs. 14 and 27); in *distincta* the enlargement of the plate of the ED has hidden the stalk which is visible in *holmgreni* and *reprobus*. In *Islandiana* (Fig. 28) the conformation is of exactly the same type but the ED has developed an additional branch.

The genus *Erigone* has clear and obvious characters which make it probable that it is a monophyletic genus. All the species have the same basic conformation (Fig. 29). The duct runs into the ED via a stout stalk which is sometimes partly visible. The ED is relatively complex in all the European species except *vagans* Aud. (the type species) (Fig. 30) which never-



Figs. 27-35: Male palps. **27** *Halorates reprobus* (Cambr.); **28** *Islandiana alata* (Emert.); **29** *Erigone remota* L. Koch; **30** *E. vagans* Aud.; **31** *"Collinsia" hibernica* Simon; **32** *"Centromerus" quadridentatus* Wund., ED (left palp); **33** *Milleriana inerrans* (Cambr.); **34** *Gongylidiellum vivum* (Cambr.); **35** *G. latebricola* (Cambr.).

theless has the same basic conformation; the much simpler form of the ED, and the rather different epigyne, indicates that this species must form a separate branch within the genus. *Islandiana* has an ED close to those of *Erigone*, and the probable derivation of the *Erigone* conformation by a transition of the type: *H. excisa* (Fig. 14) → *Halorates* (Figs. 26, 27) → *Islandiana* (Fig. 28) → *Erigone* (Fig. 29) is clear. *H. reprobus* has the same chaetotaxy as *H. excisa*, but the subsequent species in the series have lost both the second spine on tib. IV and the trichobothrium on MTIV.

The species *Anerigone fradeorum* Berl., from the Azores, seems to be a fairly typical *Eperigone*, except that the patella has a small ventral process at the distal end. *"Collinsia" hibernica* Sim. (Fig. 31) (tib. spines 2211) and *"Centromerus" quadridentatus* Wund. (tib. spines 2222) (Fig. 32) have ED's rather similar to *Eperigone*, but probably do not belong in that genus. These two species possibly bear the same relationship to *Halorates* or *Islandiana* as *E. vagans* does to the other *Erigone* species, having simplified ED's of the *Halorates* type. The position of the two species must be left open until a revision of *Eperigone* and related species has been carried out.

Milleriana inerrans (Cambr.) (Fig. 33) has the same basic conformation as the other members of this group, but the ED has become even more complex; the chaetotaxy is similar to that of *C. distincta*. *Milleriana* may possibly be a synonym of *Catabrithorax* Chamberlin 1920.

In order to gain a more complete picture of the genera in this group, it will be essential to study the N.American species of *Erigone* and related genera (Crosby and Bishop, 1928) which seem to show a much wider range of forms than is present in the European fauna. The diversity of species present in N.America suggests that this group may have originated there and subsequently spread to Europe.

6. *Gongylidiellum* (Figs. 34, 35)

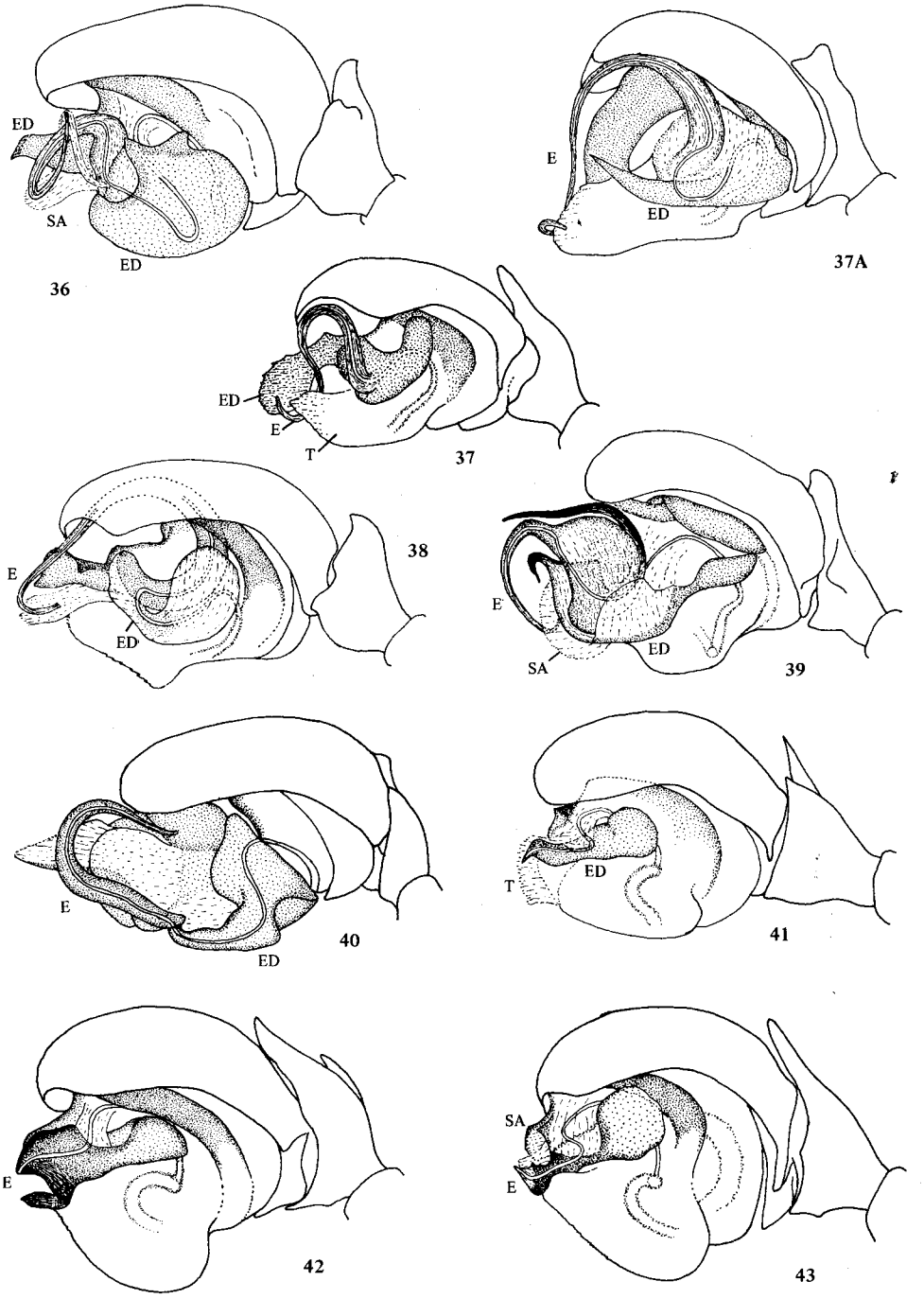
Although at first sight the genus *Gongylidiellum* Simon 1884 may appear to be close to *Asthenargus* (Section C 15, p. 40, Fig. 155), in fact the form of the ED is different, the embolus being a sclerite which is more or less distinct from the large plate forming the radix (Figs. 34, 35). It seems most likely that *Gongylidiellum* has originated from close to *Hilaira* (Section C 3, p. 8). *G. latebricola* (Cambr.) (Fig. 35) is not dissimilar to *H. pervicax* (Fig. 16) in its conformation and ED, and is also fairly close in conformation to the linyphiine species *"Oreonetides" abnormis* (Section D 7, p. 48, Fig. 194).

7. *Mioxena* Group (Figs. 36-40)

The following current genera (all monotypic) are placed in this group:

Mioxena Simon 1926
Tapinocyboides Wiehle 1960
Trichoncoides Denis 1950
Wiehlea Braun 1959
Sisicus Bishop and Crosby 1938
Heterotrichoncus Wund. 1970

These species each have a similar type of conformation (Figs. 36-40). After leaving the suprategulum the duct runs down through the basal part of the ED, which is a plate-like sclerite, and then on to a fairly long stout embolus. The ED shows some differentiation into separate sclerites, as in most linyphiine species. The 6 species are similar in having TmI 0.3-0.45 and no TmIV, but the tibial spines range from 1111 in *Tapinocyboides* through 2211 in *Mioxena, Trichoncoides, Heterotrichoncus* and *Wiehlea* to 2222 in *Sisicus*. *H. pusillus* (Miller) is very close to *Trichoncoides*, and should possibly be placed in that genus. It is postulated that this group of species has arisen from a branch close to *Hilaira*; the form of the ED could fairly readily have been derived from the form present in the *H. montigena* group (Fig. 17), though in the present group the duct leaves the suprategulum much closer to the base of the palp. These species are on the whole more erigonine that linyphiine in character: *Trichoncoides* has 3 trichobothria on the male palpal tibia, *Mioxena, Heterotrichoncus* and *Tapinocyboides* have 2, and *Wiehlea* and *Sisicus* have 1, and all the species have at least a small tibial apophysis on the male palp. Several linyphiine genera (Section D 6, p. 48) have virtually the same conformation as this group, and are probably closely related.



Figs. 36-43: Male palps. **36** *Mioxena blanda* (Simon); **37** *Heterotrichoncus pusillus* (Miller); **37A** *Tapinocyboides pygmaea* (Menge); **38** *Trichoncoides piscator* (Simon); **39** *Wiehlea calcarifera* (Simon); **40** *Sisicus apertus* (Holm); **41** *Tapinocyba praecox* (Cambr.); **42** *T. insecta* (L. Koch); **43** *T. affinis* Less.

8. *Tapinocyba* **Group** (Figs. 41-56)

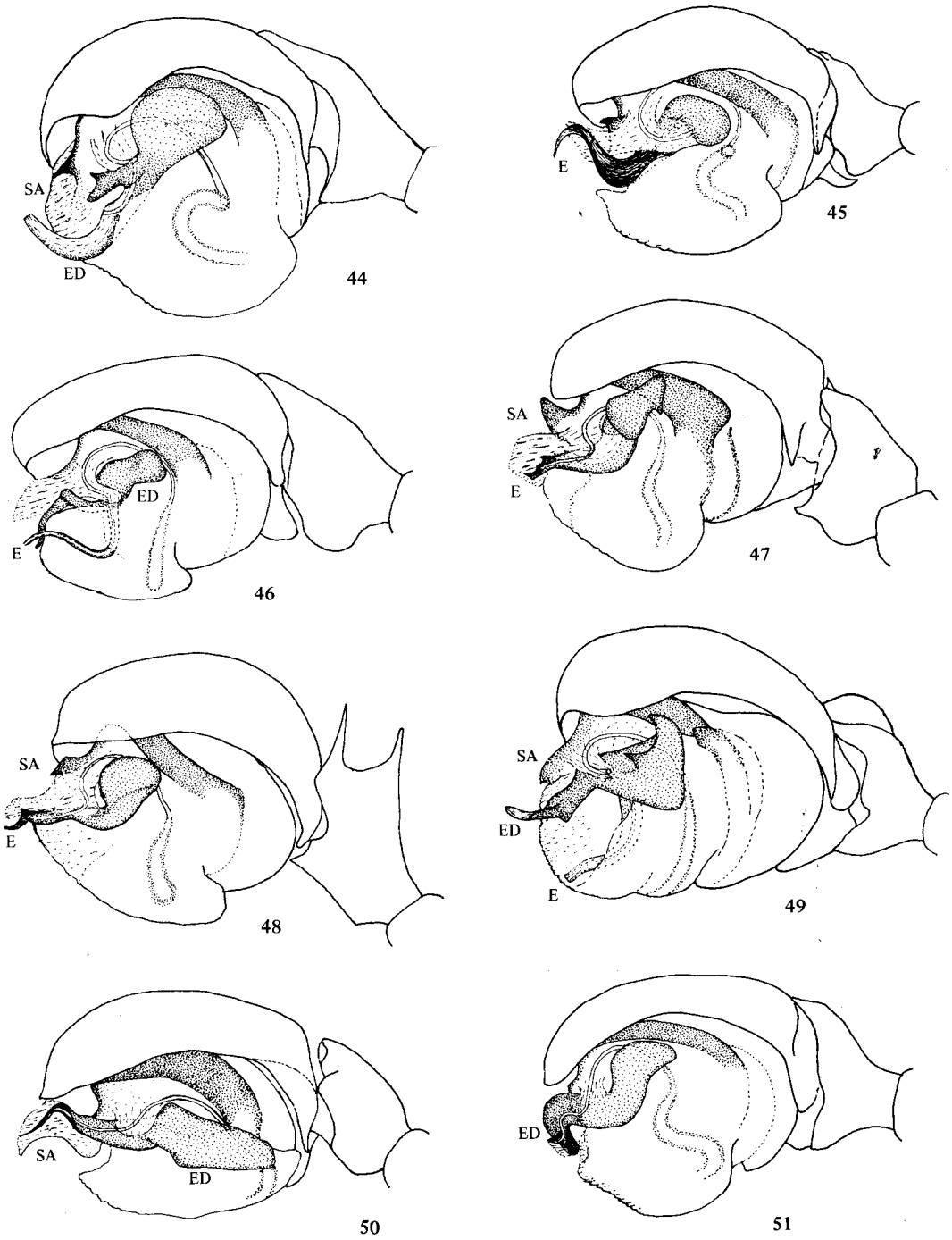
In this group, the duct runs well to the anterior end of the palp before entering the ED, via the membranous stalk, on the mesal or at least the dorso-mesal side (e.g. Fig. 41). The ED's are often relatively simple in shape with a short embolus, but in a few cases the embolus is longer. The following current genera/species are included in this group:

Tapinocyba Simon 1884
Ceratinops Banks 1905
Mecynargus Kulcz. 1894
Rhaebothorax Simon 1926
Conigerella Holm 1967
Latithorax Holm 1943
Thyreosthenius Simon 1884
Acartauchenius Simon 1884
Trachelocamptus Simon 1884
"Trichopterna" thorelli (Westr.)

The genus *Tapinocyba* illustrates several points of interest for the phylogenetic analysis of the erigonines. All the European species are closely similar in general appearance, in chaetotaxy, and in the possession of highly pectinate tarsal claws; all have male palps with the tegulum protuberant ventrally, and the duct within the tegulum is sinuous with a sudden constriction in diameter at the end of the sinuous part (only in *praecox* (Cambr.), the smallest species, is the tegulum less developed ventrally). *T. praecox* (Fig. 41), *mitis* (Cambr.), *insecta* (L.K.) (Fig. 42), *affinis* Less. (Fig. 43) and *corsica* Sim. each have the typical conformation, with simple ED's in which the embolus is relatively short. In *T. pallens* (Cambr.) (Fig. 44) the basic conformation is the same, but the ED has become significantly more complex and the duct entry has moved backwards and more to the mesal side. In *T. silvestris* Georgescu (Fig. 45) the embolus has become much longer to form a spiral, and the duct entry to the ED has moved even further back so that it has become looped round the ED; in addition, the stalk has developed a forward-directed membranous apophysis. The conformation of *T. silvestris* will in fact place it in the same group as *Pelecopsis* (Section C 9, p. 19, Figs. 66, 67). *T. silvestris* is in most respects a typical member of the genus: chaetotaxy, enlarged tegulum, pectinate claws; the paracymbium is abnormal in that it bears a prominent tooth, and the female epigyne is perhaps rather atypical. If *silvestris* is properly a *Tapinocyba* (and it seems to be in spite of these small anomalies), then this is a further indication that within a genus considerable development of the ED can occur, and that in addition this can be accompanied by a shift of the duct entry, though the basic duct conformation (viz. in this case duct entry on the mesal side of the ED) remains unchanged. The progression within *Tapinocyba* from *praecox* to *pallens* to *silvestris* suggests a probable route by which the genera possessing spiral emboli (Section C 9, p. 19) have arisen from species with simple ED's having short emboli. The actual mechanics of the change is not however clear, but it is possible that somewhere in the world fauna a key to this transformation (in the form of intermediates) will be found. *Aulacocyba* (Section C 11, p. 34, Fig. 140) is quite distinct from *Tapinocyba.*

The species *Ceratinops pectinata* (Tullg.) (Fig. 46) seems to be close to *Tapinocyba* (particularly to *pallens* and *silvestris*) in conformation and in chaetotaxy (tib. spines 1111, TmI 0.45, no TmIV); it differs in possessing a very rugose integument. A number of species are placed in the genus *Ceratinops* in N. America (Crosby and Bishop, 1933), but whether all are correctly placed is uncertain. The genus requires further study before its relationships can be usefully commented on. (On the basis of the female, *C. pectinata* seems to be a synonym of *Troxochrota scabra* Kulcz.; comparison of males has not yet been possible).

The genera *Rhaebothorax* (Fig. 48) and *Mecynargus* (*longus* Kulcz.) (Fig. 47) have virtually identical conformations, and highly developed stridulatory areas (with a honeycomb-like structure different from the stridulatory areas present in other genera) on the book lungs and adjacent ventral areas of the abdomen in the majority of species (weakly developed in *R. monticola* Holm and *R. paetulus* (Cambr.); very strongly developed in *M. longus*). This specialised structure can be regarded as an autapomorphous character for this group of species. All the species have tibial spines 2221 (though the second spine on tib. III seems sometimes to be missing (Holm, 1943)), but whereas *Mecynargus* has a TmIV and TmI 0.85, *Rhaebothorax* has no TmIV and TmI ranges from 0.45 to 0.75. The species *R. sphagnicola* Holm (Fig. 50) has the same basic conformation, but



Figs. 44-51: Male palps. **44** *Tapinocyba pallens* (Cambr.); **45** *T. silvestris* Georg.; **46** *Ceratinops pectinata* (Tullg.); **47** *Mecynargus longus* Kulcz.; **48** *Rhaebothorax brocchus* (L. Koch); **49** *Latithorax faustus* (Cambr.); **50** *R. sphagnicola* Holm; **51** *Conigerella borealis* (Jacks.).

the tegulum is much more horizontal than in the other species, possibly as the result of the longer tail of the ED; this species is typical in the strong development of the stridulatory areas. On the basis of the conformation and the stridulatory equipment, *Mecynargus* and *Rhaebothorax* can be inferred to be a monophyletic group; *Rhaebothorax* should probably therefore be regarded as a junior synonym of *Mecynargus* (syn.n.). The heterogeneity of the chaetotaxy within this group of species indicates that there has been a significant degree of branching, though the much higher value of TmI in *longus* may be associated with its larger size and more elongated shape (cf. Palmgren, 1976, p. 5).

Conigerella (Fig. 51) is very close to *Mecynargus/Rhaebothorax* and to *Tapinocyba* in conformation; there are no stridulatory areas on the abdomen. Tibial spines are 2221, TmI is 0.45, and the male head is somewhat similar to that of *M. longus*, while the tarsal claws have fairly long teeth like *Tapinocyba* but less pronounced. Apart from the tibial spines, *Conigerella* is closer to *Tapinocyba* than to *Mecynargus/Rhaebothorax*. *R. paetulus*, with TmI 0.45, and with weakly developed stridulatory equipment, is intermediate between *Conigerella* and the typical *Mecynargus/Rhaebothorax* species.

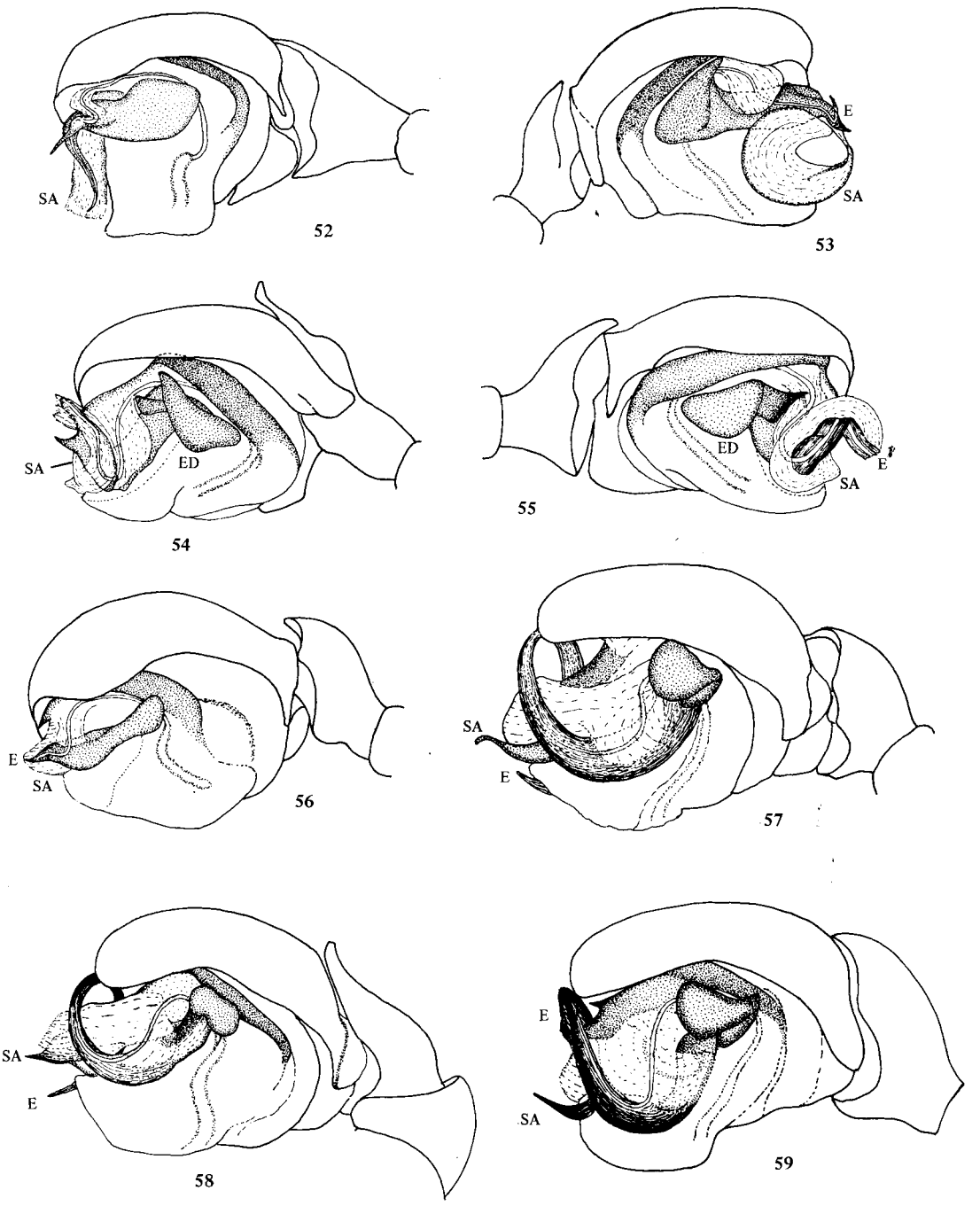
Latithorax (Fig. 49) which was incorrectly synonymised with *Eboria* (Locket and Millidge, 1953), seems to occupy the same position relative to *Mecynargus/Rhaebothorax* as does *T. pallens* to *T. praecox*, etc.; a longer embolus has developed towards the middle of the ED, and the duct entry has moved backwards with the duct entering via a loop. *Latithorax* is in other respects a fairly typical *Mecynargus/Rhaebothorax*, with rather weakly developed stridulatory areas (but of the same honeycomb type), and if *T. pallens* is to be retained in *Tapinocyba* (which seems to be correct) then it may be logical to move the *Latithorax* species into *Mecynargus/Rhaebothorax*.

The genus *Thyreosthenius* (Fig. 52) has the same basic conformation as *Tapinocyba*; its ED is still relatively simple but has developed a fairly long slender curved embolus at the anterior end. *Thyreosthenius* is closer to *Tapinocyba* than to *Mecynargus/Rhaebothorax*, having tib. spines 1111 and no stridulatory region on the abdomen; this genus has the prominent tegulum usually present in *Tapinocyba* and (to a lesser extent) in *Mecynargus/Rhaebothorax*.

Acartauchenius scurrilis (Cambr.) (the type species: Fig. 53) is similar to some *Mecynargus/Rhaebothorax* species in the shape of the ED, but the SA has developed significantly into a flat membrane which coils round the embolus. *Trachelocamptus nasutus* Cambr. (the type-species: Fig. 54) is similar in conformation to *Acartauchenius*, with a similar type of SA, but the embolus has lengthened. *A. depressifrons* Sim. (Fig. 55), which has the male head rather like *A. scurrilis*, has the ED nearer to *Trachelocamptus* than to *scurrilis*. It is questionable whether the differences in ED between *scurrilis* and the *Trachelocamptus* species are really enough to justify the maintenance of two genera. The reduction of leg spines in *scurrilis* (1111, cf. 2211 in the other species) may be associated with its myrmecophile habit; all the species have TmI 0.35-0.40, no TmIV. For the time being, however, it is proposed to retain *Trachelocamptus*; examination of the other alleged members of this genus (from N.Africa) will be necessary before a balanced conclusion can be reached.

"Trichopterna" thorelli (Westr.) (Fig. 56), which cannot be regarded as congeneric with *T. cito* (Cambr.) (Section C 9, p. 25, Fig. 86), also belongs in this group. Its chaetotaxy (tib. spines 1111, TmI 0.9, TmIV present) is different from the other species in this group, indicating that it represents a separate branch from *Tapinocyba* and *Mecynargus/Rhaebothorax*. Although it is correctly placed in this group on the basis of its conformation, it should perhaps be regarded as monophyletic with the genus *Baryphyma* (Section C 9, p. 19, Fig. 57), though it cannot be placed in that genus. It is not proposed to create a new genus for it at the present time.

It seems probable that the members of this group have evolved in several separate lines which arose from species with the *Lophomma* conformation type (Section C 1, p. 6), as the result of a relatively small movement of the stalk and the duct towards the mesal side of the ED. *Tapinocyba*, *Mecynargus/Rhaebothorax* and *"T." thorelli* are regarded as forming separate lines. *Thyreosthenius*, *Acartauchenius* and *Trachelocamptus* are probably side branches from either the *Tapinocyba* or *Mecynargus/Rhaebothorax* lines, but there is at present insufficient evidence to indicate the positions of these side branches. It is



Figs. 52-59: Male palps. **52** *Thyreosthenius biovatus* (Cambr.); **53** *Acartauchenius scurrilis* (Cambr.), (left palp); **54** *Trachelocamptus nasutus* (Cambr.); **55** *A. depressifrons* Simon, (left palp); **56** *"Trichopterna" thorelli* (Westr.); **57** *Baryphyma pratense* (Bl.); **58** *Praestigia duffeyi* Mill.; **59** *Acanthophyma gowerense* (Locket).

postulated that species of the *Tapinocyba* conformation are the ancestors of the members of the *Pelecopsis* group (Section C9).

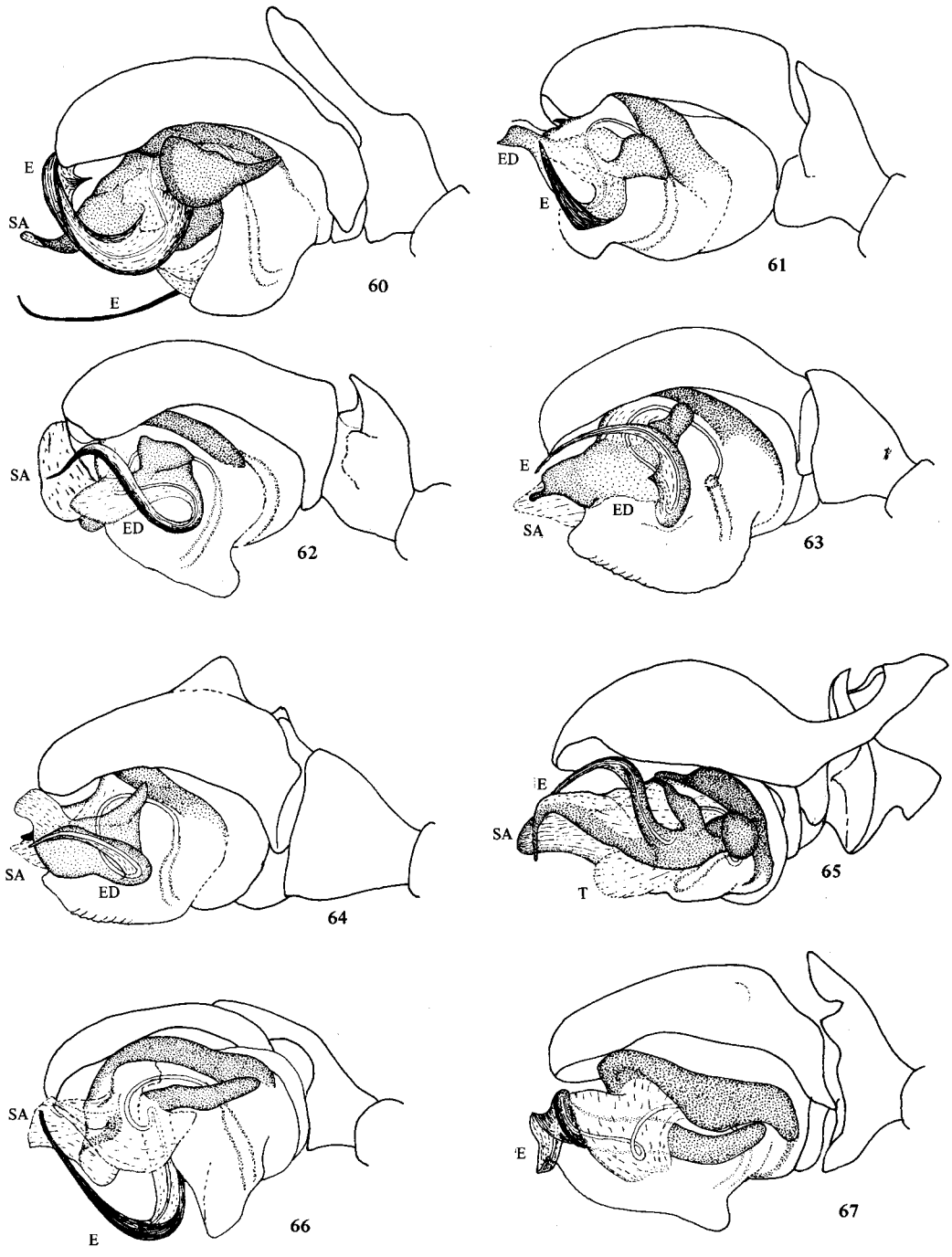
9. *Pelecopsis* Group (Figs. 57-109)

In this group of genera the embolus is in the form of a coil or part coil, which arises from the radical part of the ED; the duct enters the embolus on the dorso-mesal or mesal side via a non-sclerotised stalk which is in most cases produced anteriorly into a membranous apophysis which may be fused to the SA (e.g. Fig. 68); in a few species (e.g. Fig. 80), the stalk carries in addition a sclerotised apophysis. The radical part may be simple, with a "tail" of variable length, but in some genera is more complex with a forward-directed part anterior to the junction with the embolus (Fig. 87). Some species with an "intermediate" type of conformation (i.e. of a rather similar type to *Tapinocyba pallens* (Section C 8, p. 15, Fig. 44)) are also included in this group. A large number of what have been regarded as "typical" erigonine species have this conformation, differing only in the detail of the ED, SA and tegulum. The current genera included in this group are as follows:

Baryphyma Simon 1884
Minyrioloides Schenkel 1929
Praestigia Millidge 1954
Acanthophyma Lock., Mill. & Merr. 1974
Dresconella Denis 1950
Peponocranium Simon 1884
Maso Simon 1884
Minicia Thorell 1875
Minyriolus Simon 1884
Pelecopsis Simon 1864
Exechophysis Simon 1884
Hypselistes Simon 1884
Mecopisthes Simon 1926
Panamomops Simon 1884
Panamomopsides Denis 1962
Microstrandina Charit. 1937
Lochkovia Miller & Vales. 1962
"Micrargus" kaestneri Wiehle
Plaesianillus Simon 1926
Cnephalocotes Simon 1884
Nematogmus Simon 1884
Lessertiella Dum. & Miller 1962
Trichopterna Kulcz. 1894
Trichoncus Simon 1884
Metopobactrus Simon 1884
"Abacoproeces" ascitus Kulcz.
Lasiargus Kulcz. 1894
Silometopus Simon 1926
Cineta Simon 1884
Hypomma Dahl 1886
Gonatium Menge 1866
Kratochviliella Miller 1938
Dismodicus Simon 1884
Abacoproeces Simon 1884
Ceratinella Emerton 1882
Ceratinopsis Emerton 1882
Grammonota Emerton 1882
Micrargus Dahl 1886
Caledonia Cambr. 1894
Cochlembolus Crosby 1929
Scotinotylus Simon 1884
Lessertia F. P. Smith 1908
Scotoneta Simon 1910

The species in *Baryphyma, Minyrioloides, Praestigia* and *Acanthophyma* (Figs. 57-60) have virtually identical conformations, with similar radical parts to the ED, and similar chaetotaxy (tib. spines 2211, TmI 0.8-0.95, TmIV present). On the basis of these characters, there seems to be every justification to unite these into one genus (*Baryphyma* has priority) **(syn.n.)**. In addition, they all have rows of stout bristles beneath the anterior femora and tibiae, as in *"T." thorelli,* which has TmI 0.9, TmIV present, and male head of similar type to *Minyrioloides.* Bearing in mind the evolutionary sequence: *Tapinocyba praecox* → *T. pallens* → *T. silvestris,* it is postulated that *Baryphyma* (s.lat.) has arisen in a similar sequence from the *thorelli* line (*thorelli* itself not necessarily a direct ancestor).

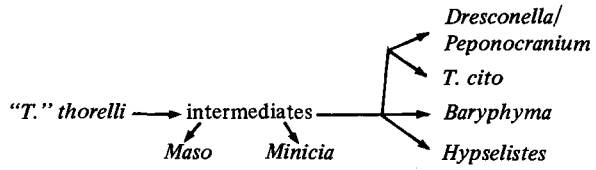
As an intermediate species (approximately equivalent in the evolutionary process to *T. pallens* in the *Tapinocyba* sequence), or more likely as derived from such an intermediate (which may no longer exist), one can postulate the species *Dresconella nivicola* (Sim.) (Fig. 61) (spines 1111, TmI *ca.* 0.8, TmIV present). A species with a conformation of this type can in turn have given rise to *Peponocranium* (Fig. 62) (spines 1111, TmI *ca.* 0.9, TmIV present). *Dresconella* is in some respects so similar to *Peponocranium,* e.g. in the form of the male head, that it



Figs. 60-67: Male palps. **60** *Minyrioloides trifrons* (Cambr.); **61** *Dresconella nivicola* (Simon); **62** *Peponocranium ludicrum* (Cambr.); **63** *Maso sundevalli* (Westr.); **64** *M. gallica* Simon; **65** *Minicia marginella* (Wid.); **66** *Pelecopsis elongata* (Wid.); **67** *P. nemoralis* (Bl.).

may be justified to include *nivicola* in *Peponocranium* as a more primitive member of the genus. Also derived from the intermediate species one can postulate the *Maso* species (spines 1111, TmI 0.9, TmIV present) which have ED's intermediate in form (Figs. 63, 64) between the simple *thorelli* and the coiled embolus of *Baryphyma,* and which have developed exaggerated versions of the bristles on the undersides of the anterior legs. *Minicia* (Fig. 65) has essentially the same type of conformation as *Maso,* but the ED is more complex and the cymbium has a most unusual (for an erigonine) posterior extension; *Minicia* may represent another side branch which originated close to *Maso. Hypselistes* (Fig. 76) and *Trichopterna cito* (Fig. 86) may also have arisen from this phylogenetic line (see later).

The evolutionary sequence postulated is shown schematically as follows, where the species/genus names represent a type of conformation:



If this type of evolutionary sequence (which on the data available seems clear enough in *Tapinocyba*) is accepted, then *thorelli* shows more or less the same relationship to *Baryphyma* as *T. praecox* does to *T. silvestris. "T." thorelli* must be part of the overall monophyletic group shown in the scheme, but cannot be regarded as part of the monophyletic genus *Baryphyma* unless this were taken to include *all* the species/genera shown. A similar problem arises with the genus *Tapinocyba* if there are side branches in this sequence also (e.g. *Panamomops* and *Trichoncus* as possibilities), i.e. *T. praecox* could not then be congeneric with *T. silvestris.*

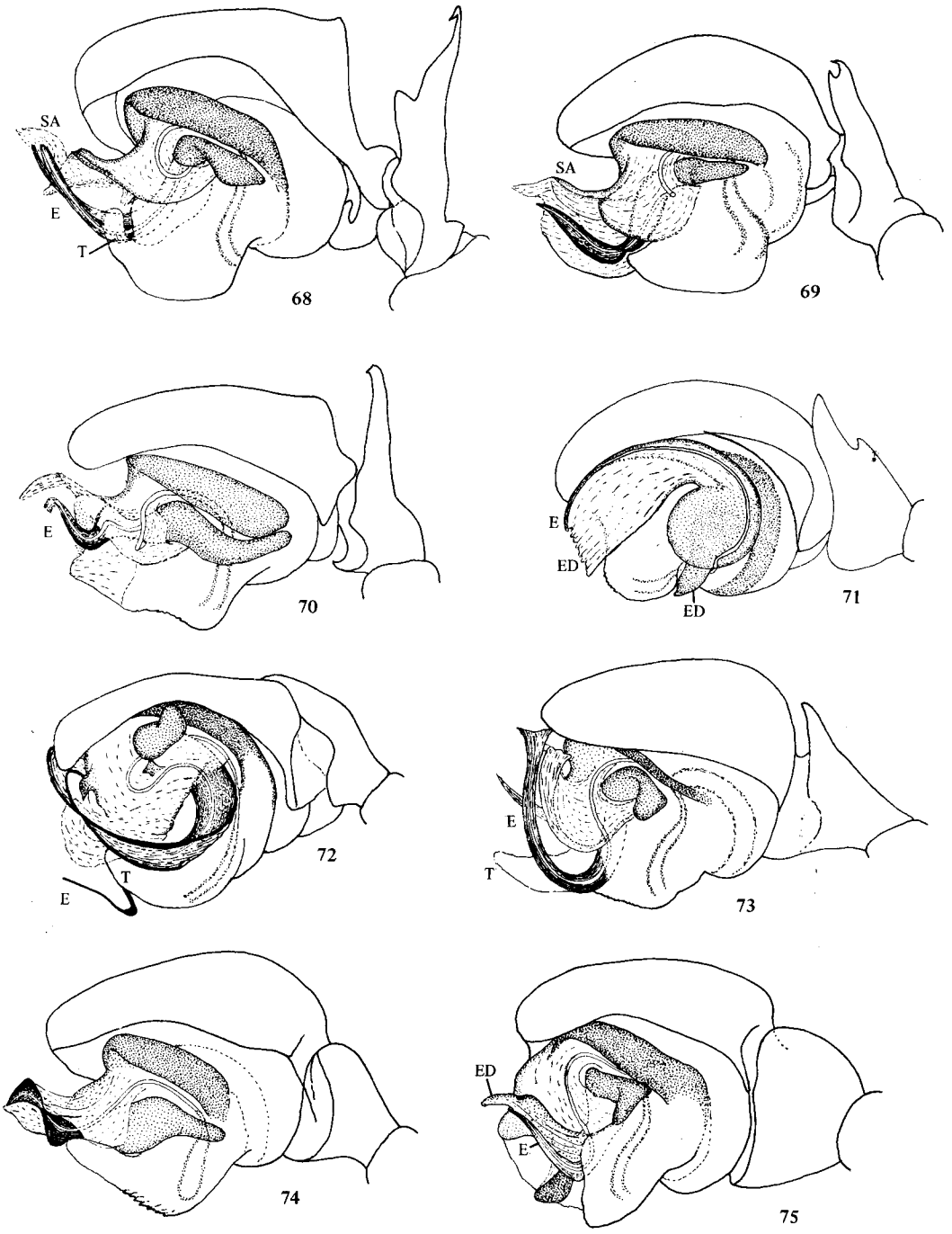
In the genus *Pelecopsis,* the sperm duct loops back to enter the ED (Fig. 66). Whereas in *elongata* (Wid.) (the type species) the embolus is a long coil of typical form, in the *nemoralis* group of species (Fig. 67) the embolus has become short and sometimes screw-like, though the duct entry is still of the same type; in addition, the tegulum is differently shaped, perhaps because it no longer has to accommodate the long embolus. The *Pelecopsis* species (excluding *medusa*: see p. 23) are so similar in all other respects that the wide differences in the shape of the ED are not sufficient to justify splitting the genus, since the basic conformation remains the same. It seems possible that the direction of morphological change of the ED has been from the more complex (in *elongata*) to the simpler (in *nemoralis*) since there has been a concommitant reduction in the trichobothria on the male palpal tibia from two to one (one being probably more apomorphous than two). The species with the "reduced" ED should be placed in a separate species group.

Exechophysis (only *bucephalus* (Cambr.) (Fig. 68) has been examined) is so close to *Pelecopsis* in conformation, in chaetotaxy (tib. spines 1111, TmI 0.6, no TmIV) and the possession of abdominal scuta (in both sexes) that it should be regarded as a somewhat exotic *Pelecopsis* and placed in this genus in a separate species group (syn.n.). *P. radicicola* (L.K.) (Fig. 69) should probably be regarded as a "reduced" form of the *Exechophysis* group (corresponding to *nemoralis*); it has the abdominal scutum in the female, and in the male the tegulum and suprategulum are much the same shape as in *bucephalus* and differ from the *nemoralis* type. The SA is also closer to *bucephalus* than to *elongata.*

The species *P.(Trichopterna) mengei* (Sim.) (Fig. 70) offers some problems; although it seems to agree quite closely in conformation and other characters with *Pelecopsis,* its chaetotaxy is significantly different (TmI 0.85, TmIV present) and its suprategulum differs in shape from those of the "reduced" *Pelecopsis* species. It may show closer similarities to some of Holm's African *"Trichopterna"* species (which almost certainly are not congeneric with *T. cito*) (Holm, 1962) than to *Pelecopsis,* and might represent the "reduced" form of these species. It may also be fairly close to *Hypselistes*: it has a pronounced row of bristles on the ventral side of the anterior tibiae, the SA is quite close to that of *Hypselistes* and the anterior tegular apophysis is more pronounced than in *Pelecopsis* species.

The species *"P." bacelarae* (Cap.) and related species (Fig. 71) from central Africa (e.g. Locket, 1974) have a conformation completely different from that of *Pelecopsis,* and cannot belong in this genus. The conformation is unlike that of any European species.

The phylogenetic line leading to *Pelecopsis* is ob-



Figs. 68-75: Male palps. **68** *Exechophysis bucephalus* (Cambr.); **69** *Pelecopsis radicicola* (L. Koch); **70** *P. (Trichopterna) mengei* (Simon); **71** *"Pelecopsis"* sp. (Africa); **72** *Minyriolus pusillus* (Wid.); **73** *"P." medusa* (Simon); **74** *"Trichopterna" cucurbitina* (Simon); **75** *"T." rufithorax* (Simon).

scure. The possibility is mentioned below that *Minyriolus* could possibly represent one of its forebears; it is also a possibility that *Pelecopsis* has entered Europe from Africa, and that it may be that Holm's *"Trichopterna"* species and *Pelecopsis* are closely related branches. If so, representatives of the ancestors of these two groups should eventually be found there. It is also not impossible that species with the *Dresconella* type of conformation may represent ancestors of the *Pelecopsis* line.

The genus *Minyriolus* (Fig. 72) has a similar conformation to *Baryphyma,* but differs in chaetotaxy (tib. spines 1111, TmI 0.5, no TmIV). The species *"Pelecopsis" medusa* (Sim.) (Fig. 73) has a closely similar conformation and chaetotaxy (1111, TmI 0.45, no TmIV), and should almost certainly be moved into *Minyriolus* **(comb.n.)**; the presence of the poorly developed scutum in the male need not preclude this move. It is possible that *Minyriolus* represents an intermediate on the way to *Pelecopsis,* as *Baryphyma* was postulated above to be an intermediate (or a branch from an intermediate) on the line to *Hypselistes,* but there are no data to connect other genera with this possible line.

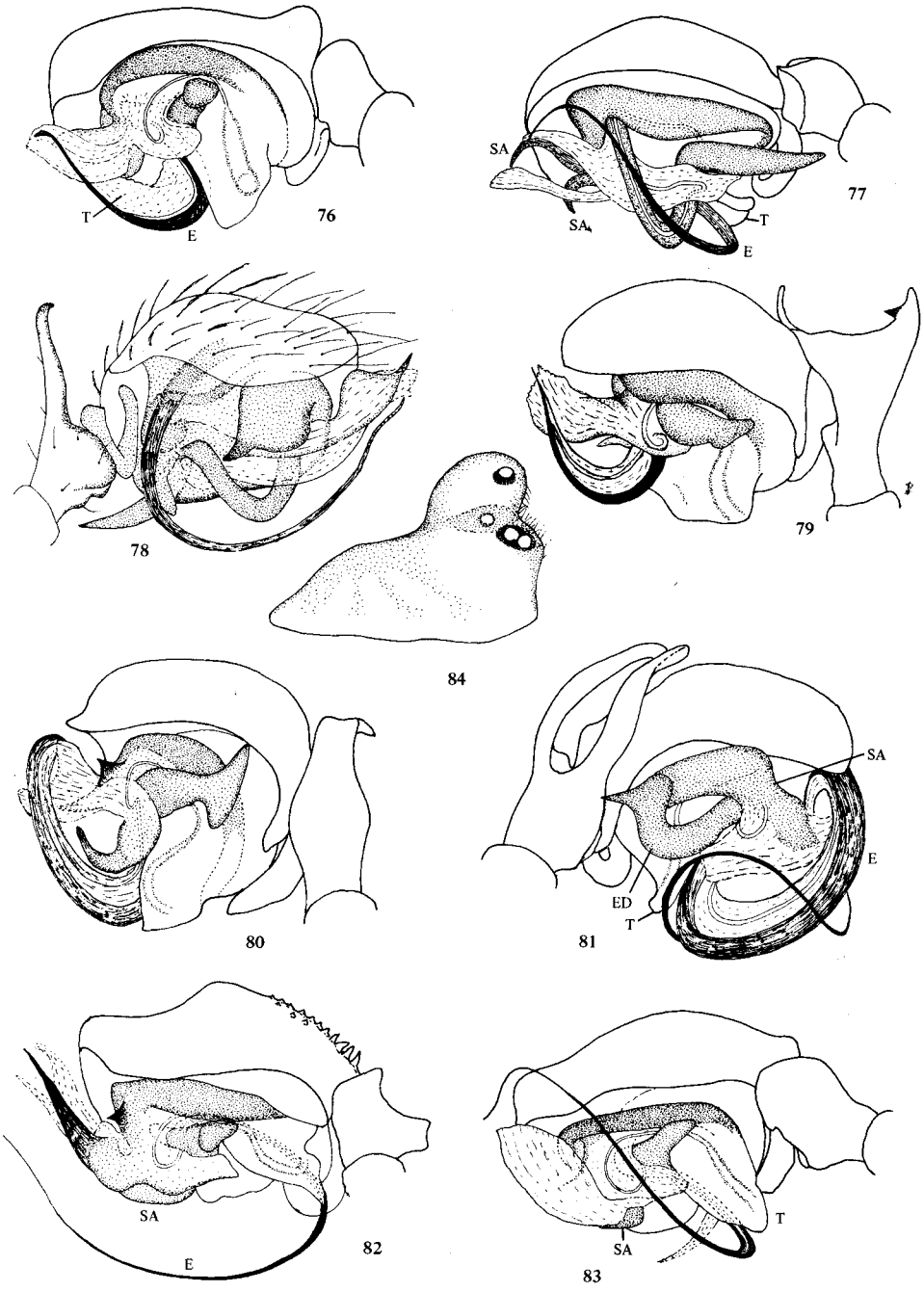
The species *"Trichopterna" cucurbitina* (Sim.) (Fig. 74) seems to occupy the same relationship to *Minyriolus* as *P. nemoralis* does to *P. elongata*; it has the same chaetotaxy as *Minyriolus pusillus* (Wid.), has a pronounced cephalic lobe and no scutum in the male. *"Trichopterna" rufithorax* (Sim.) (Fig. 75) (with the same chaetotaxy) appears to be an intermediate type (like *Tapinocyba pallens*), but whether this is also related to *Minyriolus* is unclear; despite some similarities it seems unlikely, since in particular the SA is very different.

Hypselistes (Fig. 76) shows a close resemblance to *Pelecopsis* in conformation, but has a strong tegular apophysis not present in that genus. The chaetotaxy (tib. spines 1111, TmI 0.9, TmIV present; rows of stout bristles on the undersides of the anterior legs) indicates that this genus may also have been derived from the *Baryphyma* line (as mentioned above), representing an evolutionary development one stage more advanced than the *Baryphyma* type of conformation, i.e. the duct entry has moved further back and become looped.

The species in the genus *Mecopisthes* have a conformation (Fig. 77) which, though at first sight rather complex, in fact agrees perfectly with the *Pelecopsis* type. As compared with *P. elongata* (Fig. 66), the embolus has lengthened, as has the tail (though this is much shorter in some species than in Fig. 77), and the SA has become rather more complex. The tegulum has been compressed backwards even more than in *P. elongata.* The species *"Minyriolus" nicaensis* Sim. must be moved into *Mecopisthes* **(comb.n.)**; it has a typical *Mecopisthes* palp (Fig. 78) and TmI 0.6, but the male head (Fig. 84) is much more like a *Pelecopsis. Mecopisthes* seems to be very close to *Pelecopsis*: in addition to the similarity in conformation the following congruences are present: (a) the two genera have practically identical chaetotaxies, with very short and weak tibial spines; (b) all *Pelecopsis* males have abdominal scuta, several *Mecopisthes* males also; (c) the *P. nemoralis* group share with *Mecopisthes* a rather unusual form of suprategulum (Figs. 67, 77); (d) the projecting clypeus of *P. bucephala* and *P. parallela* is very like that of most *Mecopisthes* species. It therefore seems probable that *Mecopisthes* is a sister group of *Pelecopsis.*

The monotypic genera *Panamomopsides, Microstrandina* and *Lochkovia* should be combined into *Panamomops,* as already proposed by Wunderlich (1970). It seems probable that *P. mutilis* Denis, *M. fedotovi* Charit. and *L. inconspicua* Miller and Val. are in fact conspecific. The *Panamomops* species fall into 2 groups, (i) those with a simple duct membrane, extended forwards and fused to the SA as in *Pelecopsis,* and with a simple tail (Fig. 79), and (ii) those where the duct membrane bears additionally a sclerotised tooth-like apophysis, and the tail is T-shaped posteriorly (Fig. 80). The provenance of this genus is not known. The trichobothria correspond with *Tapinocyba*; the holes in the male head, from which emerge the "horns" as an exudation, could correspond with the holes in *Tapinocyba.* The question must be left open for the present. The high proportion of the species which are found in central and eastern Europe may indicate an Asian origin for this genus.

The species *"Micrargus" kaestneri* Wiehle (Fig. 81), which has been found only in Eastern Europe, is not a *Micrargus* (see later); it has tib. spines 2211, TmI 0.35, TmIV absent, and seems to show a rather similar relationship to *Panamomops* as *Mecopisthes* does to *Pelecopsis.* I propose the new



Figs. 76-83: Male palps. **76** *Hypselistes jacksoni* (Cambr.); **77** *Mecopisthes peusi* Wund.; **78** *"Minyriolus" nicaensis* Simon (lateral); **79** *Panamomops tauricornis* (Simon); **80** *P. latifrons* Miller; **81** *"Micrargus" kaestneri* Wiehle; **82** *Cnephalocotes obscurus* (Bl.); **83** *Nematogmus sanguinolentus* (Walck.).

Fig. 84: *M. nicaensis*, ♂ cephalothorax (side).

genus *Metapanamomops,* **gen.n.** for this species. *Plaesianillus cyclops* (Sim.) seems to have a conformation very close to *Panamomops,* and should possibly be placed in that genus.

The genera *Cnephalocotes* (Fig. 82) and *Nematogmus* (Fig. 83) clearly have the *Pelecopsis* type of conformation. In *Cnephalocotes* the stalk carries a sclerotised pointed process anteriorly, whereas in *Nematogmus* the corresponding process is not sclerotised. *Nematogmus* has a narrow membranous apophysis arising from the lateral side of the tegulum, not present in *Cnephalocotes.* Nevertheless the 2 species are generally so similar in chaetotaxy (spines 1111, TmI 0.35-0.40, no TmIV), and in the form of the palpal cymbium, that it is probably justified to regard *Nematogmus* as a synonym of *Cnephalocotes,* as proposed by Wunderlich (1970). *Cnephalocotes* has a tegular form reminiscent of *Silometopus* and *Mecopisthes. Lessertiella* (Fig. 85) (tib. spines 2211, TmI 0.4, no TmIV) seems to have essentially the same type of conformation as *Cnephalocotes* but the palpal organs have become somewhat twisted and the ED is obscured by the large membranous development of the SA. The phylogenetic line leading to *Cnephalocotes* (and *Lessertiella*) is unknown.

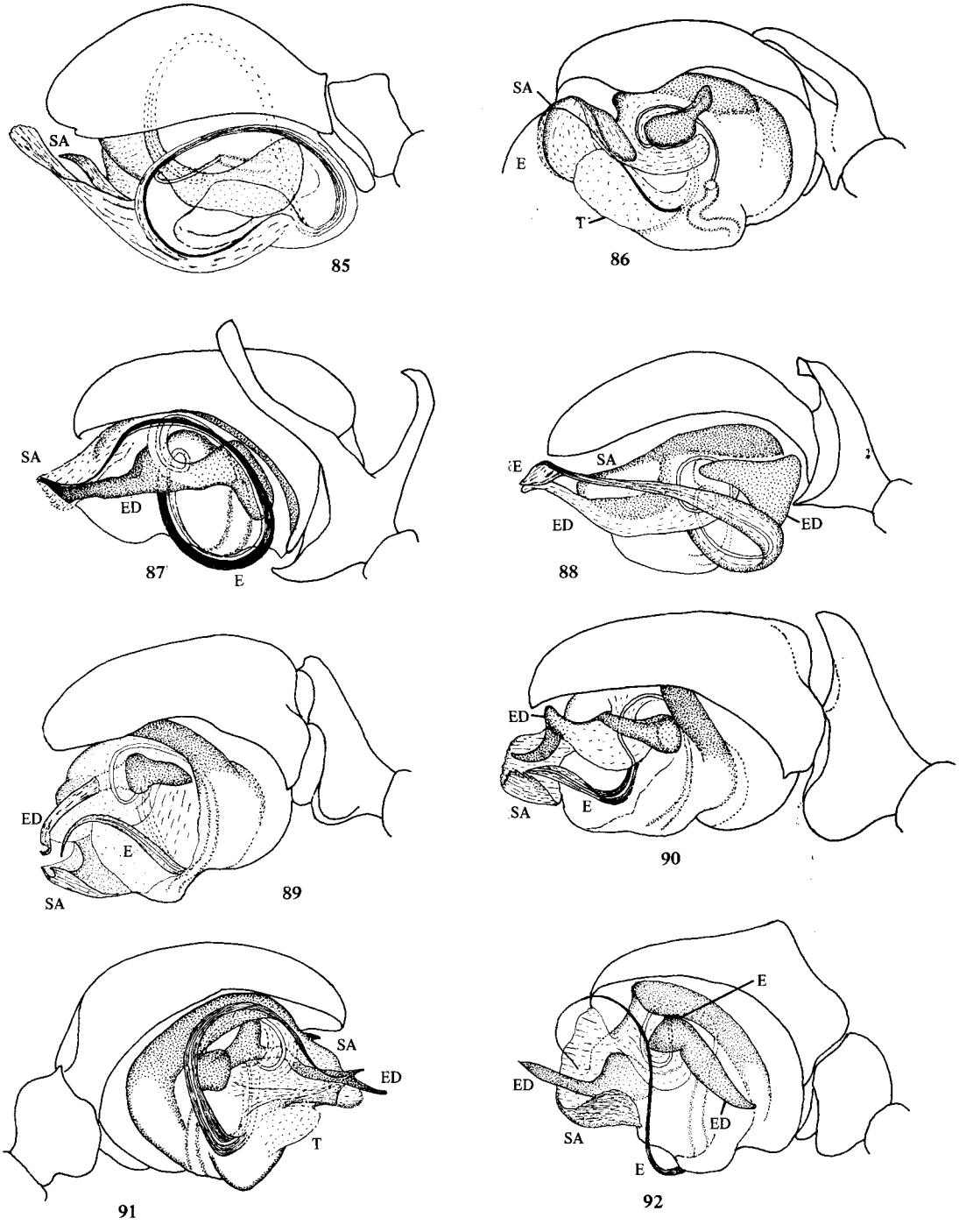
Trichopterna cito (Cambr.) (the type species and the only European species now remaining in *Trichopterna*) is not a *Pelecopsis* as suggested by Wunderlich (1970) **(gen.rev.)**. The conformation (Fig. 86) seems to be close to *Peponocranium* (Fig. 62); the embolus is very thin, and the SA is of the same type as in *Peponocranium.* In addition, the chaetotaxy (TmI *ca.* 0.8, TmIV present) shows a greater similarity to *Peponocranium* than to *Pelecopsis,* while the female does not have the carapace pits usually present in *Pelecopsis.* On this evidence, *Trichopterna* can be regarded as a possible sister group to *Peponocranium/Dresconella.*

The genus *Trichoncus* (Fig. 87) has the same basic conformation as *Pelecopsis,* but the ED bears a forward-directed apophysis and the stalk lacks the forward extension usually present in this group; all the species of the genus have closely similar palpal organs. The species *"Tapinocyboides" simoni* (Less.) (Thaler, 1973) has a virtually identical conformation (Fig. 88) and hence despite the presence of pectinate tarsal claws, not present in the other *Trichoncus* species, *simoni* should be regarded as a diminutive *Trichoncus* **(comb.n.)**; it has the same chaetotaxy as *Trichoncus.* The evolutionary line which has led to *Trichoncus* is uncertain. The presence (in the one species *simoni* only) of pectinate tarsal claws, and the chaetotaxy (tib. spines 1111, TmI 0.4, no TmIV) could indicate that it is a branch of the *Tapinocyba* line, derived from a *T. pallens* type ancestor; in addition it shares one unusual conformational character with *Tapinocyba,* viz. the sudden constriction of the seminal duct in the tegulum (Figs. 43, 87). At the present time, however, there is insufficient evidence to decide this question.

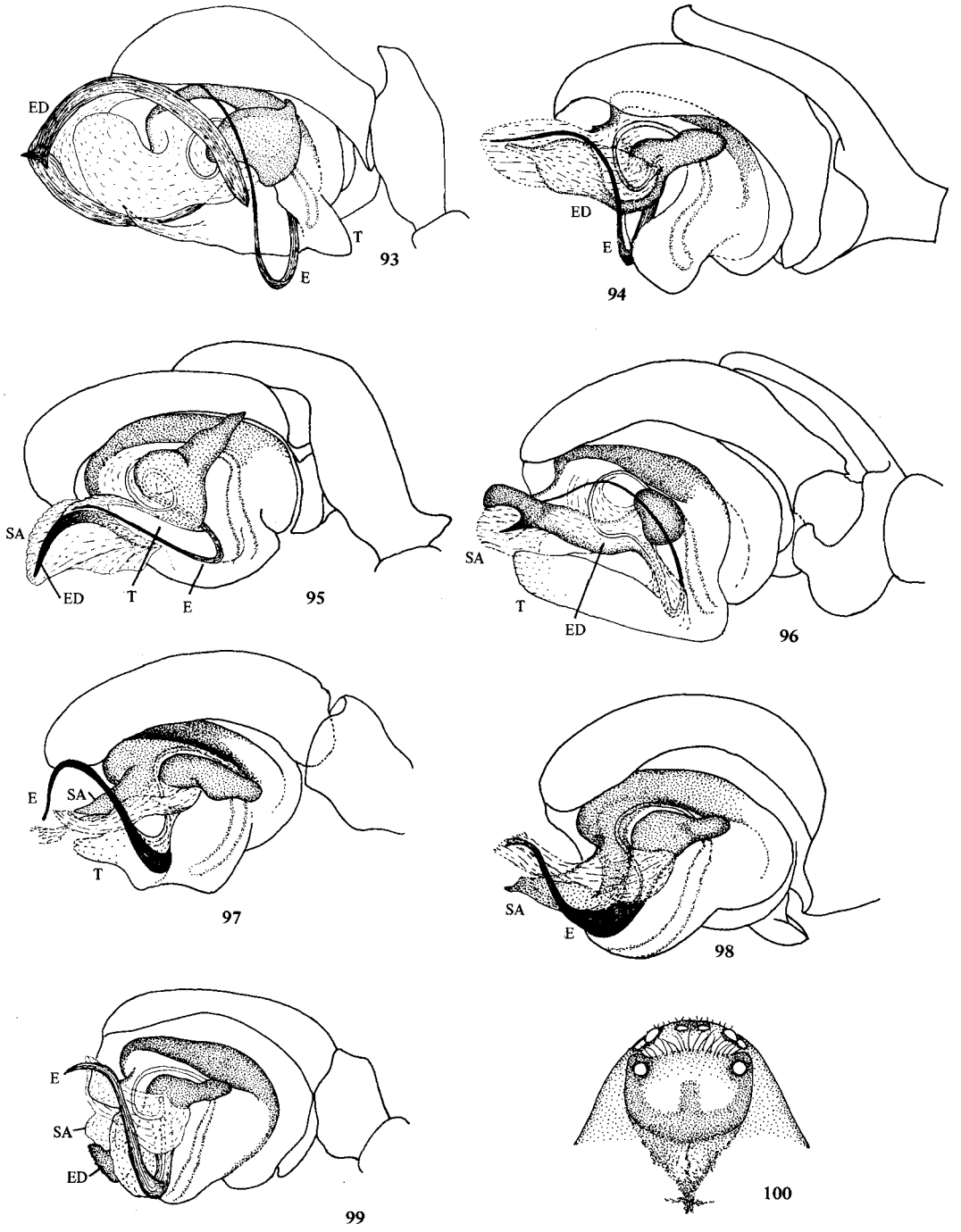
Metopobactrus (Fig. 89) has an ED rather similar to *Trichoncus,* but the SA is more highly developed. The species *"Abacoproeces" ascitus* Kulcz. (Fig. 90) seems to represent an intermediate on the way to a typical *Metopobactrus,* having a similar SA and an intermediate type of ED rather similar to those of the *Maso* species; it has the same chaetotaxy as *Metopobactrus* (tib. spines 1111, TmI 0.75, TmIV present) and a rather similar male head and female epigyne. It should perhaps be moved into *Metopobactrus. M. rayi* Sim. is somewhat abnormal, but probably belongs in *Metopobactrus.*

Lasiargus (Fig. 91) is close to *Metopobactrus* in conformation and in chaetotaxy (tib. spines 1111, TmI 0.8, TmIV present); the SA is however less highly developed. *L. hirsutus* (Menge) bears long curved bristles on the abdomen, superficially similar to those in some *Trichoncus* species and in *Baryphyma gowerense* (Locket); the significance, if any, of this character, is not known. *Lasiargus* must be regarded as phylogenetically close to *Metopobactrus* and *Trichoncus,* but the progenitors of these genera are not known. In view of their chaetotaxy it is possible that they represent yet another side-branch of the *Baryphyma* line.

The genus *Silometopus* has a rather similar conformation to *Metopobactrus;* the differences lie in (i) the greater development of the embolus, (ii) the rather greater development of the forward process of the ED, (iii) the increased length of the ED radical part, and (iv) the greater development of the SA, which is nevertheless of rather similar type (Fig. 92). The chaetotaxy of *Silometopus* is fairly close to that of *Metopobactrus* except that TmIV has been lost in all the species. *Silometopus* may have a somewhat similar relationship to *Metopobactrus/Lasiargus* as



Figs. 85-92: Male palps. **85** *Lessertiella saxetorum* (Hull) (ED is behind membrane); **86** *Trichopterna cito* (Cambr.); **87** *Trichoncus hackmani* Mill.; **88** *"Tapinocyboides" simoni* (Less.); **89** *Metopobactrus prominulus* (Cambr.); **90** *"Abacoproeces" ascitus* Kulcz.; **91** *Lasiargus hirsutus* (Menge), (left palp); **92** *Silometopus elegans* (Cambr.).



Figs. 93-99: Male palps. **93** *Cineta gradata* (Simon); **94** *Hypomma bituberculatum* (Wid.); **95** *Gonatium corallipes* (Cambr.); **96** *Kratochviliella bicapitata* Miller; **97** *Dismodicus elevatus* (C.L.K.); **98** *Abacoproeces saltuum* L. Koch; **99** *Metopobactrus rayi* (Simon).

Fig. 100: *A. saltuum*, ♂ head (above).

that postulated between *Mecopisthes* and *Pelecopsis*. *Cineta gradata* (Sim.) (Fig. 93) is somewhat similar in conformation to *Silometopus*; the forward process of the ED has reached a stage of extreme development, while the radical part is less elongated. The chaetotaxy (tib. spines 1111, TmI 0.6, no TmIV) is similar to *Silometopus*, and it seems likely that *Cineta* has originated from close to *Silometopus*.

The genus *Hypomma* has the basic *Pelecopsis* conformation; the ED has a forward-directed apophysis which is only lightly sclerotised (Fig. 94). *Gonatium* has a similar conformation (Fig. 95); all the species have the same type of palp, varying only in the degree of complexity of the forward apophysis on the ED (which is more highly sclerotised than in *Hypomma*) and of the SA. A tegular apophysis (extension) is usually present in *Gonatium* but absent in *Hypomma*. These two genera are so similar in conformation and in chaetotaxy that it seems likely that they are sister groups. *Gonatium* differs from *Hypomma* in having pectinate tarsal claws, but this is a character (probably primitive) which occurs sporadically throughout the erigonines.

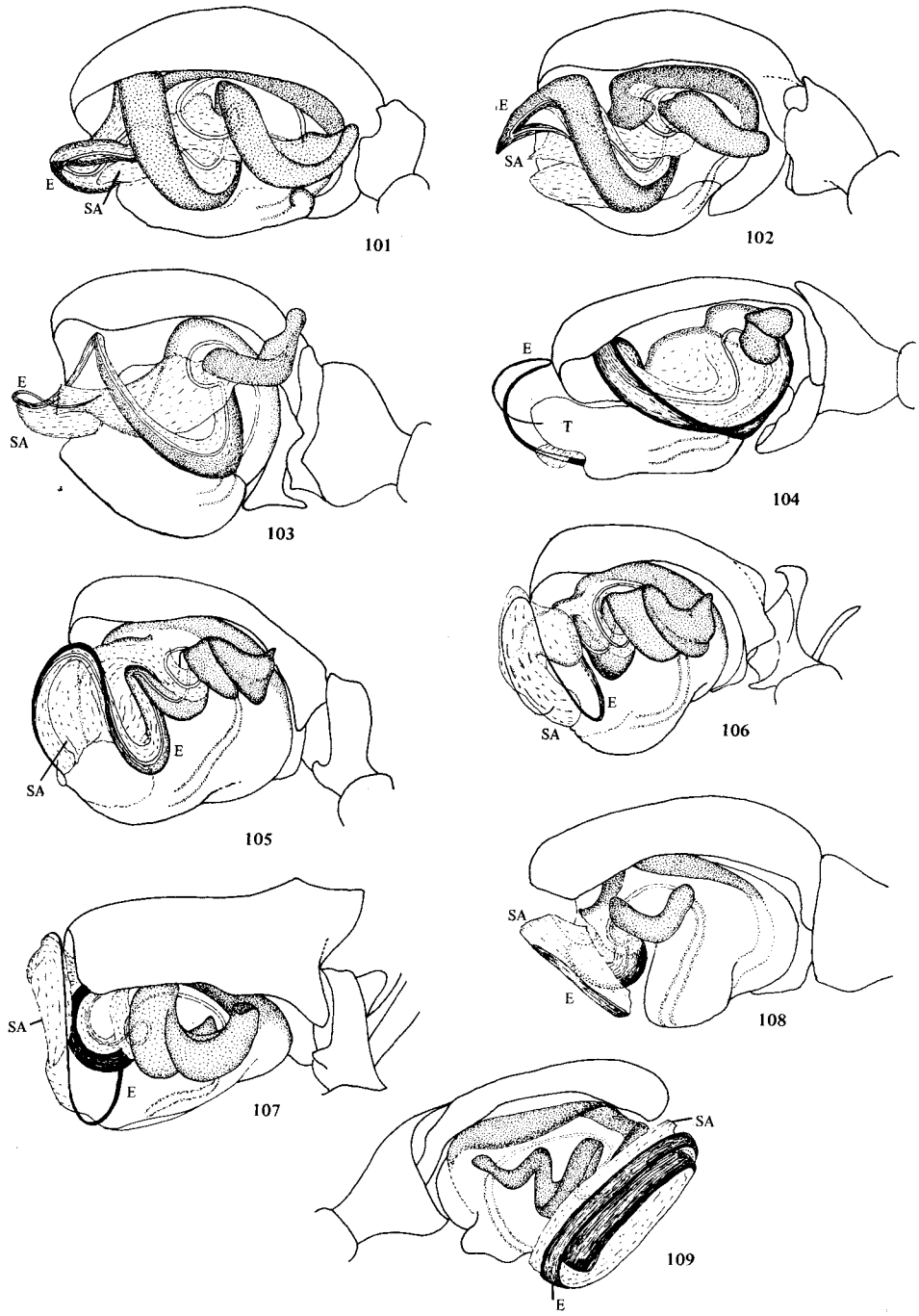
The species *Kratochviliella bicapitata* Miller (Fig. 96) seems to represent an intermediate stage (or perhaps a branch from an intermediate stage) on the way to *Hypomma*; the ED is of the intermediate type, the chaetotaxy is similar (almost identical with that of *H. cornutum*), the tibial apophysis is similar to that of *Hypomma* and the species has the reddish colour often present in *Hypomma*, but a marked tegular apophysis is also present. *Kratochviliella* should possibly be regarded as a synonym of *Hypomma*; it is certainly not a *Pelecopsis* as claimed by some recent authors.

The *Dismodicus* species have a rather similar conformation to *Hypomma*, but simpler, with the duct entry to the embolus direct (without a loop); the anterior process of the ED is completely membranous and non-sclerotised (Fig. 97). The similarity to *Hypomma* in chaetotaxy (tib. spines 1111, TmI 0.75-0.8, TmIV present), in the male head and in the conformation indicates a fairly close relationship: because the conformation is of the (assumed) more primitive type (i.e. embolus entry not looped), it is postulated that this branch arose probably slightly prior to the branch leading to *Kratochviliella*.

Abacoproeces saltuum L.K. (the type species) is very close to *Dismodicus* in conformation (Fig. 98); the chaetotaxy (tib. spines 1111 (Wiehle, 1960, seems to be wrong in giving 2211), TmI 0.85, TmIV present) is also similar, and the male head (Fig. 100) is of rather similar type. It seems possible that *Abacoproeces* represents a sister group of *Dismodicus*.

The phylogenetic derivation of the group *Hypomma, Gonatium, Kratochviliella, Dismodicus* and *Abacoproeces* is obscure, but from the chaetotaxy and the form of the male heads in many species it is possible that this group also is a side branch (or side branches) of the *Baryphyma* line.

The European species placed in the genus *Ceratinella* (Fig. 101) and *Ceratinopsis* (Fig. 102) have the same basic conformation as *Pelecopsis* (Fig. 66); the embolus is a stout broad ribbon with the anterior end turned backwards into the final coil, and probably resting on the membranous part of the rather simple SA. These two genera have almost identical conformations, as suggested by Merrett (1963). All the species have a similar chaetotaxy, except that *Ceratinella* has a TmIV, absent in *Ceratinopsis*. The *Ceratinella* species differ by the presence of abdominal scuta, usually in both sexes (absent in *C. brevipes* (Westr.) ♀); in *Ceratinopsis* the abdomens are merely rather coriaceous. At least some of the N.American species of the genus *Ceraticelus* Sim. (Crosby and Bishop, 1925) appear to fall into *Ceratinella*: the distinguishing feature given (lack of double curvature of cheliceral fang) may be of little significance (e.g. *C. scabrosa* (Cambr.) in Europe has the fang with a single curve), and the figures of the palps of many of the species indicate a virtual identity of conformation with that of *Ceratinella*. The large number of species of *Ceraticelus, Ceratinella* and *Ceratinopsis* in N.America, and the relative paucity of species in Europe, may indicate that this group originated in N.America. The European species of *Ceratinella* and *Ceratinopsis* are obviously very closely related (? sister groups), but no valid conclusions on the relationship can be reached without a complete study of the N.American species. The conformation appears to be a relatively simple elaboration of the *Pelecopsis* type, but it is probably unsafe to make any deductions on the phylogeny of this group of species without a prior study of the N.American fauna, since any ancestral forms or intermediates are likely to be found there rather than in Europe.



Figs. 101-109: Male palps. **101** *Ceratinella scabrosa* (Cambr.); **102** *Ceratinopsis stativa* (Simon); **103** *Micrargus laudatus* (Cambr.); **104** *M. apertus* (Cambr.); **105** *Caledonia evansi* Cambr.; **106** *Scotinotylus antennatus* (Cambr.); **107** *Cochlembolus clavatus* (Schenk.); **108** *Lessertia dentichelis* (Simon); **109** *Scotoneta barbara* Simon (left palp).

The two European species *Micrargus subaequalis* (Westr.) and *laudatus* (Cambr.) (Fig. 103) have conformations of the same type as *Ceratinella/Ceratinopsis,* and their chaetotaxy differs only in the tibial spines (2211 cf. 1111 in *Ceratinella*). These two species appear to belong in the genus *Grammonota* **(comb.n.)**: compare e.g. figs. 4 and 9 of Crosby and Bishop (1932) with Fig. 103 of *laudatus.* Once again, from the relatively large number of species and variety of forms of the N.American species of *Grammonota,* it seems probable that this genus may also be of N.American origin. In view of the close similarity of the conformations, *Grammonota* could be the sister group of *Ceratinella/Ceratinopsis/Ceraticelus,* but obviously a study of the numerous N.American species would be necessary before such a hypothesis could be supported.

The species *Micrargus apertus* (Cambr.) (Fig. 104) and its siblings (Millidge, 1975(2)) differ somewhat in conformation from *subaequalis/laudatus,* e.g. the duct does not loop back when entering the embolus; for the present, therefore, it is best not to transfer these species into *Grammonota,* but to retain for them the genus *Micrargus. "Baryphyma" longitarsum* (Em.) (Crosby and Bishop, 1933) seems to be close to *herbigradus.*

The genera *Caledonia* (Fig. 105), *Scotinotylus* (Fig. 106) and *Cochlembolus* (Fig. 107) have virtually identical conformations of the *Pelecopsis* type. The ED has a long spiral embolus and a short and rather screw-like radical part, while the SA is in the form of a flattish membranous piece anteriorly which possibly acts as a protector for the embolus. All the species have a similar chaetotaxy (tib. spines 2221, TmI 0.4-0.5, no TmIV). In view of the conformation and the chaetotaxy, this group of species should be regarded as monophyletic, and placed in the genus *Scotinotylus* **(syn.n.)**.

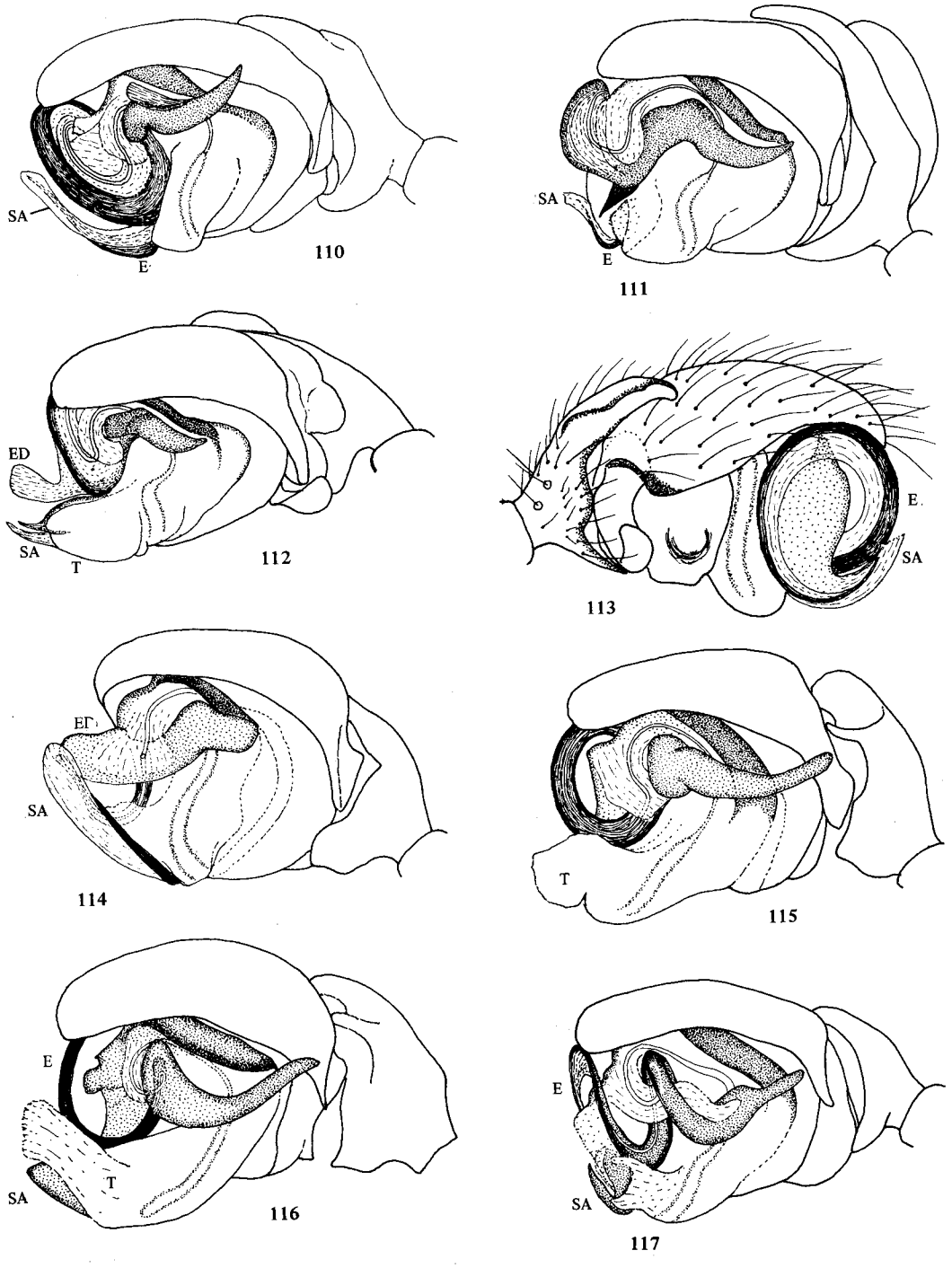
The genera *Lessertia* (*dentichelis* (Sim.)) and *Scotoneta* (*barbara* Sim.) have similar conformations (Figs. 108, 109), which seem to be fairly close to that of *Scotinotylus.* Both have a long spiral embolus, and the radical part of the ED is similar in both species; the SA is in the form of a long membranous piece which circles round the front of the palp, following and perhaps protecting the final turn of the embolus. The embolus and the SA are more highly developed in *Scotoneta.* Both species have the same chaetotaxy (tib. spines 2221, TmI *ca.* 0.4, no TmIV), and both species tend to be troglodytic, *dentichelis* occurring over a wide area of W.Europe while *barbara* has been found only in S.Spain and N.Africa. It is proposed that *Scotoneta* should be regarded as a junior synonym of *Lessertia* **(syn.n.)**. *Coreorgonal* Bishop and Crosby 1935 seems to have similar palpal organs to *Lessertia,* but specimens have not been examined. *Scotinotylus* (s.lat.) and *Lessertia* (s.lat.) are the only genera with the *Pelecopsis* conformation type which have the tibial spines 2221. No conclusions can be drawn on the origins of this group.

10. *Walckenaera* Group (Figs. 110-121)

In this group, the ED has a well-defined tail, and the duct runs directly into the base of the embolic coil, entering on the mesal side (e.g. Fig. 110); the stalk does not have a forward-directed membranous apophysis as in the *Pelecopsis* group (Section C 9, p. 19). The coil of the embolus passes over the SA to the lateral side and then runs downwards and forwards with the SA which is a long membranous piece (Fig. 113). In *Walckenaera* the tip of the SA is gutter-shaped, and the distal end of the embolus lies in the "gutter". The following genera/species are included in this group:

Walckenaera (s.lat.) Bl. 1833
Evansia Cambr. 1900
Moebelia Dahl 1886
Araeoncoides Wunderlich 1969
"Saloca" strandi Syst.
Perimones Jackson 1932
Typhochrestus Simon 1884

The genus *Walckenaera* is one of the few erigonine genera which can be characterised readily by a combination of somatic characters (Locket and Millidge, 1953, p. 191). All the European species of the genus have the same basic conformation (Figs. 110-113). This constancy of conformation, despite considerable differences in the length of the embolus and the presence of an apophysis on the SA in some species (e.g. *unicornis* Cambr.), forms part of the supporting data for the postulate that conformation is constant within well-defined genera. *W. dysderoides* (Wid.) has the same basic conformation (Fig. 114) but is somewhat aberrant; it has a shorter embolus which does not pass over the SA, and the radix of the ED



Figs. 110-117: Male palps. **110** *Walckenaera acuminata* Bl.; **111** *W. unicornis* Cambr.; **112** *W. nudipalpis* (Westr.); **113** *W. vigilax* (Bl.), (lateral side); **114** *W. dysderoides* (Wid.); **115** *Evansia merens* Cambr.; **116** *Moebelia penicillata* (Westr.); **117** *"Saloca" strandi* Syst.

projects forwards with the embolus arising from the middle of the radix. The SA also shows small differences, having a sclerotised margin ending in a dark point, not present in the other species; the tarsal claws are highly pectinate as in the other species. It is probable that *Walckenaera* should be split into several species groups, but the fine structure of the conformation does not entirely support the divisions suggested by Wunderlich (1972(2)). The wide variations in the position of the metatarsal trichobothria among the species indicate a good deal of branching within the genus.

The species *Evansia merens* (Cambr.) (Fig. 115), *Moebelia penicillata* (Westr.) (Fig. 116), *"Saloca" strandi* Syst. (Fig. 117) and *Araeoncoides berolensis* Wund. (Fig. 118) have conformations similar to each other and to *Walckenaera.* The palp of the unique male of *Araeoncoides* is slightly expanded, but comparison with a slightly expanded palp of *M. penicillata* (Figs. 118 and 119) shows how similar the two genera are in conformation. The male palpal tibiae are also similar in form to one another and to some *Walckenaera* species. *Perimones* (Fig. 120) is also similar in conformation to *Moebelia,* and the small differences are no greater than those existing within the genus *Walckenaera.* There are considerable differences in chaetotaxy between the species: *merens* 1111, TmI 0.5, TmIV absent; *penicillata* 2211, TmI 0.6, TmIV present; *strandi* 2211, TmI 0.4, TmIV absent; *berolensis* 1111, TmI 0.8, TmIV present; *arenarius* (Emert.) (*britteni* (Jackson)) 1111, TmI 0.65, TmIV absent. Despite the variations in the chaetotaxy, the close relationship shown by the virtually identical conformations should possibly be recognised by uniting these species into one genus (cf. Merrett, 1963, p. 462): if this were done, *Moebelia* would have priority. In view of the variability in chaetotaxy, however, such a genus would have to be regarded as composed of several branches. *Moebelia* is not a synonym of *Entelecara* (Section C 13, p. 37) as suggested by Wunderlich (1970) (gen.rev.).

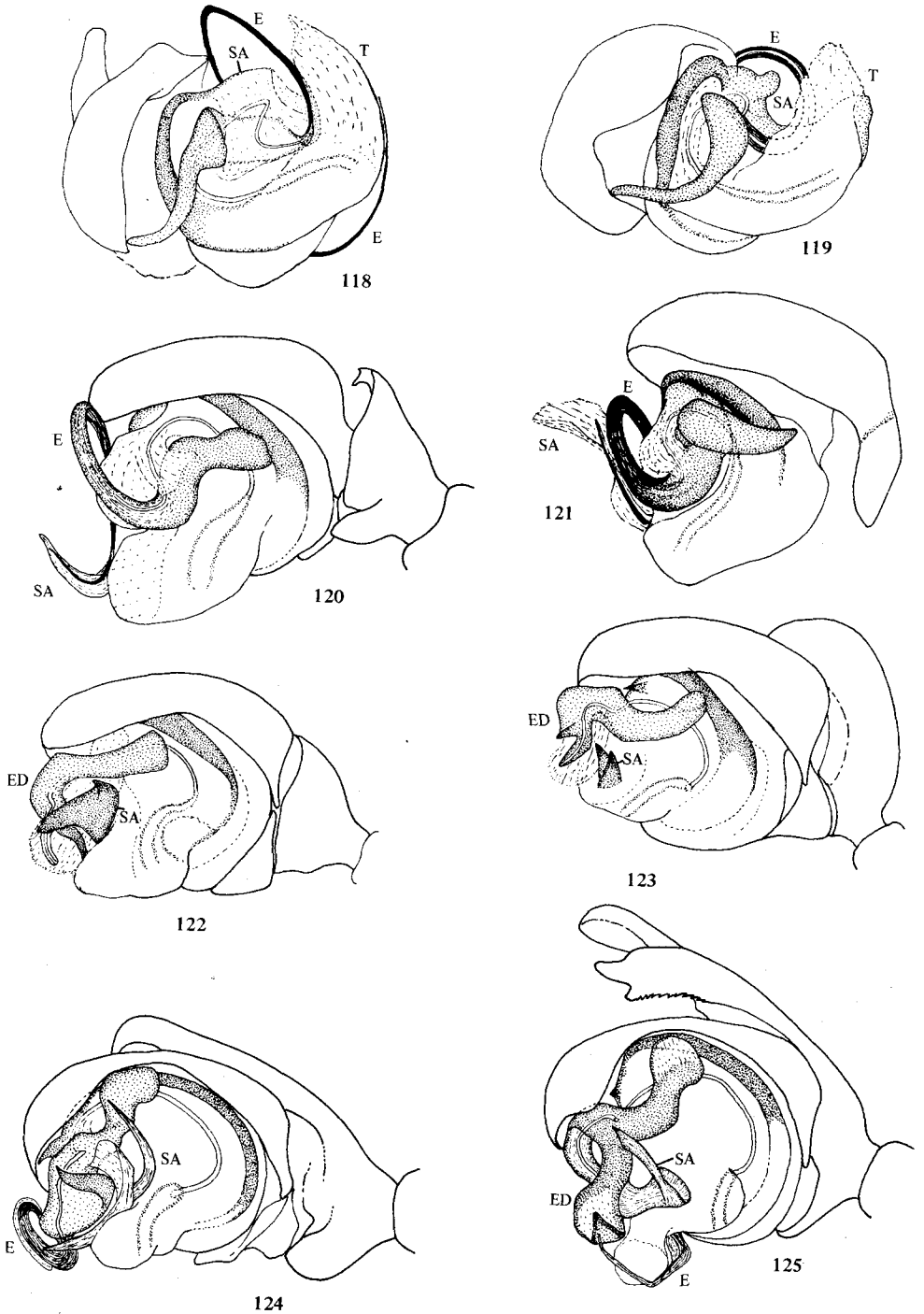
Typhochrestus also has a conformation of the *Walckenaera* type; the ED's are similar, particularly in *simoni* (Fig. 121) (which lacks the pointed, forward-directed apophysis on the ED present in *digitatus* (Cambr.) and *tenuis* Holm), but the SA's are different in form.

The genera in this group can probably be regarded, on the basis of their conformation, as forming a monophyletic group, with *Walckenaera* forming one branch and *Moebelia* (s.lat.) + ? *Typhochrestus* forming another. The evolutionary route to this conformation is obscure. *W. dysderoides* may possibly offer a clue: the ED of this species may represent an intermediate type of ED, and perhaps the group was derived from an intermediate of this type which subsequently lost the anterior part of the radix, while the length of the embolus increased. An alternative route to this type of conformation could be via the *Thyreosthenius* (Fig. 52) or *Trachelocamptus* (Fig. 54) types, with *dysderoides* remaining as an unexplained anomaly. All the *Walckenaera* species (except *dysderoides*) have the (probably) primitive character of 3 trichobothria on the male palpal tibia (as in e.g. *Hilaira, Ostearius, Leptorhoptrum*) and this should indicate that the group has arisen from one of the more primitive forms, but there are no data to indicate in which phylogenetic area the group arose. It is assumed in Fig. 200 that its ancestors were somewhere in the *Lophomma* conformation area, but that the *Walckenaera* group arose in a line probably quite separate from the *Tapinocyba* and *Pelecopsis* lines.

11. *Savignya* Group (Figs. 122-144)

In this group the stalk is located fairly well forward on the palp, with the duct entering the ED on the dorsal or lateral side. The ED varies a good deal in complexity, and normally has a tail; the embolus may be short or long. An important feature of the conformation is that the SA runs downwards along the front of the tegulum and then turns inwards and upwards to give an inner (mesal) arm, so that the SA forms a kind of "hook" above which lies the ED (e.g. Fig. 126); the complexity of the SA shows considerable variation, and in a few species the hook is but poorly developed. All the species except one in the group have tibial spines 2211, TmI is 0.4-0.55 (with only 2 species having TmI 0.35), and, with the exception of *Dicymbium,* TmIV is absent. The following current genera are included in this group; they are split into 3 groups on the basis of differences in the detail of the conformation:

(i) *Savignya* Genus Group
Savignya Bl. 1833
Diplocephalus Bertk. 1883



Figs. 118-125: Male palps. **118** *Araeoncoides berolensis* Wund., (left palp, slightly expanded); **119** *Moebelia penicillata* (left palp, slightly expanded); **120** *Perimones arenarius* (Emert.); **121** *Typhochrestus simoni* Less.; **122** *Diplocephalus picinus* (Bl.); **123** *Glyphesis servulus* (Simon); **124** *Dicymbium nigrum* (Bl.); **125** *Araeoncus anguineus* (L. Koch).

Erigonella Dahl 1901
Araeoncus Simon 1884
Dicymbium Menge 1867
Saloca Simon 1926
Glyphesis Simon 1926
Alioranus Simon 1926
Diastanillus Simon 1926
Delorrhipis Simon 1884

(ii) *Dactylopisthes* Genus Group
Dactylopisthes Sim. 1884

(iii) Miscellaneous
Aulacocyba Simon 1926
Janetschekia Schenkel 1939
Thaumatoncus Simon 1884

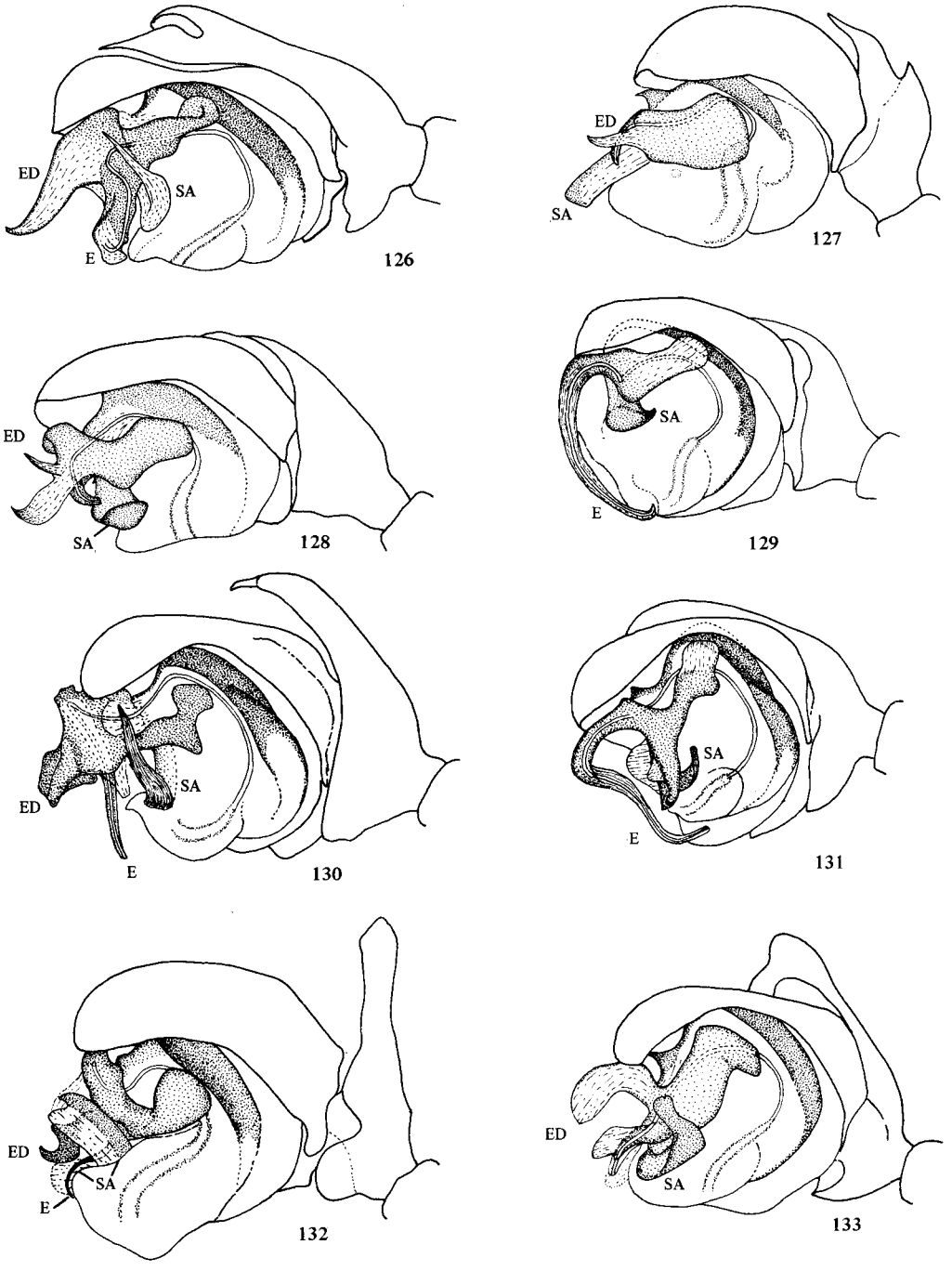
(i) All the species in this sub-group have a similar conformation, and most have epigynes of similar type. The separation of these species into genera has been based almost entirely on the form of the male head, and on the presence of TmIV but absence of cephalic lobe in *Dicymbium*. The ED's of these species range from relatively simple in *D. picinus* (Bl.) (Fig. 122) and *Glyphesis* (Fig. 123) to relatively complex in e.g. *Dicymbium* (Fig. 124), *Araeoncus* (Fig. 125) and *D. cristatus* (Bl.) (Fig. 126). The SA's range from a vestigial inner arm in *Araeoncus prospiciens* (Thor.) (Fig. 127) through a short inner arm in *Glyphesis* (Fig. 123), *D. picinus* (Fig. 122), *Alioranus* (Fig. 128) and *Diplocephalus dentatus* Tullg. (Fig. 129) to the more complex form present in many species (e.g. Fig. 124). The forms of the ED's in *D. protuberans* (Cambr.) and *helleri* (L.K.) (Figs. 130, 131) (both with *Diplocephalus* type male heads) are much closer to *Araeoncus* than to *D. cristatus* (palp identical with the type species, *D. foraminifer* (Cambr.)); *D. picinus* (also with a *Diplocephalus* type head) has both ED and SA closer to *Glyphesis* than to *D. cristatus*. Within the fairly wide range of complexity of the ED's and SA's of the species in this sub-group (all of which have the same basic conformation) it is difficult or impossible to perceive any natural breaks which correspond with current generic boundaries (apart from probably *Saloca* (Figs. 132)), and this casts doubts on the validity of these boundaries. If it could be agreed that it is an undesirable practice to create separate genera for every tiny group of sibling species, then it would be logical to recognise the close relationship of all these species, as shown by the conformation and the chaetotaxy, by combining all these genera into one (with the probable exception of *Saloca*). (Holm *(in litt.)* has already suggested to the author that *Savignya* is not really distinguishable from *Diplocephalus*). This procedure would have the disadvantage that the commonly used name *Diplocephalus* would be lost (*Savignya* has priority), but would have the advantage that the close relationship of the species would be evident in their binomial names. The large genus resulting could then be divided into species groups on the basis of the finer details of the conformation, e.g. as follows (only some species of the groups are included by way of illustration):

a) *cristatus* species group: embolus runs down an arm of the ED on mesal side of palp. Species in descending order of palpal complexity:
D. procerus Sim., *D. cristatus* (Fig. 126), *D. permixtus* (Cambr.) (Fig. 133), *Alioranus* (Fig. 128), *Glyphesis* (Fig. 123).
b) *humilis* species group: embolus usually long and curved, running initially to lateral side of palp. Species in descending order of complexity:
Araeoncus (Fig. 125), *D. latifrons* (Cambr.) (Fig. 134), *S. frontata* (Bl.) (Fig. 135), *D. protuberans* (Fig. 130), *D. helleri* (Fig. 131), *D. dentatus* (Fig. 129), *Araeoncus prospiciens* (?) (Fig. 127).
c) *nigrum* species group: embolus forms coil at anterior end of ED.
Dicymbium (Fig. 124), *Delorrhipis* (Fig. 136), *Erigonella* (Fig. 137), *Diastanillus* (Fig. 138).

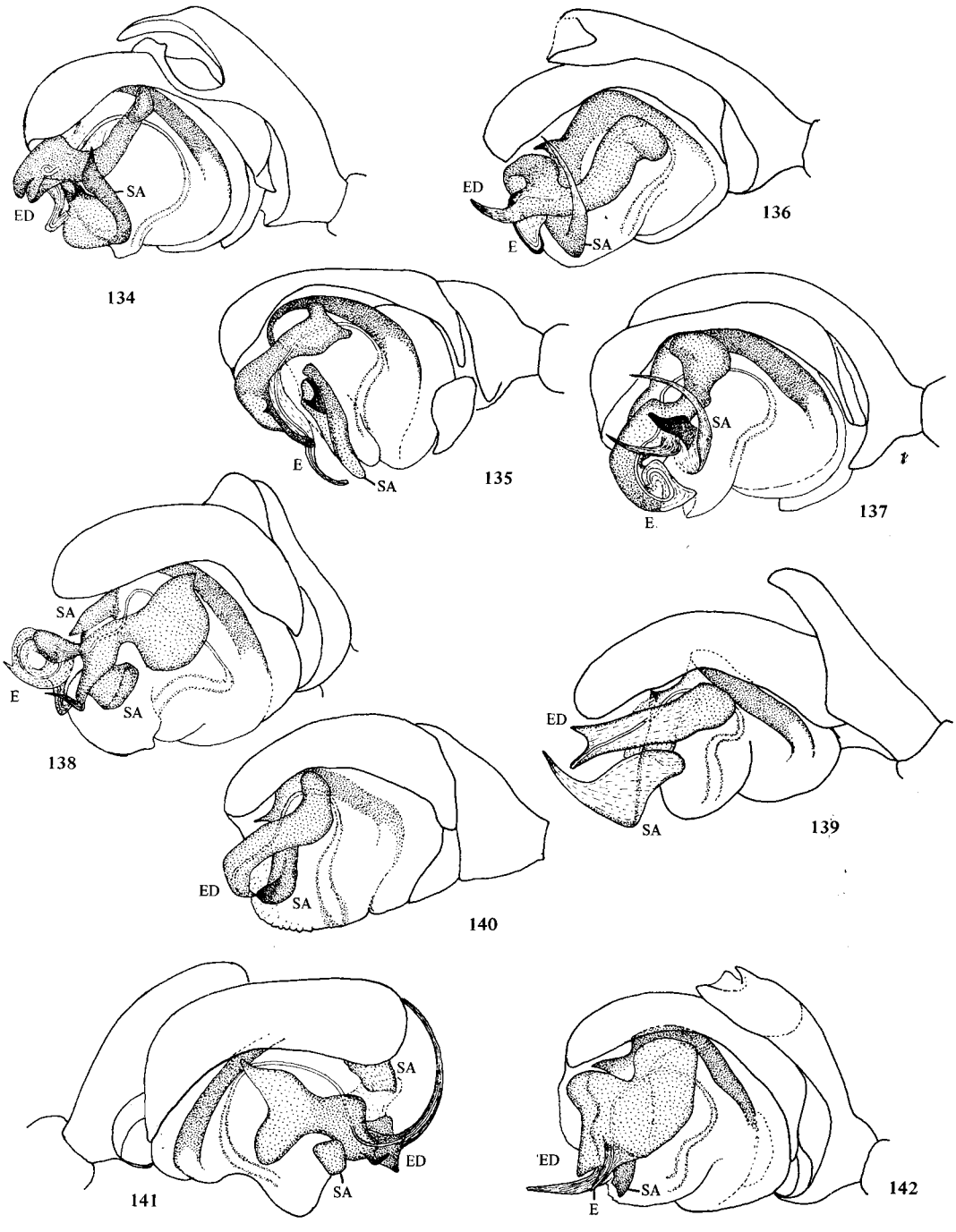
At this stage, however, these should not be regarded as firm proposals.

(ii) *Dactylopisthes digiticeps* Sim. (Fig. 139) (the only member of the genus) seems to fall in this group, but is abnormal in possessing a very simple ED coupled with a much more highly developed SA. Its phylogenetic position is uncertain; if further species of this genus could be found, e.g. in Asia or N.Africa, its relationships might become clearer.

(iii) The monotypic genera *Aulacocyba* (Fig. 140), *Janetschekia* (Fig. 142) and *Thaumatoncus* (Fig. 141) have a conformation basically similar to that of the *Savignya* group, but with ED's of rather different form and with the inner arm of the SA scarcely developed. These species may represent primitive forms of the *Savignya* group.



Figs. 126-133: Male palps. **126** *Diplocephalus cristatus* (Bl.); **127** *Araeoncus prospiciens* (Thor.); **128** *Alioranus pauper* (Simon); **129** *D. dentatus* Tullg.; **130** *D. protuberans* (Cambr.); **131** *D. helleri* (L. Koch); **132** *Saloca diceros* (Cambr.); **133** *D. permixtus* (Cambr.).



Figs. 134-142: Male palps. **134** *Diplocephalus latifrons* (Cambr.); **135** *Savignya frontata* (Bl.); **136** *Delorrhipis fronticornis* Simon; **137** *Erigonella subelevata* (L. Koch); **138** *Diastanillus pecuarius* (Simon); **139** *Dactylopisthes digiticeps* Simon; **140** *Aulacocyba subitanea* (Cambr.); **141** *Thaumatoncus indicator* Simon (left palp); **142** *Janetschekia monodon* (Cambr.).

Aulacocyba seems to represent the most primitive branch of this group, having a very simple ED; the tibial spines (1111) are different from the other species of this group, and the tarsal claws are pectinate. It shares with *Alioranus* and *Janetschekia* the presence of a wide seminal duct in the tegulum (Figs. 143, 144). *Janetschekia* has a much larger, plate-like ED with a short embolus and a pointed apophysis, while *Thaumatoncus* bears a long curved embolus and has a more complex SA.

The species in the *Savignya* group have probably originated from an ancestor with the *Lophomma* type of conformation, by growth of the SA and elaboration of the ED; e.g. a transition sequence in the ED's from the *Troxochrus* type (Fig. 9) through *Alioranus* (Fig. 128) to *D. cristatus* (Fig. 126) seems possible. The simpler palp's could have been derived from a species with a simple conformation of the *Aulacocyba* type.

12. *Erigonoplus* Group (Fig. 145)

This small group of species seems to have essentially the same basic conformation as the *Savignya* group, but the SA is simpler and the ED has a characteristic sickle shape (Fig. 145). Only two genera are included in the group:

Erigonoplus Simon 1884
Cotyora Simon 1926

Following my earlier revision of the genus *Erigonoplus* (Millidge 1975(1)) I would now transfer *Cotyora castellana* (Cambr.) into *Erigonoplus,* but place it in a separate species group because of the difference in the tibial spines (**syn.n.**).

It is postulated that this group also arose from a *Lophomma*-like conformation. It is possible that it is a sister group of the *Savignya* or *Savignya/Entelecara* lines; it has TmI 0.45, similar to the *Savignya* group, and *E. globipes* (L.K.) has a swollen tibia I in the male not unlike that of *Dicymbium tibiale* (Bl.).

13. *Entelecara* Group (Figs. 146-148)

The following genera are placed in this group:

Entelecara Simon 1884
Stajus Simon 1884
Hybocoptus Simon 1884

In these genera there is a lightly sclerotised radical part, which is fairly distinctly separated from the embolus. The duct enters the ED on the lateral side and forms a loop inside the radical part before entering the embolus.

Entelecara (Fig. 146) and *Stajus* (Fig. 147) are very close in conformation. Their tibial apophyses are of similar type, and the position of the metatarsal trichobothria is the same (TmI 0.5: *Stajus,* like some *Entelecara* species, has no TmIV); *Stajus* has tibial spines 1111 instead of 2211 as in *Entelecara.* The male head of *Stajus* is different from those of the *Entelecara* species, but this is probably of no significance. Despite the difference in tibial spines, it is proposed that *Stajus* should be regarded as a junior synonym of *Entelecara* (first reviser, **syn.n.**). The genus *Entelecara* may have originated from the *Savignya* phylogenetic line. The two genera have the same basic type of SA, with an upturned end, and an almost identical chaetotaxy apart from the presence in most *Entelecara* species of a trichobothrium on metatarsus IV. The ED has a tail as in most *Savignya* group species, and the *Entelecara* type of ED could probably be derived from a precursor of the *Savignya* group (C 11, p. 32) by a morphological change (growth of the duct within the radix) which does not appear too difficult.

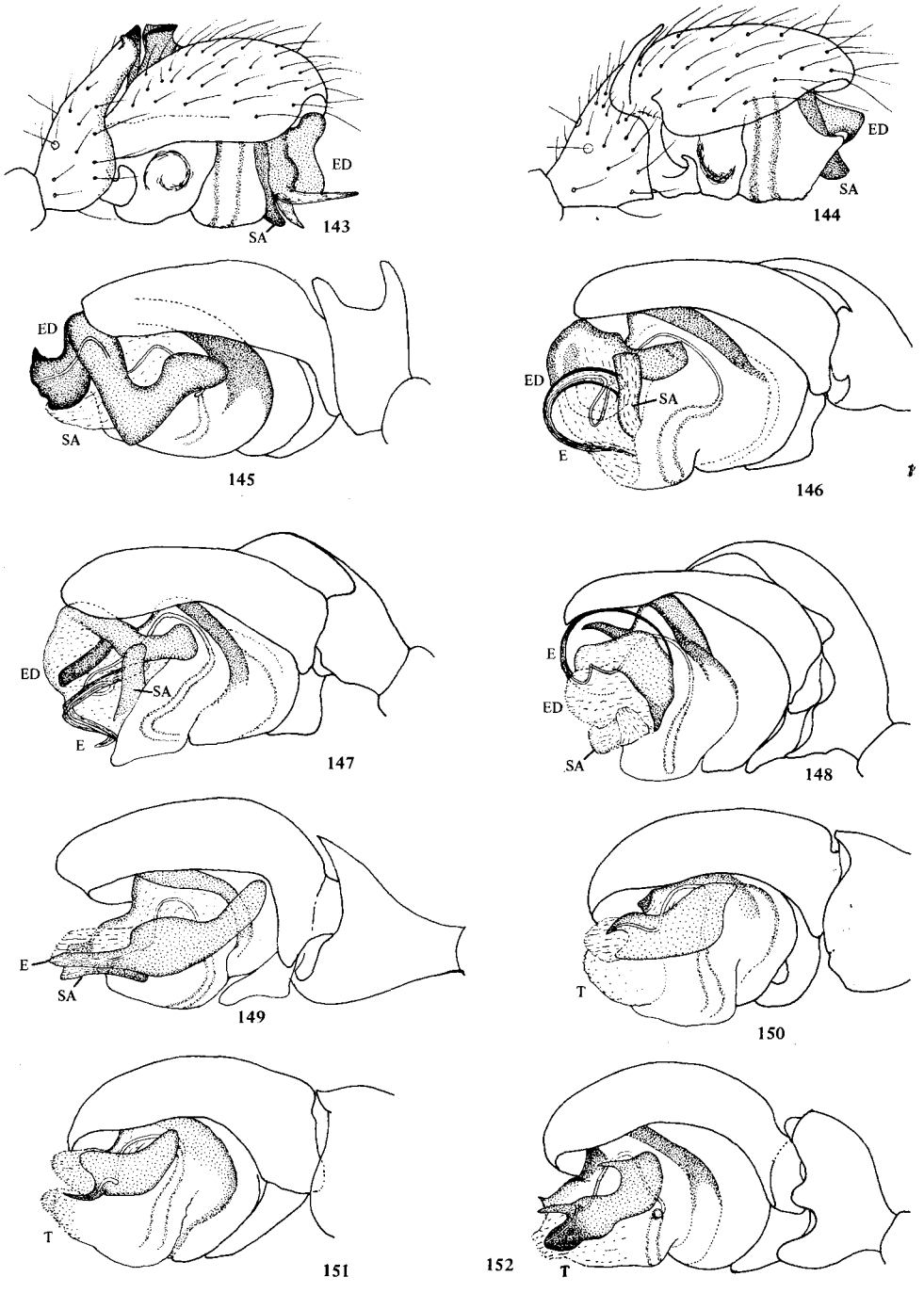
Hybocoptus (Fig. 148) bears some resemblance to *Entelecara* in conformation; it has a somewhat similar type of SA, but the ED has no tail. It is grouped here with *Entelecara,* though there is no solid evidence which links the two genera.

14. *Tmeticus* Group (Figs. 149-153)

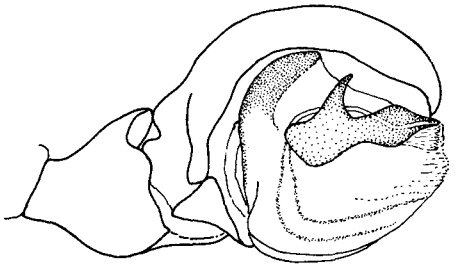
In this group the duct enters the ED on the lateral side, and towards the anterior end of the palp. The ED is usually a relatively simple plate, and the embolus is a short stub. The following current genera are included in this group:

Ostearius Hull 1911
Tmeticus Menge 1866
Donacochara Simon 1884
Eboria Falconer 1910
Sciastes Bishop and Crosby 1938

Ostearius (Fig. 149), which may not be European in origin, seems to be rather a primitive genus; but *Tmeticus* (Fig. 150), *Donacochara* (Fig. 151), *Eboria* (Fig. 152) and *Sciastes* (Fig. 153) each have a simple



Figs. 143-152: Male palps. **143** *Janetschekia monodon* (lateral); **144** *Aulacocyba subitanea* (lateral); **145** *Erigonoplus jarmilae* (Miller); **146** *Entelecara flavipes* (Bl.); **147** *Stajus truncatifrons* (Cambr.); **148** *Hybocoptus decollatus* (Simon); **149** *Ostearius melanopygius* (Cambr.); **150** *Tmeticus affinis* (Bl.); **151** *Donacochara speciosa* (Thor.); **152** *Eboria caliginosa* Falc.



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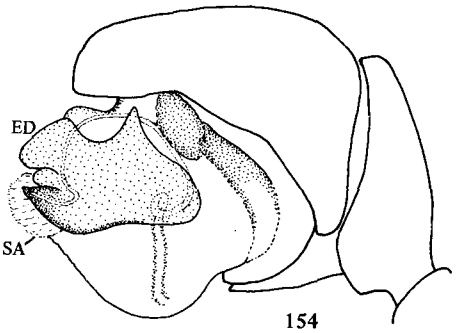

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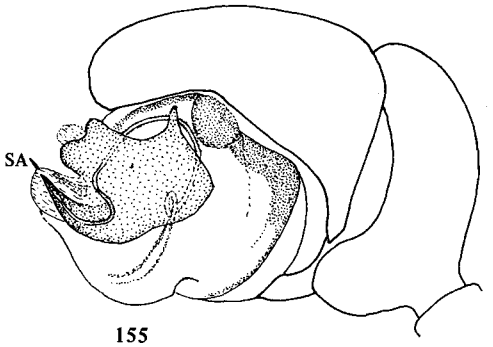

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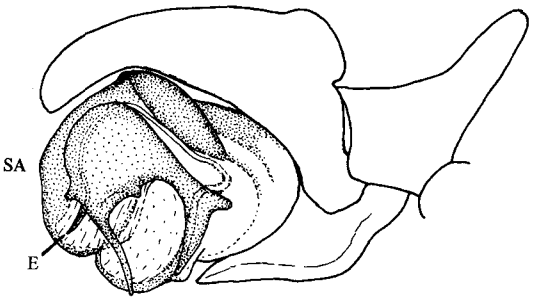

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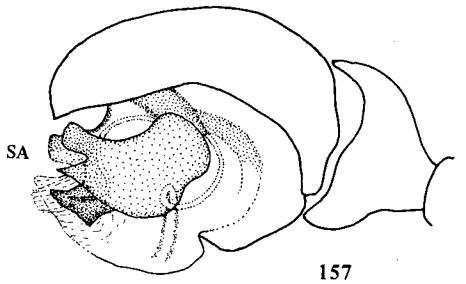

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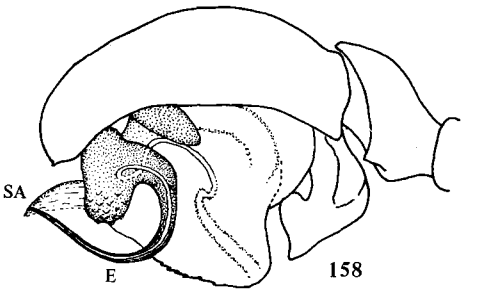

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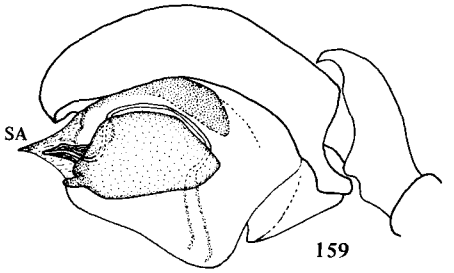

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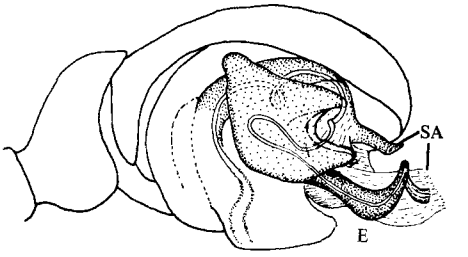

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Figs. 153-160: Male palps. **153** *Sciastes carli* (Less.); **154** *Asthenargus helveticus* Schenk; **155** *Asthenargus paganus* (Simon); **156** *Tibioplus diversus* (L. Koch); **157** *Jacksonella falconeri* (Jacks.); **158** *Carorita limnaea* (Cros.& B.); **159** *C. paludosa* Duffey; **160** *Microcentria rectangulata* (Emert.) (left palp).

conformation of the same type. The close apparent similarity of *Tmeticus* and *Donacochara* has been noted many times; the ED's are in fact rather different, and *Donacochara,* like *Zornella* and *H. nubigena,* has the unusual number of 5 trichobothria on the male palpal tibia (cf. 3 in *Tmeticus* and all the other species except *Eboria,* which has 2). *Sciastes* and *Eboria* are very close in conformation, but differ in the tibial spines (2222 in *Sciastes,* 2221 in *Eboria*) and in the absence in *Sciastes* of the ridges on the lung books; the N.American species placed in *Sciastes* (Bishop and Crosby 1938) probably do not all belong in that genus.

The species in this group seem to represent the more primitive forms of the phylogenetic branch (Fig. 200) where the duct entry to the ED is on the lateral side. This type of conformation is thought to have given rise to the *Asthenargus* group (next Section).

15. *Asthenargus* Group (Figs. 154-160, 166)

The species in this group have the same basic conformation as in the *Tmeticus* group. The following current genera are included in the group:

Asthenargus Simon and Fage 1922
Tibioplus Chamberlin and Ivie 1947
Jacksonella Millidge 1951
Carorita Duffey and Merrett 1963
Microcentria Schenkel 1925

Asthenargus (Figs. 154, 155) and *Tibioplus diversus* (L.K.) (the type species) (Fig. 156) have the same basic conformation and the same chaetotaxy, the differences lying mainly in the greater complexity of the ED and of the paracymbium in *diversus.* Chamberlin and Ivie (1947) noted the similarity of *Tibioplus* to *Asthenargus. Jacksonella* (Fig. 157) is very close to *Asthenargus,* and despite the loss of the second spine on tibia III *Jacksonella* should now be regarded as a synonym of *Asthenargus* **(syn.n.).** The *Asthenargus* and *Tibioplus* species have a sinuous duct (usually with a loop) within the tegulum, and in some species their epigynes show a tendency towards the development of a scape. The ED's of the typical *Asthenargus* species show a superficial resemblance to those of *Eperigone* (Section C 5, p. 13) but the embolus occupies a different position on the ED.

Carorita has the same basic conformation as *Tmeticus* or *Asthenargus. C. paludosa* Duffey (Fig. 159) is similar in its ED to *Tmeticus* or to *Asthenargus falconeri* (Jacks.), but the duct in the tegulum follows a less sinuous path than in *Asthenargus. C. limnaea* (Crosby and B.) (Fig. 158) and *paludosa* are so similar in most characters, viz. tibial spines 2211, and the unusual presence (for this spinal formula) of a prolateral spine on tibia I; TmI 0.3-0.35, no TmIV; similar SA's; and the basic palpal conformation, that it is probable that the two species should be regarded as forming a monophyletic group. They differ markedly, however, in the form of the ED, in particular by the fact that in *limnaea* (the type species) the embolus arises at the posterior end of the ED. This indicates again how great a range of variation is possible in the ED within what seems to be a good genus.

Microcentria (Fig. 160) has a similar basic conformation to *Asthenargus* or *Carorita,* but the duct forms a loop within the ED. The chaetotaxy (tibial spines 2221, TmI 0.4-0.45, no TmIV) is close to *Asthenargus,* and the species has the duct loop in the tegulum as in that genus. *Microcentria* is not a synonym of *Diplocentria* (Fig. 2), as claimed by Wunderlich (1970), but should be regarded as a branch from *Asthenargus* **(gen.rev.).**

Sintula (Fig. 165) also seems to be close to *Asthenargus*; although the tibial spines are 2211, this genus should probably be regarded as linyphiine, and is dealt with in Section D 1 (p. 43).

16. Doubtful Genera (Figs. 161-164)

Caracladus Simon 1884
Monocephalus Smith 1906
Pocadicnemis Simon 1884
Gnathonarium Karsch 1881
Hybauchenidium Holm 1973
Lessertinella Denis 1947

Monocephalus (Fig. 161) and *Caracladus* (Fig. 162) have conformations which are probably basically the same. In both genera there is a lightly sclerotised radical part which carries a small membranous apophysis, and the embolus forms a fairly distinct sclerite attached to the radical part. The duct enters the ED on the lateral side, and forms a loop (more developed in *Monocephalus* than in *Caracladus*) inside

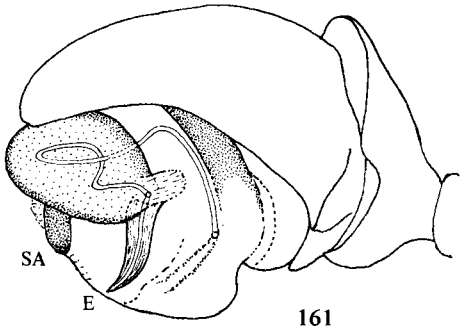
the radical part. In *C. leberti* (Roewer) (which I have not examined in detail) the duct loop seems to be scarcely present (Thaler, 1973). *Monocephalus* and *Caracladus* have virtually identical chaetotaxy, and in *C. leberti* the male head is similar to *Monocephalus*. It seems probable that these two genera are related, but their precursors are not known. From their basic conformation it is possible that they originated in the *Hilaira* region (C 3, p. 8), but there is no supporting evidence for this.

Pocadicnemis (Fig. 163) has a conformation different from that of any other genus, and its relationships are unknown. *Gnathonarium* (Fig. 164) is also impossible to place at present; the duct enters the ED at the posterior end of the palp, which may indicate a derivation from the *Hilaira/Drepanotylus* region.

Hybauchenidium has a complex palp with a long embolus; it is probable that this genus will be related to some N. American or Siberian species rather than to European species. *Lessertinella* also has a complex palp with a long embolus; it has not been possible to reach a conclusion on its relationships.

D. Linyphiine Genera

Only a limited selection of linyphiine species have been examined. The results indicate that there are a number of distinct conformations in the linyphiines, most of which can be identified by their similarities



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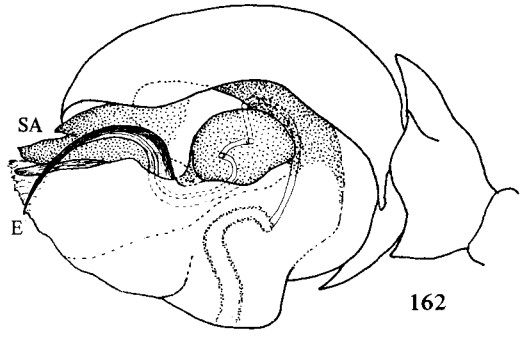

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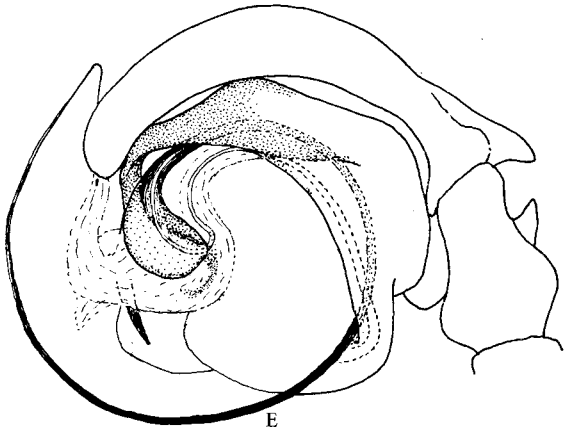

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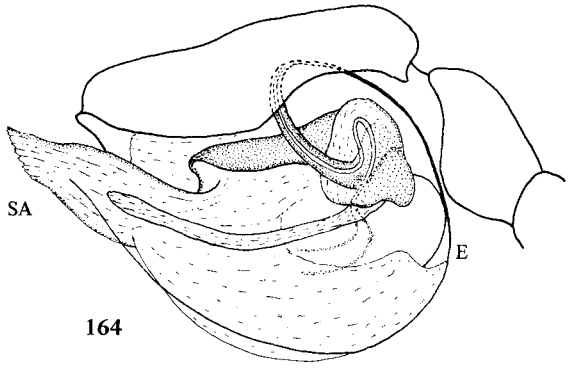

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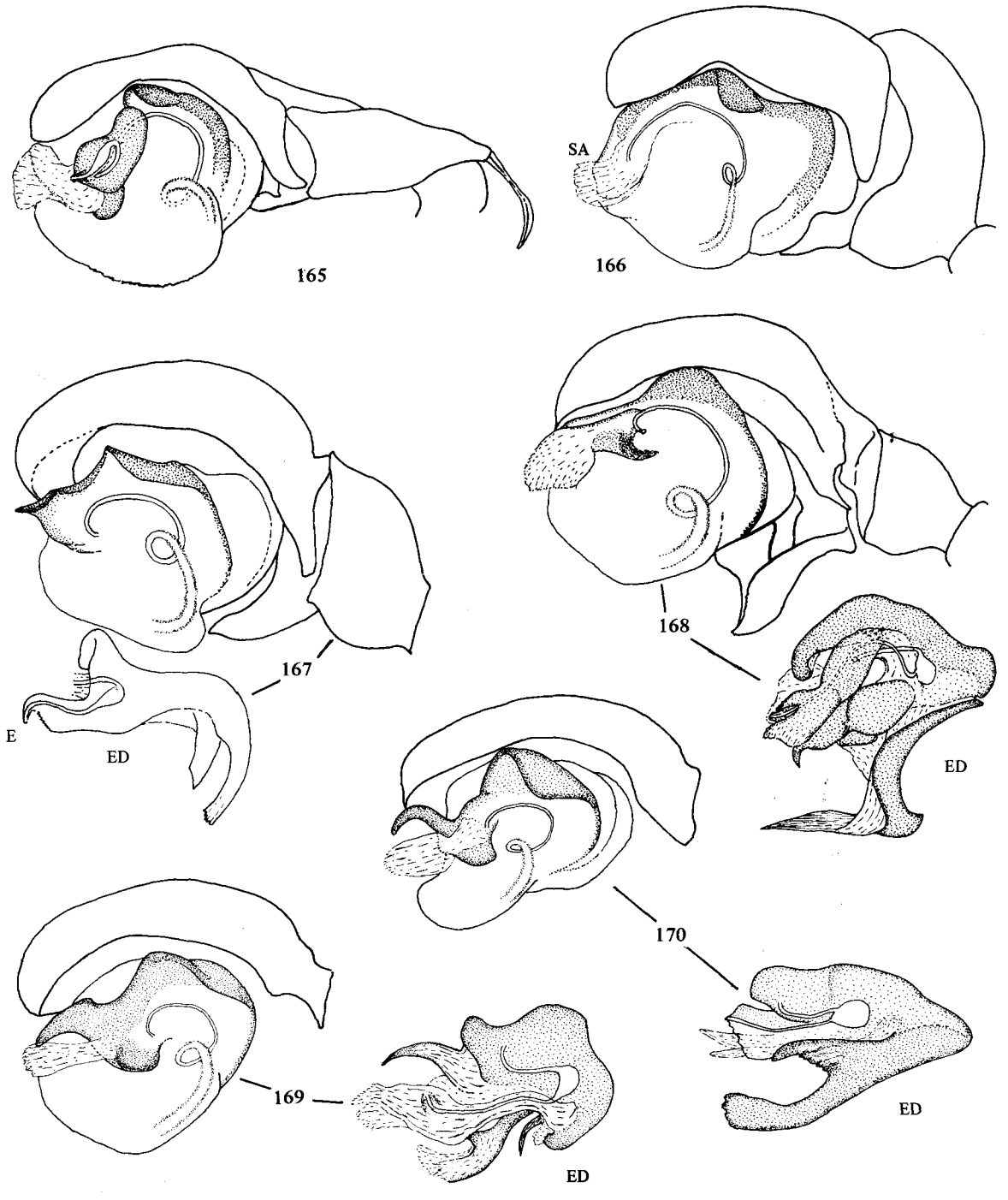
Figs. 161-164: Male palps. **161** *Monocephalus castaneipes* (Simon); **162** *Caracladus avicula* (L. Koch); **163** *Pocadicnemis pumila* (Bl.); **164** *Gnathonarium dentatum* (Wid.).



Figs. 165-170: Male palps. **165** *Sintula cornigera* (Bl.); **166** *Asthenargus paganus*, ED removed; **167** *Centromerus expertus* (Cambr.), ED separate; **168** *Lepthyphantes zimmermanni* Bertk., ED separate; **169** *C. arcanus* (Cambr.), ED separate; **170** *L. pallidus* (Cambr.), ED separate.

to certain erigonine conformations as having originated, with some degree of probability, from more than one region of the phylogenetic tree.

The genera examined are split into 10 groups on the basis of their conformations.

1. *Lepthyphantes* Group (Figs. 165, 167-170)

The following current genera are included in this group:

Sintula Simon 1884
Lepthyphantes Menge 1866
Bolyphantes C.L.K. 1837
Poeciloneta Kulcz. 1894
Drapetisca Menge 1866
Centromerus Dahl 1886
Centromerita Dahl 1882
Syedra Simon 1884

The conformation of all the members of this group is identical in principle with that of *Sintula* (Fig. 165), the difference lying only in the complexity of the ED and the SA (Figs. 167, 170). In all cases, the duct forms a loop within the tegulum, and after entering the ED on the lateral side it runs backwards for a short distance, makes a U-turn and then runs to the embolus. The duct within the embolus has a short enlarged part (sometimes called "Fickert's gland") in all the species, though this is poorly developed in *Centromerus dilutus* (Cambr.); the form of the enlargement is different in *Lepthyphantes* from that in *Centromerus* (cf. Figs. 169, 170). The combination of the sinuous duct in the tegulum with the relatively anteriorly placed position of the stalk (cf. *Linyphia* etc., Groups D 4, D 5), is regarded as an apomorphous character indicating that *Asthenargus* (Section C 15), *Sintula* and the *Lepthyphantes* and *Microneta* groups form a monophyletic group (cf. Figs. 165-168).

Centromerus expertus (Cambr.) (Fig. 167) has one of the simplest ED's in the group, with the "apophyses" still fused to the radix, and it is not difficult to envisage the derivation of an ED of this sort from an ED like that of *Tibioplus diversus* (Fig. 156), or even from *Sintula* by relatively minor extensions of the embolus and the growth of simple apophyses. Apart from the simplicity of the ED, *expertus* seems to be a typical *Centromerus*; it also has exactly the same type of duct enlargement in the ED as the other *Centromerus* species. It is considered, therefore, that it is preferable to regard *expertus* simply as a primitive member of the genus, rather than to split it off as a separate genus (*Tallusia*: Lehtinen and Saaristo, 1972), which will merely serve to hide its close relationship with the other *Centromerus* species. *Syedra* is very close to *Centromerus* (Merrett, 1965), with a similar duct enlargement, and it seems doubtful whether *gracilis* (Menge) should be separated from the *Centromerus* species; unfortunately *Syedra* would then have priority. *Centromerita* has a conformation close to *Centromerus*, with the same type of duct enlargement.

Bolyphantes, *Poeciloneta* and *Drapetisca* have a conformation close to that of *Lepthyphantes* (Figs. 168, 170), with the same type of duct enlargement as in that genus. *Poeciloneta/Drapetisca* have a very different chaetotaxy from *Lepthyphantes/Bolyphantes*, and it seems reasonable to postulate that, as appears to have occurred in some erigonine groups, there has been more than one line of development leading to an almost identical conformation. *Poeciloneta* and *Drapetisca* are probably sufficiently close to be united into one genus (*Drapetisca* would have priority, syn.n.).

Within both genera, *Lepthyphantes* and *Centromerus*, there is a wide range of complexity of the ED's, resulting from a variable degree of growth of the various appendages of the ED; this variation in the ED should not in itself be taken as a reason for splitting these genera, except into species groups.

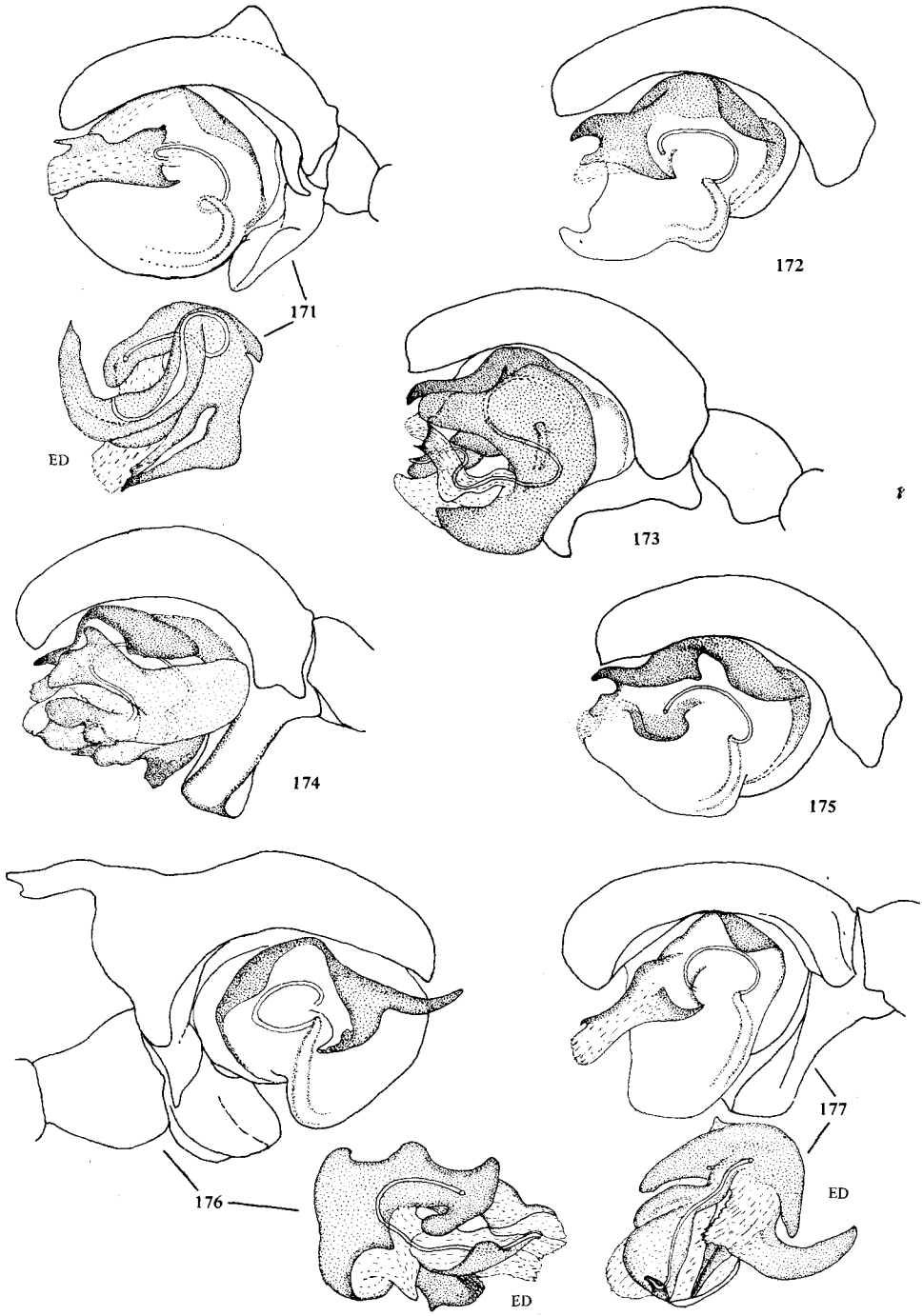
There are probably 3 phylogenetic lines in this group, *Sintula* being regarded as derived from a primitive form:

(i) *Lepthyphantes*, with *Bolyphantes* as a side branch or sister group;
(ii) *Syedra/Centromerus*, with *Centromerita* as a side branch or sister group;
(iii) *Poeciloneta/Drapetisca*

2. *Microneta* Group (Fig. 171)

The following current genera are included in this group:

Meioneta Hull 1920
Syedrula Simon 1929
Theonina Simon 1929
Microneta Menge 1868
Agyneta Hull 1911



Figs. 171-177: Male palps. **171** *Agyneta subtilis* (Cambr.), ED separate; **172** *Oreonetides vaginatus* (Thor.), ED removed; **173** *O. vaginatus;* **174** *Montetextrix glacialis* (L. Koch); **175** *M. glacialis,* ED removed; **176** *Tapinopa longidens* (Wid.), ED separate (left palp); **177** *Macrargus rufus* (Wid.), ED separate.

The conformation in this group is shown in Fig. 171. This is close to that of the *Lepthyphantes* group, but is also similar in general principle to that of *Microcentria* (Fig. 160). The duct enters the ED on the lateral side, and runs in a short loop inside the radix; in a few species only there is a slight swelling of the duct inside the embolic part. It is postulated that this group of species, like Group D 1, has arisen from the *Asthenargus* region of the phylogenetic tree; the duct within the tegulum is looped as in Group D 1.

Syedrula should be regarded as a synonym of *Meioneta* (Saaristo, 1973(1)). A male of *Theonina cornix* (Sim.) has not been examined, but it is practically certain (Saaristo, 1974) that this species belongs here, and it seems likely that, despite the presence of a trichobothrium on the 4th metatarsus, *Theonina* should be regarded as a synonym of *Meioneta*. *Agyneta* and *Meioneta* have conformations of exactly the same type (Saaristo, 1973(1)), but in view of the wide differences in trichobothrial formula (*Agyneta:* TmI 0.7-0.9, TmIV present) the existence of parallel lines of development is probable. Thus the views of Saaristo (1973(1)), and Wunderlich (1976) that *Agyneta* is a synonym of *Meioneta* are not accepted **(gen.rev.)**.

There are probably two phylogenetic lines in this group:

(i) *Meioneta* (s.lat.)
(ii) *Agyneta,* with *Microneta* as a side branch or sister group

3. *Oreonetides* Group (Figs. 172-177)

The following current genera are included in this group:

Oreonetides Strand 1901
Tapinopa Simon 1887
Floronia Westr. 1851
Montetextrix Denis 1963
Macrargus Dahl 1886

The conformation of this group is basically similar to those of Groups D 1 and D 2, but the form of the ED differs in detail, and the form of the SA is also slightly different (Figs. 170, 172). There is no swelling of the duct within the ED, and the duct in the tegulum is not quite so looped, but the group is nevertheless regarded as closely related to Groups D 1 and D 2 because of the general similarity in conformation.

Saaristo's contention (1972) that only *vaginatus* properly belongs in *Oreonetides* is borne out by the present work (for the other species, see Group D 7, p. 48). *Montetextrix glacialis* (L.K.) (Figs. 174, 175) is close to *O. vaginatus* (Figs. 172, 173) in conformation, but its metatarsal trichobothria (TmI *ca.* 0.8, TmIV present) seem to indicate a parallel line of development as in Groups D 1 and D 2.

Tapinopa (Fig. 176) and *Floronia* fall in this group, and have conformations which are similar to one another; in addition they have a similar chaetotaxy. The maintenance of both genera does not seem to be justified, and *Tapinopa* should probably be regarded as a junior synonym of *Floronia* **(syn.n.)**. It is thought probable that *Macrargus* (Fig. 177) belongs in this group, but it does show some differences from the other members; Merrett (1963) regards it as closer to *Centromerus*.

There are probably two phylogenetic lines in this group:

(i) *Oreonetides, Floronia* and (?) *Macrargus*
(ii) *Montetextrix*

The three Groups D 1, D 2 and D 3, which are postulated to have arisen from the *Asthenargus* region, have the common feature that each seems to have two parallel lines of development differing in the trichobothrial formula; this feature is absent in the remaining linyphiine groups (at least in Europe).

4. *Cresmatoneta* Group (Figs. 178, 180, 181)

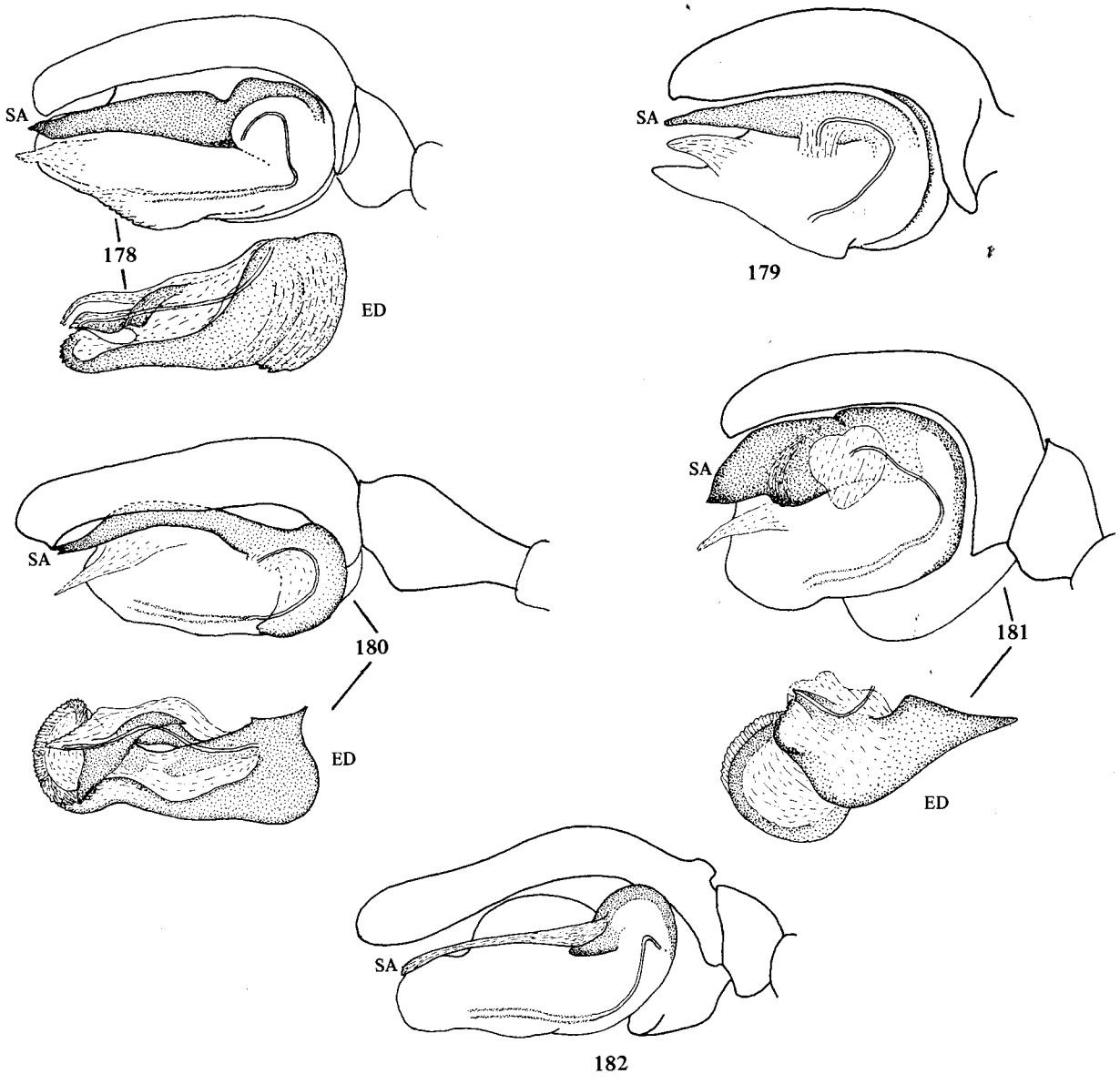
This group includes the following current genera:

Kaestneria Wiehle 1956
Cresmatoneta Simon 1929

The species in this group have a basic conformation almost identical with that of *Leptorhoptrum* (cf. Figs. 178, 179). The conformations of *K. pullata* (Cambr.) (Fig. 178) and *K. dorsalis* (Wid.) (the type species) (Fig. 181) are basically similar, but in *dorsalis* the SA is broader and less pointed and the ED has developed a larger terminal apophysis which is beginning to show similarities to the *Linyphia* type (Fig. 184). *Cresmatoneta mutinensis* (Canest.) (Fig. 180) has a conformation very close to that of *K. pullata*,

but with the terminal apophysis intermediate in size between *pullata* and *dorsalis*. The three species should be regarded as forming a monophyletic genus (*Cresmatoneta* has priority, **syn.n.**), the ant-like shape of *mutinensis* being regarded merely as an adaptive specialisation within the genus.

The close similarity in conformation to that of *Leptorhoptrum* indicates that this group of species originated from the *Leptorhoptrum* region of the phylogenetic tree, i.e. the *Cresmatoneta* group is part of a monophyletic group comprising *Leptorhoptrum* and the *Linyphia* group (Group D 5).



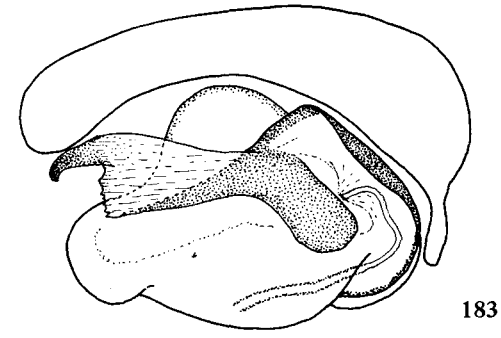
Figs. 178-182: Male palps. **178** *Kaestneria pullata* (Cambr.), ED separate; **179** *Leptorhoptrum robustum* (Westr.), ED removed; **180** *Cresmatoneta mutinensis* (Canest.), ED separate; **181** *K. dorsalis* (Wid.), ED separate; **182** *Diplostyla concolor* (Wid.), ED removed.

5. ***Linyphia* Group** (Figs. 183-186)

This group includes the following current genera:

Linyphia (s.lat.) Latreille 1804
Microlinyphia Gerhardt 1928

The basic conformation of the species in this group also appears to be close to that of *Leptorhoptrum* (*L. montana* Fig. 183; *L. triangularis* is almost identical). The ED's of *L. montana* (Fig. 184) and *triangularis* (Fig. 186) are similar, the differences being only of degree, viz. a longer embolus and a more highly developed terminal apophysis in *triangularis*. The two ED's in fact differ in much the same way as do the ED's of *Hilaira pervicax* (Fig. 187) and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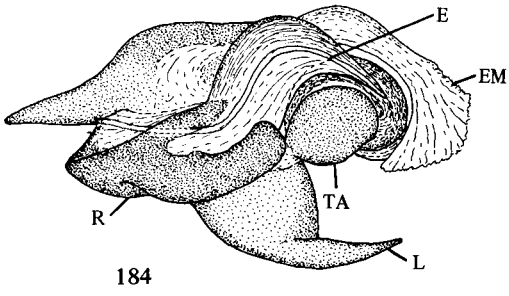

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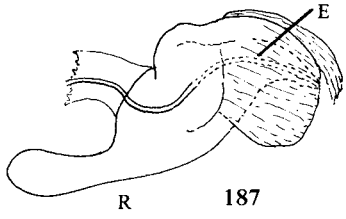

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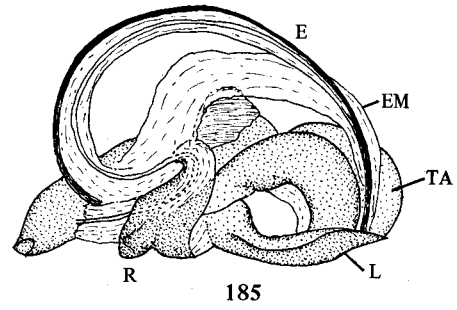

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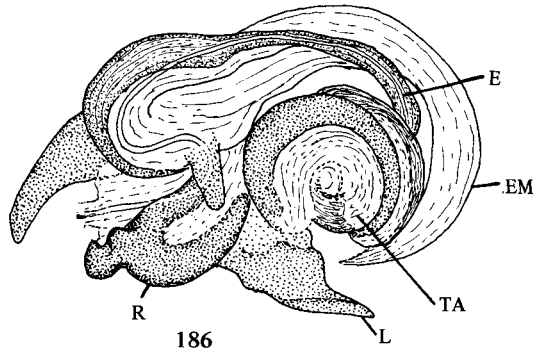

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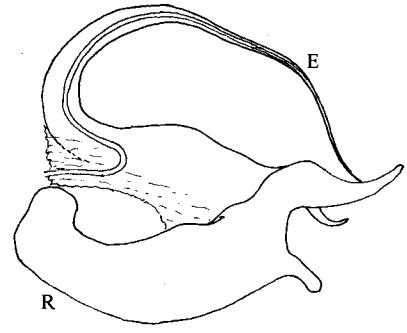


Fig. 183: Male palp. *Linyphia montana* (Cl.), ED removed.

Figs. 184-188: Embolic divisions, lateral side: L = lamella, R = radix, EM = embolic membrane, TA = terminal apophysis. **184** *L. montana;* **185** *L. hortensis* Sund.; **186** *L. triangularis* (Cl.); **187** *Hilaira pervicax;* **188** *H. montigena.*

montigena (Fig. 188), but the ED's are of course more complex in *Linyphia.* Within the genus *Linyphia* (s.lat.) there is a considerable range of variation of the ED, with emboli of various lengths and terminal apophyses of various sizes (e.g. *L. hortensis* Fig. 185), and splitting of the genus on the basis of morphology is almost certainly not justified. Splitting on the basis of the mechanics of copulation (Helsdingen, 1969) seems to the author to be unjustified, since the obvious relationship of the species as indicated by their morphology should be shown in the generic name. Within a given genus of the Linyphiidae there are often species with both short and long emboli, and it is probable that a lengthening of the embolus must often, for mechanical reasons alone, force on to the spider the necessity to change, at least to some extent, the procedure in copulation. It is clearly a matter of degree, and to that extent subjective, but the author considers that it would be very undesirable if every change of habit required, as a general rule, the erection of a new genus.

The genus *Microlinyphia* has basically the same conformation as *Linyphia,* the differences lying only in the detail of the shapes of the parts of the ED, and it is doubtful therefore whether it is justified to split off *Microlinyphia* as a separate genus.

This group is also postulated to have arisen from the *Leptorhoptrum* region; it is possible that the *Linyphia* and *Cresmatoneta* groups are sister groups.

6. *Porrhomma* Group (Figs. 189-192)

This group includes the following current genera:

Porrhomma Simon 1884
Bathyphantes Menge 1866

The basic conformation of these genera is fairly close to that of Groups D 4 and D 5, but less close to that of *Leptorhoptrum.* The ED has a plate-like structure mesally, and the embolus is a separate sclerite attached to the lateral side of the plate (Figs. 189-192). *B. approximatus* has the same basic conformation but the embolus has become long and spirally coiled. The conformation is closely similar to that of the *Mioxena* group (Section C 7, p. 13), and these two groups should be regarded as being of common parentage and perhaps standing in a sister-group relationship. This group is postulated as having arisen from the *Hilaira* region of the tree.

7. *Aphileta* Group (Figs. 193-195)

This group includes the following current genera/species:

Aphileta Hull 1920
"Oreonetides" abnormis (Bl.) and *firmus* (Cambr.)
Maro Cambr. 1906

The basic conformation of this group is close to that of *Hilaira pervicax* (Figs. 16, 193-195); *Aphileta* (Fig. 193) can be regarded as a rather primitive form of this conformation, while *"O." abnormis* (Fig. 194) and *Maro* (Fig. 195) (Saaristo, 1971) are more complex. Saaristo (1972) pointed out that *abnormis* and *firmus* did not belong to *Oreonetides,* and I therefore propose that these two species should be placed in the new genus *Saaristoa,* gen.n.

Because of their basic similarity in conformation to some *Hilaira* species, this group is postulated to have arisen from the *Hilaira* region.

8. *Diplostyla* (Fig. 182)

The species *Diplostyla concolor* (Wid.) (Fig. 182) has essentially the same basic conformation as *Cresmatoneta* (Fig. 180), with a long forward-directed SA as in that genus; the ED is however of a much more complex type. This species presumably arose from the same general region of the tree as *Cresmatoneta,* but as a separate branch.

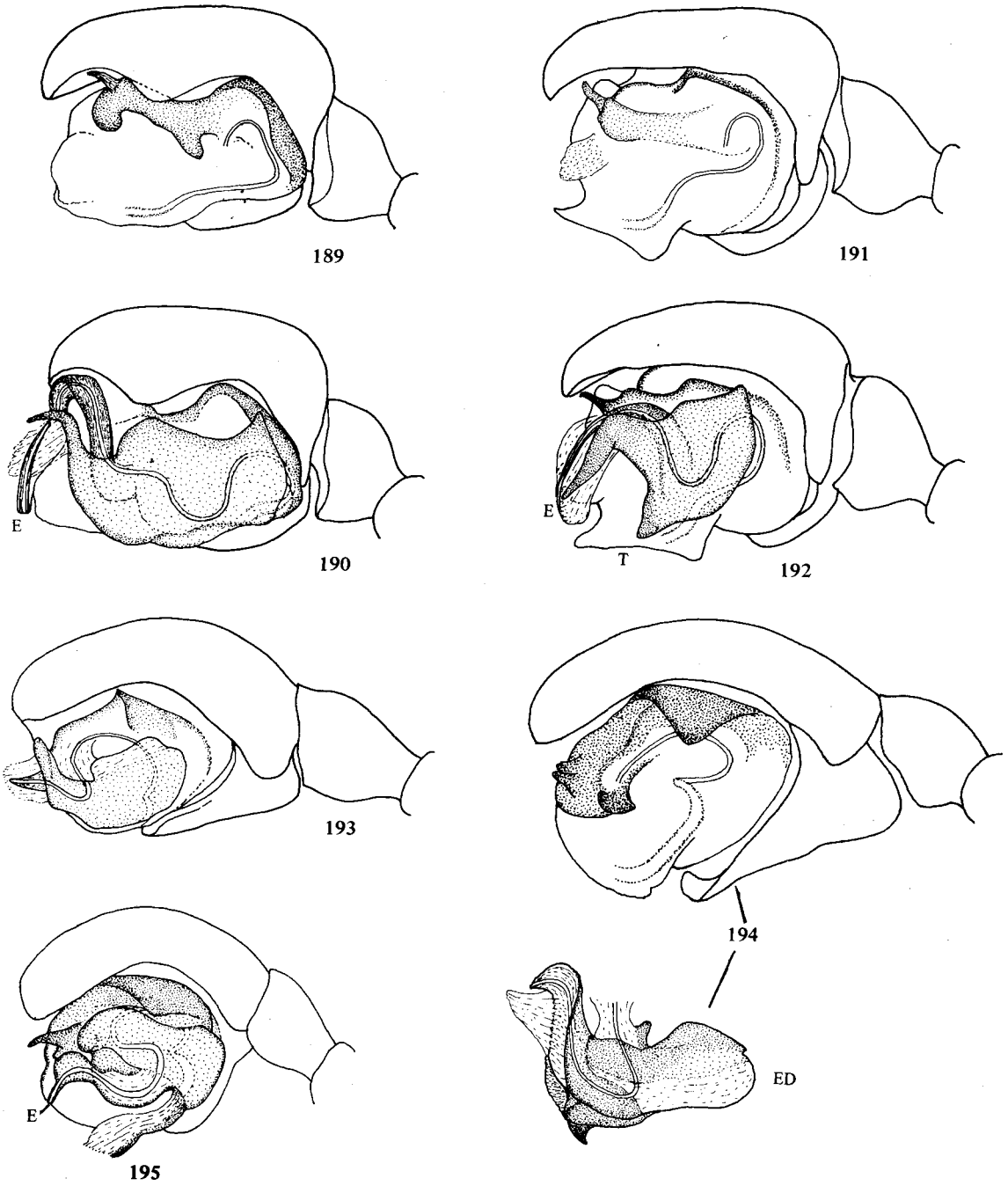
9. Genera with Erigonine Conformations (Figs. 196-198)

The following current genera are included here:

Taranucnus Simon 1884
Allomengea Strand 1912
Helophora Menge 1866

These 3 genera have palpal organs of the erigonine type; the SA's are complex as in many of the erigonines, and in *Taranucnus* and *Helophora* the tegulum is more or less vertical.

Taranucnus (Fig. 196) has a conformation rather like that of *Monocephalus* (Fig. 161) or possibly *Microcentria* (Fig. 160), and on this basis it seems



Figs. 189-195: Male palps. **189** *Bathyphantes gracilis* (Bl.), ED removed; **190** *B. gracilis;* **191** *Porrhomma convexum* (Westr.), ED removed; **192** *P. convexum;* **193** *Aphileta misera* (Cambr.), **194** *"Oreonetides" abnormis* (Bl.), ED separate; **195** *Maro minutus* Cambr.

probable that it originated in the same region of the phylogenetic tree as one or other of these genera. *Helophora* (Fig. 198) has a fairly simple erigonine-type coiled embolus, on which has grown the long lamella; the SA is complex. The provenance of this species is obscure, but it could possibly be an offshoot from the *Baryphyma* region of the tree. *Allomengea* (Fig. 197) has a distinctly erigonine type of SA (reminiscent of e.g. *Dismodicus* (Fig. 97)), and the ED consists of a fairly simple radical part bearing a coiled embolus, this radical part having superimposed on it a large lamellar structure. This conformation could conceivably have arisen from the *Maso/Minicia* area (Section C 9, p. 21, Figs. 63-65); *Allomengea* has a similar trichobothrial formula to these species, and has a somewhat similar cymbial form to *Minicia*.

Each of these 3 species has a fairly high value of TmI, and TmIV is present. Why so few linyphiine spiders have arisen with the erigonine type of palp is a mystery.

10. *Stemonyphantes* Menge 1866 and *Labulla* Simon 1884 (Fig. 199)

Stemonyphantes (Fig. 199) has basically the same conformation type as Groups D 4, D 5 and D 6, with the duct leaving the tegulum and entering the ED near the posterior end of the palp. It is, however, very different in detail, with a curious anterior development of the tegulum, and a strikingly different form of ED. Because of its basic conformation, it presumably arose from the same general phylogenetic region of Groups D 4-D 6, but nothing more than this can be said of its relationships.

Labulla is also difficult to place; it seems to be closer in basic conformation to the *Lepthyphantes* area (Groups D 1-D 3) than to the *Linyphia* area (Groups D 4-D 6).

E. Discussion and Conclusions

On the basis of the palpal conformation it has been possible to carry out a partial phylogenetic analysis of the Linyphiidae. The assumptions made in this analysis are (i) that the plesiomorphous conformation was simple, and that the apomorphous conformations are more complex; (ii) that regression from complex to more simple conformations has been absent or infrequent; and (iii) that conformation is an apomorphous character which can be used to show phylogenetic relationship, i.e. that the conformations present today are the results of separate phylogenetic lines of development of the palp and of the spiders themselves. What is postulated is that the wide range of palpal forms present today have arisen by radiative elaboration from a simple plesiomorphous form. The complicated palpal organs of most contemporary species have therefore been formed by an increase in the complexity of the ED and to a lesser extent of the SA, and by less obvious changes to other parts of the palpal organs. Evolutionary development of the palp in this way appears to be the most logical pathway to the wide range of palpal forms present today. In agreement with the assumption (iii) it has been found that conformation is more or less constant within well-defined genera.

Conformation can be considered at various levels of detail. At the family level, the generalised conformation as summarised on p. 4 and Fig. 1, is a synapomorphous character for the family Linyphiidae. Various examples are given in Section C of conformation at the generic level, and when considered in its ultimate detail each species has its own particular conformation.

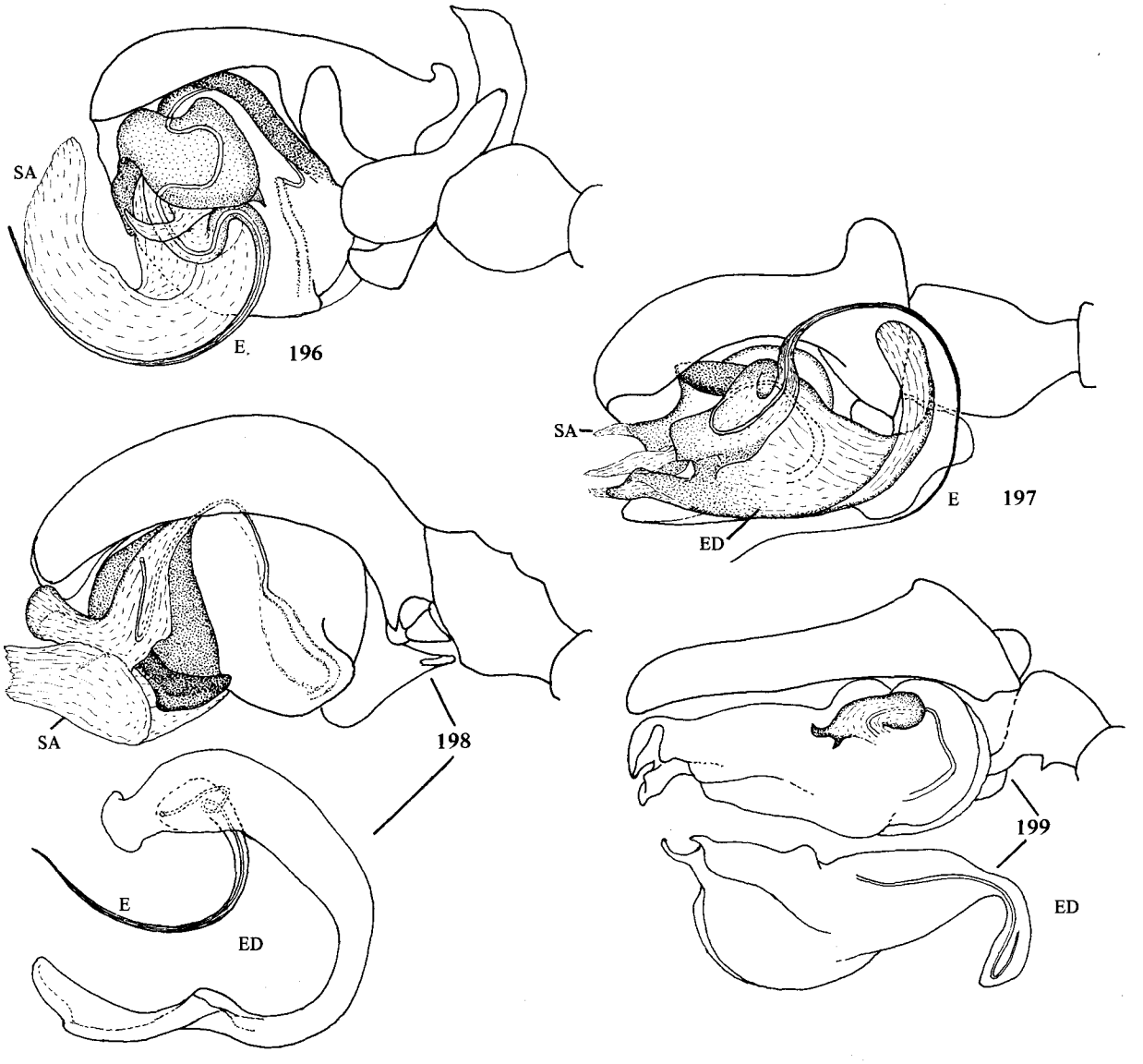
This analysis of conformation, coupled with the use of some other characters, has permitted the synthesis of a provisional phylogenetic system for the Linyphiidae, including both erigonine and linyphiine members. The morphological transitions within and between the various groupings postulated appear to be on the whole relatively simple and straightforward, requiring no undue stretch of credulity. The analysis indicates that both erigonine and linyphiine spiders have evolved from several different areas of the phylogenetic tree. The so-called transitional genera, which have caused a good deal of discussion and disagreement amongst arachnologists, fit naturally into the system proposed and pose no problems. There are, however, a small number of genera which cannot at present be placed. In considering the results obtained, and the theory proposed, it is important to bear in mind that the analysis has been limited to the European fauna; in other geographical areas some conformations and conformational relationships not found here will undoubtedly be present. The theory

put forward is of course descriptive and correlative only; the *reasons* for the various evolutionary changes which have occurred in the palp and in other characters, and the actual morphological pathways for some of the palpal changes suggested, are quite unknown at the present time.

The phylogenetic system proposed for the Linyphiidae is summarised schematically in Fig. 200, which is based on the results reported in more detail in Sections C and D.

Some points to be taken into consideration in the interpretation of this diagram are as follows:

(i) The arrangement is schematic, indicating the pathways to the palpal conformations of the various



Figs. 196-199: Male palps. **196** *Taranucnus setosus* (Cambr.); **197** *Allomengea scopigera* (Grube); **198** *Helophora insignis* (Bl.), ED separate; **199** *Stemonyphantes lineatus* (L.), ED separate, long embolus hidden.

groups and genera. This is not to be taken to mean that e.g. *Hilaira* is a direct ancestor of *Erigone,* but rather that the *Erigone* species have been derived from an ancestor with a conformation like today's species of *Hilaira.*

(ii) The most uncertain areas of this scheme are considered to be the relationships shown in the lower part of Fig. 200. The *Tmeticus* and *Lophomma* groups contain a somewhat heterogeneous mixture of species, the derivation of which from the hypothetical stem species is capable of several interpretations. More phylogenetically useful characters are needed to clarify the position of these genera in particular; additional characters, if they can be found, will also be of the utmost value for testing the other relationships postulated in Fig. 200.

(iii) The stem species is postulated to have had a very simple conformation (but of the linyphiid type). The duct entry to the ED could have been either dorsal or lateral; one form is convertible into the other by a relatively small shift in the stalk and duct, and there is no evidence to show which was in fact the primitive form. There is of course, no direct information on any other characters of this stem species, but a few inferences can be drawn. Many of the species existing today with what appear to be the most primitive types of palps (e.g. *Leptorhoptrum, Ostearius, Sciastes, Donacochara*) have tibial spines 2222, and some of these have a trichobothrium on metatarsus IV. If one makes the postulate (which appears a reasonable one on present knowledge) that the trichobothrium on metatarsus IV changes always in the direction of loss, and that the *dorsal* tibial spines also change always or almost always in the direction of loss, then the primitive members of the family can be inferred, with some reasonable degree of probability, to have had tibial spines 2222 and to have possessed TmIV. On the same basis, it seems probable that the primitive members had no significant cephalic elevation in the adult male. Another character which seems to give some indication of primitiveness is the number of trichobothria on the male palpal tibia. The more primitive species seem to have 3 trichobothria (perhaps more, since in 3 exceptional cases there are 4 or 5); this number decreases to 2 or 1 in most of the erigonine species, but remains at 3 in most of the linyphiines. Thus it seems that the linyphiines tend to have retained some of the primitive somatic characters of the family, viz. tibial spines 2222, 3 or 4 trichobothria on male palp, no cephalic lobe in male (and perhaps the tracheal system, p. 55).

(iv) It is assumed that the stem species split, in the usual manner, into two species which then led to the two main branches of the family. It is postulated that the right-hand branch (Fig. 200) carried the character of dorso-mesal or mesal entry of the duct into the ED, while the left-hand branch carried the character of lateral entry of the duct into the ED. It is to be noted that subsequent elaboration and growth of the parts of the ED has often obscured the position of entry of the duct, i.e. it seems probable that apomorphous characters common to members of a monophyletic group may sometimes become hidden during the evolution of the group. The truth or otherwise of the assumption, that the family split fairly early in its history into two branches differing essentially in the position of duct entry to the ED, may be capable of proof or disproof when a wider fauna than that of Europe has been properly studied. It cannot be ruled out at this stage that species with the lateral duct entry have arisen more than once, from species with dorsal entry, or vice versa.

(v) The analysis does not support the existence of the commonly used sub-families Erigoninae and Linyphiinae. The results indicate that both erigonine and linyphiine species have arisen from several parts of the phylogenetic tree, but that the linyphiine species are in 2 or 3 main groups which have arisen quite separately from one another. These findings are in general agreement with the views of Lehtinen (1975) that the phylogeny of Linyphiidae is significantly more complex than indicated by the simple bifurcate splitting of the family into the two traditional sub-families.

In view of the doubts cast by the present work on the existence of these sub-families, and in view of the many questions which still remain unanswered, it is strongly recommended that taxonomists should for the time being abandon the use of these sub-families, at least in faunal lists. If this is not done, some genera will continue to be shifted from one sub-family to another, by different arachnologists, to the detriment of all those biologists who use the results of taxonomy. The terms "erigonine" and "linyphiine" when used should be regarded as morphologically des-

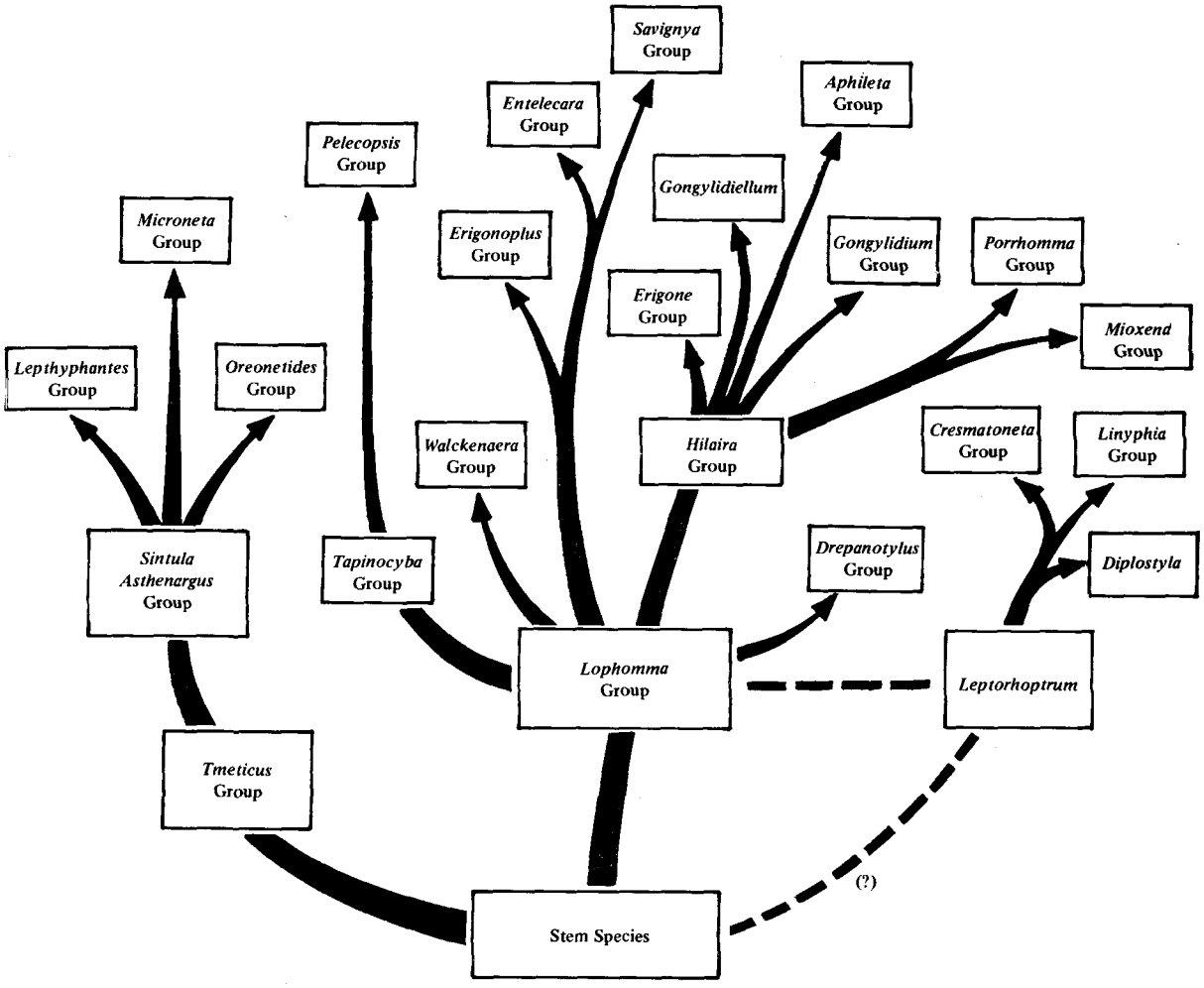


Fig. 200: Partial phylogenetic classification of the Linyphiidae.

criptive and not phylogenetically descriptive.

(vi) If the two main branches shown in Fig. 200 are accepted as a workable hypothesis, they must eventually be named as sub-families, while the smaller branches (even though their exact limits may be difficult to define) must also be named, as tribes, subtribes, etc. Family group names are subject to the same laws of priority as any other name, a fact which seems to have been lost sight of by some arachnologists. The sub-family name for the right-hand branch of Fig. 200 must be the nominate sub-family Linyphiinae since it contains the family's nominate genus *Linyphia*. The earliest available family group name for the left-hand branch is Micronetinae Hull 1920. As recommended in (v) above, however, these names should not be used for the present in faunal lists.

(vii) It is obvious that, for reasons unknown, there is an inbuilt genetic tendency for the linyphiine members of the family to develop ED's of ever-increasing complexity, by the growth of parts attached to the radix. This is true even of those few linyphiine species which have erigonine types of palp. If it is accepted that the linyphiine spiders have arisen from several distinct lines of development, then it is probably no longer justified to infer that the various

parts ("lamella", etc.) arising from the radix in the different lines are homologous. No doubt it will be convenient to retain the names already given to the parts, for descriptive purposes, so long as it is realised that the names do not automatically confer homology.

(viii) There seems to be quite a strong tendency for the position of the metatarsal trichobothria (measured on the adult) to remain reasonably constant within the smaller phylogenetic lines (particularly in genera): e.g. *Erigone, Savignya/Diplocephalus* group, *Tapinocyba, Meioneta, Centromerus*). While it cannot be said that *all* monophyletic genera have the position of the trichobothria constant, nevertheless where there are marked differences in the trichobothrial position within a conformation group (e.g. one well < 0.5, one well > 0.5), then the existence of more than one phylogenetic line must be suspected. On this basis, parallel lines of development leading to almost identical conformations have been postulated in the *Tapinocyba* and *Pelecopsis* groups, and in several of the linyphiine groups. The loss of TmIV seems to have occurred relatively easily, and erratically, in the various branches. No species are known which have lost TmIII as well.

Within the various phylogenetic lines, the loss of dorsal tibial spines appears to have been a relatively easy process. The dorsal spines on tibiae I and II must be genetically linked, since there seem to be no species with tibial spines 2111.

(ix) The ED can show a considerable range of variation from species to species within a genus, while the SA usually tends to be more stable.

(x) It is a valid question to ask whether a corresponding phylogenetic analysis could be carried out on the basis of the detailed structure of the female sex organs, and whether such an analysis would lead to a different answer? With the erigonines the problem is that the fine structure of the vulva is usually difficult to see, and that in any case the vulva is often very simple. It has therefore been difficult or impossible to find any significant correlations between the epigyne/vulva structure of erigonine spiders of different groups. Attempts to carry out taxonomic analysis on the basis of the structure of female organs in some linyphiine species (where the complexity of the organ is greater) have been more successful (e.g. Saaristo, 1972, 1973(1)). It seems clear, in the erigonines, that there is little or no correlation between palpal structures and vulva structures; while the male palp retains a more or less constant conformation, as in e.g. *Walckenaera*, the female epigyne/vulva can show considerable variations. Another example is provided by the 2 species *Pelecopsis elongata* and *P. (Exechophysis) bucephala*: these have almost identical palpal conformations, yet the vulva of *bucephala* is much more complex than that of *elongata*. If the hypothesis proposed in this paper is accepted, then it seems that the form of the epigyne/vulva may often be of minor importance phylogenetically, at least in the erigonines, and that changes in the female organ, while the palpal conformation remains more or less unchanged, are the results of minor branching of the phylogenetic lines. If so, such changes do not justify the setting up of new genera, though the erection of species groups may well be justified.

Changes in the detail of the sex organs can probably lead to changes in mating procedure; such changes will be forced on the spider, if it is to survive, by the changed geometrical situation which it faces (all such changes, morphological and adaptational, will of course occur gradually, in small steps). It seems to the author that such changes in mating procedure, if they are solely the result of relatively small morphological changes (such as lengthening of the embolus), which represent only minor phylogenetic branches, are not sufficient to justify the splitting off of the species concerned into a new genus, though a sub-genus or species group may be justified. Clearly in such cases it is a matter of degree, but if every small change in mating (or other) habit required the erection of a new genus, there would indeed be a proliferation of genera! As stated in the Introduction, it seems preferable, particularly in a family such as the Linyphiidae which is so rich in species, to use generic names to show relationships rather than to show differences, i.e. to avoid splitting off every minor phylogenetic branch as a new genus.

In an interesting paper on the tracheal arrangements in the Linyphiidae published recently, Blest (1976) suggests that some of the simpler palpal forms (particularly those of the transitional genera) have been derived from linyphiine forms by "reduction" of the complex to the simple. The view expressed in the present paper, that the linyphiine palps have all been formed by elaboration of simpler palps, and that

the transitional forms are in fact intermediates or side branches on the way to the linyphiine forms, appears to the author to give a more logical phylogenetic picture of the Linyphiidae. Although there must be doubts on the value of the tracheal arrangement as a reliable character for phylogenetic analysis (e.g. Levi, 1967; Levi and Kirber, 1976), and although Blest's conclusions are at variance with those reached here, his *results* are not necessarily in disagreement with most of the present findings. If the linyphiine tracheal arrangement is the more plesiomorphous form of the character, and the erigonine arrangement is the more apomorphous form, as seems probable, then the retention of the plesiomorphous form of this character by the linyphiines would be in line with their retention of some other probably primitive somatic characters (this Section, iii, p. 52). Thus Blest's results need not be regarded as in serious disagreement with the scheme of Fig. 200. Only *Lessertiella* appears to be quite anomalous.

This paper makes a serious attempt to investigate the phylogeny of the Linyphiidae, and the author intends to develop the theme in subsequent papers. The approach is of course speculative, and it is not pretended that the analysis carried out represents more than a preliminary and partial attack on the numerous problems of linyphiid taxonomy/phylogeny. For example, it will clearly be impossible to identify all the sister group relationships within the family on the basis of a study of the European fauna only, rich in species though this may be. Nor is any claim made at this stage that the theory and scheme proposed are "right"; in the absence of extensive fossil evidence a theory of this kind can never be "proven". Like any other scientific hypothesis, it must be judged on the basis of its ability to give a reasonable fit to the known data, and to new data as these appear. If the hypothesis put forward encourages others to develop a system which shows a better fit to *all* the known data, then the author will be well satisfied.

Quite apart from the phylogenetic inferences made, the concept of conformation described in this paper gives a practical basis for analysing, in a logical manner, the structure of the palp, thus offering a better basis for comparing species with one another and for organising species and genera into more accurately defined and recognisable higher taxa.

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Appendix

During the course of the work described in this paper the following synonyms were established:

1. *Aulacocyba parisiensis* (Simon 1884) (Tube No. 2324.B.948, M.N.H.N. Paris) = *Aulacocyba subitanea* (Cambr. 1875).
2. *Collinsia foenaria* (Simon 1884) (♂♂ Tube No. 4791.B.938, M.N.H.N.) = *Milleriana inerrans* (Cambr. 1884): on grounds of usage, *inerrans* should continue to be used.
3. *Collinsia harmsi* Wunderlich 1972 (♀♂ from Senckenberg Musuem) = *Gongylidiellum mediocre* Simon 1884 (Tube No. 4505.B.904, M.N.H.N., ♂ palp).
4. *Diplocephalus pulicarius* (Thorell 1875) (syntype ♀, Coll. Thorell 115/467, Naturh.Riksmus.Stockholm) = *Aulacocyba subitanea* (Cambr. 1875): on grounds of usage, the name *subitanea* should continue to be used.
5. *Diplocephalus tauricus* (Thorell 1875) (♂ palp from holotype, Coll. Thorell 115/468, Naturh.Riksmus.Stockholm) = *Ceratinopsis romana* (Cambr. 1872).
6. *Gongylidiellum maderianum* Schenkel 1938 (♀ paratype, Tube 1544a, Naturh.Mus.Basel) = *Aulacocyba subitanea* Cambr. 1875).

7. *Janetschekia lesserti* Schenkel 1939 (♀♂ from Dr K. Thaler, Innsbruck) = *Janetschekia (Erigone) monodon* (Cambr. 1872) (type ♂ from Hope Dept., Oxford; several ♀♂ (labelled *Erigone monodon*) from Koch Coll., B.M.N.H., London).
8. *Troxochrus sulcatus* Simon 1926 (♂, Tube No. 22840.B.883, M.N.H.N., Paris) = *Thyreosthenius parasiticus* (Westr. 1851).

References

BISHOP, S. C. and CROSBY, C. R., 1935: Studies in American spiders: miscellaneous genera of Erigoneae. Part I. *Jl.N.Y.ent.Soc.* **18**: 217-281.

BISHOP, S. C. and CROSBY, C. R., 1938: Studies in American spiders: miscellaneous genera of Erigoneae. Part II. *Jl.N.Y.ent.Soc.* **46**: 55-107.

BLEST, A. D., 1976: The tracheal arrangement and the classification of linyphiid spiders. *J.Zool.* **180**: 185-194.

BRISTOWE, W. S., 1938: The classification of spiders. *Proc. zool.Soc.Lond.* (Ser.B), **108**: 285-322.

CHAMBERLIN, R. V. and IVIE, W., 1947: The spiders of Alaska. *Bull.Univ.Utah biol.Ser.* **37**, 51.

CROSBY, C. R. and BISHOP, S. C., 1925: Studies in New York spiders (*Ceratinella* and *Ceraticelus*). *Bull.N.Y. St.Mus.* **264**: 1-46.

CROSBY, C. R. and BISHOP, S. C., 1928: Revision of the spider genera *Erigone, Eperigone* and *Catabrithorax* (Erigoneae). *Bull.N.Y.St.Mus.* **278**: 1-98.

CROSBY, C. R. and BISHOP, S. C., 1932: Studies in American spiders: the genus *Grammonota. Jl.N.Y.ent.Soc.* **40**: 393-421.

CROSBY, C. R. and BISHOP, S. C., 1933: American spiders: Erigoneae, males with cephalic pits. *Ann.ent.Soc.Am.* **26**, 105-182.

HELSDINGEN, P. J. van, 1969: A reclassification of the species of *Linyphia* Latreille based on the functioning of the genitalia (Araneida, Linyphiidae) I. *Zool.Verh., Leiden*, **105**: 1-303.

HENNIG, W., 1966: *Phylogenetic Systematics.* Univ. of Illinois Press, Urbana. Chicago and London.

HOLM, Å., 1943: Zur Kenntnis der Taxonomie, Ökologie und Verbreitung der schwedischen Arten der Spinnengattungen *Rhaebothorax* Sim., *Typhochraestus* Sim. und *Latithorax* n.gen. *Ark.Zool.* **34A**: 1-32.

HOLM, Å., 1962: The spider fauna of the East African mountains. *Zool.Bidr.Upps.* **35**: 19-204.

HOLM, Å., 1975: A new species of the genus *Erigone* Sav. and Aud. (Araneae: Erigonidae) from Swedish Lapland. *Ent.Tidskr.* **96**: 17-23.

HULL, J. E., 1920: The spider family Linyphiidae: an essay in taxonomy. *Vasculum*, **6**: 7-11.

JACKSON, A. R., 1932: On new and rare British spiders. *Proc.Dorset nat.Hist.archaeol.Soc.* **53**: 200-214.

LEHTINEN, P. T., 1975: Notes on the phylogenetic classification of Araneae. *Proc.6th Int.Congr.Arachnol.1974:* 26-29.

LEHTINEN, P. T. and SAARISTO, M., 1970: Principles in limiting supraspecific taxa of Linyphiidae. *Bull.Mus. natn.Hist.nat., Paris* **41** (2): 155-160.

LEHTINEN, P. T. and SAARISTO, M., 1972: *Tallusia* gen.n. (Araneae, Linyphiidae). *Ann.Zool.Fenn.* **9**: 265-268.

LEVI, H. W., 1961: Evolutionary trends in the development of palpal sclerites in the spider family Theridiidae. *J.Morph.* **108**: 1-10.

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

LEVI, H. W. and KIRBER, W. M., 1976: On the evolution of tracheae in arachnids. *Bull.Br.arachnol.Soc.* **3**(7): 187-188.

LOCKET, G. H., 1974: Notes on some African Linyphiid spiders. *Publçoes cult.Co.Diam.Angola*, **88**: 167-176.

LOCKET, G. H. and MILLIDGE, A. F., 1953: *British Spiders* **2**: 1-449. Ray Soc., London.

MERRETT, P., 1963: The palpus of male spiders of the family Linyphiidae. *Proc.zool.Soc.Lond.* **140**: 347-467.

MERRETT, P., 1965: The palpal organs of *Acartauchenius scurrilis* and *Syedra gracilis* (Araneae: Linyphiidae). *J.Zool.* **146**: 467-469.

MILLIDGE, A. F., 1975(1): A taxonomic revision of the genus *Erigonoplus* Simon 1884 (Araneae: Linyphiidae: Erigoninae). *Bull.Br.arachnol.Soc.* **3**(4): 95-100.

MILLIDGE, A. F., 1975(2): Re-examination of the erigonine spiders *"Micrargus herbigradus"* and *"Pocadicnemis pumila"* (Araneae: Linyphiidae). *Bull.Br.arachnol.Soc.* **3**(6): 145-155.

MURGATROYD, J. H., 1954: Anomalous specimens of *Erigone longipalpis* (Sund.) (Araneae: Linyphiidae). *Entomologist's mon.Mag.* **90**: 231.

MURPHY, F., 1974(1): Occurrence of TmIV on *Erigone longipalpis* (Sund.) *Newsl.Br.arachnol.Soc.* **9**: 9.

MURPHY, F., 1974(2): Two field meetings at Hackhurst Downs, Surrey. *Newsl.Br.arachnol.Soc.* **9**: 9.

PALMGREN, P., 1976: Die Spinnenfauna Finnlands und Ostfennoskandiens. VII. Linyphiidae 2. *Fauna fenn.* **29**: 1-126.

SAARISTO, M., 1971: Revision of the genus *Maro* O. P. Cambridge (Araneae: Linyphiidae). *Ann.Zool.Fenn.* **8**: 463-482.

SAARISTO, M., 1972: Redelimitation of the genus *Oreonetides* Strand 1901 (Araneae, Linyphiidae) based on an analysis of the genital organs. *Ann.Zool.Fenn.* **9**: 69-74.

SAARISTO, M., 1973(1): Taxonomical analysis of the type species of *Agyneta, Anomalaria, Meioneta, Aprolagus* and *Syedrula* (Araneae: Linyphiidae). *Ann.Zool.Fenn.* **10**: 451-466.

SAARISTO, M., 1973(2): Delimitation of the sub-family Lepthyphantinae (Araneae, Linyphiidae) according to the secondary genital organs. *Ann.Zool.Fenn.* **10**: 388-390.

SAARISTO, M., 1974: Taxonomical analysis of *Theonina cornix* (Simon 1881), the type species of the genus *Theonina* Simon 1929 (Araneae, Linyphiidae). *Ann. Zool.Fenn.* **11**: 240-243.

THALER, K., 1973: Über wenig bekannte Zwergspinnen aus den Alpen, III (Arachnida: Aranei, Erigonidae). *Ber.naturw.-med.Ver.Innsbruck*, **60**: 41-60.

WIEHLE, H., 1960: Spinnentiere oder Arachnoidea (Araneae) XI. Micryphantidae – Zwergspinnen. *Tierwelt Dtl.* **47**: 1-620.

WUNDERLICH, J., 1970: Zur Synonymie einiger Spinnen-Gattungen und -Arten aus Europa und Nordamerika (Arachnida: Araneae). *Senckenberg biol.* **51**: 403-408.

WUNDERLICH, J., 1972(1): Neue und seltene Arten der Linyphiidae und einige Bemerkungen zur Synonymie (Arachnida: Araneae). *Senckenberg biol.* **53**: 291-306.

WUNDERLICH, J., 1972(2): Zur Kenntnis der Gattung *Walckenaeria* Blackwall 1833 unter besonderer Berücksichtigung der europäischen Subgenera und Arten (Arachnida: Araneae: Linyphiidae). *Zool.Beitr.* **18**(3): 371-427.

Index to Genera and Species

Main text references in **bold** type, page numbers of figures in *italics*