Some comments on the anatomy of spiders

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In Nephila clavipes (L.), N. maculata (Fabr.), Azilia affinis (O.P.-Cambridge) and Cyrtophora moluccensis (Doleschall) the anatomy of the musculature and of the intestinal caeca of the prosoma characterizes these spiders as typical Araneidae

without any tetragnathid features.

In Comaroma simoni Bertkau, classified by recent authors as a theridid, the tergo-coxal and endosterno-coxal musculature appear to be unique (three symmetrically arranged tergo-coxal muscles; no upper endosterno-coxal muscles). Dissection of Ceratinella brevis (Wider) (Micryphantinae), Crustulina guttata (Wider), Steatoda bipunctata (L.), Dipoena tristis (Hahn) and Pholcomma gibbum (Westring), Theridiidae, suggests that the peculiarities of Comaroma cannot be interpreted as an adaptation to the strong sclerotization of the prosoma or as a general character of the smallest Theridiidae. The isolated taxonomic position of Comaroma is thus brought out. Comaroma lacks lungs and is perhaps related to the very heterogeneous Symphytognathidae complex.

The anatomy of *Psechrus argentatus* (Doleschall) and two other *Psechrus* spp. (not determined with certainty), Psechridae, is described (prosoma and opisthosoma).

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1. Anatomy of the genera Azilia, Nephila and Cyrtophora (Araneidae)

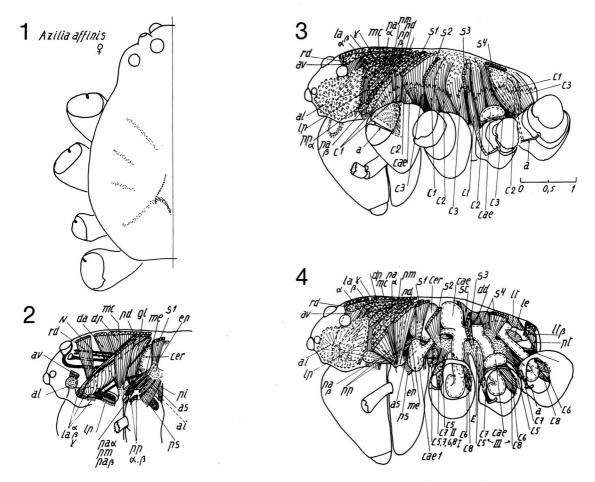
As shown in three earlier papers (Palmgren 1978 a & b, 1979), all species of the family Tetragnathidae studied by me differ from all species of other araneomorph spider families that I have dissected in the following respects: They have a posterior unpaired dorsal caecum (behind the dorsal apodeme) and lateral caecal branches extending not only to the coxae of the walking legs but also to the chelicers and, with the possible exception of Tetragnatha (Eugnatha) striata, to the pedipalps; these lateral branches protrude between the tergo-coxal muscles as pouches which extend more or less along the margin of the cephalothorax and contain guanine crystals. None of the species of the family Araneidae, including the genus Meta, share these features with the tetragnathids. The conclusion that Meta should not be included in the family Tetragnathidae (cf. Locket et al. 1974) is in accordance with Homann's views, founded on the anatomy of the eyes.

Professor H.W. Levi pointed out to me that the anatomy of the genera *Azilia*, *Cyrtophora* and *Nephila* would be of interest as an argument in a

discussion of their systematic position and the distinction between the subfamilies of Araneidae (incl. "Tetragnathinae"), and he kindly provided me with some specimens (\$\partial{\Phi}\$\Phi\$) of Azilia affinis (O.P.-Cambr.) and Nephila clavipes (L.) from Florida, and of Cyrtophora moluccensis (Doleschall) and Nephila maculata (Fabr.) from New Guinea (Wau). The preservation of Azilia was excellent. In the other specimens, the brain and the cheliceral and pedipalpal ganglia in particular had suffered maceration, but all essential features of the musculature and the intestinal organs could be clearly distinguished. When necessary, two specimens were compared.

Azilia affinis

Azilia (Figs. 1—4) corresponds almost completely to the European species of Araneidae dissected by me. The only differences observed are the following: M.antero-medialis verticalis (av) of the chelicera is extremely weak. M.tergo-pedipalpalis posterior (pp) arises as two portions. (M.tergopedipalpalis anterior (pa) has two fans, as in Araneus cornutus. It seems to be of very little taxonomic importance whether the tergo-pedipalpal muscles have one or two portions, and



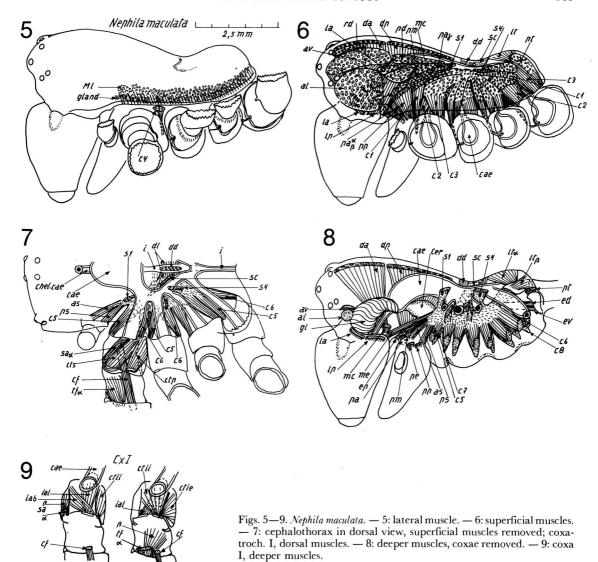
Figs. 1—4. Azilia affinis. — 1: cephalothorax, dorsal surface. — 2: superficial muscle layer. — 3: deeper muscles of chelicera and pedipalp. — 4: superficial muscles removed from pedipalp backwards, of leg I only trunks of muscles c 5—8 left.

individual variation appears probable.) The suspensor IV is cleft, with the origin of one fan on the dorsal apodeme, which is a very rare finding. The caecal branches to legs I and III give off small pouches between the anterior and posterior median tergo-coxal muscles (c_2 and c_3), a feature typical of the Tetragnathidae.

Nephila clavipes and maculata

The Nephila species (Figs. 5—9) have a very much stronger cheliceral m.antero-medialis verticalis than Azilia and thus resemble the Araneidae earlier dissected by me. N.clavipes has a cleft suspensor IV, N.maculata a single one; this feature is apparently of little taxonomic value.

The anterior tergo-pedipalpal muscle (pa) is double-fanned in N. clavipes, but triple-fanned in *N.maculata.* The m. tergo-coxalis anterior profundus $(c_1,$ "anterior rotator") of the first leg arises in N.clavipes as two broad portions; in N.maculata one of the portions is very narrow. None of the *Nephila* species has caecal pouches protruding between the tergo-coxal muscles. In N.clavipes the dorsal pouch is short. In N.maculata it extends to the base of the chelicerae and sends a very narrow tube into them, a feature reminiscent of the Tetragnathidae. In this species the poison gland is short, while in N.clavipes it extends to the dorsal apodeme. I have previously drawn attention to the apparent competition for space between the poison glands and the dorsal caecum.

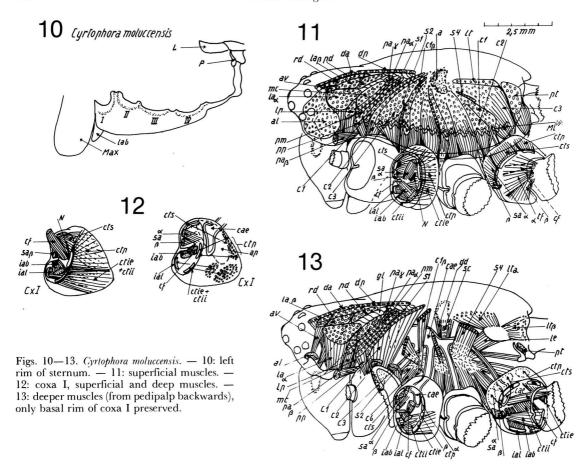


Cyrtophora moluccensis

Cyrtophora moluccensis (Figs. 10—13) possesses a lateral muscle (Ml) consisting of unusually bulky muscular lobes. The tergo-coxal musculature of leg IV is very powerful, especially the posterior-most of the median muscles $(c_3,$ the "posterior levator"; the m.plagulo-tergalis (pt) is also very bulky. Of the cheliceral muscles, m.lateralis anterior (la) is represented by two distinct muscles, a not uncommon variation; the m. antero-medialis verticalis (av) is very weak, as is

also the m.medialis pro-descendens (pd), but the m.retro-descendens (rd) is unusually strong. The tips of the poison glands and the dorsal caecum do not overlap.

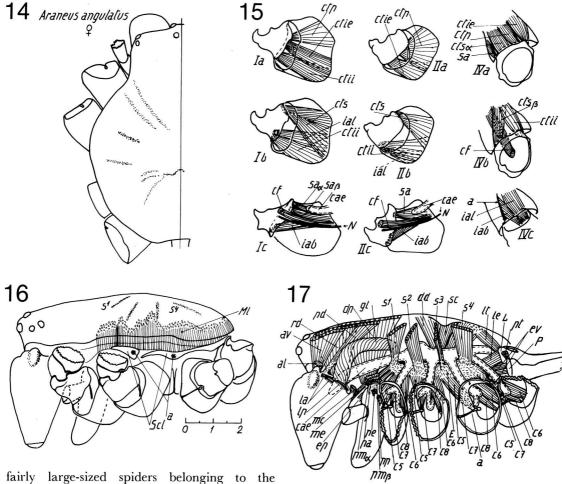
The caecal branches to the legs have a very typical araneid structure: they enter the coxae near the dorsal margin of the aperture, run downwards to the bottom of the coxae and bend under the ventral ganglion mass (cf. Millot). At the top of the coxa a small diverticulum protrudes along the axis of the coxa.



Araneus angulatus

All araneid species previously dissected by me are fairly small, the biggest being Araneus cornutus, whereas Nephila and Cyrtophora include larger species. For the sake of comparison, I dissected a female of Araneus angulatus Clerck (Figs. 14—18), which is of about the same size. The cheliceral m.lateralis anterior (la) is as clearly doubled as in Cyrtophora. Of the m.tergo-pedipalpalis muscles, the medius (pm) is two-fanned, the others are simple. A m.tergo-pedipalpalis externus (pe) is present, which is rare in non-amaurobid spiders. This finding corroborates the view previously expressed by me (1978 a), that bigger species need a more diversified set of muscles. In A.angulatus the dorsal caecal pouch proved to be very long and narrow, extending well into the basal portion of the chelicers, leaving ample space for the poison gland parallel to the caecal pouch.

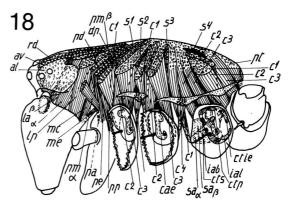
The musculus lateralis (Ml) is noticeably weaker in Nephila than in Araneus, the fibres being shorter. The cause of this is probably the completely sclerotized pleurae (connecting carapace and sternum) of Nephila, which apparently allow only a very small amount of depression of the margin of the carapace. In Araneus angulatus (and in A.cornutus) the pleurae contain discrete, triangular sclerites. The musculus lateralis has generally been credited with the generation of a raised body fluid pressure, causing extension of the leg joints lacking extensor muscles. It remains to be shown how Nephila generates sufficient power to straighten the very long legs. The coxae must also be much less mobile in Nephila than in Araneus. This is reflected by the absence of musculi tergo-coxales posteriores profundi (c_4 , "posterior rotators"), whereas A.angulatus has such muscles in legs I—II, A.comutus in I—III. They arise from the small sclerites in the pleurae. These muscles have been found chiefly in the



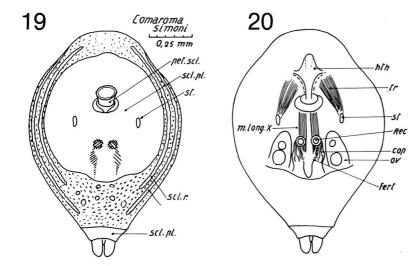
fairly large-sized spiders belonging to the amaurobides complex, sensu Lehtinen. Cf. the m.tergo-pedipalpalis externus of *A. angulatus!* The systematic value of these muscles should clearly not be overrated, as the crucial factor determining their presence is simply a large body size (Palmgren 1978a:19).

It is perhaps worth mentioning that Azilia, Cyrtophora and Nephila all have a pair of strong muscles running from the lorum backwards to the hind margin of the carapace ($ll\beta$). The same muscles were found in Araneus cornutus (but not in A.angulatus!), in Drassodes, Callilepis (Gnaphosidae) and in Clubiona. The interpretation seems difficult: is this muscle a posterior portion of m.lorotergalis (cf. Whitehead & Rempel) or the hindmost portion of the lateralis muscle?

The above-mentioned traces of resemblance to tetragnathid spiders do not, in my opinion, alter the isolated position of that group. Cf., however, the arguments of Levi in a most recent publication (1980)!



Figs. 14—18. Araneus angulatus. — 14: cephalothorax, dorsal surface. — 15: muscles of coxae I, II and IV. — 16: lateral muscle. — 17: deeper muscles. — 18: superficial muscles.



Figs. 19—20. Comaroma simoni. — 19: ventral surface of opisthosoma, petiolus cut. — 20: organs immediately adjacent to the integument.

2. Muscular anatomy of Comaroma simoni Bertkau, Ceratinella brevis (Wider), and several small theridids

The genus Comaroma has been placed in the family Theridiidae by several recent authorities (Oi, Levi & Levi, Thaler), as it originally was by Bertkau. Simon considered it more or less intermediate between the Micryphantidae and Theridiidae (Pholcomma), Wiehle discussed Comaroma simoni in connection with the Micryphantidae, but remarked that its taxonomic position was uncertain. The extrinsic coxal musculature is very peculiar: One median tergo-coxal muscle is inserted in the middle of the superior margin of the coxa, and two lateral muscles of the same length and strength are inserted symmetrically fairly low on the lateral margins, thus preventing the development of the upper endosterno-coxalis muscles ("promotors" and "remotors" of earlier authors, c_5 and c_6 in my nomenclature, Palmgren 1978a).

This muscular equipment, found in no other spiders studied by me, could theoretically be interpreted 1) as an adaptation to the very strongly sclerotized prosoma, or 2) as a character also to be found in other very small theridids. To test these hypotheses, specimens ($\varphi\varphi$) of several genera were dissected (Ceratinella brevis Wider, Fig. 21, Crustulina guttata (Wider), Fig. 22, Steatoda bipunctata (L.), Figs. 23—24, Dipoena

tristis (Hahn), Figs. 25—27, Pholcomma gibbum (Westring), Fig. 28). Unfortunately, only material preserved in alcohol was available. The outlines of the brain, ganglia and intestinal caeca could not be clearly discerned in all cases.

The extrinsic musculature of the coxae displayed the normal features of spiders. — Comaroma is also distinguished by the replacement of book-lungs by tracheae (Figs. 19—20). Posterior tracheae appear to be absent. Comaroma might thus be related to the very heterogeneous Symphytognathidae complex, although the chelicerae are free and a pedipalp present in the female. The external resemblance to Chasmocephalon shantzi Gertsch is striking (cf. Gertsch, Fig. 4). Another observation of interest is that in general even very small species, with a cephalothorax less than 1 mm long, have the normal set of leg muscles (cf. also Minyriolus, Palmgren 1978a, fig. 19:3—4).

A few comments may be added on the special features of the above-mentioned species.

The lateral muscle (Ml) is very poorly developed in Ceratinella and Crustulina, just as in Comaroma. As I have pointed out (1978 a), strong sclerotization of the carapace and pleurae more or less excludes compression of the prosomal space, which is the supposed function of Ml; this leaves unanswered the question of the extensor mechanism of the leg joints. In Steatoda and Dipoena the Ml is strong; in Pholcomma the muscle is quite continuous, but its fibres are short.

The cheliceral and pedipalpal muscles are on the whole only weakly developed, leaving the poison gland laterally exposed for part of its length. This accords with the weak development of the chelicers and pedipalps.

The poison gland is long in all species. This is apparently a general character of theridids, whereas *Ceratinella* appears to be unique among the Micryphantinae in this respect (cf. Palmgren 1978a).

Ceratinella: The celebrum is high and has a lateral lobe. There seems to be no median dorsal caecal pouch (owing to competition for space with the poison glands and the cerebrum?), but the tube draining the coxal caecal branches is enlarged.

Crustulina: The tergo-coxal c_1 I ("anterior rotator") is very small and hidden behind c_2 I; c_2 is progressively weaker from I—IV. The poor state of preservation prevented observation of the caeca.

Steatoda: The progressively greater strength of all tergo-coxal muscles from I to IV is very striking; the plagulo-tergalis muscle (pt) is also unusually conspicuous. The cerebrum is flanked laterally by the paired parts of the dorsal caecal pouch. The branches to the coxae are wide.

Dipoena: The contrast between the long, though slender, cheliceral muscles and the extremely short tergo-pedipalpal muscles is striking; only the retro-descending muscle (rd) to the median margin of the chelicer is strong. The tergo-coxal muscles are long and thin; only c_3 IV is unusually powerful. The dorsal caecal pouch occupies the usual space between the tip of the poison gland and the dorsal apodeme. The branches to the legs form small pouches protruding between muscles c_2 and c_3 , a feature attaining its extreme development in the tetragnathids.

Pholcomma: The "dome" of the prosoma lacks muscle origins, but is filled by the poison glands and the cerebrum. It was impossible to distinguish any traces of the caecal system. The very short tergo-pedipalpal muscles could not be differentiated in this tiny spider. The tergo-coxal muscles of the first leg are unusually strong, compared with those of the other legs.

3. Psechrus

Professor H. W. Levi kindly provided me with a specimen of the not readily accessible *Psechrus argentatus* (Doleschall) from New Guinea, Wau

(Figs. 29—38). It is apparently a not fully mature &, abnormal in that the left palp bears a typical combed claw (female character); the tarsus of the right clawless palp is 30 % longer than that of the left, but not turgid. The specimen was preserved in Bouin's fluid and in good condition. Lehtinen (1967) remarks on the lack of anatomical information concerning this isolated group.

The lateralis muscle forms a continuous sheet of median height and strength from the pedipalps to the petiolus. Two somewhat individualized fibre bundles are inserted on triangular sclerites in the pleurae behind the first and second coxae. From these sclerites small muscles of the type called "posterior rotators" by earlier authors, c_4 in my nomenclature (Palmgren 1978a), run to the hind margins of coxae I and II.

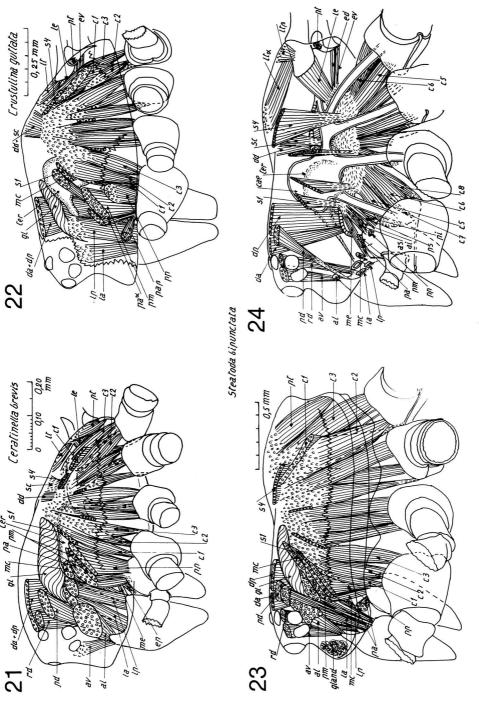
The tergo-coxal muscles (c_1-c_3) are bulky. Their shape is reminiscent of Tegenaria (Palmgren 1978a, fig. 12:8—9). Tegenaria also displays the two foremost "posterior rotators" c_4 . No systematic conclusions should be attempted. Suspensor I is very weak, suspensor III has two fans which partly cross each other. Suspensor IV and the suspensor centralis are unusually strong. The endosterno-coxal muscles do not deviate in any way from the normal and the same is true of the intrinsic coxotrochanteric muscles.

The pedipalp has a differentiated set of tergal muscles: An externus muscle (pe) is present, the posterior and median muscles are cleft (pp) and (pm) and the anterior muscle (pa) is strong. The set of endosterno-pedipalpal muscles (ai, as, pi, ps) is of the usual pattern. The intrinsic coxotrochanteric muscles are depicted.

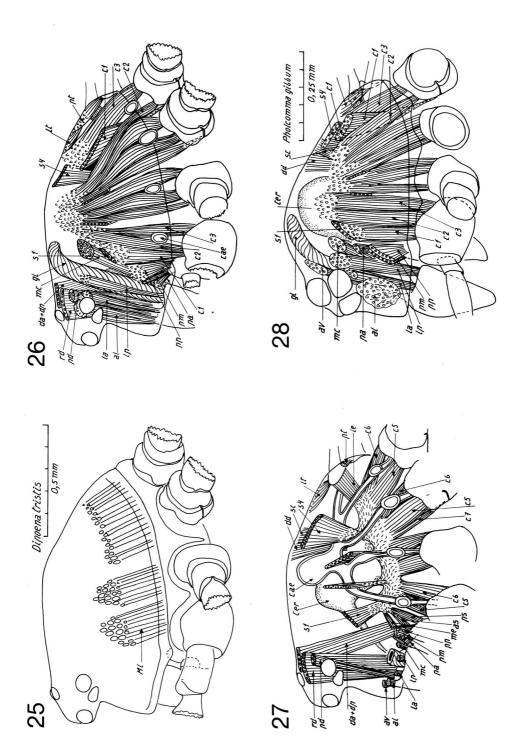
As would be expected, the bulky chelicers are served by powerful muscles of the usual configuration. The intrinsic cheliceral muscles are very simple; the flexor is not composed of many converging tracts.

The opisthosoma (Figs. 34—36) is encased in a sheet of circular integumental muscle fibres, strongest near the pulmonary furrow and decreasing in strength towards the spinnerets. The fibres are rather flat and divided into compartments (Fig. 35). The muscles between the segmental apodemes and between them and the integumental insertion points do not deviate from the general type (cf. e.g. Whitehead & Rempel 1959). The same applies to the muscles of the spinnerets.

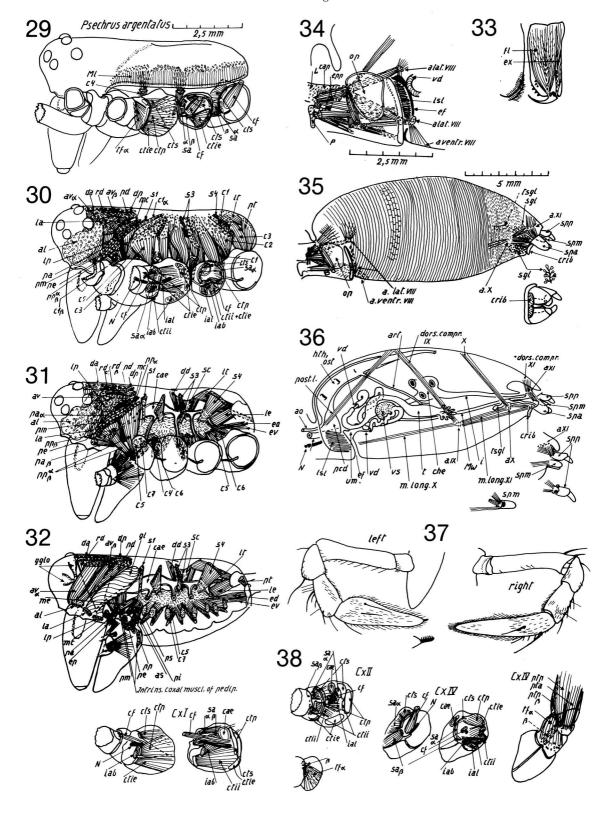
The pockets of the lungs are very narrow. The pericardial sac, which originates from the space surrounding the lungs and receives the blood from the petiolus, is narrow. The heart has three

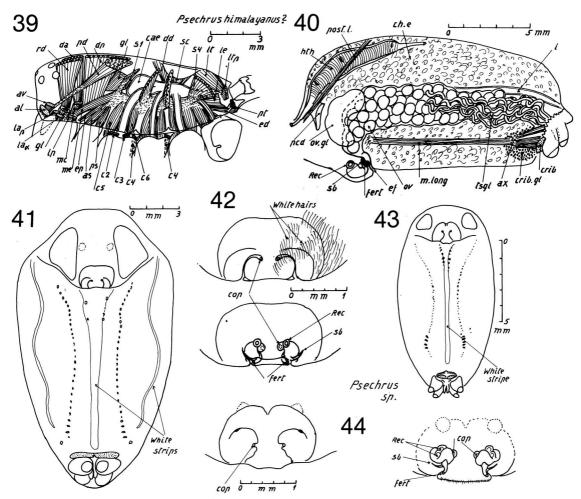


Figs. 21-24. — 21: Ceratinella brevis, superficial muscles. — 22: Crustulina guttata, superficial muscles. — 23: Steatoda bipunctata, superficial muscles. — 24: Steatoda bipunctata, deeper muscles.



Figs. 25–28. — Dipoena tristis. — 25: lateral muscle. — 26: superficial muscles. — 27: deeper muscles. — 28: Pholoomma gibbum, superficial muscles.





Figs. 29—44. — Psechrus argentatus, subad. δ . — 29: lateral muscle, superficial muscles of coxae II—IV. — 30: superficial muscles of cephalothorax, deeper coxal muscles. — 31: deeper muscles from pedipalp backwards. — 32: deepest view of muscles. — 33: cheliceral muscles, anterior view. — 34: foremost segmental muscles of opisthosoma. — 35: integumental musculature of opisthosoma and part of segmental muscles. — 36: internal features of opisthosoma. — 37: left pedipalp. — 38: coxal muscles I, II and IV (cf. also Fig. 29). Psechrus himalayanus? ς . — 39: deeper layer of muscles. — 40: internal features of opisthosoma. — 41: ventral surface of opisthosoma. — 42: epigyne and "vulva" (dorsal view). Psechrus sp. ς . — 43: ventral surface of opisthosoma. — 44: epigyne and "vulva" (dorsal view).

pairs of ostia, the third being almost rudimentary. Unfortunately, all but the hindmost part of the tracheal tubes was destroyed.

In the middle of the intestinal tract a large pouch-like structure gives off diverticula which ramify and form the dorsal digestive parenchyma. The bladder was filled with faecal crumbs. The point of origin of the ventral part of the parenchyma could not be detected. The anal bladder is conspicuous. Owing to poor preservation the ramification of the Malpighian vessels remained obscure.

Only three kinds of silk glands could be discerned. The cribellar glands are bushlike and aciniform. The mass of the glands are lengthy and ampullate. Only a few typical tubuliform glands are found.

Owing to the imperfect penetration of the fixative (Bouin's fluid) the structure of the genital organs could not be established in full detail. On the whole, it corresponds to the findings of Crome (1951). The testes are digitated, however. The long and coiled vas deferens incorporates a bulky structure to be regarded as

the vesicula seminalis. Between this and the testis is an intercalated enlargement. The vesiculae and the vasa deferentia are strongly sclerotized, the later being covered by a soft, apparently glandular tissue. The part of the duct between the vesicula and the "uterus masculinus" is much narrower than the part between the vesicula and the testis, and the ultimate part has no glandular investment.

Dr. F. R. Wanless has kindly provided me with two undetermined Psechrus females from the collections of the British Museum of Natural History. One is apparently P. himalayanus (Nepal, Darsan, 3000', 16. VI. 1954, leg. K. H. Hyatt). The identity of the other remains obscure (Saravak, Dee Cave 24. IV. 1978, leg. P. Chapman, Mulu Expedition). The epigynes and "vulvae" are depicted in Figs. 42 and 44. The muscular anatomy of the prosoma corresponds closely, of course, to the anatomy of the P. argentatus male. The intestinal caecal pouch seems not to extend narrowly into the chelicerae, as in the male, perhaps corresponding to the bulkier state of the poison glands in the females. In the opisthosoma, the ovaries (filled with eggs) are in close contact. The other organs were rather poorly preserved.

Figures

Structures hidden behind other structures are drawn with interrupted lines. The endosternum and tendons are depicted with short strokes. Areas of origin of muscles are indicated with rings or crescents. Cut areas of muscles are indicated with dots. If the lateral muscle is not explicitly depicted, its margin is denoted across the superficial muscles of the cephalothorax as an angular line.

Unless otherwise mentioned, the figures are drawn perpendicularly from the left. The scale (in mm) is

indicated separately for each species.

Abbreviations

apodeme (alat lateral, aventr ventral) aal m.antero-medialis lateralis ai m.endosterno-pedipalpalis antero-inferior aperture coxa-prosoma ap m.endosterno-pedipalpalis antero superior as m.antero-medialis verticalis m.tergo-coxalis anterior profundus c_1 ("anterior rotator") c_2 m.tergo-coxalis medius anterior m.tergo-coxalis medius posterior c_3 m.tergo-coxalis posterior profundus ("posterior rotator")

m.endosterno-coxalis antero-superior c_5 m.endosterno-coxalis postero-superior c_6 m.endosterno-coxalis antero-inferior c_7 m.endosterno-coxalis postero-inferior CR cae intestinal caecum anterior compressor of pedicel cap Cercerebrum m.coxo-femoralis cf che chylenteron posterior compressor of pedicel cpp crib.gl cribellar silk glands ctie m.coxo-trochantericus inferior externus ctii m.coxo-trochantericus inferior internus m.coxo-trochantericus posterior ctp cts m.coxo-trochantericus superior Cxda m.dilator pharyngis anterior ddm.dilator proventriculi dorsalis dpm.dilator pharyngis posterior Ĕ. endosternum edm.plagulo-endosternalis dorsalis m.plagulo-endosternalis ventralis ev ex cheliceral extensor fl cheliceral flexor glpoison gland ovarial gland gl.ov. iab m.infra-apodemicus brevis ialm.infra-apodemicus longus Llorum le m.loro-endosternalis 11 m.loro-tergalis m.postero-medialis carapacis mc m.postero-medialis endosterni me Mlm.lateralis m.long. longitudinal median muscle N nerve P plagula m.tergo-pedipalpalis anterior pa pd m.medialis prodescendens m.tergo-pedipalpalis externus pe pet.scl. petiolus sclerotization pi m.endosterno-pedipalpalis postero-inferior m.tergo-pedipalpalis medius pm pp m.tergo-pedipalpalis posterior m.endosterno-pedipalpalis postero-superior ps pt m.plagulo-tergalis pta patellar depressors (a ant., p. post.) rd m.medialis retro-descendens suspensors 1-4 51-54 m.supra-apodemicus (α superior, β inferior) sa supensor centralis SC pleural sclerite scl scl.pl. sclerotized plate sclerotized ridges scl.r. tfm.trochantericus femoris sb supporting bar spinneret (a anterior, m median, p posterior) sp st stigma testis tf m. trochantericus femoris tubuliform silk glands tsgl "uterus masculinus" umvdvas deferens

vesicula seminalis

References

- Crome, W. 1951: Die grobe Morphologie des männlichen Genitalapparates einiger Araneen. — Deutsche Zool. Zeitschr. 1:169—186.
- Gertsch, W.J. 1960: Descriptions of American spiders of the family Symphytognathidae. — Amer. Mus. Novitates 1981:1—40.
- Homann, H. 1950: Die Nebenaugen der Araneen. Zool. Jahrb. Anat. 71:56—144.
- Lehtinen, P. 1967: Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Ann. Zool. Fennici 4:199—468.
- Levi, H. 1980: The orb-weaver genus Mecynogea, the subfamily Metinae and the genera Pachygnatha, Glenognatha and Azilia of the subfamily Tetragnathinae north of Mexico (Araneae: Araneidae).
 Bull. Mus. Comp. Zool. Harvard Univ. 149 (1):1—75
- Levi, H. & Levi, L. R. 1962: The genera of the spider family Theridiidae. — Bull. Mus. Comp. Zool, Harvard Coll. 127 (1):1—71.
- Locket, G. H., Millidge, A. F. & Merrett, P. 1974: British Spiders III. — Ray Society 149:1—X + 1—315.

- Millot, J. 1931: Anatomie comparée de l'intestin moyen cephalothoracique chez les Araignées vraies. — C. R. Acad. Sci. 192:375—377.
- Oi, R. 1960: Linyphiid spiders of Japan. J. Inst. Polytechnics Osaka city Univ. (D) 11:137—244.
- Palmgren, P. 1978a: On the muscular anatomy of spiders.

 Acta Zool. Fennica 155:1—41.
- —»— 1978b: Taxonomic position of the genus Meta (Araneida). — Ann. Zool. Fennici 15:241—242.
- —»— 1979: On the internal taxonomic characters of the genus Leucauge White (Araneida). — Bull. Brit. Arachnol. Soc. 4 (9):394—395.
- Thaler, K. 1978: Bodenspinnen aus der Steiermark und ihren Nachbarländern, gesammelt von Prof. Dr. R. Schuster. — Mitt. Abt. Zool. Landesmus. Joanneum 7:173—183.
- Whitehead, W. F. & Rempel, J. G. 1959: A study of the musculature of the Black Widow spider, Latrodectus mactans (Fabr.). — Canad. J. Zool. 37: 831—870.

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