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New data on the epigastric apparatus of male spiders

André Lopez
Laboratoire de Pathologie comparée,
Ecole pratique des Hautes Etudes,
Université des Sciences et Techniques du Languedoc,
Place E. Bataillon,
34 060 Montpellier, France

and

Michel Emerit
Laboratoire de Zoologie,
Université des Sciences et Techniques du Languedoc,
Place E. Bataillon,
34 060 Montpellier, France

Summary

A comparative study of the epigastric area has been carried out by means of a scanning electron microscope in male spiders belonging to 28 families.

The fusule pattern of their acinoid epigastric glands shows an evolutionary sequence from the "dispersed" type (Mygalomorphae) to a genuine "epigastric organ" (Metidae, Tetragnathidae).

In addition to these data, there are histological clues supporting an appendicular origin of the whole "epigastric apparatus" (acinoid epigastric glands, gonoporal organs, pheromonal glands).

Introduction

Male spiders possess characteristic organs located in the anterior lip of the genital furrow, showing an exocrine glandular appearance and accordingly named "epigastric" or "epiandrous" glands.

These organs can be divided into two distinct types. On the one hand, there are the properly so-called epigastric glands which are multicellular and acinoid, each consisting of an epithelial secretory body and a single excretory duct; this duct opens forward of the epigastric furrow, via a hollow fusule implanted in the ventral integument. On the other hand, there are the "gonoporal organs" (Lopez, 1972, 1974, 1977) which have the aspect of unicellular glands forming two symmetrical clusters. These clusters open inside the epigastric furrow via tiny individual ducts devoid of terminal fusules. While the gonoporal organs seem to exist in all the male spiders we have so far studied histologically (perhaps with the exception of Telemidae), the fusulate acinoid epigastric glands are found less constantly.

Discovered by Fage & Machado (1950) in Ochyroceratidae, the fusules were found later on, again in Ochyroceratidae but also in *Scytodes* and *Pholcus* by the second author using cleared preparations (Machado, 1951). He then supposed that the fusules corresponded to the endings of hypothetical glands. Such glands were observed for the first time by Melchers (1964) in histological sections of Theraphosidae, seen again three years after by Marples (1967) in Gradungulidae and since then, have been extensively reviewed in numerous spiders by one of us (Lopez, 1977) under the name of "pregonoporal acinous epigastric glands".

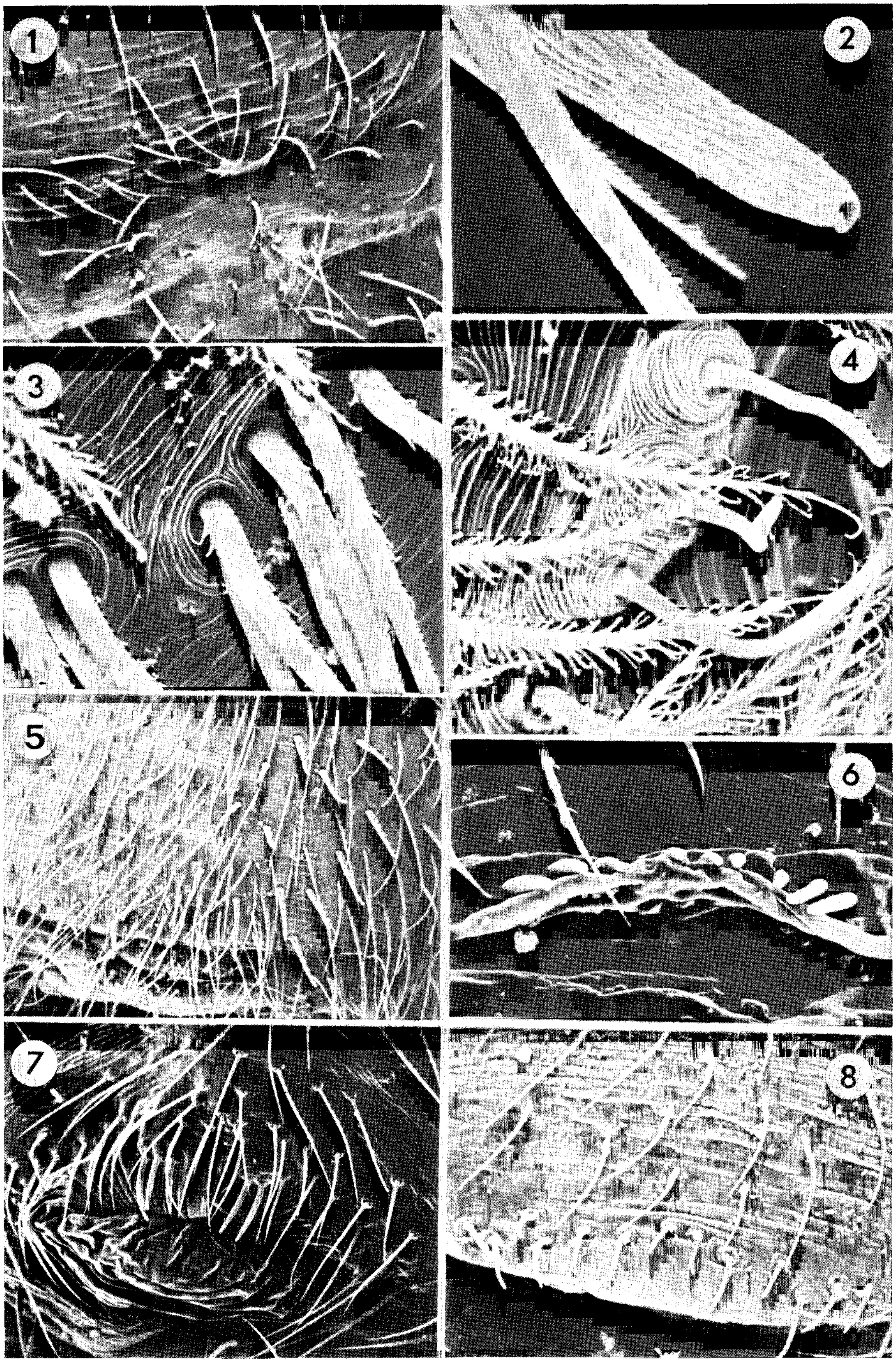
Marples (1967) has reported the presence of fusules in 17 families of spiders that it would be tedious to enumerate here, but which are distributed over nearly the whole order of Araneae and without obvious bearing on classification, at first sight. It is simpler to list the families in which Machado and Marples could not find fusules: Amaurobiidae, Dictynidae (Cribellatae), Leptonetidae, Segestriidae, Zoropsidae, Symphytognathidae and Thomisidae (Ecribellatae). It now looks as though these exceptions do not perhaps have any value as a familial criterion, as we show below. Moreover, it must be confessed that the simple examination of cleared preparations with a stereomicroscope is not an infallible way to discover the epigastric fusules. Although Machado (1951) did not see them and therefore considered them absent in Leptonetidae, we have easily observed and photographed fusules in *Leptoneta infuscata minos* Simon (Fig. 4) and in *Leptoneta microphthalma* Simon. In fact, this technique is perfectly adapted to the study of epigastric fusules that satisfactorily withstand desiccation. If we exclude a previous investigation performed on *Ochyrocera thibaudi,* when describing this new ochyroceratid species (Emerit & Lopez, 1985), we present here, for the first time, a comparative study of the epigastric area in male spiders carried out by means of a scanning electron microscope. Their abdomens, preserved in alcohol, were successively treated with acetone and — when too fragile — liquid carbon dioxide at its critical temperature, or with Gurr's "Supercedrol" (an original technique developed by Michel Emerit), coated with gold, and subsequently examined then photographed using the scanning electron microscope JEOL SM 35.

Our observations bear upon the presence or absence of epigastric fusules, their shape and connection with the integument and their distribution, in a sample of 28 spider families. In fact, they represent a preliminary to further more exhaustive work.

Absence of fusules

First, let us emphasize that the presence of fusules is remarkably inconstant. The forelip of the epigastric furrow shows only simple or plumose tactile hairs in several species belonging to the most varied families: *Synaema globosum* (Fabricius) (Thomisidae) (Fig. 1), *Zoropsis* sp. (Zoridae), *Archaea workmani* (O. Pickard-Cambridge) (Archaeidae), *Oxyopes heterophthalmus* (Latreille) (Oxyopidae), *Pseudanapis parocula* (Simon) (Anapidae), *Chiracanthium punctorium* (Villers) (Clubionidae), *Pardosa hortensis* (Thorell) and *Alopecosa fabrilis* (Clerck) (Lycosidae).

Nevertheless, it is noteworthy that in the last of these families, we were able to observe, for the first time, the endings of pregonoporal organs, their discovery being facilitated by a location which is more superficial than in other spiders. They appeared as two fields of minute independent acuminate nipples, apparently devoid of orifices. Their appearance would seem to discount the presence of underlying excretory ducts, which were however revealed by histological



Figs. 1-8: Epigastric areas of various male spiders. **1** *Synaema globosum* (Salticidae), epigastric furrow without fusules (× 210); **2** *Micrommata roseum* (Sparassidae), detail of a fusule (× 850); **3** *Amaurobius erberi* (Amaurobiidae), spinulate epigastric fusules (× 1900); **4** *Leptoneta infuscata minos* (Leptonetidae), one of the two groups of fusules (× 2500); **5** *Nemesia caementaria* (Ctenizidae), field of solitary fusules (× 80); **6** *Scytodes thoracica* (Scytodidae) (× 1000); **7** *Holocnemus pluchei* (Pholcidae) (× 210); **8** *Nesticus cellulanus* (Nesticidae) (× 260).

sections; it could place doubt upon the glandular nature of gonoporal organs, which may have the status of relict appendicular structures (Lopez & Emerit, 1987).

Fusule shape

The fusules are cone-shaped, more often slender than truncated as in *Pholcus phalangioides* (Fuesslin), almost straight (Figs. 5, 7, 9-12, 16), arched (Figs. 6, 8) or contorted (Figs. 4, 14). Histological sections show that each of them is hollow and perforated lengthwise by the excretory duct of the corresponding epigastric gland. This duct opens at their blunt tip via a pore, which sometimes appears slightly everted (Fig. 2).

As a rule, the epigastric fusules are somewhat fluted (Figs. 2, 12) and similar to those of the silk glands. Nevertheless, they are obviously spinulate in *Amaurobius erberi* (Keyserling) (Fig. 3) which is the only case of this kind we have met in all our observations. It is not yet possible to assert that spinulation is the survival of a plesiomorphic character; it is accompanied by an unusual pattern of the acinoid epigastric gland bodies which appear very small and as if "under-developed" in histological sections.

In accordance with Melchers' observations in Mygalomorphae (1964), there is no modification of profile at the base of epigastric fusules, unlike that observable for silk gland spigots. We always noticed a perfectly regular stem, without conical or bulbous foot enlargement.

Great variety exists at the point where the fusule joins the ventral integument. In *Nemesia caementaria* (Latreille) (Fig. 5), *Atypus affinis* Eichwald and *Anelosimus eximius* (Keyserling), each fusule protrudes directly from the integumentary surface, without being implanted in a socket, an appearance that could lead us to assume it to be the beginning (or the end) of an evolutionary sequence. In *Filistata insidiatrix* (Forskål), the integument has a tendency to form a slight pad surrounding the base of the fusule. In all other spiders we have studied, this base is sunk into a socket so that it is surrounded by a circular furrow, e.g., *Amaurobius* (Fig. 3). Finally, the furrow can be rimmed by a more or less prominent cuticular pad and often gives the erroneous impression of being a cup like that of sensillae. The pad is smooth in *Salticus scenicus* (Clerck), although the ventral integument is streaked elsewhere (Fig. 13), and in *Pholcus phalangioides*. On the other hand, it is decorated with concentric cuticular ridges in *Leptoneta infuscata minos* (Fig. 4) and in *Ochyrocera thibaudi* Emerit & Lopez (Emerit & Lopez, 1985: plate I, fig. B). Curiously, the fusules of *Pachygnatha clercki* Sundevall and *Tetragnatha extensa* (Linn.) (Tetragnathidae) are provided with a very prominent columnar table-topped pad and an incomplete furrow at their base (Fig. 15).

Fusule patterns

The epigastric area of Mygalomorphae (*Nemesia, Atypus*) is occupied by a large number of solitary fusules seemingly randomly distributed over almost its whole extent (Fig. 5).

In the Araneomorphae, the fusules can be few, isolated or arranged in one row. *Scytodes thoracica* (Latreille) (Fig. 6) exhibits 9 fusules, regularly spaced forward of the genital cleft, and *Ochyrocera thibaudi,* only 5. *Nesticus cellulanus* (Clerck) possesses 13 or 14 fusules tending to lie in two rows (Fig. 8). In *Pholcus phalangioides,* they are limited to 5 and have a strong tendency to be gathered into two groups, one of 3 and the other of 2 fusules, indicating an evolutionary trend towards a genuine bipartite pattern. Such a pattern is achieved in a second pholcid, *Holocnemus pluchei* (Scopoli) (Fig. 7), in the theridiids *Anelosimus eximius* and *Argyrodes cognatus* (Blackwall) whose 4 to 6 fusules are gathered into two very distinct "brushes", as well as in *Leptoneta infuscata minos*. This cave spider is provided with two equal groups of fusules. In addition to the above-mentioned individual basal pads, a low integumentary fold rises around and encircles each group (Fig. 4). In *Saitis barbipes* (Simon) (Fig. 14), there are also two distinct groups of 3-5 fusules, but here they protrude from the bottom of a cleft.

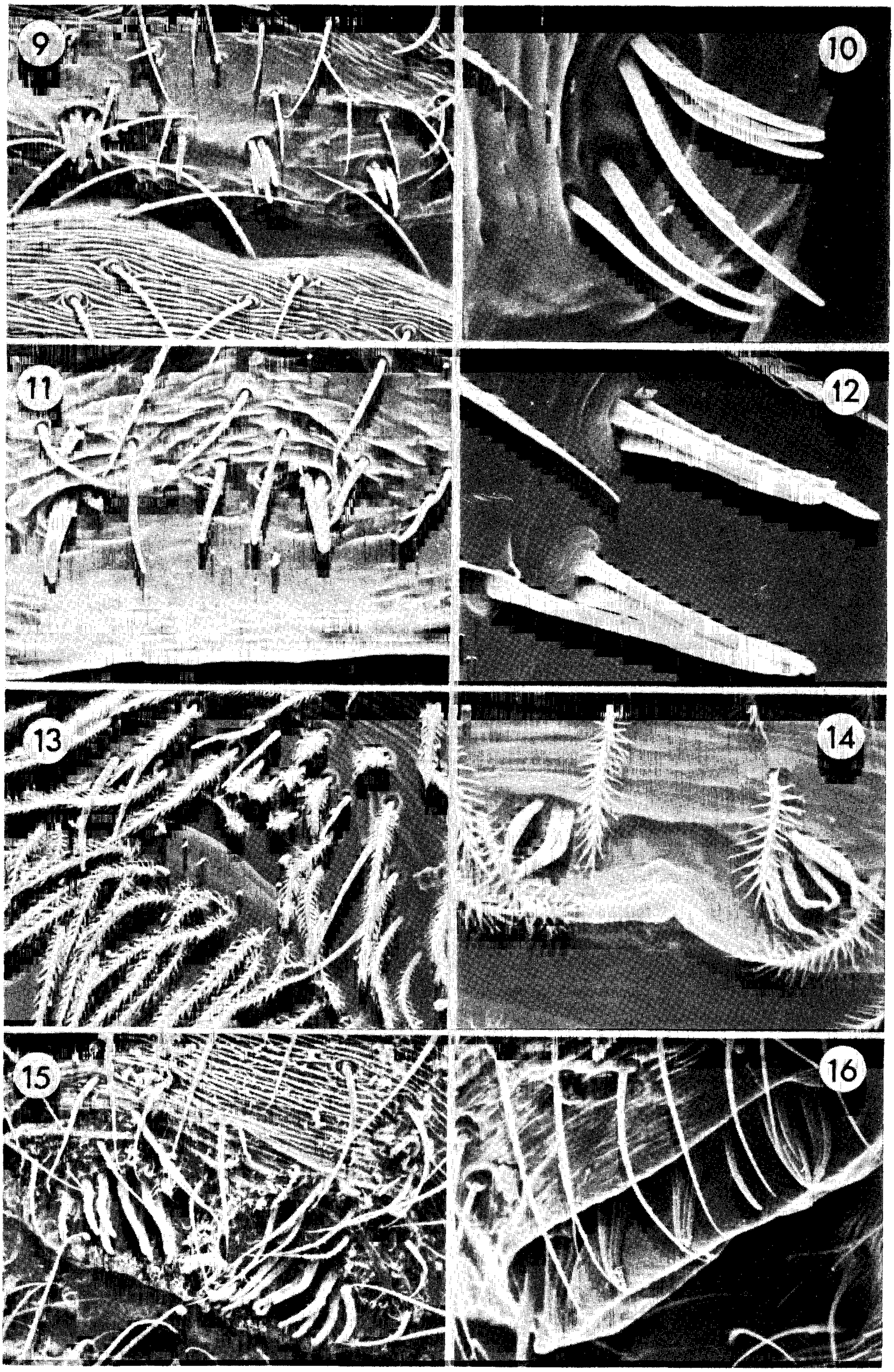
Lastly, a more general pattern is achieved by the arrangement of fusules into several small groups, all disposed along a transverse line. This is the pattern in Araneidae, namely *Argiope argentata* (Fabricius) (Fig. 9), *Nephila senegalensis senegalensis* (Walckenaer), *N. inaurata madagascariensis* (Vinson), *Araniella cucurbitina* (Clerck) (Fig. 10), *Gasteracantha versicolor* (Walckenaer) which shows a trend towards the reduction in fusule number, and *Micrathena schreibersi* (Perty) (Fig. 11) where this trend is completed by the existence of isolated fusules. An analogous pattern is also present in the Linyphiidae that we have examined, namely *Linyphia triangularis* (Clerck) and *Florinda coccinea* (Hentz), in the gnaphosid *Drassodes lapidosus* (Walckenaer), in the agelenid *Tegenaria inermis* Simon, and lastly in the uloborid *Philoponella republicana* (Simon), the fusules of which, though similarly aggregated (Fig. 12) are devoid of sockets. *Micrommata roseum* (Clerck) (Eusparassidae) also possesses small groups of fusules but, in this species, there is a slight tendency for them to be spread out in several rows.

It is noteworthy that a kind of "epigastric organ" seems to become visible in the eresid *Eresus niger* (Petagna): numerous fusules, assembled in several groups, are enclosed in a single large pit located forward of the epigastric furrow. A previous histological investigation (Lopez, 1977: plate 2, fig. 4) allowed such a peculiarity to be foreseen. It is likely that these fusules are the source of a prominent band of silk, coming from the epigastric region, which has been observed when the male *Eresus niger* is spinning its sperm web (P. Merrett, pers. comm.).

The cases of Metidae and Tetragnathidae

It is in the families Metidae and Tetragnathidae that we have found the most fascinating examples of complex "fusulotaxy" types.

The fusules of *Meta bourneti* Simon and *Meta menardi* (Latreille) are arranged in numerous small



Figs. 9-16: Epigastric areas of various male spiders. **9** *Argiope argentata* (Araneidae) (× 270); **10** *Araniella cucurbitina* (Araneidae) (× 860); **11** *Micrathena schreibersi* (Araneidae) (× 660); **12** *Philoponella republicana* (Uloboridae), two groups of fusules (× 2200); **13** *Salticus scenicus* (Salticidae), 8 fusules in arched line (× 50); **14** *Saitis barbipes* (Salticidae), 8 fusules in two groups (× 750); **15** *Tetragnatha extensa* (Tetragnathidae), fusules in two symmetrical tegumentary depressions (× 450); **16** *Leucauge argyra* (Metidae), the fusular "trough" (× 580).

unequal groups, which are in turn laid out in an irregular pattern with their bases on a level with the integumentary surface (Lopez & Emerit, 1986). In *Tetragnatha extensa* (Fig. 15), and apparently also in *Pachygnatha clercki* (Tetragnathidae), the fusules nest in two shallow round symmetrical tegumentary depressions separated by a low ridge. This unusual appearance is enhanced by the unique form of the fusule pad. In *Leucauge argyra* (Walckenaer) (Metidae), the fusules are mostly assembled in "brushes" and are buried to their full height within a large transverse, jutting, trough-shaped tegumentary fold. This real epigastric organ is located just forward of the epigastric furrow which it slightly overhangs (Fig. 16).

Concerning the Metidae, we must emphasize that besides acinoid epigastric glands and gonoporal organs, we have met another type of exocrine gland which is unicellular or paucicellular in appearance (Lopez & Emerit, 1986, 1987). In the sections, it can be identified among the epidermal cells of the epigastric forelip where it lies scattered. Each gland cell is provided with a tiny "reservoir", probably corresponding to an "end apparatus", and with an excretory ductule, leading to a pore on the integument surface. These are the pores that we first discovered with the scanning microscope and which put us on the track of the underlying glands. In the genus *Meta,* these pores open haphazardly between the bases of the fusules, whereas, in *Leucauge argyra,* they open on the posterior slope of the "trough". Given the presence of a presumed "end apparatus" in these gland cells, we hypothesize that they produce a pheromonal secretion that could feature in sexual life. Moreover, they are probably not characteristic of the Metidae, for we have recently found analogous pores and "organules" in *Zoropsis* and *Amaurobius* as well (Lopez & Emerit, 1987).

Conclusions

In our opinion, the fusulate epigastric glands, the gonoporal organs and the supposed pheromonal glands can be considered as a complex forming the "epigastric apparatus". This term can currently be considered as the mere topographical name of three different formations that do not have the same physiological activity but could originate from a common "epiandrous" appendicular anlage. Such a notion is supported by the even-numberedness of gonoporal organs, by the strong tendency of acinoid gland fusules to bipartition and by the association of supposed pheromonal glands. Indeed, tiny glands similar to the latter are often located close to the base of appendages: chelicerae, rostrum, maxillae, leg coxae, spinnerets.

In the light of our observations and taking into account their limited number, it is hardly possible to correlate definitively the existence and patterns of epigastric fusules with phylogeny. Indeed, certain Clubionidae such as *Phrurolithus flavitarsis* (Lucas) are provided with acinoid glands and fusules, whereas *Chiracanthium punctorium* lacks them. In Salticidae, the fusules of *Salticus scenicus* stand in one curved row (Fig. 13) while those of *Saitis barbipes* are gathered into two groups (Fig. 14). Differences can also appear between different species of the same genus: owing to its extremely reduced number of fusules (usually 2), the theridiid *Argyrodes elevatus* Taczanowski is radically different from *Argyrodes cognatus* (Blackwall) (two groups of 4-5 fusules). Nevertheless, it seems that a general type emerges distinctly in the Araneidae and perhaps also in the Theridiidae.

The epigastric organ of Metidae, owing to its symmetry, could suggest some ancient appendicular structure, but how to explain the arrangement of this structure compared with the dispersed fusules in mygalomorphs which are "primitive" spiders?

Another presumption of an appendicular origin of the epigastric apparatus could be founded on the similarity between the epigastric glands and the silk glands (Lopez, 1977).

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References

EMERIT, M. & LOPEZ, A. 1985: *Ochyrocera thibaudi* n.sp. et autres Ochyroceratidae des Petites Antilles (Araneae). *Revue Arachnol.* **6**: 81-89.

FAGE, L. & MACHADO, A. de B. 1950: Quelques particularités remarquables de l'anatomie des ochyroceratidés (Araneae). *Archs Zool.exp.gén.*(Notes et Revues) **87**: 95-103.

LOPEZ, A. 1972: Morphologie et rapports particuliers des glandes épigastriques dans deux familles d'araneides: les Dysderidae et les Clubionidae (Note préliminaire). *Bull.Soc.zool.Fr.* **97**: 113-119.

LOPEZ, A. 1974: Glandes épigastriques et classification des araneides. *Bull.Ass.Anat., Paris* **58**: 899-904.

LOPEZ, A. 1977: *Contribution à l'étude des caractères sexuels somatiques chez les mâles des araneides.* Thèse Doct.Etat es Sci., U.S.T.L., Montpellier.

LOPEZ, A. & EMERIT, M. 1986: Présomptions en faveur de glandes à phéromone chez des mâles de Metidae (Araneae). *Bull.Soc.Étude Sci.nat.Béziers* (NS) **11**: 56-60.

LOPEZ, A. & EMERIT, M. 1987: Seminario de anatomia: Analogies and homologies in the sensory and glandular systems of the Arachnida. *Actas X Congr.Int.Aracnol.* (Jaca, 1986) **2**: 25-40.

MACHADO, A. de B. 1951: Ochyroceratidae (Araneae) de l'Angola. *Publções cult.Co.Diam.Angola* **8**: 9-87.

MARPLES, B. J. 1967: The spinnerets and epiandrous glands of spiders. *J.Linn.Soc.*(Zool.) **46**: 209-223.

MELCHERS, M. 1964: Zur Biologie der Vogelspinnen (Fam. Aviculariidae). *Z.Morph.Okol.Tiere* **53**: 517-536.