

FURTHER STUDIES ON *GEOPHILUS CARPOPHAGUS* (SENSU LATO), AND A REINTERPRETATION OF THE STRUCTURE OF ITS LABRUM

Malcolm Haswell¹, Henrik Enghoff² and Wallace Arthur^{3*}

¹ Electron Microscope Unit, University of Sunderland, Sunderland SR1 3SD, United Kingdom

² Natural History Museum of Denmark (Zoological Museum), Universitetsparken 15 DK-2100 Koebenhavn OE, Denmark

³ Department of Zoology, National University of Ireland, Galway, University Road Galway, Ireland. Email: wallace.arthur@nuigalway.ie

* Author for correspondence.

INTRODUCTION

The order Geophilomorpha includes about 1000 named species in total (Lewis 1981). Only one of these, *Geophilus carpophagus* Leach 1817, has been the subject of a previous search for possible cryptic species (Arthur et al. 2001). We now build on that earlier study in two ways: achieving greater resolution of morphological features; and looking at specimens from a wider geographical area – not just British populations.

As will be seen, our results both confirm the existence of the recently described species *Geophilus easoni* (Arthur et al 2001), and suggest the possible existence of a species complex or group. We also show that the conventional interpretation of the structure of the labrum is incorrect for this species, and perhaps for the family Geophilidae in general. This is important because there has been considerable controversy about the nature of the arthropod head (see, for example, Budd 2002), including the issue of homologies between various head structures among different arthropod classes. Discussion of this issue relies on having a correct understanding of the structures concerned.

MATERIALS AND METHODS

All of the British specimens were collected from the field. All other specimens, from continental Europe, north Africa and the Canaries, were from collections held in the Natural History Museums in Copenhagen (University of Copenhagen), London, Vienna, and Berlin (Humboldt University). After examining the segment numbers of all specimens to provide a connection with previous work using this character (Arthur & Kettle 2001; Kettle & Arthur 2000), we selected approximately 50 specimens (a mixture of British field-caught ones and material from the Copenhagen collection) for the SEM work. This figure was a compromise between the need for information on variation between individuals and the problem that this work required the destruction of the specimens concerned, some of which had been held in the museum collection for several decades.

The morphological characters examined were the number and shape of projections on the labrum. These were visible only after (a) separating the head and first few trunk segments from the rest of the body to facilitate more detailed work in this region, and (b) dissecting away the forcipules, and the first and second maxillae. After dissection, the specimens were prepared for SEM work by removing from preservative (70% ethanol) and air-drying for approximately 24 hours. They were then transferred to aluminium stubs of 25 mm diameter, three specimens per stub. The specimens were secured to the stubs using silver DAG paint. They were not coated.

The microscope used was a Hitachi S-3000N variable-pressure SEM. All work was carried out at a pressure of 70 Pa and at an accelerating voltage of 20 Kv using the backscattered electron detector. Images were captured digitally in TIF format over a wide range of magnifications, at working distances of 10-15 mm. The magnifications used to produce the images displayed in our figures herein were 200-250 (whole clypeus) and 1000-1200 (close-ups of 'teeth').

RESULTS

Segment numbers

British specimens can be readily assigned to either *Geophilus carpophagus* (sensu stricto) or *Geophilus easoni* using the number of segments alone (Arthur et al. 2001; Arthur et al. 2002). So the first step in the present study was to compare the specimens at our disposal from outside Britain with the segment number ranges of British populations – see Table 1.

On the basis of segment number alone, the Danish specimens appear to be *G. carpophagus*, the ‘Europe’ material a mixture of the two species, which is perhaps unsurprising as this is a combined collection of small numbers of specimens from several countries in central and southern Europe. The North African material may be *G. easoni*, and the Canarian material *G. carpophagus*, with the slight upward shifts in segment numbers that are to be expected in more southerly populations (Arthur & Kettle 2001; Kettle & Arthur 2000). However, all of these interpretations are very tentative. We now look to see if information arising from the SEM studies can render them any less so.

SEM studies of ventral head characters

Figure 1 shows one specimen each of British *G. carpophagus* and *G. easoni*. We examined the *shape* of the central ‘teeth’ and the *number* of filamentous projections (fimbriae) flanking the teeth in several specimens. These were both reliable characters for separating the two species in Britain, while the ‘converse’ characters (number of teeth, shape of fimbriae) were not. Therefore, they potentially afford an opportunity to determine the identity of each non-British specimen, and hence to clarify the rather tentative conclusions reached from the segment number data.

On the basis of the shape of the central teeth, the French specimens, with their blunt-ended teeth (see Figure 2) seem to be unambiguously *G. easoni*. This is perhaps not surprising, as both specimens were from Finistère in Brittany. With regard to the material from further afield, the situation is much less clear. Many specimens from the other source countries come out as failing to align clearly with either of the two British species on the basis of tooth shape: for example, the Algerian specimen shown in Figure 3.

Counts of the total number of fimbriae on the labrum (Figure 4) show clearly separated distributions for British *G. carpophagus* (12-19) and *G. easoni* (30-46). The non-British material spans across these two ranges (19-38). If the different source countries are separated out, the situation does not get any clearer. For example, the largest European sample, from Denmark, which looks to be *G. carpophagus* on the basis of segment number data (Table 1) has a range of 25-36, that is, corresponding approximately with British *G. easoni*.

Although these SEMs of ventral head characters have failed to clarify the species status of the non-British material, they have produced an unexpected, and very clear, result in relation to the structure of the ‘labrum’ of *Geophilus carpophagus* (sensu lato). This is emphatically *not* a 3-piece structure, as it is normally drawn (Eason 1964). The ‘mid piece of the labrum’ is no such thing – rather it is a projection of the clypeus (Figures 1, 2 and 3).

DISCUSSION

British material

Our results confirm the existence of two separate species, *G. carpophagus* and *G. easoni*, as proposed in earlier papers (Arthur et al. 2001; Arthur et al. 2002; Lewis 1985), and extend the range of characters that can be used to separate the two.

Non-British material

In spite of having both segment number data and information on ventral head structures from the SEM work, it is currently impossible to be certain of the species status of most of the European and African specimens. At least three hypotheses can be advanced regarding this material: 1. All specimens from all places belong to *G. carpophagus* or *G. easoni*, with anomalies merely representing intraspecific variation. 2. There is at least one further cryptic species represented among the material we examined. 3. There is, in at least some places, a species complex in the

FIGURE 1

SEM photographs of the clypeus/labrum, and the 'mid-piece of the labrum' (bottom) from specimens of British *G. easoni* (left) and *G. carpophagus* (right).

FIGURE 2

SEM photographs of the clypeus/labrum, and the 'mid-piece of the labrum' (bottom) from a specimen of *G. easoni* from Brittany, France.

FIGURE 3

SEM photographs of the clypeus/labrum, and the 'mid-piece of the labrum' (bottom) from an Algerian specimen.

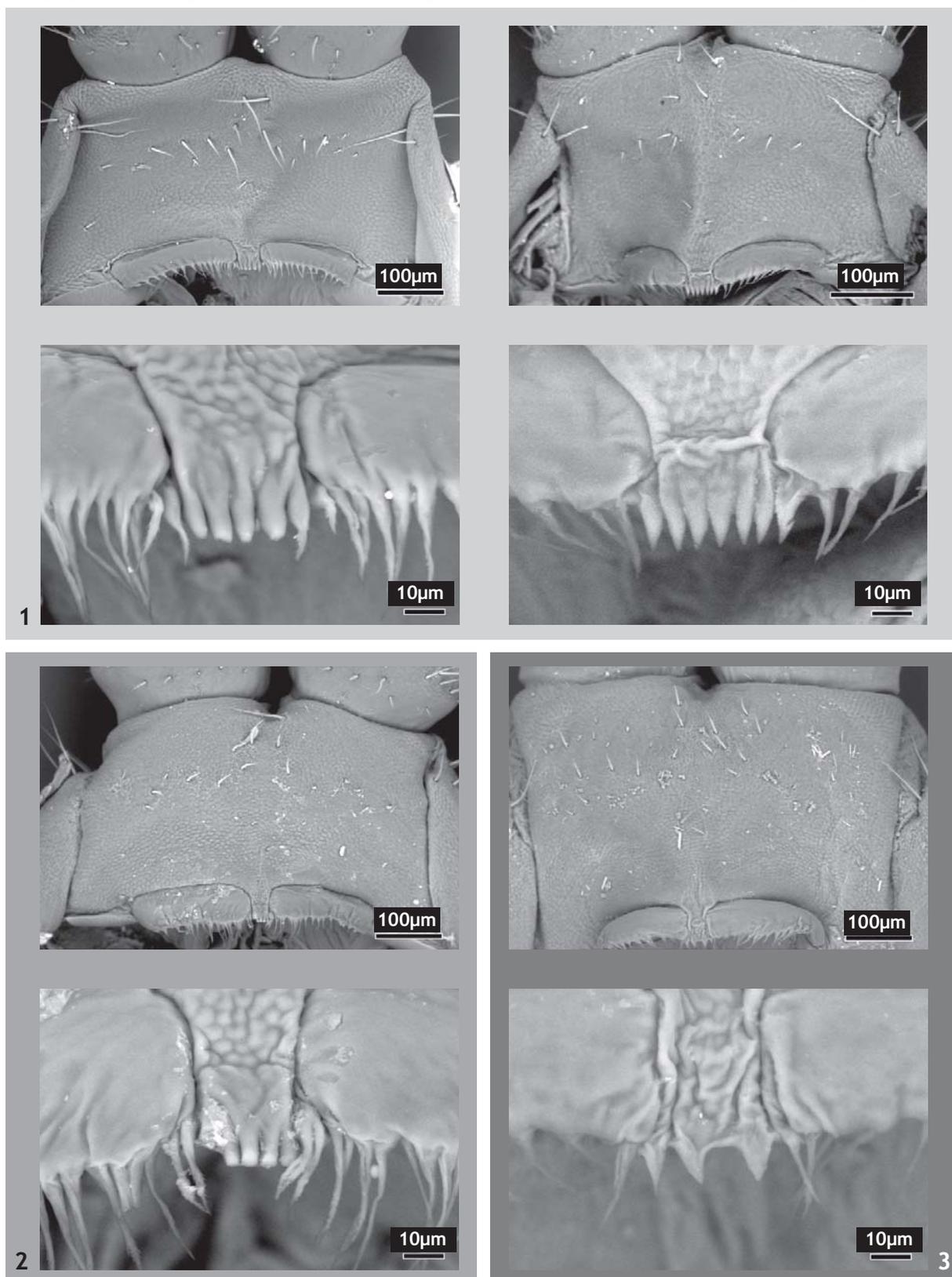


FIGURE 4

Frequency distributions for the number of fimbriae on the side pieces of the labrum in British *G. carpophagus* (top), British *G. easoni* (centre) and all non-British specimens examined (bottom).

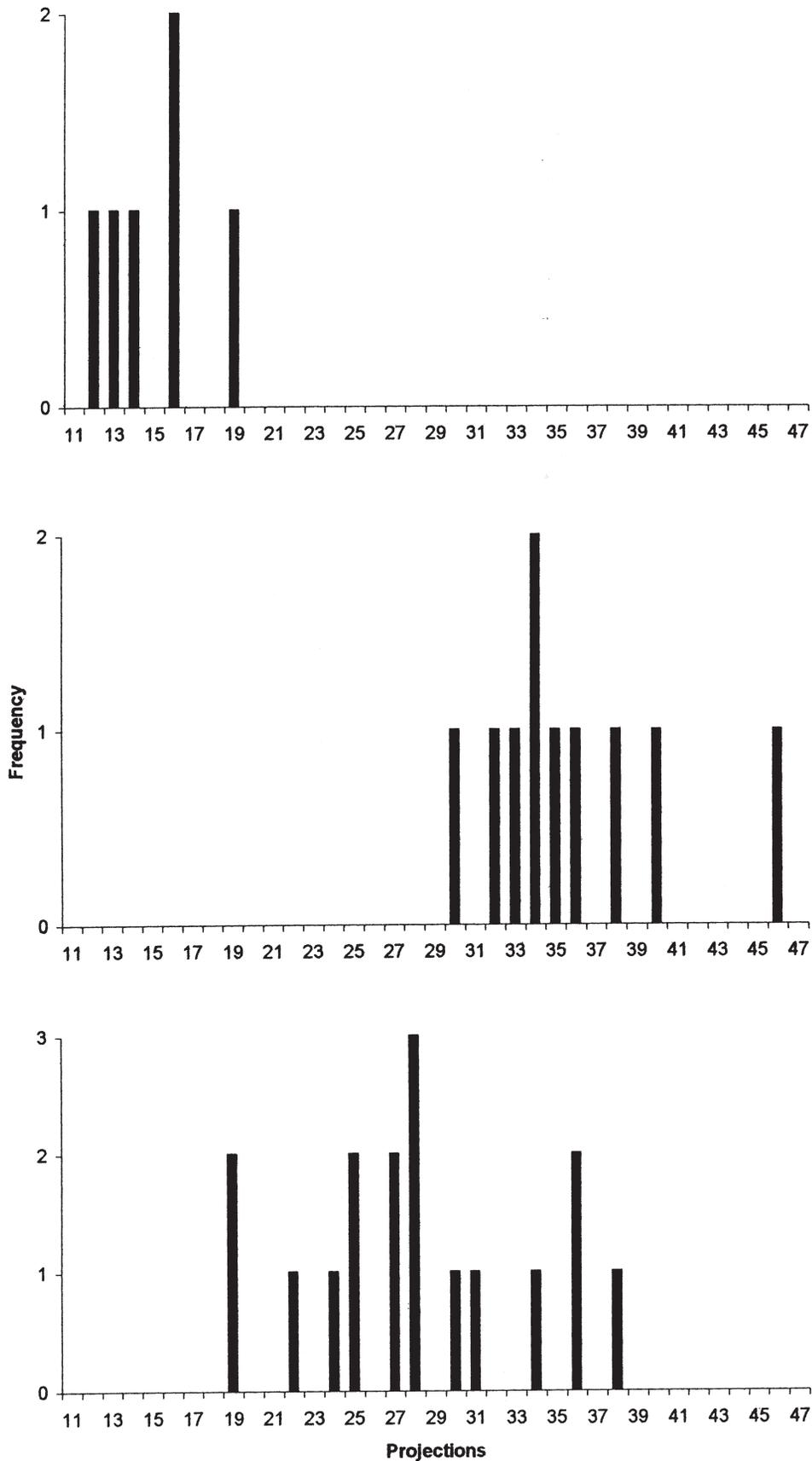


TABLE 1

Segment numbers of males (left side of table) and females from *G. easoni* and *G. carpophagus* (British specimens); and in specimens of as-yet uncertain species status from outside Britain. Source countries for Europe were: France, Austria, Spain, Portugal and Greece. The north African specimens were from Algeria and Tunisia.

SEGMENTS	47	49	51	53	55	57	59	47	49	51	53	55	57	59	61
<i>easoni</i>	80	12						2	73	5					
<i>carpophagus</i>			1	22	3						3	27	11		
Denmark				4							3	21	2		
Europe	1	4	2	4	2				1	5	3	3	3		
North Africa		9							6	9	4				
Canaries				8	1	0	3					2	4	15	4

sense of partial interbreeding and perhaps incipient reproductive isolation. Further studies will be required to distinguish between these hypotheses.

The nature of the labrum

It is conventional, in the myriapodological literature, to refer to the labrum of geophilids as consisting of three pieces, a mid-piece and two flanking side pieces (Eason 1964; Lewis 1981). Drawings of the labrum typically show clear boundaries between these pieces, and also between all three of them and the clypeus. However, it is apparent from the present study that this description is inaccurate, at least for *G. carpophagus* and *G. easoni*. The side pieces are indeed distinct morphological units, but the 'mid-piece' is an extension of the clypeus. This can be seen clearly from Figure 1. In many cases it is less clear, because there is a tendency for a slight crumpling or fold to develop at the base of the midline extension of the clypeus. It is likely that misinterpretation of this fold as a discontinuity or joint, in light-microscopical studies, has been responsible for the incorrect idea that the central piece of tissue is part of the labrum.

The next question is whether this reinterpretation of the nature of the labrum in *G. carpophagus* and *G. easoni* should be extended to a wider group of species – the family Geophilidae for example. In order to address this question, the next phase of this work will be to examine the clypeus/ labrum of several other geophilids. It may also be informative to examine other species chosen to represent families that are distantly related according to our current view of the phylogeny of the Geophilomorpha (Foddai 1998; Foddai & Minelli 2000), as the structure of the labrum varies markedly between families (Eason 1964).

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