

Observations on the structure of the fore-gut of spiders

B. J. Marples

1 Vanbrugh Close,
Old Woodstock,
Oxford

Summary

A survey was made of the muscles of the fore-gut of 43 species of spiders belonging to 29 families. Six pairs of muscles are attached to the pharyngeal portion, and their arrangement is extraordinarily uniform throughout. Exceptions were found in the liphistiomorph *Heptathela*, in mygalomorphs *Hexathele* and a theraphosid, and in araneomorphs *Hypochilus* and *Ectatosticta*. The muscle arrangement of the post-cerebral part of the fore-gut, the sucking stomach, is the same in all groups.

Introduction

In an earlier investigation (Marples, 1968) a comparison was made between 5 species of spiders which had at times been regarded as forming a subordinal group, the Hypochilomorpha, intermediate between the Mygalomorpha and the Araneomorpha. It is convenient in a discussion such as this to refer to the suborders without becoming involved in questions of their validity. It was concluded that *Hypochilus* and *Ectatosticta* were closely related and should be placed in a family Hypochilidae, while the others belonged to separate families; Hickmaniidae, Thaididae and Gradungulidae. Although the Hypochilidae have some primitive features, all these families were included in the Araneomorpha, and the suborder Hypochilomorpha was thought to be unnecessary. Among the peculiarities of the Hypochilidae are the details of the structure of the pharyngeal muscles, which tend to resemble those of the liphistiomorph *Heptathela* rather than the majority of spiders. This focussed attention on these muscles, and, when it was found that abnormalities also occurred in the Filistatidae, it was decided to check these structures in as many families as possible. The results of this survey are presented here.

Material examined

It must be emphasised that the material available was limited and of very unequal value. Sometimes there were good series of sections in all three planes, at others perhaps very fragmentary ones in one plane only, and opportunity does not offer to improve on these. The sections were cut usually at 10 μ and stained with Mallory's stain. Those of the mygalomorphs and *Gradungula* were prepared by Dr V. E. Davies, the rest by myself, and the work was done in the Department of Zoology of the University of Otago, New Zealand. It is hoped that the material will eventually be deposited in the Hope Entomological Collections of the University Museum, Oxford. Usually there were sections of only one member of a genus or family, and these were seldom, specifically identified. It is hoped that even such a superficial survey may indicate something of the variability in this area, and help to form a basis for future workers. With these limitations, sections of 43 species belonging to some 29 families were examined.

LIPHISTIOMORPHA

Liphistiidae. *Heptathela*, *Liphistius*

MYGALOMORPHA

Antrodiaetidae. *Antrodiaetus*

Atypidae. *Atypus*

Ctenizidae. *Cantuarina*, *Nemesia*

Dipluridae. *Hexathele*, *Porrhothele*

Migidae. *Migas*

Theraphosidae.

ARANEOMORPHA

Agelenidae.

Araneidae. *Araneus*, *Cyclosa*, *Zygiella*

Dictynidae. *Amarara*, *Amaurobius*, *Dictyna*,
Ixeuticus, *Matachia*

Dinopidae. *Dinopsis*

Filistatidae. *Filistata*

Gradungulidae. *Gradungula*

Hickmaniidae. *Hickmania*

Hypochilidae. *Ectatosticta*, *Hypochilus*

Lycosidae. *Lycosa*

Oecobiidae. *Oecobius*

Oonopidae. *Oonops*

Pholcidae. *Pholcus*

Psechridae. *Psechrus*

Scytodidae. *Scytodes*

Segestriidae. *Ariadna*, *Segestria*

Symphytognathidae. *Patu*

Thaididae. *Thaida*

Thomisidae. *Diaea*

Toxopidae. *Cycloctenus*

Uloboridae. *Hyptiotes*, *Uloborus*

Urocteidae. *Uroctea*

Zoropsidae. *Zoropsis*

General structure of the fore-gut

The fore-gut, or stomodaeum, of the chelicerates consists of a pharynx, an oesophagus which is a simple tube piercing the nerve mass, and, in some, a post-cerebral portion. With the possible exception of the Phalangida, all ingest liquid food only, and the sucking apparatus is the fore-gut, especially the pharynx. This may be provided with both dilator and constrictor muscles, both of which are best developed in the Phalangida. Of the 10 orders, 5 have no elaboration of the fore-gut behind the nerve mass, but it unites immediately with the mid-gut. In the Phrynichida, however, there is a well developed sucking apparatus, with both dilator and constrictor muscles, behind as well as in front of the nerve mass. The Araneida have a very similar sucking stomach behind the nerve mass, but their pharynx is simpler and has no constrictor muscles. In the Scorpionida, Schizomida and Solpugida there is only a slight development of a post-cerebral sucking apparatus.

The external structures around the mouth of spiders have been described by Kästner (1952, 1954) and will not be mentioned here except to state that the mouth lies between the rostrum and the lower lip. There are a number of glands in the region of the mouth. The most obvious is the rostral gland, but there may be others in the rostrum, lip and maxillae, and also underlying the cuticle of the epi- and hypopharynx (Legendre, 1953). These vary considerably in size and in their occurrence in different species, but they are not considered here. Nor are the special sense organs, such as those described by Millot (1936) at the sides of the pharynx.

It will be convenient to give a generalised account of the cuticular lining of the fore-gut, and of its muscles, before commenting upon the differences which were observed. The mouth is a slit, and the pharynx extends more or less vertically upwards from it as a broad cleft, flattened antero-posteriorly.

The cuticle of the anterior wall, the epipharynx, is thickened while that of the hypopharynx is thinner, and they are joined laterally by a very flexible region. The surface of the epipharynx is marked with fine transverse ridges and up its middle line runs a deep groove, circular in section and with strongly sclerotised walls. There may also be rod-like thickenings of the cuticle supporting various parts of the pharynx. The pharynx is rectangular as seen from the front, and, from the middle at the top, the oesophagus runs backwards at right angles to it through the nerve mass. The oesophagus is tubular with thick dorsal and lateral walls, and is essentially a continuation of the groove in the epipharynx. Where the oesophagus begins, the thick lateral cuticle is more extensive and is prolonged upwards into the pharyngeal lobes. Behind the nerve mass the fore-gut expands into the sucking stomach. This has thickened plates in its dorsal and lateral walls, and these plates are connected by flexible cuticle; the whole has a somewhat T-shaped cross section.

A number of papers have dealt with the muscles of the fore-gut in more or less detail, and important among them are those of Brown (1939), Whitehead & Rempel (1959), Palmgren (1978) and Meyer (1981). There is some variation in the nomenclature used by different authors, and, as in the present paper it is not intended to enter into discussion of homologies or details of anatomy, only simplified diagrams and names are presented here.

The muscles associated with the fore-gut fall into two groups, those in front and those behind the nerve mass. The pharynx has 6 pairs of muscles inserted upon it (Figs. 1-3). The dorsal pharyngeal m. (M1) originate on the mid-dorsal area of the carapace and are inserted on the pharyngeal lobes. These are the largest of the muscles, and between and in front of them the anterior pharyngeal m. (M2) originate and insert on the epipharyngeal groove. Inserted immediately below these on the groove are the median pharyngeal m. (M3) which originate on the anterior wall of the rostrum, dorsal to the rostral gland. Lateral pharyngeal m. (M6) also originate here and insert on the lateral margins of the epipharynx. The large labial m. (M4) originate on the lower lip and insert on the pharyngeal lobes, and immediately posterior to this point is the insertion of the oesophageal dilator m. (M5). These originate on the anterior

horns of the endosternite and run transversely to the walls of the oesophagus. There are other muscles in this region which, though not inserted on the pharynx, may play some part in its movements and in changing the shape of the rostrum. In the rostrum are 2 muscles, the dorsal and ventral transverse rostral m. (M9 & 10), running horizontally from one side to the other. The lateral rostral m. (M8) run more or less vertically up the sides of the rostrum, and the anterior endosternal m. (M7) originate on the anterior wall of the rostrum, close to M6, and insert on the anterior horns of the endosternite.

It is difficult to imagine the exact function of some of these muscles. The transverse rostrals must produce distortion of the cuticle and so affect the mouth, while the anterior and median pharyngeal m. (M2 & 3) and the oesophageal dilators (M5) serve to increase the lumen of the fore-gut. There are no constrictors, such as occur in other arachnid orders. The dorsal pharyngeal m. (M1) and the labial m. (M4) are the best developed, and they are curious in that they extend in the same direction forming a link between the dorsal carapace and the lower lip, the pharyngeal lobes being interposed in the middle. Together they presumably pull back the lip and so open the mouth. One might imagine that this would have been effected by a muscle originating on the endosternite rather than by two muscles in series, but probably there is some phylogenetic reason for the existing disposition. Legendre (1961, 1962) has discussed the mode of action of the fore-gut and how liquid food is taken in by dilation of the pharynx and sucking stomach and is passed to the mid-gut. He describes valves at the junction of the oesophagus and sucking stomach in *Archaea* and some other genera. These have not been observed in the present survey.

The oesophagus is capable of dilation as it has a thin flexible floor, but it has no muscles attached to it apart from the anterior pair (M5) already mentioned. The sucking stomach, however, is very well provided with muscles. A dorsal series of dilators originate on the carapace at the point indicated by the fovea, and insert on the dorsal surface of the sucking stomach, and there is a series along each side originating on the endosternite. Between these bundles of muscle fibres, of which there are usually about a dozen, constrictor muscles encircle the

sucking stomach. With minor differences the structure of the sucking stomach seems to be essentially the same in all spiders.

Behind the sucking stomach is the beginning of the mid-gut, and it immediately gives off a pair of lateral diverticula which constitute the thoracenteron. In *Hypochilus* a pair of very slender muscles originates on the dorsal carapace immediately anterior to the origin of the muscles to the waist. They run obliquely downwards to ramify over the bases of these diverticula, and slender fibres also extend on each side from the endosternite to the same region of the gut. These dorsal and lateral muscles are posterior to and distinct from the muscles of the sucking stomach. The material available in the present study is not good enough to enable the presence of these muscles to be confirmed in many other species, but they appear to be of widespread occurrence. *Hickmania* and *Filistata* appear to resemble *Hypochilus*, while the transverse fibres were seen in *Heptathela*, *Thaida* and *Ixeuticus*.

Results

Liphistiomorpha

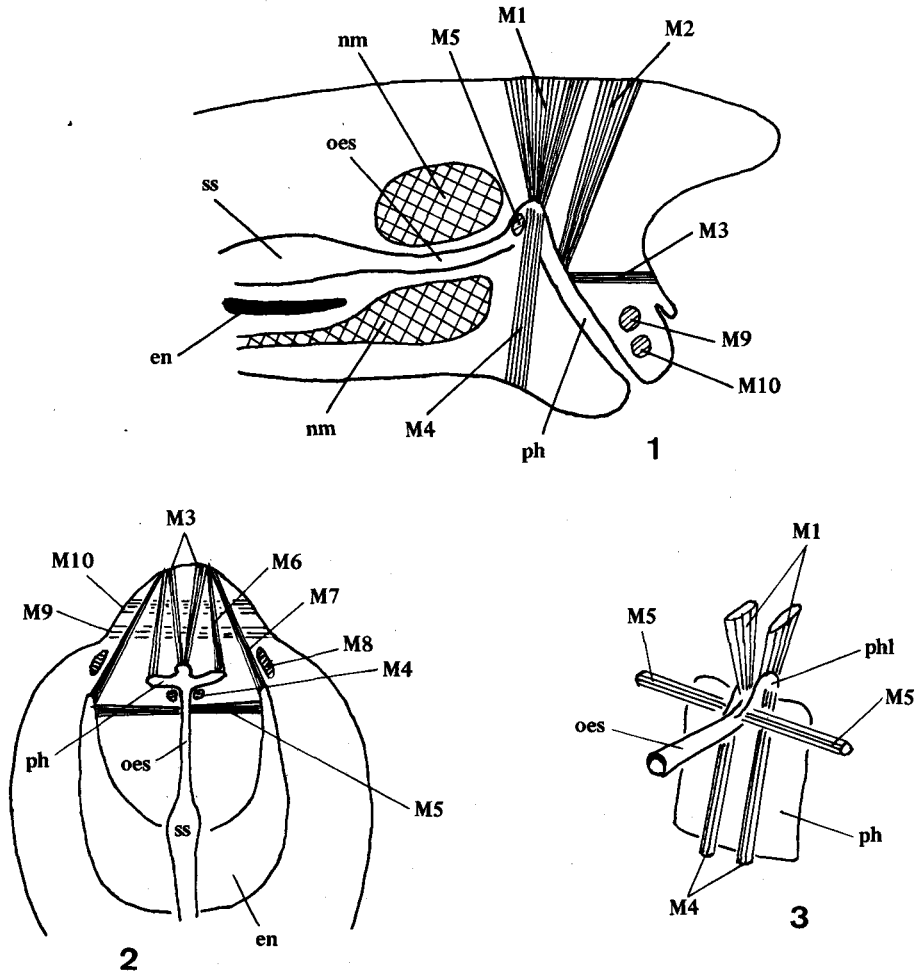
The following account is based on *Heptathela*, but as far as could be determined from the material available the structure of *Liphistius* seems essentially the same.

The pharynx rises vertically and forms an angle of about 90° with the oesophagus. It is slightly concave on its anterior side and the epipharyngeal groove is small. The rostrum is large and thin-walled, and the epi- and hypopharyngeal glands are well developed. The pharyngeal lobes are very large and hollow, the lining of the oesophagus is thin, and the sucking stomach is I-shaped in cross section.

The intrinsic muscles of the pharynx are unusual (Fig. 5). What appears to represent the dorsal pharyngeal m. (M1) consists of a very few muscle fibres inserted on the edges of the pharyngeal lobes but originating not on the dorsal carapace but ventrally between the chelicerae at the base of the rostrum. There is, however, in addition a pair of large dorso-lateral muscles. These diverge from the pharyngeal lobes at an angle of about 90°. They originate on the carapace and the space between them is partly

occupied by an anterior prolongation of the mid-gut. The pharyngeal lobes are joined in the mid line, and on their lateral faces are inserted the dorso-lateral muscles and also the labial m. (M4). These originate from the base of the lower lip, underly the hypopharyngeal glands as wide fan-shaped sheets, and insert as about half a dozen distinct bundles. These bundles alternate with those of the dorso-lateral muscles, and to some extent also with those of the oesophageal dilator m. (M5). There is thus an alter-

nating arrangement of muscle bundles directed dorso-laterally, laterally and ventrally, somewhat similar to that seen on each side of the sucking stomach, where the dilator and constrictor muscles alternate. It may be that M1 in *Heptathela* is in two parts, the large dorso-lateral part originating on the carapace and the small ventral part originating at the base of the rostrum. However, in all other spiders examined, M1 is inserted on the median side, or perhaps the edge of the pharyngeal lobes, not on the



Figs. 1-3: Diagrams to show the relations of the 10 muscles, or pairs of muscles, associated with the pharynx of an idealised spider. 1 Section in a slightly parasagittal plane; 2 The lower half seen from a frontal plane passing through the upper part of the pharynx; 3 The oesophagus and upper part of the pharynx, showing the pharyngeal lobes and the insertions of muscles M1, M4 and M5. (en = endosternite, M1-M10 = muscles, nm = nerve mass, oes = oesophagus, ph = pharynx, phl = pharyngeal lobe, ss = sucking stomach.)

lateral side as is the dorso-lateral muscle in *Heptathela*. This may be evidence that the dorso-lateral muscles are not part of M1 and are unique to the liphistiomorphs.

No other example of such dorso-lateral muscles was encountered, but Meyer (1981) describes and figures a similar arrangement in a salticid. Here the pharyngeal lobes appear to be large, with a dorso-lateral muscle from each side inserted on them. This he labels *M. dilator pharyngis dorsalis*. In the other families he considered, Agelenidae, Lycosidae, Araneidae and Theraphosidae, there were two dorsal dilators, anterior and posterior, inserted on the median side of the pharyngeal lobes and originating on the dorsal carapace near the middle line. It is not clear where those in the salticid are inserted, nor whether they are to be regarded as the anterior and posterior muscles running together or whether the anterior dilator is absent.

The anterior pharyngeal muscle (M2) of *Heptathela* also has a ventral origin at the base of the rostrum (Fig. 5), instead of on the carapace as is the normal pattern (Fig. 4). Inserted immediately ventral to it on the epipharyngeal groove is a large median pharyngeal m. (M3), and below this is a small muscle which was not observed in other spiders. It consists of two groups of 2 or 3 fibres only. They originate laterally on the sides of the rostrum, and, passing below M10, insert on the epipharyngeal groove immediately ventral to the insertion of M3. The pharynx of the liphistiomorph is thus interesting in that it is exceptionally well provided with dilator muscles. Though no constrictors are present it may still be regarded as being somewhat closer to the original arachnid condition than are the majority of spiders.

Mygalomorpha

In almost all respects the fore-gut of members of this group seems to conform to what may be called the normal spider structure. The pharynx is vertical with a small epipharyngeal groove, and forms a right angle with the oesophagus. This is usually down-curved, except in *Hexathele* where it is straight, and its thick dorsal cuticle may be transversely ridged. In *Atypus* the pharynx slopes backwards at an angle of about 45°, and so is more nearly in line with the

oesophagus.

With a few interesting exceptions the muscles of the fore-gut also conform to the normal pattern. The dorsal pharyngeal m. (M1), labial m. (M4), oesophageal dilator m. (M5), lateral pharyngeal m. (M6), anterior endosternal m. (M7) and transverse rostral m. (M9 & 10) were present in all genera examined, but the lateral rostral m. (M8) appears to be absent. The median pharyngeal m. (M3), which extends between the anterior wall of the rostrum and the pharyngeal groove, is double in the Dipluridae and in *Atypus* but appears single in the members of the other four families which were available. The anterior pharyngeal m. (M2), which originates on the dorsal carapace and inserts on the upper part of the pharyngeal groove, is normal in *Antrodiaetus*, the ctenizids *Cantuaria* and *Nemesia*, and in *Migas*. In *Atypus*, however, it is absent. The dorsal pharyngeal m. (M1) in this species is large, and the median one (M3) is double, while the pharynx forms an obtuse angle with the oesophagus, but these peculiarities do not seem to be enough to account for the absence of M2.

The other mygalomorphs are more remarkable. In the theraphosid (Fig. 6) M2 is small and has a ventral origin at the base of the chelicerae, not on the dorsal carapace. The diplurids are even more peculiar. In *Hexathele* (Fig. 7) M2 has very few fibres. Some originate on the dorsal carapace in the usual way and run parallel to M1, but the rest have a ventral origin on the thick cuticle between the chelicerae, similar to the condition seen in the theraphosid. Both groups of muscle fibres insert on the pharyngeal groove in the usual way. *Porrhothele*, on the other hand, has a larger M2 which has the normal relations and does not seem to have any ventral portion. The existence of fibres of this muscle with a ventral origin in the theraphosid and in *Hexathele* recalls the arrangement seen in the liphistiomorphs. In the present study it has not been noticed in any other spiders except, as described below, in the Hypochilidae. Meyer (1981), however, describes and figures a different arrangement in a theraphosid. Here his *M. dilator pharyngis dorsalis anterior* and *posterior* originate along the mid line of the carapace and insert, one behind the other, on the median sides of the pharyngeal lobes. There appear to be no muscles extending between the pharyngeal groove

and the wall of the rostrum apart from *M. dilator pharyngis rostralis medialis*, here called M3. Clearly this region of the mygalomorphs requires further investigation.

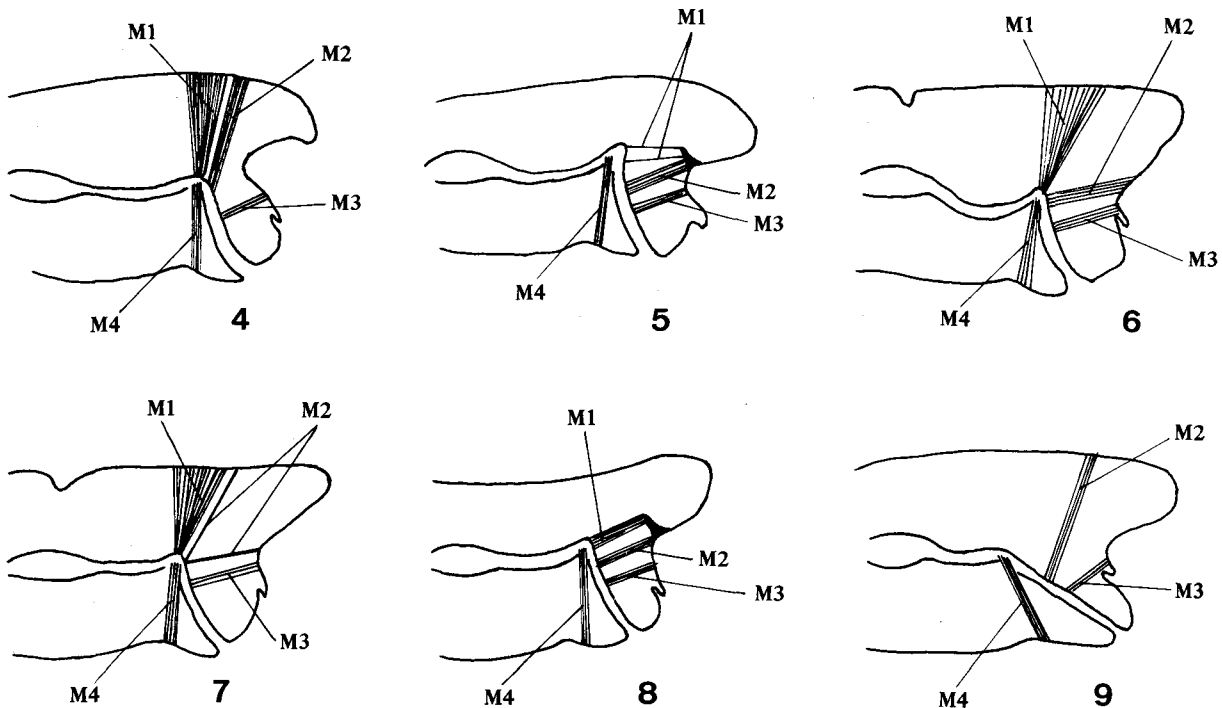
Araneomorpha

As would be expected in such a diverse assemblage as the araneomorphs, there is much variation in the proportions and details of the mouthparts and foregut. Branches of the thoracenteron extend into the rostrum in *Hypochilus*, *Ectatosticta*, *Dinopis* and also in *Eresus* (Millot, 1931). The extent and size of the rostral and other glands varies, and in at least *Hypochilus*, *Hickmania* and *Ixeuticus* there may be glands in the lip. The lip may have lateral grooves to receive ridges on the maxillae, as in *Pholcus*, *Uloborus*, *Uroctea* and others.

The angle between the pharynx and the oesophagus is usually rather more than 90° , and in the filistatids (Fig. 9) the two are more or less in a straight line, more so than in any other group examined. The pharyngeal lobes are not remarkable except in *Pholcus* and *Oonops* where they are moderate in size but extend laterally instead of dorsally. The oesophagus is more or less downcurved, and the sucking stomach is of the usual type.

With a few notable exceptions the number and relations of the muscles are the same throughout the group, and it will be convenient to deal with them in turn.

M1. Dorsal pharyngeal m. It will be recalled that in *Heptathela* this muscle is represented by a few fibres which originate ventrally at the base of the rostrum. *Hypochilus* (Fig. 8) and *Ectatosticta* differ from all



Figs. 4-9: Simplified diagrams of sagittal sections to show the normal arrangement of pharyngeal muscles M1, 2, 3 and 4, and some unusual exceptions. 4 *Ixeuticus*. Normal arrangement; 5 *Heptathela*. M1 very small with ventral origin, M2 also with ventral origin. There are large dorso-lateral muscles inserted on the pharyngeal lobes but they are not visible in this plane, nor are the muscle fibres passing to the pharynx ventral to M10; 6 Theraphosid. M1 normal, M2 with ventral origin; 7 *Hexathele*. M1 normal, M2 very small and in two parts with dorsal and ventral origins; 8 *Hypochilus*. M1 and M2 with ventral origins; 9 *Fillistata*. M1 absent.

the other araneomorphs in that they have this same ventral origin for M1 on an apodeme at the base of the rostrum, not on the dorsal carapace. It is, however, a medium sized muscle not a few fibres only. M1 varies considerably in size in different araneomorphs, and it is absent altogether in *Filistata* (Fig. 9). The unusual situation described by Meyer in the salticid has been mentioned above in comparison with *Heptathela*.

M2. Anterior pharyngeal m. Here again *Hypocheilus* and *Ectatosticta* are unlike all other araneomorphs, and resemble *Heptathela*. M2 are large muscles originating at the base of the rostrum and inserted on the epipharyngeal groove. *Hexathele* and the theraphosid also have some fibres of M2 with a ventral origin, but they were observed in no other spiders.

M3. Median pharyngeal m. This is usually double, but it is single in *Filistata*, *Uroctea* and *Ariadna*, and perhaps also in *Hickmania*.

M4. Labial m. This varies considerably in size but is present in all. In *Hickmania* there is the usual large pair of muscles originating on the lip, but towards their ventral ends small lateral bundles, which arise from the cuticular rods at the sides of the hypopharynx, converge with them. The arrangement is the same in *Uloborus*, and here the lateral bundles are distinct up to their insertion on the pharyngeal lobes. In *Pholcus* and *Oonops*, where the pharyngeal lobes extend horizontally instead of vertically, M4 are inserted on their ventral surface while M1 insert dorsally and in the median groove of the upper surface.

M5. Oesophageal dilator m. These are absent in *Ariadna* and apparently also in *Oonops* and *Patu*.

M6. Lateral pharyngeal m. This appears to be present

in all except perhaps *Dinopis*.

M7. Anterior endosternal m. This is present in all.

M8. Lateral rostral m. This is absent in *Hypocheilus*.

M9 & 10. Transverse rostral m. Normally there are two of these, but in *Dinopis* only one is present. A unique arrangement is seen in *Filistata*. Here there is a distinct transverse bundle which seems to represent the dorsal muscle M9. In front of it fibres arising on each side fan out obliquely, and, crossing one another, insert on the opposite side of the rostrum.

References

- BROWN, R. B. 1939: The musculature of *Agelena naevia*. *J.Morph.* **64**: 115-166.
- KÄSTNER, A. 1952, 1954: Die mundswerkzeuge der Spinnen. *Zool.Jb.* **72**: 101-146; **73**: 47-68.
- LEGENDRE, R. 1953: Recherches sur les glandes prosomatiques des araignées du genre *Tegenaria*. *Annls Univ.sarav.* **4**: 305-333.
- LEGENDRE, R. 1961: Le mechanism de la prise de nourriture chez les araignées. *C.r.hebd.Séanc.Acad. Sci., Paris* **252**: 312-323.
- LEGENDRE, R. 1962: La structure et la fonctionnement du tube digestif anterior des Archaeidae. *C.r.hebd.Séanc. Acad.Sci., Paris* **254**: 3034-3036.
- MARPLES, B. J. 1968: The hypocheilomorph spiders. *Proc. Linn.Soc.Lond.* **179**: 11-31.
- MEYER, W. 1981: Observations on the morphology and histochemistry of the fore-gut muscles of spiders. *J.Morph.* **170**: 113-131.
- MILLOT, J. 1931: Les diverticules intestinaux du cephalothorax chez les araignées vrais. *Z.Morph.Okol.Tiere* **21**: 740-764.
- MILLOT, J. 1936: Le sens du gout chez les araignées. *Bull. Soc.zool.Fr.* **61**: 27-38.
- PALMGREN, P. 1978: On the muscular anatomy of spiders. *Acta zool.Fenn.* **155**: 1-41.
- WHITEHEAD, W. F. & REMPEL, J. G. 1959: A study of the musculature of the black widow spider *Latrodectus mactans* (Fabr.) *Can.J.Zool.* **37**: 831-870.