The genera *Mecopisthes* Simon and *Hypsocephalus* n.gen. and their phylogenetic relationships (Araneae: Linyphiidae)

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Summary

The genus *Mecopisthes* Simon is revised, and the species *dahli, huberti, nesiotes* and *paulae* are transferred into *Hypsocephalus* **n.gen.** The sister group relationship of *Pelecopsis* and *Mecopisthes* is supported by a cladistic analysis of selected characters. The phylogenetic relationships of *Hypsocephalus* with *Pelecopsis/Mecopisthes* and with *Silometopus* are discussed, and investigated by cladistic analysis; a scheme showing the inferred relationships is given. *Mecopisthes latinus* **n.sp.** is described.

Genus *Mecopisthes*

The genus *Mecopisthes* Simon 1926 has, up to now, been regarded as composed of the following species:

M. silus (Cambr.) – type species
M. crassirostris (Simon)
M. dahli (Lessert)
M. huberti Millidge
M. nesiotes (Simon)
M. nicaensis (Simon)
M. paulae (Simon)
M. peuceticus Caporiacco
M. peusi Wunderlich

An additional species, *M. latinus* n.sp. can now be added to this list (for description, see later in this paper).

Wunderlich (1972) regards *dahli* (Lessert 1909) as a synonym of *pusillus* Menge 1869; there is some evidence for this from Menge's figure, but in the absence of any specimens named by Menge, and in view of the confusion surrounding the use of the name *pusillus* Menge in the past, stability of nomenclature will probably best be served by regarding *pusillus* as a *nomen dubium.*

M. pictonicus Denis 1949 (described on the female only) was synonymized by Denis himself (1964(1)) with *M. silus,* but Thaler has suggested *(in litt.)* on the basis of Denis' figures that *pictonicus* may be a senior synonym of *peusi.* It has not been possible so far to clear up this point, as specimens of *pictonicus* have not been obtainable.

Re-examination of the male palps of all the species listed above (except *huberti*: male unknown) now shows that only *crassirostris, latinus, nicaensis, peuceticus* and *peusi* are congeneric with the type.

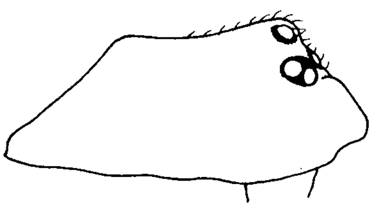
The genus *Mecopisthes* comprises small spiders (2 mm or less in length) which have no dorsal tibial spines in the male, and in the female have either very short spines (1-1-1-1) or none; TmI is *ca* 0.6, and metatarsus IV has no trichobothrium. The males have a projecting clypeus, and the cephalothorax in both sexes is high anteriorly, sloping sharply posteriorly (Figs. 1-5) (exception: *M. nicaensis* ♂ which has a cephalic lobe rather like *Pelecopsis* (Millidge, 1977)).

The palpal organs of the true *Mecopisthes* species are all closely similar in form (conformation), and this conformation is regarded as a synapomorphous character indicating that the genus is monophyletic. The embolic division (ED) (Fig. 7) has a long tail, tapering to a point posteriorly; the embolus is a coil, stout at the base but becoming very thin distally. The duct enters the ED on the mesal side, near the base of the tail, and loops back along the embolus (Millidge, 1977). The ED is almost identical in all the species, though there may be small differences in the length of the tail (Wunderlich, 1972). The suprategulum (ST) is stout and runs more or less along the margin of the cymbium on the mesal side. The suprategular apophysis (SA) is made up of several parts (Fig. 7), best seen when the palp is viewed from in front (Figs. 8-16): (1) a semi-membranous part, with a dark pointed tip; (2) a thin transparent membranous piece arising from near the base of (1) – this is shown only in Figs. 7, 8, 11, 14; (3) a more or less sclerotised apophysis composed of a pointed tooth (a) and an adjacent section (b) of variable shape; (4) in *silus* and *peuceticus* there is a prominent curved tusk-like apophysis arising at the base of (1). Parts (1) and (2) are closely similar in form in all the species, but the apophysis (3b) differs from species to species (though *silus, peuceticus* and *peusi* are fairly close) and gives a reliable means for separating the males in most cases. There are small variations in 3b within a species.

So far as the males of *Mecopisthes* are concerned, *silus* and *peuceticus* are immediately recognisable by the presence of apophysis 4 (Figs. 8, 11). There seems to be a good deal of minor variation in the shape of apophysis 3b in specimens of *silus* from different localities (Figs. 9, 10). The apophysis 3b in *peuceticus* is very close to *silus,* while apophysis 4 seems to be shorter and stouter in *peuceticus* than in *silus*. In *peusi* 3b shows less variation (Figs. 14, 15). *M. crassirostris* has a prominent and distinctive apophysis 3b (Fig. 12); *latinus* also has this apophysis relatively large (Fig. 13). *M. nicaensis* is immediately recognisable by the form of the male head, and the lightly sclerotised apophysis 3b is triangular in shape (Fig. 16). *M. silus, peuceticus* and *latinus* have a clear dorsal abdominal scutum in the male, a character which is absent or only very weakly developed in the remaining species.

The females of *Mecopisthes* are closely similar in epigyne/vulva; I have not seen a female which can be reliably attributed to *crassirostris,* and the female of *nicaensis* is not known. *M. silus* and *peuceticus* seem to have identical epigynes; *peusi, latinus* and *silus/peuceticus* can probably be diagnosed by the shape of the epigynal opening (Figs. 18, 20, 21); in addition, *peusi,* which seems to be always more obscure in colour (in fresh specimens) with less detail of the internal vulva showing through the integument, has clear circular depressions on either side of the opening, which are normally absent or scarcely visible in *silus/peuceticus* and *latinus* (cf. however Fig. 19). The variations in the epigyne of what appears to be *silus,* but taken in different areas (cf. Figs. 18, 19), coupled with the slightly different apophyses 3b of males (Figs. 8-10) from various areas, does raise the question whether *M. silus* auct. may be a complex of sibling species, of which *M. peuceticus* would be one. This question cannot at present be resolved.

The genus *Mecopisthes* appears to be limited to Europe and N. Africa. The species *M. tokumotoi* (Oi, 1964) from Japan does not, on the basis of the figures given, belong in the genus. *M. silus* has been recorded from central, southern and eastern Europe, and from N. Africa (Denis, 1964(2)). *M. peuceticus* is based on specimens from S. Italy (Caporiacco, 1953). *M. peusi* has been taken in Britain, probably France,



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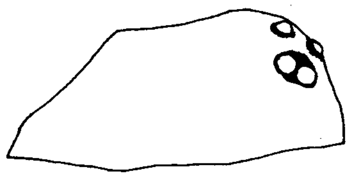

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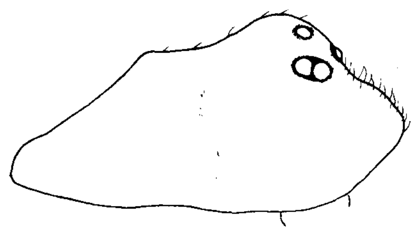

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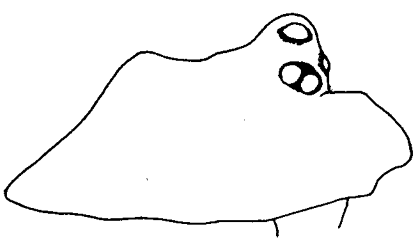

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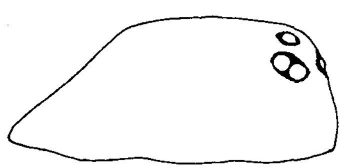

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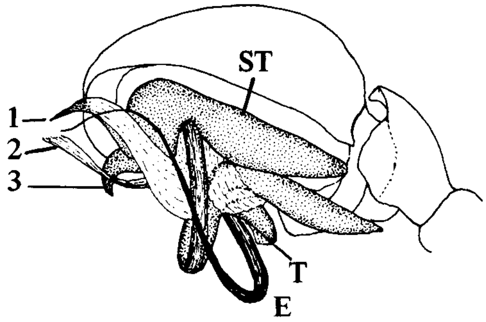
Figs. 1-5: Cephalothorax profiles. **1** *Mecopisthes silus* ♂; **2** *M. silus* ♀; **3** *M. crassirostris* ♂; **4** *M. latinus* ♂; **5** *M. latinus* ♀.

Fig. 6: *M. latinus* ♂, clypeus and eyes from above.



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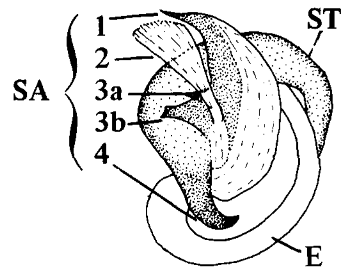

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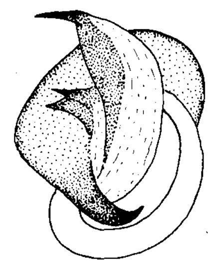

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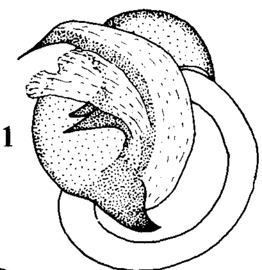

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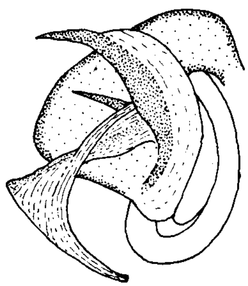

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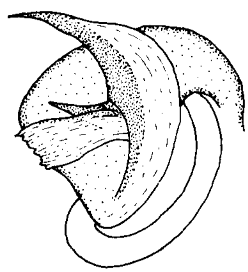

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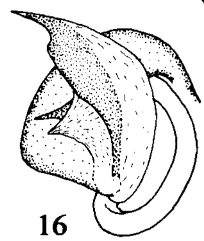

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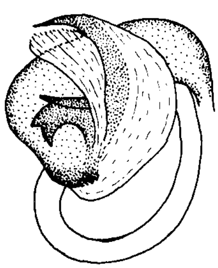

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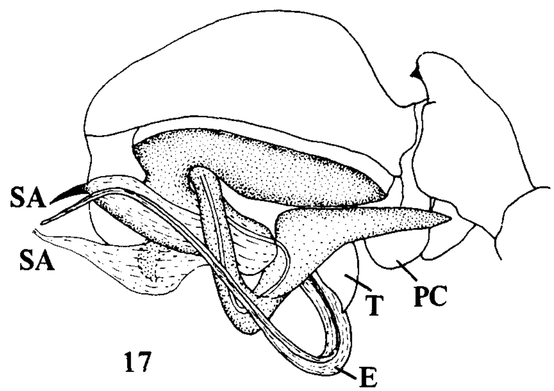

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Fig. 7: *Mecopisthes peusi* ♂ palp, mesal view.

Figs. 8-16: Palpal organs from in front. **8** *M. silus* (O. P.-Cambridge type); **9** (?) *M. silus* (Yugoslavia); **10** (?) *M. silus* (Koch Coll., BM (NH)), apophysis 3; **11** *M. peuceticus* (left palp, reversed); **12** *M. crassirostris;* **13** *M. latinus*; **14** *M. peusi* (Germany); **15** *M. peusi* (Britain), apophysis 3; **16** *M. nicaensis.*

Fig. 17: *M. latinus* ♂ palp, mesal view.

All male palps are right palps, unless otherwise stated. Abbreviations used: ST = suprategulum, SA = suprategular apophysis (for numerals, see text), ED = embolic division, E = embolus, T = tegulum, D = duct in tegulum, PC = paracymbium.

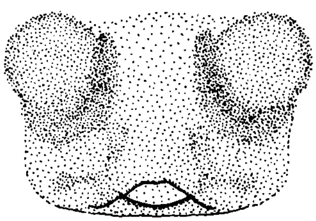
W. Germany, E. Germany and Austria. *M. crassirostris* has been recorded only from southern France, close to the Mediterranean, and from Portugal (Machado, 1949). *M. nicaensis* is based on a single male from Nice. *M. latinus* is recorded from central Italy (see below).

Description of *Mecopisthes latinus* n.sp.

Total length: ♀ *ca* 1.8 mm, ♂ *ca* 1.45 mm. *Cephalothorax:* length ♀ *ca* 0.8 mm, ♂ *ca* 0.9 mm. Orange, with slightly darker fovea and striae. ♂ with strongly projecting clypeus (Figs. 4, 6). Profiles (Figs. 4, 5). *Chelicerae:* stridulatory file scarcely visible. *Eyes:* fairly large, with posteriors (♀) all *ca* 1d apart. *Abdomen:* ♀ grey, with paler chevrons and 4 clear reddish impressed dots dorsally; clothed with very short hairs. ♂ with orange-brown scutum covering whole dorsal surface. *Sternum:* orange, with darker margins. *Legs:* pale orange to orange-brown, short and stout with tibia I l/d *ca* 4 (♀). All tibiae (♀♂) spineless. Metatarsi I-III with a trichobothrium, TmI (♀♂) 0.55-0.60. *Epigyne:* Fig. 21; the opening is rather small, almost circular, but difficult to see in some specimens. *Male palp:* Fig. 17; the tail is slightly different in shape from the other species. The form of the apophysis 3b of the SA (Fig. 13) distinguishes *latinus* from its congeners. The tibia (Fig. 22) is similar to *peusi*, but the lateral extension is somewhat longer. *Material:* All the specimens were taken in Italy, and sent to the author by Prof. P. M. Brignoli. 3♂ 4♀ from Riano Flaminio (Lazio), 5.3.67; 1♂ Bivgliano (Tuscany), 23.3.67; 2♀, Greve (Tuscany), 15.4.67. The ♂ holotype and a ♀ paratype from Riano Flaminio will be deposited at the M.N.H.N., Paris.

Phylogenetic position of *Mecopisthes*

The author has suggested (Millidge, 1977) that *Pelecopsis* and *Mecopisthes* may be sister groups. This hypothesis can be supported by a cladistic analysis based on the following characters:



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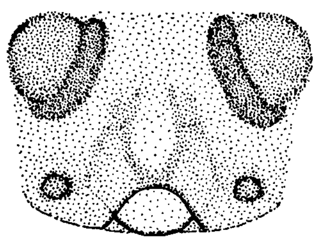

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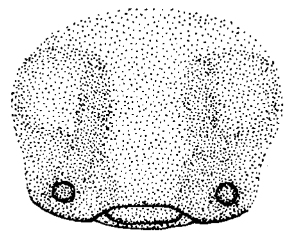

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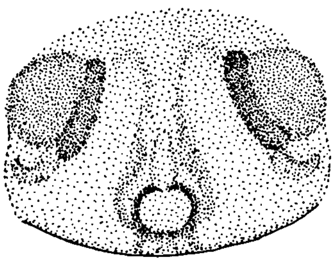

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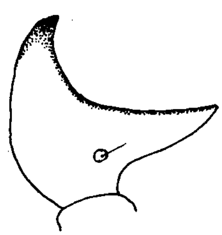

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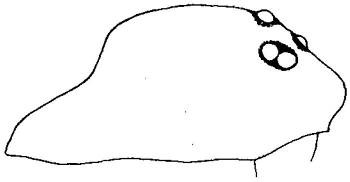
Figs. 18-21: Epigynes. **18** *Mecopisthes silus* (Austria); **19** (?) *M. silus* (Yugoslavia); **20** *M. peusi* (Britain); **21** *M. latinus*.

Fig. 22: *M. latinus* ♂ palpal tibia (dorsal).



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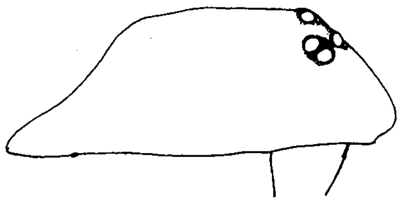

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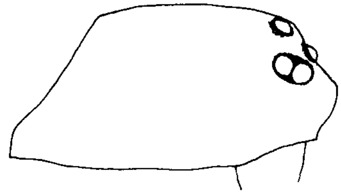

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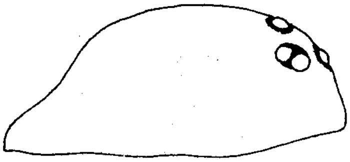

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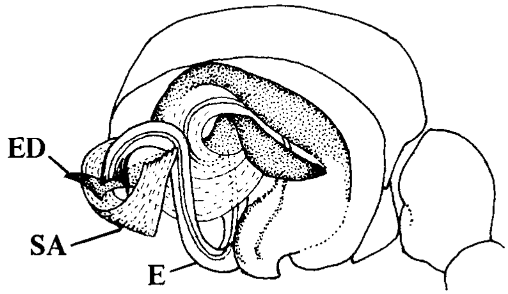

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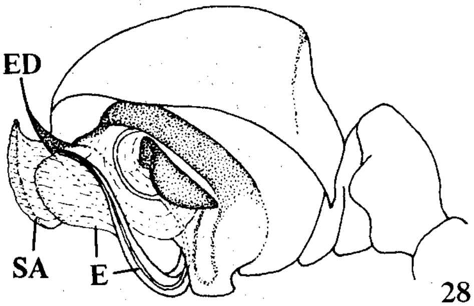

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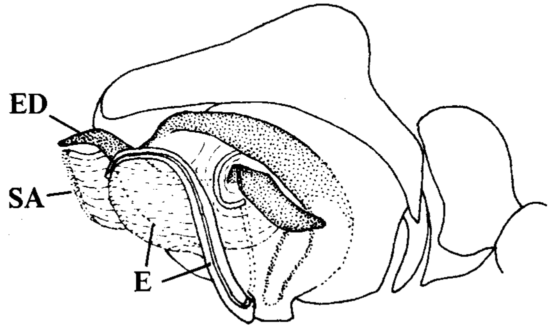

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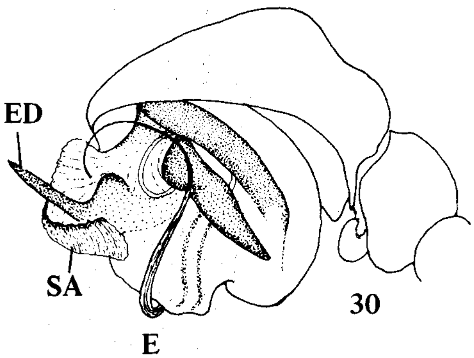

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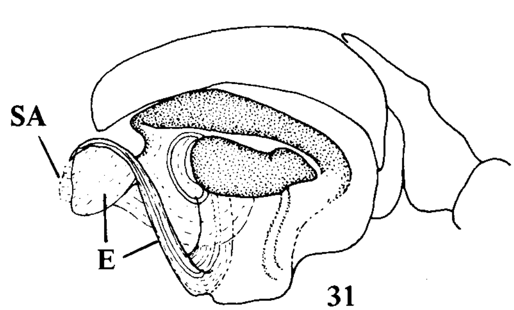

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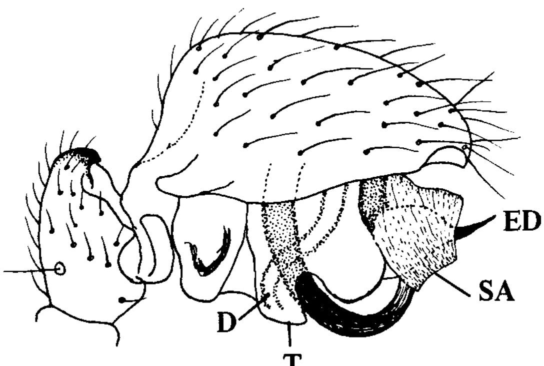
Figs. 23-26: Cephalothorax profiles. **23** *Hypsocephalus dahli* ♂; **24** *H. nesiotes* ♂; **25** *H. paulae* ♂; **26** *H. dahli* ♀.

Figs. 27-31: Male palps, mesal. **27** *H. dahli*; **28** *H. paulae*; **29** *H. nesiotes*; **30** *Silometopus ambiguus* (Cambr.); **31** *Pelecopsis coccinea*.

1. basic palpal conformation: both the *Pelecopsis* and the *Mecopisthes* conformations can be inferred to have been derived from a common ancestral form.
2. scutum on abdomen (♂, occasionally ♀): regarded as apomorphous.
3. tibial spines 1111, very short, or none: regarded as apomorphous.
4. projecting clypeus (Figs. 1, 3, 4): regarded as apomorphous.
5. raised cephalothorax, with thorax steeply sloping (e.g. Fig. 3): regarded as apomorphous (note: it is possible that 4 + 5 should be regarded as a single character).
6. distinct cephalic lobe (*Pelecopsis* type) in ♂: regarded as apomorphous.
7. trichobothrium on metatarsus IV: presence regarded as plesiomorphous, absence as apomorphous (this must however be regarded as uncertain).

It is to be noted that not all the species in either of the two genera display all the characters listed. It is suggested however that the "tendency" by a group of related species to show characters or combinations of characters in common with other groups may be regarded as a "character" for the groups concerned, because this "tendency" is presumably the visible expression of a more fundamental character, viz. some feature in the genetic coding which is common to the groups concerned.

The cladistic analysis gives the cladogram shown in



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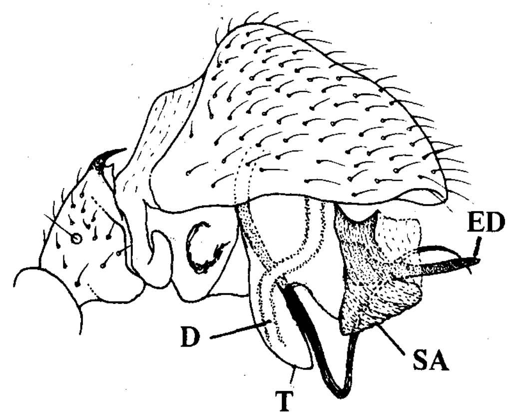

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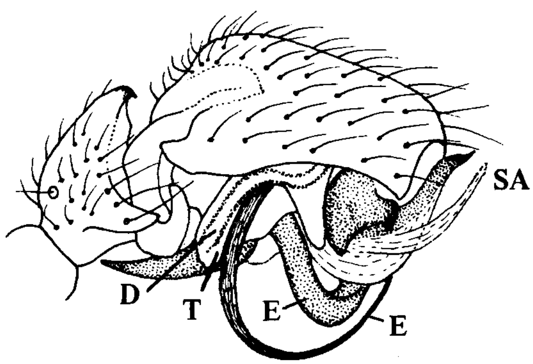

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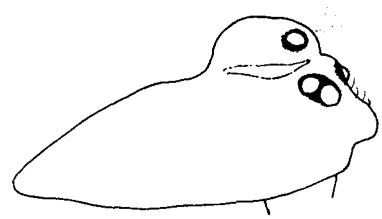

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Figs. 32-34: Male palps, ectal. 32 *Hypsocephalus dahli*; 33 *Silometopus ambiguus*; 34 *Mecopisthes peusi*.

Fig. 35: *Pelecopsis parallela* (Wid.) ♂ cephalothorax profile.

Fig. 36. This shows the presence of perhaps 6 synapomorphies, which (if the assumptions made on the characters used are correct) supports the hypothesis that *Pelecopsis* and *Mecopisthes* form a monophyletic group, i.e. are sister groups.

Genus *Hypsocephalus* n.gen.

The species *dahli, paulae* and *nesiotes*, which have the cephalothorax in both sexes like *Mecopisthes* (Figs. 23-26), have palpal conformations similar to one another, but different from *Mecopisthes*. The basic conformation (Figs. 27-29) is similar to that of *Silometopus*, the ED having a forward-directed apophysis ending in a point anteriorly (Millidge, 1977). The SA in each of these 3 species is lamellar and only lightly sclerotised, slightly curved distally towards the mesal side in *paulae* and *nesiotes*, and more strongly so in *dahli* (Fig. 27); this form of SA is rather similar to that of *Silometopus* species (e.g. Fig. 30) but quite different from *Mecopisthes*. The embolus in the *dahli* group is significantly shorter than in *Silometopus*, and terminally not whiplike. In *dahli* the embolus broadens distally into a flat lamella terminating in two points (Fig. 27). In *paulae* and *nesiotes* the embolus is broadened distally by a roughly semicircular membranous lamella (Figs. 28, 29); this unusual addendum to the embolus is present also in *Pelecopsis coccinea* (Cambr.) (Fig. 31), a N. African species which seems to be a true *Pelecopsis*, and also in *Metopobactrus rayi* Sim. (Millidge, 1977, fig. 99) which stands somewhat apart from the remaining *Metopobactrus* species. The palpal tibial apophyses (Figs. 37-39) can be regarded as intermediate between *Mecopisthes* and *Silometopus*.

The author is not in favour of creating new genera in the Linyphiidae, except where it appears to be absolutely necessary. This seems to be the case, however, for the small group of species comprising *dahli, paulae* and *nesiotes*, which are now placed in the new genus *Hypsocephalus* (derivation: *hypsos*, height, *kephale*, head): type species *dahli*. This genus is defined on the palpal conformation of the male, combined with the form of the male cephalothorax and of the female epigyne, and the chaetotaxy (tibial spines 1111, very short, or none; TmI 0.55-0.60). The males do not have abdominal scuta.

The species concerned are:

Hypsocephalus dahli (Lessert) n.comb.
H. paulae (Simon) n.comb.
H. nesiotes (Simon) n.comb.
H. huberti (Millidge) n.comb. – see below

The males of *Hypsocephalus* can be diagnosed by the form of the palpal tibial apophysis (Figs. 37-39), but better by the palpal organs. The form of the SA, the form of the pointed anterior apophysis of the ED, and the form of the embolus distinguish *dahli* (Fig. 27), while *paulae* and *nesiotes* which seem to have very similar SA's and emboli can probably be separated by the much reduced clypeal projection in *paulae* (cf. Figs. 24, 25) and by the shape of the anterior point of the ED (Figs. 28, 29). Fresh specimens are necessary to confirm these differences.

The females of *Hypsocephalus* have epigynes/vulvae (Figs. 40-44) which are somewhat similar to, but different from, the *Mecopisthes* species; the female of *nesiotes* is not known. On the basis of the epigyne, *huberti* (Fig. 42) almost certainly belongs in *Hypsocephalus* rather than in *Mecopisthes;* as noted earlier (Millidge, 1975) *huberti* may possibly be the female of *nesiotes*. The epigynes probably differ sufficiently

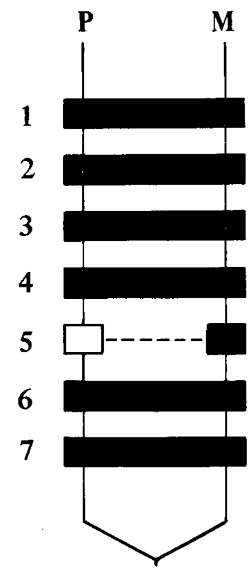


Fig. 36: Cladogram of *Pelecopsis* (P) and *Mecopisthes* (M). Numbers refer to numbered characters in text: black = apomorphous state of character, white = plesiomorphous state.

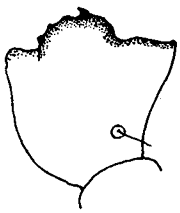
one from another to be satisfactory for diagnosis of the species, though fresh specimens of *paulae* are required to make certain of this.

The genus *Hypsocephalus* seems to be limited to central and southern Europe: *dahli* has been recorded from Switzerland, Austria, Germany and Czechoslovakia; *paulae* from the region of Menton (S. France); and *nesiotes* and *huberti* from Corsica.

Phylogenetic relationships of *Hypsocephalus*

The spiders of the genus *Hypsocephalus* exhibit a number of characters in common with species in both the *Pelecopsis/Mecopisthes* group and the genus *Silometopus*. These are:

(i) basic palpal conformation (see above)
(ii) form of SA (see above)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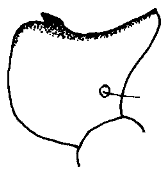
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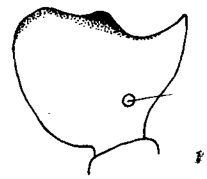
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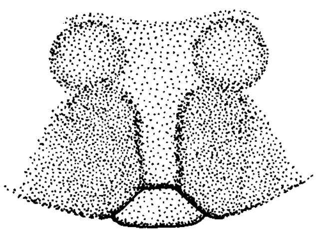
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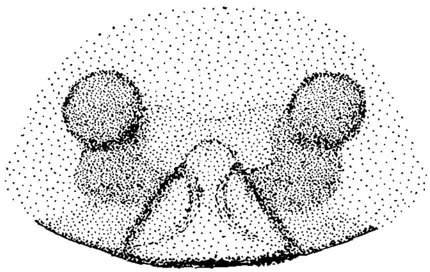
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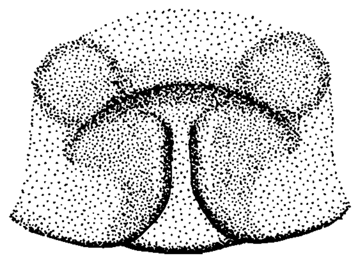
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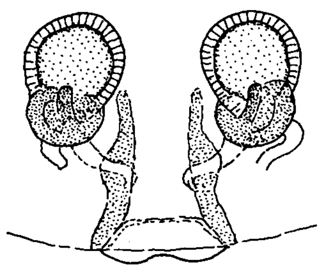
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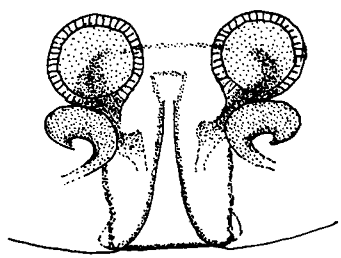
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Figs. 37-39: Male palpal tibiae, dorsal. **37** *Hypsocephalus dahli*; **38** *H. paulae*; **39** *H. nesiotes*.

Figs. 40-42: Epigynes. **40** *H. dahli*; **41** *H. paulae*; **42** *H. huberti*.

Figs. 43-44: Vulvae. **43** *H. dahli*; **44** *H. huberti*.

(iii) semicircular lamella on embolus (see above)
(iv) form of the tegulum and the duct in the tegulum, viz. on the ectal side the embolus runs down behind the tegulum (which is flattened in this area) and emerges from a notch in the tegulum; the duct runs down the tegulum in a double bend across the line of the embolus (Figs. 32-34): character present in *Silometopus* and *Mecopisthes.*
(v) projecting clypeus in ♂: present in *Mecopisthes* and some *Pelecopsis* species (Fig. 35).
(vi) carapace profile (Figs. 23-26): as in *Mecopisthes*
(vii) very short tibial spines or none: as in *Pelecopsis, Mecopisthes* and *Silometopus.*
(viii) TmI 0.55 or higher.

It is to be noted that, as in the *Pelecopsis/Mecopisthes* case discussed above, not all the species in the genera mentioned display all the characters listed.

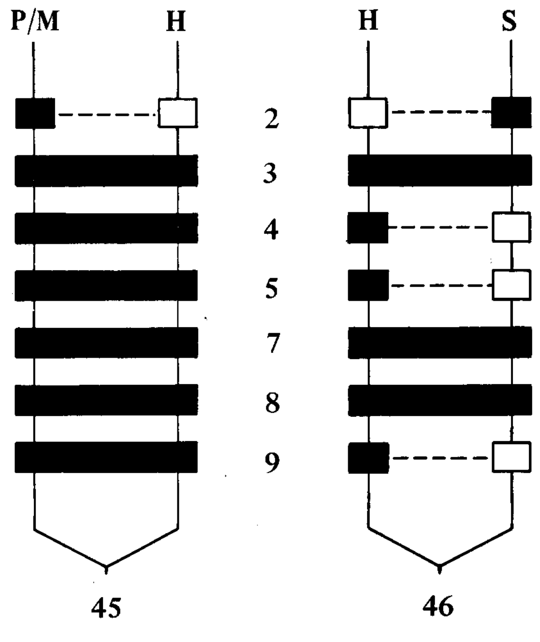
The possession by *Hypsocephalus* of characters in common with both the *Pelecopsis/Mecopisthes* group and the genus *Silometopus* (some at least of these characters being probably apomorphous with respect to the hypothetical ancestral species of these genera) suggests that *Hypsocephalus* forms part of a monophyletic group which includes these genera, and that it occupies a phylogenetic position somewhere between *Pelecopsis/Mecopisthes* and *Silometopus.* This hypothesis, that the genus *Silometopus* is monophyletic with *Pelecopsis/Mecopisthes* (plus *Hypsocephalus*) cannot be properly supported at present by a cladistic analysis, but is based additionally on the inference that the palpal conformations of the *Pelecopsis* type and of the *Silometopus* type can both be derived from a conformation of an intermediate type (Millidge, 1977) present in an ancestral species, in the former case by loss of the anterior portion of the ED and in the latter case by development or modification of this anterior part of the ED.

The two phylogenetic possibilities for the genera concerned are shown in Figs. 47, 48. The two hypotheses given can be examined by cladistic analysis, on the basis of characters 2, 3, 4, 5 and 7 given earlier (p. 118) for the *Pelecopsis/Mecopisthes* case, plus two additional ones:

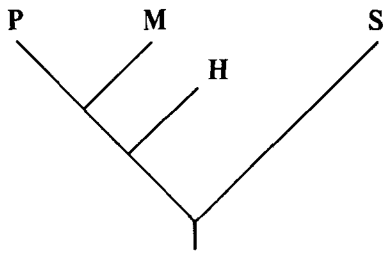
8. character (iv) above (form of tegulum and duct): assumed to be apomorphous.
9. character (iii) above (lamella on embolus): assumed to be apomorphous.

(Note: Character 1 is not used in this analysis, as it is uncertain whether the *Hypsocephalus* and *Silometopus* conformations should be regarded as apomorphous or plesiomorphous relative to the ancestral form; in character 2, use is made of the fact that a scutum is present in a new species of *Silometopus* to be described soon by Dr K. Thaler (Innsbruck); character 6 has been omitted as probably not relevant to the present analysis).

The cladograms are given in Figs. 45, 46. Since both hypotheses (Figs. 47, 48) cannot be correct, it can be inferred that characters 3, 7 and 8 which indicate synapomorphy in both possibilities must be eliminated, on the ground that they probably represent parallelisms. This leaves 3 synapomorphies in Fig. 45, which supports the hypothesis that *Pelecopsis/Mecopisthes* and *Hypsocephalus* form a monophyletic group and are sister groups. Thus the phylo-



Figs. 45-46: Cladograms. **45** *Pelecopsis/Mecopisthes* (P/M) and *Hypsocephalus* (H); **46** *Hypsocephalus* (H) and *Silometopus* (S). Numbers refer to numbered characters in text: black = apomorphous state of character, white = plesiomorphous state.



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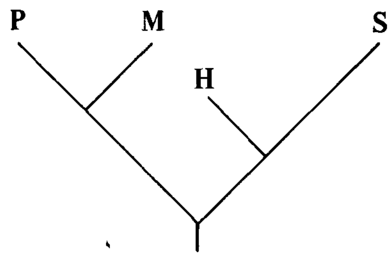

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Figs. 47-48: Possible phylogenetic schemes for the genera *Pelecopsis* (P), *Mecopisthes* (M), *Hypsocephalus* (H) and *Silometopus* (S).

genetic scheme given in Fig. 47 is regarded as the best hypothesis on the basis of the data used. Strictly speaking, on the basis of this hypothesis, the *dahli* group of species *(Hypsocephalus)* must be of supra-generic rank, since it is the sister group of the complex comprising two genera. It is however proposed to ignore this problem.

Because of the few characters available, most of which refer to the male sex, and because of the assumptions which have to be made regarding these characters, it must be admitted that these cladistic analyses may be regarded as not wholly convincing. They do serve, however, to draw attention to the possibilities that may exist for cladistic analysis within the Linyphiidae, as well as to the difficulties and uncertainties associated with such analyses at the present time.

Conclusions

An attempt has been made in this paper to deduce the phylogenetic relationships within a small part of the family Linyphiidae. In an exercise of this kind, based on limited data, it is impossible to avoid uncertainties and ambiguities, and the result is always in the nature of a hypothesis. Nevertheless, despite the problems, the author is hopeful that, working on the basis of a combination of the palpal conformation and other characters (Millidge, 1977, and this paper), it should in time be possible to build up useful phylogenetic "models" of a number of sections of the Linyphiidae. The word "model" is used advisedly, because the phylogenetic schemes produced will always be models (in the scientific sense), that is, representations the purpose of which is to aid our understanding and to suggest further lines of investigation. Although these models, unlike their (usually) more mathematical counterparts in the physical sciences, can never be directly tested by experiment, they can nevertheless be regarded as proper scientific hypotheses which are potentially refutable by further data. The derivation of such models should serve a useful purpose: the phylogenetic approach, by injecting more scientific discipline into taxonomic studies, should bring a greater degree of order into the somewhat confused systematics of the Linyphiidae.

Acknowledgements

The author gratefully acknowledges the generous gifts and loans of specimens from the following: Prof. P. M. Brignoli (L'Aquila); Mrs C. Deeleman (Ossendrecht); Prof. F. Miller (Brno); Dr K. Thaler (Innsbruck); J. Wunderlich (Neuenbürg); Muséum Nat. d'Hist. Naturelle, Paris (M. Hubert); British Museum (Nat. Hist.), London (F. Wanless); Hope Department, Oxford (E. Taylor); Natur-Museum, Senckenberg, Frankfurt (M. Grasshoff); Museo Civico di Storia Naturale, Trieste (R. Mezzana).

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The genera *Saaristoa* n.gen. and *Metapanamomops* Millidge (Araneae: Linyphiidae)

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In a paper published recently (Millidge, 1977) the author erected two genera, *Saaristoa* and *Metapanamomops*. By an oversight, the type species of these two genera were not designated. *Metapanamomops* is available by monotypy, but *Saaristoa* is unavailable under Rule 13b of I.C.Z.N. It is the purpose of this short note to designate the type species of *Saaristoa* and to make the generic name available from the date of publication of the present paper.

Genus *Saaristoa* n.gen.

This genus is erected for the species *abnormis* Bl. and *firmus* Cambr., previously placed in the genus *Oreonetides* Strand 1901. The genus is named for M. Saaristo, who indicated (1972) that these species are not congeneric with the type species (*vaginatus* Thor.) of *Oreonetides*. The type species of *Saaristoa* is *abnormis*. The genus is defined by the conformation of the male palp (Millidge, 1977) and by the chaetotaxy: the species have 2 dorsal spines on the tibiae, and there are no metatarsal spines; TmI (♀) is 0.35-0.45, and metatarsus IV has no trichobothrium.

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