

Filtration mechanisms in the mouthparts of tetrapulmonate arachnids (Trigonotarbida, Araneae, Amblypygi, Uropygi, Schizomida)

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Summary

The comparative anatomy of filtration mechanisms in the mouthparts of living and extinct tetrapulmonate arachnids is described. All taxa studied possess plumose, preoral setae. A pharyngeal palate plate is an autapomorphic filtering mechanism for spiders. Amblypygi and Uropygi have no such pharyngeal filter; however, these orders have a dense mat of filtering setae on the pedipalpal coxae which in Uropygi lines a preoral trough formed in conjunction with the labrum, but comprises a more open preoral channel in Amblypygi. The extinct trigonotarbids had a series of cuticular projections between the labrum and labium which is interpreted as being a preoral filtration mechanism, similar to that reported for palpigrades. Comparisons are made between these tetrapulmonate filtration mechanisms, and the term preoral cavity is considered inappropriate for some arachnids. A filtering structure in the fossil record dates liquid feeding in tetrapulmonates to at least the Lower Devonian.

Introduction

The arachnid taxon Tetrapulmonata (Shultz, 1990) is defined by the possession (at least primitively) of two pairs of book-lungs and comprises the orders Araneae, Amblypygi, Uropygi and Schizomida and includes the extinct Palaeozoic order Trigonotarbida (Shear *et al.*, 1987), which ranged from the Upper Silurian (Jeram *et al.*, 1990) to the end of the Carboniferous and which also had two pairs of book-lungs (Claridge & Lyon, 1961). The trigonotarbids have been placed as the phylogenetically primitive sister taxon of the living tetrapulmonates (Shear *et al.*, 1987).

Trigonotarbid fossils include unusually well preserved specimens from the Devonian Rhynie Chert, Aberdeenshire (Hirst, 1923; Hirst & Maulik, 1926; Shear *et al.*, 1987), in which there has been excellent preservation of the cuticular anatomy. The Rhynie trigonotarbids were placed in the family Palaeocharinidae (Hirst, 1923) and appear, morphologically, to be the most primitive, but not the oldest (Jeram *et al.*, 1990), of the trigonotarbids, retaining primitive features such as multifaceted lateral eyes (Hirst & Maulik, 1926; Shear *et al.*, 1987). The Rhynie Chert arthropods preserve detail of cuticular structures in three dimensions, including setae, tendons, book-lung lamellae (Claridge & Lyon, 1961) and, in some specimens, structures interpreted as the mouthparts.

All extant tetrapulmonates, like most arachnids, practice preoral digestion, pouring enzymes on to prey held in a preoral cavity and then ingesting the liquified food (Snodgrass, 1948). The preoral cavity is defined by Snodgrass (1948) as the space between the labrum and the palpal coxae, but this definition is less appropriate

for arachnids such as spiders and Amblypygi which have relatively simple labra and palpal coxae. Therefore a reappraisal of the concept of a preoral cavity is presented here.

Externally, preorally digested liquid has to be filtered to prevent large particles entering the gut and potentially blocking it (Foelix, 1982). In all tetrapulmonates, the small size of the mouth and the general "hairiness" of the mouthparts with their dense brushes of setae help to achieve this. However, in spiders a further fine filtering mechanism occurs within the pharynx. This palate plate (Bartels, 1930; Foelix, 1982) consists of rows of microscopic platelets which trap any remaining particles of food. Dense setae with a filtering function in the preoral trough between the labrum and fused palpal coxae of the Uropygi and on the palpal coxae of the Amblypygi have also been described by Pocock (1902).

To my knowledge, a palate plate has not been identified in the pharynx of the Uropygi and Amblypygi even in the studies of Pocock (1902) and Snodgrass (1948) and, with the exception of the dense setae around the mouthparts, the method, if any, by which these groups fine filter the food in the pharynx is unknown. The excellent preservation of the Rhynie Chert trigonotarbids allows this comparative anatomy to be extended into an extinct order, regarded as the most phylogenetically primitive of the tetrapulmonates.

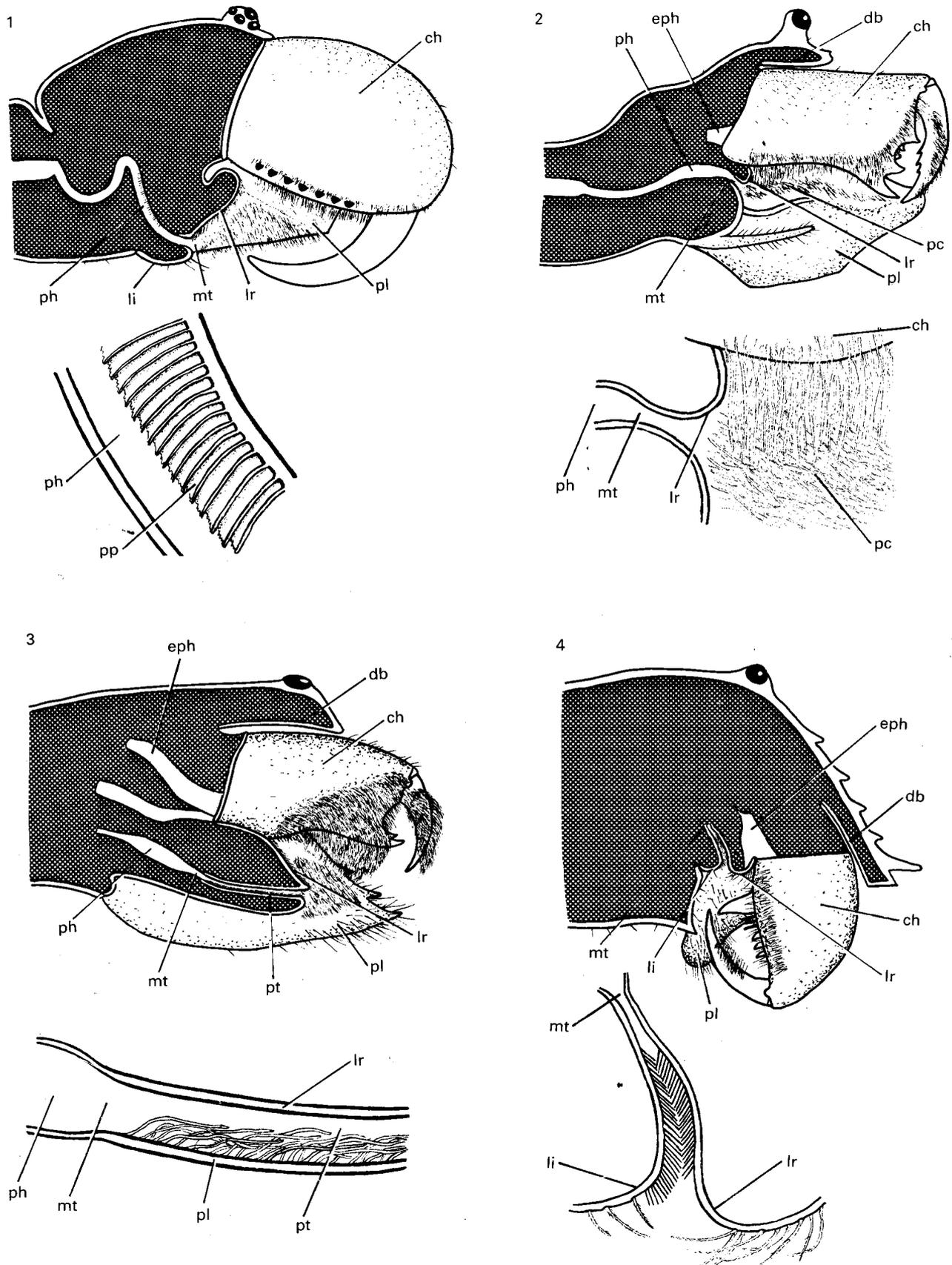
Methods

Representative specimens of each of the extant orders of tetrapulmonate arachnids were obtained for comparative anatomy. *Mastigoproctus giganteus* (Lucas) (Uropygi), *Heterophrynus* sp. (Amblypygi) and *Grammostola cala* Chamberlin (Araneae: Theraphosidae) were used. No schizomid specimen was available, but the mouthparts of this taxon are anatomically similar to those of the closely related Uropygi (Van der Hammen, 1989; Shultz, 1990).

Specimens were sectioned longitudinally and vertically to one side of the midline of the prosoma, and the morphology of the mouthparts, the distribution of their filtering setae and the position of the foregut were examined using a Wild M8 stereomicroscope. The prosoma was cleared of soft tissue by heating in KOH and the remaining cuticular structures investigated.

The pharynx, mouth, and in the case of the Uropygi the structures surrounding the preoral trough, of each group were dissected free as a single unit. With the exception of the delicate Amblypygi pharynx, the structures were opened out by easing the dorsal and ventral surfaces of the pharynx apart to examine the internal surfaces of the pharynx. The pharynges of all three groups were examined under high power using a Nikon Optiphot biological microscope. The open foregut and preoral structures of the Araneae and Uropygi were mounted on stubs, dried and gold coated for examination using a Jeol 2020 scanning electron microscope.

The trigonotarbid material consisted of thin sections and slides of fragments of chert from the British Museum (Natural History), specimen numbers BM



Figs. 1-4: Comparative anatomy of filtration mechanisms in the mouthparts of the tetrapulmonate arachnid orders, showing gross morphology in lateral section of the prosoma and a section of detail of the fine filtering mechanism. **1** Araneae, showing detail of palate plate; **2** Amblypygi, showing detail of setae surrounding the mouth; **3** Uropygi, showing detail of setae lining the lower surface of the pre-oral food trough; **4** Trigonotarbida (not to scale), showing detail of setae lining the labrum and labium; note orientation of the chelicerae hanging downwards. Abbreviations: ch = chelicerae, pl = palpal coxa, lr = labrum, li = labium, mt = mouth, ph = pharynx, db = doublure of carapace, eph = epipharyngeal sclerite, pp = palate plate, pc = preoral channel, pt = preoral trough.

(NH) In 24675, In 27756, In 27759 and In 27364. The Rhynie Chert is of Lower Devonian (Pragian) age and interpreted as having been preserved in siliceous sinters in a hot springs environment (Trewin & Rice, 1992). These specimens were examined under high power and transmitted light using the Nikon microscope. Drawings were made with the aid of a camera lucida.

Results

Araneae

Preorally, the dense setae interpreted as having a filtering function are located principally on the labrum, on the chelicerae either side of the tooth row and especially on the palpal coxae (Fig. 1). The labral setae are short and wholly external, i.e. they do not continue on to the inner surface of the labrum (the preoral cavity). Similarly, the labium has no dense setae on either its external or internal surface. The cheliceral setae are longer on the lateral side of the tooth row compared with the mesal side. The fang has no setae, an autapomorphic condition for spiders (Selden *et al.*, 1991). The palpal coxae are most densely setose on the ventro-mesal surface of the podomere. The setose area is roughly triangular and widest at the proximal end of the palpal coxae where they converge towards the mouth.

As has been described previously in spiders (Bartels, 1930; Foelix, 1982), the dorsal (labral) wall of the theraphosid pharynx is modified into a palate plate. This roughly oval plate is widest near the top of the pharynx (Fig. 5) and consists of successive rows, approximately 15 μm apart, of thin cuticular platelets with serrated margins, arranged on either side of a median groove (Fig. 6). These platelets are orientated at a shallow angle towards the mouth. The ventral (labial) wall of the pharynx is not modified into a filtering device.

Amblypygi

Preorally, the setae occur on the chelicerae and the palpal coxae (Fig. 2). The labrum is very small (cf. Uropygi) and unlike that of spiders bears few setae. The labium is poorly defined owing to fusion of the palpal coxae, and there are few setae immediately below the mouth. The chelicerae are most densely setose in a large brush on the ventral surface of the proximal end of the basal segment. Setae also line the tooth row of the chelicera which, with the fang, lies parallel with the junction of the basal segment to the prosoma; whereas in spiders the tooth row and fang lie perpendicular to it. The position of the cheliceral setae is such that they are densest where they overhang the entrance to the preoral cavity and hence the mouth. The fang is setose.

The greatest distribution of setae is on the palpal coxae with their large, anteriorly projecting processes (Pocock, 1902). As noted above, the palpal coxae are fused beneath the mouth and the setae on each process form a hairy V-shaped channel in which ingested food must be channelled through the dense setae towards the mouth (Fig. 2). This preoral channel or gutter (Pocock,

1902) underlies the setose proximal region of the chelicerae and thus forms a mass of setae surrounding the mouth both dorsally and laterally (Fig. 2).

The Amblypygi pharynx is a simple expanded tube leading into a narrower oesophagus. The thin nature of the pharynx walls allows the internal surface to be examined under light microscopy. No modifications of the pharynx wall were visible in terms of a palate plate or similar filtering structure. The mouth itself is surrounded by a sclerotised ring of cuticle formed from the labrum and labium, but this structure bears no setae or other filtering device. The Amblypygi filtering system is therefore interpreted as being wholly preoral, relying on the palpal coxae and chelicerae.

Uropygi

Preorally, setae occur mainly on the chelicerae and palpal coxae (Fig. 3), as in Amblypygi. Setae are also present on the labrum; however, the palpal coxal setae are part of a more complex structure, the preoral trough (Pocock, 1902).

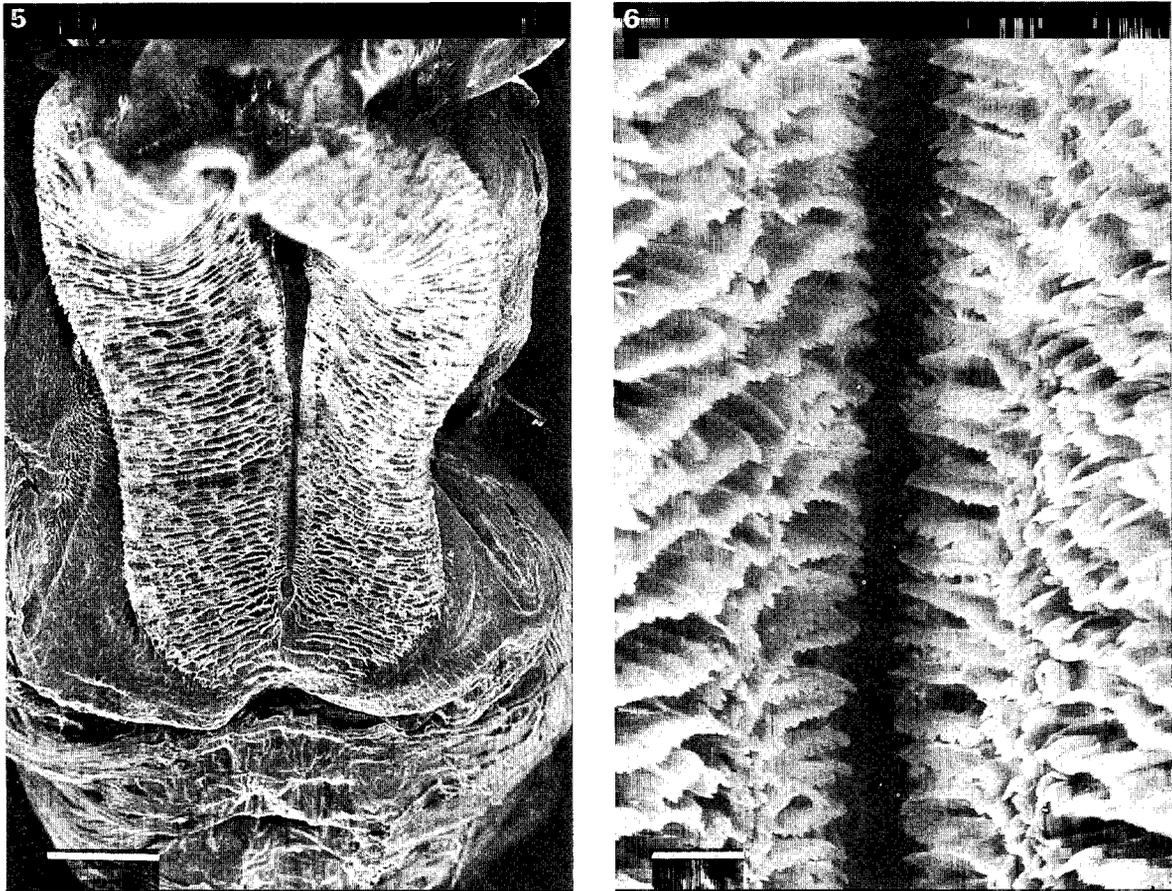
The chelicerae are morphologically similar to those of Amblypygi, with the fang and tooth row lying parallel with the junction of the basal segment to the prosoma. The fang is highly setose, but the setae on the basal segment are more distal and mesal than those of amblypygids. These cheliceral setae do not overhang the mouth as in Amblypygi, but are densest in a more anterior position, guarding the entrance to the preoral trough (Fig. 3).

The preoral trough is a narrow channel, crescentic in transverse section, which tapers towards the mouth. The floor of this trough is formed by the dorsal surface of the fused palpal coxae while its roof is formed from the ventral surface of the labrum (Fig. 3). A dense mat of setae, interpreted as having a filtering function, lines the floor of this narrow trough (Figs. 3, 7–8), i.e. the dorsal surface of the palpal coxae as in Amblypygi, with the individual setae estimated as being 100 μm long. Setae were figured on the roof of the trough by Petrunkevitch (1949). Detailed examination of the ventral surface of the labrum under both light and scanning electron microscopy revealed no setae on this surface.

However, a fringe of longer hairs is present on both the labrum and the palpal coxae at the entrance to the preoral trough (Pocock, 1902; Fig. 3). The palpal coxae also bear a small setose pad on the mesal face of the coxal processes, either side of the entrance to the preoral trough (Fig. 3). This is similar to the setae on the Amblypygi palpal coxae, except that there they guard the entrance to the mouth itself. The labrum bears short setae on its dorsal surface. The Uropygi pharynx is larger and more complex than that of the Amblypygi, with distinct dorsal and ventral surfaces. However, examination of both surfaces of the pharynx revealed no specialised filtering structures on either surface.²

Trigonotarbida

Three Rhynie Chert specimens show the mouthparts of these palaeocharinid trigonotarbids in detail (Figs.

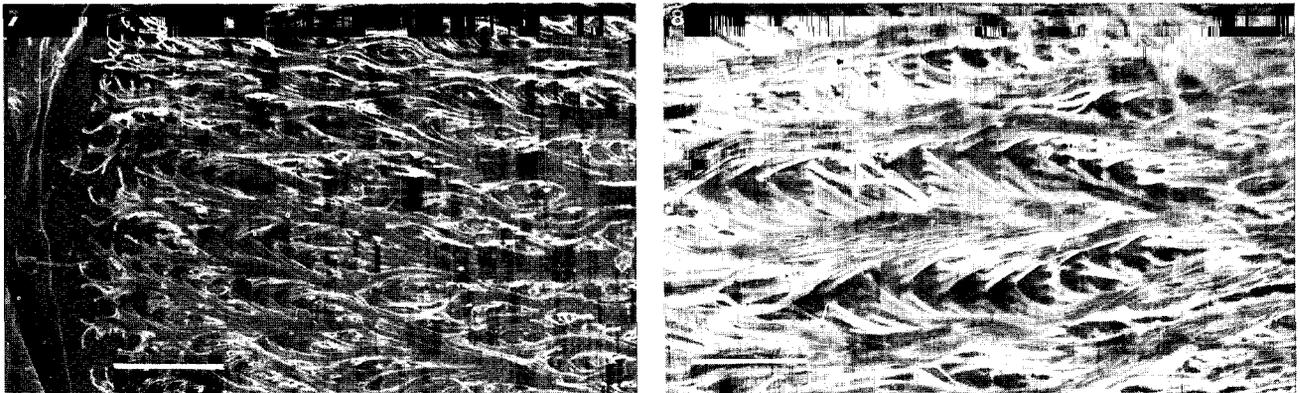


Figs. 5-6: Scanning electron micrograph of palate plate of the theraphosid *Grammostola cala*, showing the rows of platelets to filter food particles from ingested liquid prey. **5** Overview of palate plate (scale line = 200 μm); **6** Detail of individual platelets surrounding the central groove (scale line = 20 μm).

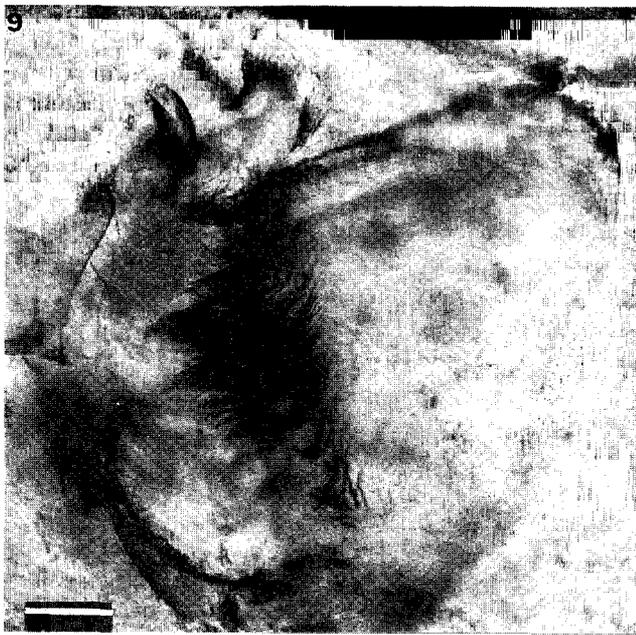
9-12): BM(NH) In 24675, two fragments each containing part of the same animal (In 27756/27759), and In 27364, a thin section. Numerous additional fragments show more general views of the animal and the position of the elements of the mouthparts and their setal distribution. The chelicerae in trigonotarbid are constructed like those of a spider in terms of the position of the fang and tooth row and are paraxial like those of a mygalomorph spider. However, they hang down between the palpal coxae, in the same plane as the other limb coxae (Figs. 4, 9-12). This appears to represent a previously

undescribed cheliceral orientation in arachnids. The trigonotarbid chelicerae and their orientation are currently being fully described (Dunlop, in preparation).

Preorally, setae are preserved on the chelicerae, the labrum and the palpal coxae, which also have proximal coxal processes. Under very high power these setae are seen to be of the plumose type with fine filaments projecting from the main shaft. The mouthpart setae of the other tetrapulmonates studied were also of the plumose type. The chelicerae have reasonably dense setae along their tooth row and also on the fang itself,



Figs. 7-8: Scanning electron micrograph of dorsal surface of the fused palpal coxae of Uropygi forming the floor of the preoral trough, showing a mat of dense setae interpreted as having a filtering function. The mouth is to the left in both cases. **7** Setose lining at entrance to the mouth (scale line = 100 μm); **8** Detail of setae, showing their arrangement in rows (scale line = 50 μm).

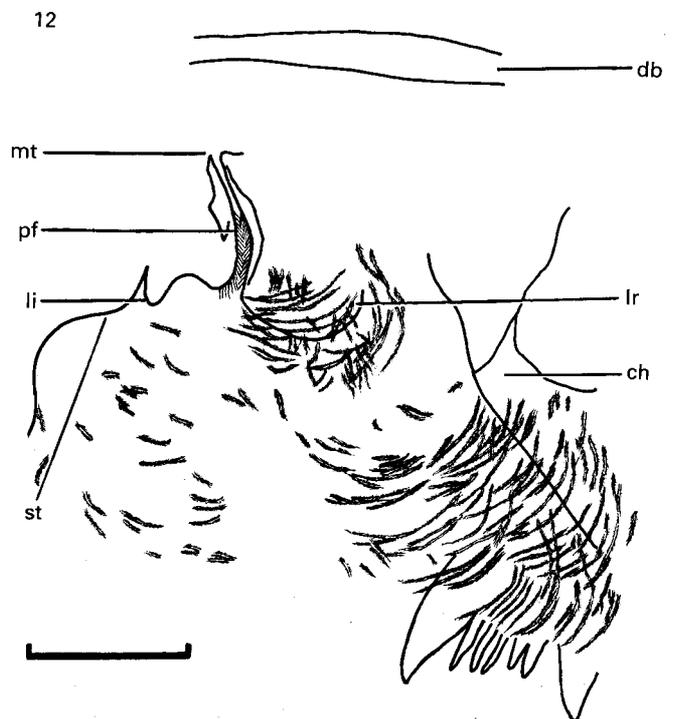
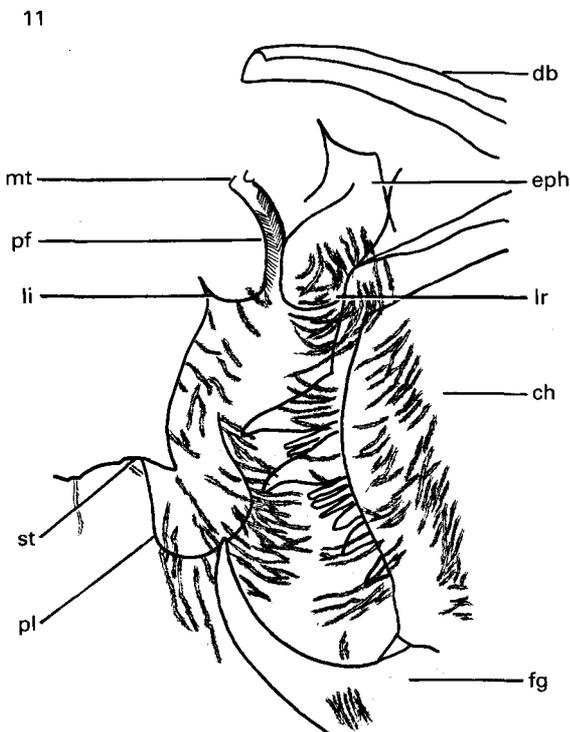


Figs. 9–10: Mouthparts of palaeocharinid trigonotarbids from the Rhynie Chert, Aberdeenshire. **9** In 25675; **10** Thin section In 27364. Scale lines = 0.05 mm.

but in both cases this setation is less dense than in *Amblypygi* and *Uropygi*. The two small plates anterior to the sternum are interpreted as the palaeocharinid labium and labrum respectively. The labrum is quite setose externally, but the labium probably had too few setae to have had any significant filtering effect, at least on its external surface. The palpal coxae have some setation, most prominent on the coxal processes, but

this is considerably less dense than in the living tetrapulmonates.

The three principal specimens also show a small dark, sclerotised structure at the base of the chelicerae and between the labrum and labium, with which it is continuous. The structure appears tubiform, but this is based on a lateral view only, and is most clearly visible on specimens In 24675 and 27364 (Figs. 9–12: pf),



Figs. 11–12: Interpretative drawings of palaeocharinid mouthparts shown in Fig. 4. **11** In 25675, the less distorted of the two, interpreted as being close to life position. Note the two superimposed chelicerae in vertical orientation. **12** In 27364, distorted specimen with the sternum and chelicerae skewed away from the mouth. Abbreviations: mt = interpreted position of mouth, pf = preoral filtering structure, li = labium, st = sternum, pl = palpal coxa, db = structure interpreted as doublure of carapace, eph = structure interpreted as epipharyngeal sclerite, lr = labrum, ch = chelicera, fg = fang. Scale line = 0.1 mm.

27756/27759 being rather opaque. Under high power this structure contains rows of opposing, stiff setae angled downwards, strongly suggesting a filtering function for fluid being drawn through this structure. It is possible that these "setae" could represent cross sections of platelet-like cuticular projections, similar to the spider palate plate, but this is impossible to determine from lateral sections of the fossils alone.

What is not apparent is whether this structure represents a preoral structure formed from the labrum and labium or alternatively the pharynx itself. The arguments for it being the pharynx are that there is no cuticular structure preserved anterior to it, i.e. if this structure is not the pharynx then why is one not present? The inner lining of the trigonotarbid pharynx and oesophagus was probably sclerotised, but such structures are likely to have been delicate and could easily have been broken off during preservation.

A small cuticular element is preserved anterior to this structure (Figs. 9–12: eph) which in comparison to Amblypygi and Uropygi is interpreted with reservations as the epipharyngeal sclerite. In uropygids (Fig. 3) this structure lies above the pharynx and acts as a muscle attachment site for the pharyngeal dilators (Shultz, 1993). This cuticular element in the Rhynie chert trigonotarbid lies above the setae-bearing structure, but this is seen in In 24675 (Figs. 9, 11), a laterally compressed specimen, and its position may have been distorted.

In favour of the preoral interpretation is the small size of the structure if it were a pharynx, compared with other tetrapulmonate pharynges, and the lack of any obvious muscle attachment sites on it for pharyngeal dilators. A setae-based pharyngeal filtration system would be unique among tetrapulmonates. The apparent narrowing at the top of this structure (Figs. 10, 12) could be interpreted as the mouth itself, and if this were the case the epipharyngeal sclerite could still provide a muscle attachment site for pharyngeal muscles as in Uropygi.

The exact position of the mouth in animals with preoral structures can be hard to define, especially when the fossils are only preserved in lateral section. On balance, this setae-bearing structure is probably preoral rather than postoral, but in either case this does not detract from the presence of a specific filtering mechanism either just outside or inside the mouth.

Discussion

In all tetrapulmonates preoral filtration mechanisms are present and involve to a greater or lesser degree the brushes of plumose setae on the chelicerae, labrum and especially the palpal coxae (Figs. 1–4), with the exception of amblypygids which have a poorly setose labrum (Fig. 2). This setation around the mouth, in particular of the chelicerae and the palpal coxae, was present in the Lower Devonian Rhynie Chert trigonotarbids (Fig. 4), but was not so well developed. The palpal coxae of the Middle Devonian trigonotarbid *Gilboarachne* appear to have been more setose than the Rhynie form (Shear *et al.*, 1987).

In addition to the general distribution of setae, spiders have a specialised additional filter, the palate plate. No homologous structure was found on the dorsal wall of the pharynx in Amblypygi or Uropygi. The pharynx plate is therefore considered autapomorphic for the Araneae and appears to be the most specialised of the tetrapulmonate filtration systems.

If the trigonotarbid filtering setae are indeed preoral then the Araneae are the only order to use postoral filtration. Van der Hammen (1989) placed the spider mouth at the top of the pharynx, behind the pharynx plate, and considered the pharynx as part of the preoral cavity. I place the mouth in its traditional position, in front of the pharynx, since the spider pharynx is a roughly tubular structure with muscle attachments and a sucking function (Foelix, 1982) like that of the other extant tetrapulmonate pharynges, which Van der Hammen (1989) does not dispute.

The Amblypygi and Uropygi rely solely on their preoral setae on the chelicerae and coxal endites, and coxal setae are also seen in spiders. The Uropygi, however, have a specialised enlargement of the labrum to form an enclosed preoral trough between itself and the palpal coxae. The amblypygid system presents a more open preoral channel which Pocock (1902) considered as a simpler version of the uropygid morphology. The amblypygid morphology is probably the more primitive of the two, being the most similar to trigonotarbids.

The trigonotarbids, at least the Rhynie Chert form, had an alternative fine filter interpreted as a preoral lining of setose cuticular projections from the inner surface of the labrum and labium. This trigonotarbid structure is not seen in any living tetrapulmonate nor does it appear to be directly ancestral to any of them. If pharyngeal, it cannot be easily homologised to the spider palate plate. It is superficially, and probably functionally, similar to the Uropygi and Amblypygi structures. However, neither of these orders have dense setae on the labrum, except at its anterior margin, and their principal setation comes from the palpal coxae, not the labium.

To date, later Devonian and Carboniferous trigonotarbid material has not been found preserved in sufficient detail to determine whether the filtering mechanism in the Rhynie Chert animals was present in all members of this order, or whether it underwent subsequent evolution. As might be expected, the palaeocharinid filtration system appears to be the most primitive and least specialised of the tetrapulmonates.

It might be predicted that overall, the palaeocharinid system was less effective than that of the extant orders. It would be interesting to compare the relative effectiveness of the alternative filtration systems of the three extant tetrapulmonates, the spider palate plate being capable of filtering particles out of Indian ink (Bartels, 1930), and the relative contributions of the different elements of the systems in living animals.

It may be significant to note that the palpigrades, regarded as the phylogenetically primitive sister taxon of the tetrapulmonates by Shultz (1990), are reported to

have a buccal cavity, anterior to the pharynx, lined with cuticular projections (Rowland & Sissom, 1980). These projections were interpreted by these authors as functioning to filter food, and the palpigrade buccal cavity appears to represent the closest analogue among living arachnids to the palaeocharinid system of ingestion. This in turn may suggest that this filtering system based on cuticular projections may be the primitive condition for tetrapulmonate arachnids.

The only previous evidence suggesting a liquid feeding mode of life in fossil arachnids was the presence of the preoral cavity (Størmer, 1976; Selden & Jeram, 1989). The term preoral cavity applies best to scorpions and similar arachnids including Uropygi, with a projecting labrum and coxal endites which together form a genuine cavity in front of the mouth in which food is enzymically digested. However, this term applies less well to arachnids such as spiders, amblypygids and trigonotarbids in which the labrum is small and the coxae do not have strong endites enclosing a cavity. These orders, by definition, have a highly reduced preoral cavity, a fact noted by Snodgrass (1948), but still digest food enzymically and preorally while held in the chelicerae. The term preoral cavity should be used with caution and appears to be an inappropriate term for a functional structure in such animals as spiders, especially those which digest soft tissues within the prey's body itself. Here the preoral cavity is not the actual site of digestion, but simply a short conduit in front of the mouth.

That said, the earliest record of a preoral cavity is cited as being in Lower Devonian scorpions which possess coxal endites (Selden & Jeram, 1989; Rolfe, 1985), although this still does not prove liquid feeding. The presence of structures permitting liquid feeding has been considered as evidence for terrestriality (Selden & Jeram, 1989), since preoral digestion in water is thought to have been inefficient owing to dilution of digestive enzymes poured on to prey (Van der Hammen, 1989).

The presence of a filtration mechanism in the Rhynie Chert trigonotarbid is almost unequivocal evidence that this animal was a liquid feeder relying on preoral digestion. This dates the evolution of this mode of feeding to at least the Lower Devonian (approximately 398 ma). Earlier trigonotarbids, which were probably terrestrial, are present in the Upper Silurian (approximately 414 ma) (Jeram *et al.*, 1990), but their mouthparts are not preserved well enough to compare to the Rhynie Chert form. The presence of book-lungs with spiracles in the Rhynie Chert trigonotarbids (Claridge & Lyon, 1961) shows that they at least were terrestrial. Further supportive evidence for trigonotarbids feeding on liquid prey comes from a Rhynie Chert thin section (Hunterian Museum A. 2451/25) figured by Rolfe (1985: pl. 1, figs. 6–8). This shows masticated cuticular material being held in the chelicerae of a trigonotarbid and apparently being digested preorally. This suggests an overall mode of feeding in Devonian arachnids essentially indistinguishable from that of tetrapulmonates today.

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