SOIL ORGANISMS Volume 81 (3) 2009 pp. 543–556

ISSN: 1864 - 6417

The order Siphonophorida – A taxonomist's nightmare? Lessons from a Brazilian collection

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Abstract

Recent study of a collection of over 300 specimens of Siphonophoridae from Brazil, comprising several morphotypes/species, has allowed comparison between and within 'species'. Published descriptions have in the past used characters that were found to vary between individuals of the same species, or even within the same individual. Hitherto unused characters that may be useful in distinguishing between species are discussed.

Keywords: taxonomic characters, Brazil, millipedes, Diplopoda

1. Introduction: Current taxonomy

The Siphonophorida remain one of the least studied millipede orders. Hoffman (1979) described the classification of the order as 'chaotic' and in a more recent bibliographic catalogue Jeekel (2001) gives it the 'taxonomists' award for the least popular group among diplopods'. He attributes this to the lack of easily accessible complicated genital structures. Nevertheless the Siphonophorida are of special interest among the Diplopoda, they hold the 'world record' for the most number of legs (375 pairs, Marek & Bond 2006) and they also have very unusual mouthparts which are elongated into a long 'bird-like' beak.

Both Verhoeff (1941) and Attems (1951) attempted to bring some order to the group but in the absence of good generic characters many authors described new species under the genus *Siphonophora* so that over 100 species have been attributed to this genus. Jeekel's (2001) catalogue is a very useful recent list of described species with brief remarks.

The global distribution of the order is primarily pan-tropical (Central and South America, South-East Asia and Australasia) but extends into temperate regions such as California and the Himalayas; one family is found in Southern Africa.

The order Siphonophorida is characterised by separate tergites, pleurites and sternites, simple leg-like gonopods derived from legs 9 & 10 with the podometers often coalesced (generally the posterior pair being longer), ozopores starting on the 5th body ring, absence of eyes, and the head either conical or drawn out into a 'beak' of varying length with correspondingly reduced mandibles and gnathochilarium; it has been suggested that the mouth parts may be suctorial. Three families are recognised (see Jeekel 2001), the Siphonorhinidae Cook & Loomis (three genera and 10 species) have elbowed antennae that lack sensory pits on the 5th and 6th antennomeres and a conical head which is not drawn out into a long beak. The family Nematozoniidae Verhoeff (one genus and two species) is very similar to the Siphonorhinidae but differs in the relative lengths of the antennomeres. Finally the large family Siphonophoridae (10 genera and over 100 species) has straight antennae, the head drawn out into a long beak and sensory pits on antennomeres 5 and 6.

2. Materials and methods

A large collection of Siphonophoridae was made during the course of ecological studies in the Brazilian Amazonia by Joachim Adis and colleagues from the Max Plank Institute in Plön. Specimens were obtained using a variety of methods including trapping and hand sorting. The collection numbered over 300 specimens, 294 of which were analysed in detail. All specimens came from the area around Manaus but had been collected in different forest types. These included inundation forest (Igapó), primary upland forest (Reserva Ducke), secondary upland forest (Capoeira) and mixed water forest (Lago Janauarí). See Adis (2002) for more details.

Apart from general details of the collection, such as locality, date, collecting technique and ecological information (where available) the detailed characteristics were recorded for each specimen as shown in Tab. 1. The list was compiled with reference to information in previous descriptions of Siphonophorids. Some specimens were too damaged or were preserved in such a way that certain characters could not be recorded.

For several individuals a more detailed analysis of legs and antennae was made, including length and breadth of podomeres/antenomeres, relative length of accessory claw to claw and number of sensory cones on the antennae. For several males the gonopods were dissected and mounted. SEM mounts of head, telson, mid body rings and gonopods were made to look at potential microscopical characteristics in more detail.

Tab. 1 Characteristics recorded for each specimen.

Characteristic	**Method used**
Specimen number	Assigned to each individual
Body length	Estimated using a squared graticle under binocular microscope
Body width	The widest tergite in dorsal view. Measured in the same way as length
Number of body tergites	Expressed as total (including collum) + telson
Number of leg pairs	Total counted
Body shape	General description made, mostly from dorsal view
Colour of specimen	General description (note some specimens were strongly influenced by capture method)
Rostrum length measured as:	
♦ Head + rostrum	Tip of rostrum to hind margin of head
♦ Rostrum to base	Tip of rostrum to base of rostrum
♦ Rostrum to antenna base	Tip of rostrum to mid point of antennal base
Width of head was measured as:	
♦ Widest point	Maximum head width
♦ Posterior margin	Width at hind margin
♦ Width between antennae	Width between internal margin of antennal sockets
Rostrum shape/curvature	Description made in dorsal and lateral view, also approximate length
Setation on head	Description of number and position of setae
Setation on rostrum	Description of number and position of setae
Cuticle of head	Descripion was made of any surface structures
Details of antennae	
♦ Length	Estimated length using squared graticule
♦ Number of visible segments	Count of clearly visible antennomeres
♦ Sensillae/sensory pits	Location and number of sensory pits under light microscope
Collum	
♦ Length	Measured mid dorsally using squared graticule
♦ Shape	Description & sketch made from dorsal & lateral view
♦ Pilosity	Description of extent of setae
Tergite 2: Length	Tergite after the collum measured mid-dorsally
Midbody tergites, Shape & pilosity	Description & sketch made
Prozona:	
♦ Microtubercules & setae	Description made
♦ Width	Estimated mid dorsally using squared graticle
Metazona	
♦ Microtubercules & setae	Description made
♦ Width	Estimated mid dorsally using squared graticle

Tab. 1 cont.

Characteristic	Method used
Limbus	Description made using light microscope, some specimens studied under SEM
Tergal setae length	Estimated length of maximum mid-dorsal tergal seta using squared graticle
Pleurite: Shape	Shape (espcially of ventral margin) described
Sternite: Shape	Described
Telson	
♦ Length	Maximum mid dorsally
♦ Width	Maximum mid dorsally
♦ Setae	Description made of number and location of setae
Subanal Scale	Description made of shape
Ozopores:	
♦ Shape	Description made of overall shape
♦ Position	Description of position in lateral view
♦ Start on tergite no.	First tergite for which ozopores could be seen
♦ Finish on tergite no.	Last tergite for which ozopores could be seen
Female	
♦ Coxal tubercules	Description of presence and appearance of coxal tubercles on legs
♦ Vulvae	Description made if visible
Male	
Leg pairs 1–8	Description made of appearance
Leg pair 9	Description made of appearance
Leg pair 10	Description made of appearance

From these measurements the following ratios were calculated:

- The width/length of mid-body tergites
- Length of rostrum to length of head
- Antenna/rostrum ratio (rostrum length being tip to base of rostrum)
- Antenna/rostrum ratio (rostrum length being tip to antenna socket)
- For a mid-body ring the dorsal width of the prozona relative to the dorsal width of the metazonite. This gives an indication of the presence/size of the metazonal ridges, (clearly visibly enlarged tergal metazona relative to the prozona) or paranota (large lateral expansions)
- Length of mid-body maximum dorsal setae relative to the maximum width of the mid-body terga
- Length to width of the telson
- Length of legs relative to body width (only for specimens where the legs were measured accurately)
- Length of antenna relative to body width (only for specimens where the antennae were measured accurately).

3. Results

The specimens were grouped into morphospecies where possible. This proved relatively straightforward for some but very difficult for others. Two clear groups of species could be established with very different head and rostrum shapes. Within one of these it is still difficult to determine if some small individuals are juveniles or small species in their own right. Some of these small individuals have male gonopods; it is not unusual in the Siphonophorida for males of the same species to be very variable in size and apparently mature even when very small in size.

For some characteristics it proved difficult to measure them accurately in most specimens. This was particularly obvious for head length and width. In most cases the hind margin of the head was covered by the collum so measurements including this were not possible even after attempted manipulation.

The next stage of the investigation was to attempt to match the morpho-species to any species that have previously been described for the region. This has not proved easy because most were described on the basis of a small number of individuals and additionally many are tiny in size and some of the features are very difficult to see.

One outcome of this work has been the ability to evaluate some of the characters previously used to characterise genera and species, a few of which have proved reliable but many of which appear to vary considerably between indivduals of the same species.

4. Conclusions

4.1. Suitability of characters for distinguishing species

Head and rostrum shape. In the collection from Brazil this was the clearest and most reliable feature that separated two major groups of species. In one type it is abruptly constricted so the beak resembles the tooth of a narwhal, and seen from the side the head is strongly domed and sharply set off from the rostrum (Fig. 1). In the other type the beak is a more gradual extension of the head both from dorsal view and in lateral view (Fig. 2). There is the possibility that intermediate forms exist but in the current collection specimens could be easily assigned to one or the other type.

Length of antennae and antennae relative to rostrum. Many species descriptions have used the relative length and shape of the antennae as an important character, using the number of antennomeres by which the antennae surpass the tip of the rostrum. However in the current collection this varied greatly and depended to a very large extent on the state of preservation of the specimen. A 'dry' contracted specimen can appear to have antennae that are short, blunt-ended and more or less the same length as the rostrum. A more 'relaxed' specimen of the same species can appear to have longer antennae, reaching beyond the rostrum by one or even two antennomeres and with the last small antennomere clearly visible. Despite this, a broad distinction could be determined between some species with antennae substantially longer than the rostrum and some where they were more similar in length. Absolute number of visible antennomeres can also be variable between individuals of the same species for the same reason.

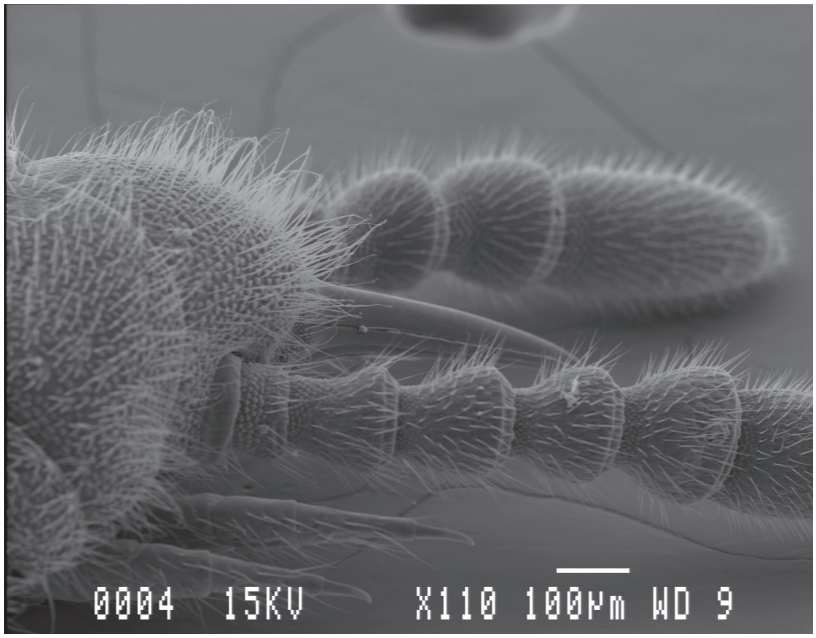

Fig. 1 Head and rostrum of a morphospecies with very abrupt demarcation between head and rostrum and relatively long antennae. Lateral view.

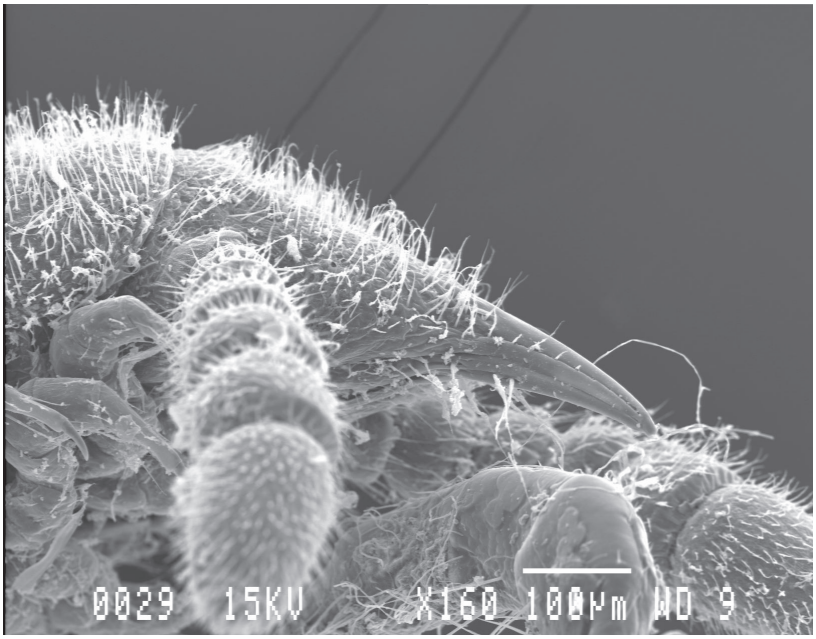

Fig. 2 Head and rostrum of a morphospecies with a gradual progression between head and rostrum and relatively short antennae. Lateral view.

Collum shape. The shape of the anterior margin of the collum is frequently described in species accounts. This may be a good character but care needs to be taken because there is frequently a thin area anteriorly, which may be hard to see under light microscopes and may give the impression of a deeply incised anterior margin. When examined carefully, or under SEM, the margin may be much less incised. The thinner, anterior region may also be sparsely setose in comparison to the posterior region (Fig. 3).

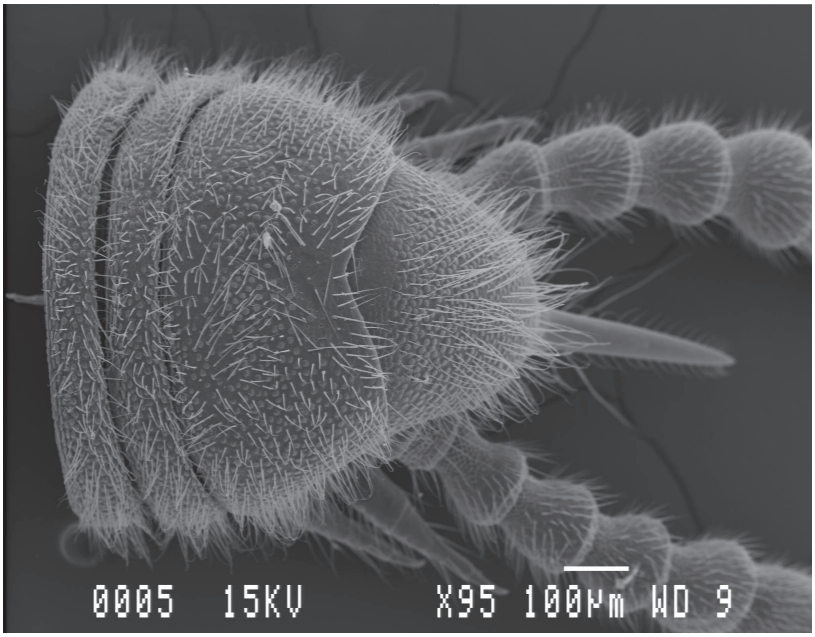

Fig. 3 Collum to illustrate the actual boundary of the anterior edge and that visible in light microscope which is appears like a more deeply cut V shape due to a thinner region with no tubercles.

Overall size and number of body tergites. As anamorphosis continues throughout life in this order, and because male gonopods are found in very small individuals there can be a large range of size/tergite numbers within each species. Like antenna length, the state of preservation also can have a huge impact on the overall length depending upon the state of preservation of the membranes between the body rings, thus it is only helpful in giving a general idea of size. Body width seems more reliable and scatter plots of width against tergite number for each sex were helpful in distinguishing some morphospecies and these can be compared with the limited data available on previously described species.

Colour. In contrast to many millipedes the Siphonophorids are generally pale and have a soft cuticle. The consequence of this is that they absorb colours easily during preservation and body colours and patterns should be used with caution. Colours apparent in life may change during preservation.

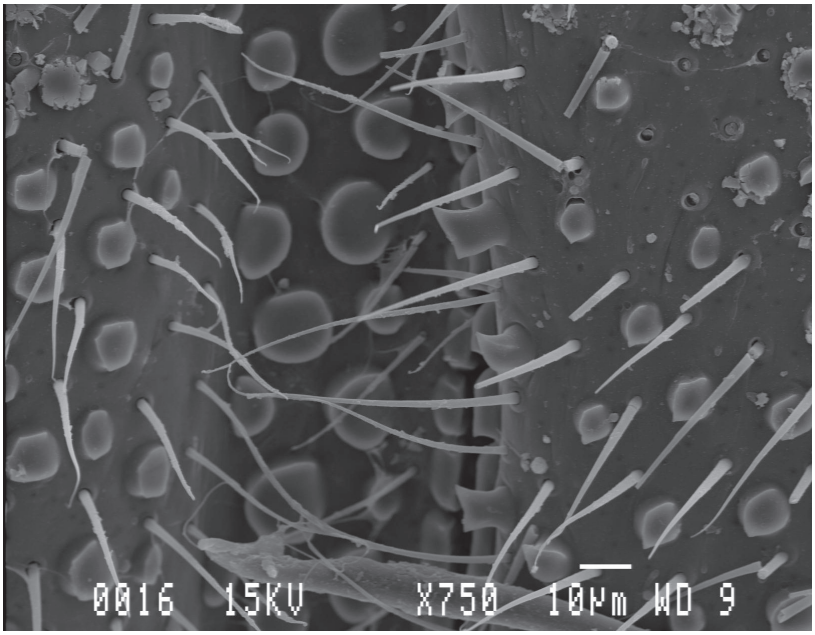

Fig. 4 Detail of the mid-dorsal region of two consecutive tergites showing tubercles in dorsal and lateral view. Some appear anchor-shaped.

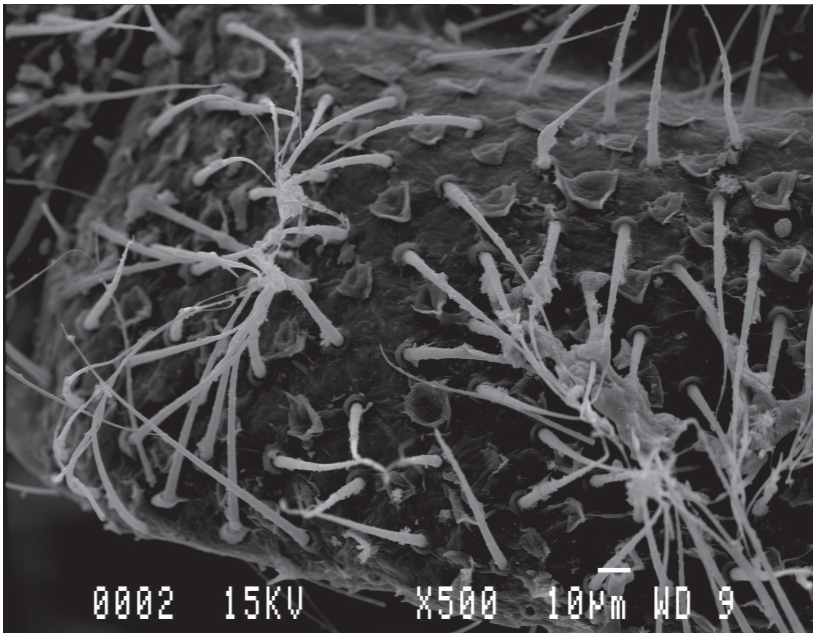

Fig. 5 Detail of the lateral metazonite from a different morphospecies to Fig. 4 showing cytoscutes and setae. Are the cytoscutes collapsed tubercles? Are the setae just dirty or might they be silk-producing as seen in *Ilacme plenipes*?

Tubercles and sculpturing. All individuals showed significant sculpturing on the head, collum and body rings. It is not clear if some of these differences are due to the relative 'expandedness' or state of collapse of tubercles or more significant variations between tubercules and cytoscutes (Figs 4, 5).

Edge of pleurite. The shape of the ventral edge of the pleurite is also frequently mentioned in descriptions. While the overall shape did not prove helpful in the current collection the microscopical shape of the edge (degree and shape of serrations) did appear to show differences, especially when viewed from 'inside', and this may be useful (Fig. 6).

Fig. 6 The posterior edge of a pleurite showing a particularly strong saw-shaped edge. The hind edge of the tergite (limbus) can also be seen to the top of the picture.

Repugnatorial glands (ozopores). The position of the gland relative to the metazonal ridges has been mentioned in previous species descriptions. However, the position frequently appears to be relatively anterior at the front end of the individual but progressively more posterior towards the caudal end of the individual. A related feature is the presence of small protuberances at the sides of the metazonal ridges on which the repugnatorial glands sit. Quite frequently these protuberances are present but they can appear much more pronounced than they are due to the ring of setae around them and also small blobs of secretion stuck to the outside (Fig. 7). The state of preservation can also make the protuberances appear substantially more pronounced on some individuals of the same species.

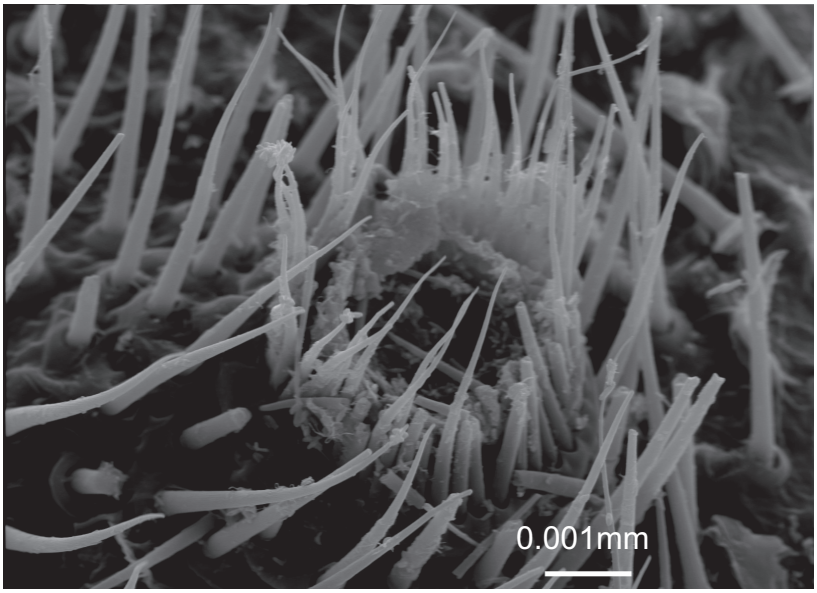

Fig. 7 Ozopore showing a ring of setae around it.

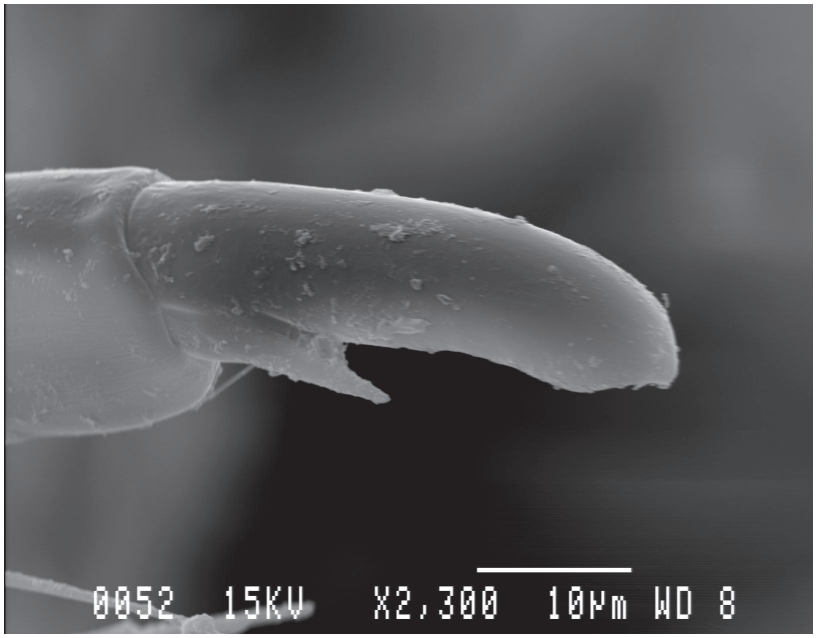

Fig. 8 Tarsal claw of the mid-body walking leg from a morphospecies showing thickened shape like that described for *R. hebetunguis.*

Claw and accessory claw. One previously described species from Brazil, *Rhinosiphora hebetunguis* Attems, 1951, has a very broad, thickened claw; this situation was observed in some individuals in the current collection (Fig. 8). The accessory claw appears to be variable between morphospecies with some showing the accessory claw dorsal to the claw (Fig. 9) and some lateral (Fig. 10).

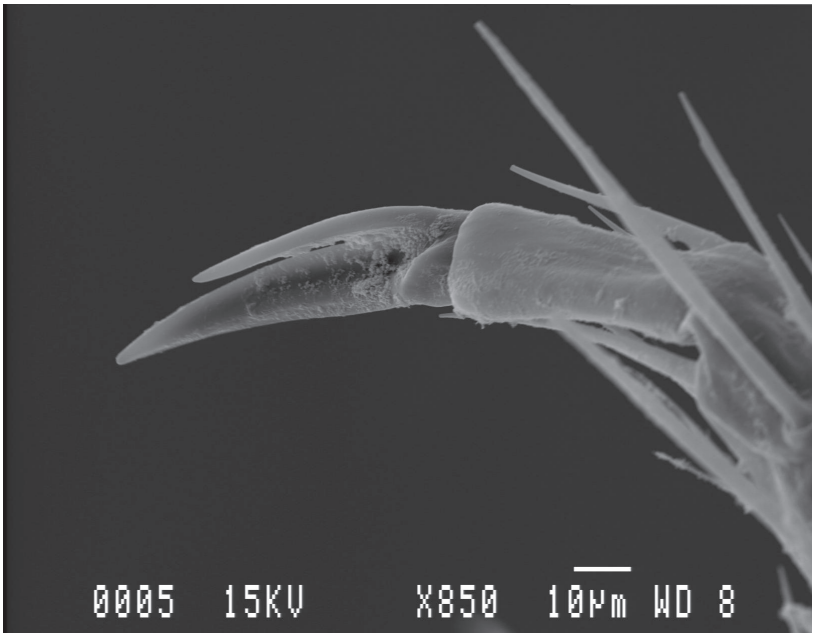

Fig. 9 Tarsal claw of a mid-body walking leg from a different morphospecies species with the accessory claw located dorsally to the claw.

Gonopod characters. In most other orders of Diplopoda differences in the gonopod structure are reliable methods of determining species. Male gonopods have been used in species descriptions for the Siphonophorida too, but considerable caution must be taken. Regarding the position of gonopods and extent to which they are 'bent'; this depends on the type of preservation. Hence the gonopods can appear strongly bent and lying closely adpressed to the body of the specimen, or they can appear almost as long as walking legs and much straighter without strong 90 degree bends. This may also be related to the relative age of the male and state of development.

The gonopods are very simple with both anterior and posterior pairs reminiscent of simplified walking legs. The number of podomeres in both parts has been used in descriptions, however, in general they proved difficult to distinguish under light microscope and not any easier using the SEM, the basal ones particularly have a tendency to coalesce.

The presence of a spine or notch on the posterior gonopods appears to be one of the few obvious features on the gonopods (Fig. 11) and is frequently mentioned in descriptions – so frequently that it can be found in the drawings of gonopods of species from different continents looking remarkably similar (Fig. 12).

Some details, such as the shape of the anterior gonopods (the presence of lobes or protuberances near the base and/or the presence of ribbon-like setae at the tip) may be useful.

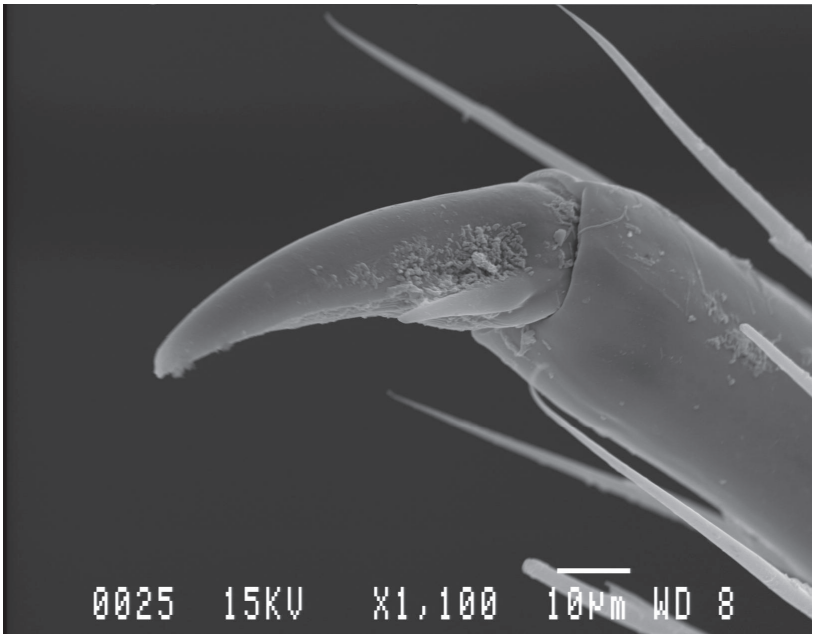

Fig. 10 Tarsal claw of a mid-body walking leg from a third morphospecies showing the accessory claw located laterally to the claw.

4.2. Relating this study to the current understanding of Siphonophorida taxonomic groups

Although we were able to sort most of the studied specimens into more or less well-circumscribed morphospecies, we have refrained from naming these. Doing so would require considerable additional work to compare them with previously described species. Of the three species previously described from Brazil, none have been found in the state of Amazonas in which Manaus is located, thus examination of other South American species would be helpful. The collection examined consists of five or more morphospecies, thus descriptions of new species will almost certainly be necessary. Comments have been compiled here on the basis of those morphospecies that are clearly defined.

The features discovered in the course of this study so far have not changed the current perception of the families of Siphonophorida. All individuals studied were confirmed as having a long rostrum drawn out into a beak shape, antennae that were not elbowed and with two sensory pits, one each on antennomeres 5 and 6. A recent re-description of *Illacme plenipes* Cook & Loomis, 1928 (family Siphonorhinidae) from southern USA based on freshly found specimens (Marek & Bond & 2006) included plates of SEM photographs. Comparison of the various features illustrated with those of the Brazilian specimens reveals many similarities, including the apex of the posterior gonopods, anchor-shaped tubercles on tergite margins and the possible presence of silk-secreting setae.

Fig. 11 Posterior gonopods from a Brazilian morphospecies.

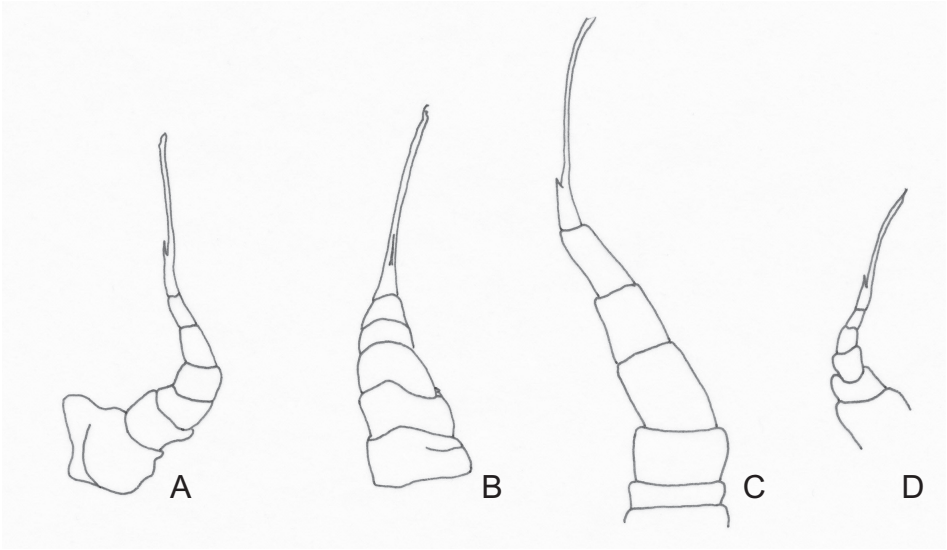

Fig. 12 Posterior gonopods from a range of previously described Siphonophoridae (redrawn from the original descriptions): A: *S. braueri* Attems, 1900 from the Seychelles; B: *S. coatochira* Attems, 1938 from Vietnam; C: *S. duschman* Golovatch, 1991 from Pakistan; D: *S. fuhrmanni* Carl, 1914 from Colombia.

In contrast to the familial characters, many of those used previously to distinguish genera and species have here been shown to be unreliable. Perhaps the only character described in the present study that is different enough to justify the validity of different genera is the shape of the rostrum, which can be linked consistently to other characters such as the antennae substantially longer than rostrum.

4.3. Recommendations for future study of Siphonophoridae

There are already substantial numbers of species described within the family Siphonophoridae on the basis of a single individual, often a small one and sometimes a single female. It is recommended that in future species should not be described on the basis of a single specimen, even if it is a male. Several specimens should be available, ideally representing more than one morphologically mature male. Small individuals observed in the current study were very difficult to assign to morphospecies because features of importance were poorly developed. In the material studied from Brazil, the tiny white specimens would have been impossible to separate to species without the larger ones of the same species being present in the collection (and even then some proved to be impossible). Whilst it seems likely that there will be some species that are genuinely tiny, at the present time, more robust, older specimens should be sought for description and identification until a better grasp of species differences has been gained. The use of an SEM added greatly to the current study and it seems prudent that, where ever possible, this should be used to help study aspects such as the tubercles and edges of tergites that are otherwise difficult to see. As the taxonomy of this group is already in a substantial mess nothing will be gained by adding to the mire by more poorly described species. These comments also mean that redescription of previously described species using only single specimens may also be of limited value, far more useful will be the study of larger collections. This may mean that the siphonophorids will remain a poorly studied and poorly understood group for the immediate future, pending more collections like the one from Brazil.

5. Acknowledgements

Financial support for this project was given by the Max Plank Institute for Limnology in Plön and work in Copenhagen was supported by a grant from the European Commission's (FP 6) Integrated Infrastructure Initiative programme SYNTHESYS (DK-TAF). I am very grateful to the late Joachim Adis for the opportunity to study his collection.

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Accepted 09 November 2009