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PROGRESS IN STUDIES ON MYRIAPODA AND ONYCHOPHORA

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Centipede antennal characters in taxonomy with particular reference to scolopendromorphs and antennal development in pleurostigmomorphs (Myriapoda, Chilopoda)

Abstract: Scolopendromorphs with a fixed antennomere number and geophilomorphs can only increase the length of a damaged antenna by antennomere elongation. Antennomere number and the distribution of antennal sensilla, are of taxonomic value, as are the sculpturing of the antennal cuticle in scolopendromorphs. A basic antennomere number of 17 in three centipede orders and similarities between the antenna of geophilomorphs and that of larva II in lithobiomorphs suggests that there may be a common developmental pattern in the pleurostigmophoran centipedes.

Key words: Chilopoda, antennae, repair, taxonomy, cuticular sculpturing, development

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INTRODUCTION

The Chilopoda show considerable variation in antennomere number. Fixed at 14 in the Geophilomorpha, it is 17 or 18 in the Craterostigmomorpha (MESIBOV 1986). In the Scolopendromorpha it varies from 17 to 34 but is usually between 17 and 22. Greater variation is seen in the Lithobiomorpha. In the Lithobiidae, for example, it varies from species in which the number is fairly constant at 17 or 19, to *Osellaebius* MATIC from Eastern Turkey with 64-72 antennomeres (EASON 1992).

In these pleurostigmophoran orders the antennae consist of similar antennomeres, whereas in Scutigermorpha the antennae differ radically, consisting of a scape of two articles and a flagellum of numerous annulations.

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THE RELATIONSHIP BETWEEN FIXED ANTENNOMERE NUMBER AND REPAIR AFTER DAMAGE

In *Scolopendra amazonica* BÜCHERL (= *S. morsitans* L.) the early adolescens stadia have 17 antennomeres and during development the number increases to 19 and very rarely to 20 by division of the subterminal antennomeres (LEWIS 1968). Regeneration after antennomere loss takes place in the same way, but is less accurate, sometimes leading to atypically high numbers.

Antennomere number in *Cryptops* is always 17 or less. Where it is less it is probably the result of damage, as are the lower numbers in *Tidops simus* CHAMBERLIN (13 antennomeres) and *Kartops guianae* ARCHEY (11 antennomeres).

In species with a fixed number of 17 antennomeres loss appears to be compensated for by an increase in the length of those remaining. A figure of a specimen of *Cryptops doriae* POCOCK (LEWIS 1999) shows a normal right antenna but the left of only eight antennomeres, the distal three of which clearly elongated. A similar condition is seen in the holotype of *C. melanotypus* CHAMBERLIN with 9 + 16 antennomeres (Fig. 1).

The same response to antennomere loss might be expected in the Geophilomorpha where the antennomere number is fixed at 14. Of interest in this respect is PEREIRA's (1999) figure of the antennae of *Schendyllops pampeanus* (PEREIRA & COSCARON 1976) with 14 antennomeres on the right, only five on the left, the distal four of which are very elongated (Fig. 2). This suggests that the response to antennomere loss is the same as in *Cryptops*.

ANTENNAL CHARACTERS AND TAXONOMY

Lithobiomorpha

EASON (1991) remarked that, in the Lithobiomorpha, the discontinuity in antennomere number (very few with 22 or 23) makes it fairly easy to separate *Bothropolys* (20) from *Eupolybothrus* (numerous) and *Monotarsobius* (20) from *Sigibius* (well in excess of 20).

The distribution of antennal sensilla in *Lithobius forficatus* L. has been described by FUHRMANN (1922) and KEIL (1977). The trichoid sensilla are mostly arranged in three irregular rows, those of the anterior row directed forwards, of the posterior row directed backwards. (In *L. variegatus* LEACH the number of rows varies with the size of the antennomeres but the arrangement of the sensilla is the same (Fig. 3)). At the apex of the terminal antennomere there is a group of small pale setae (termed *Sinneskegel* = brachyconic sensilla by KEIL 1977). One or two of these are also present on the anterior wall of the other antennomeres. *Zapfen* (= basiconic sensilla) are present on all antennomeres except the basal one, 6 to 8 on the terminal antennomere, one or two on the others.

Unfortunately there are no data for other genera so it is not known whether the arrangement of trichoid sensilla or of other sensilla seen in *L. forficatus* is characteristic of the order or not.

Craterostigmomorpha

The only data on the distribution of antennal sensilla in *Craterostigmus tasmanianus* POCOCK appears to be DOHLE's (1990) SEM showing the ventral surface of the basal two antennomeres with long and short trichoid sensilla.

Geophilomorpha

The distribution of antennal sensilla of a number of geophilomorphs (notably some, Schendylidae, Ballophilidae and Geophilidae) has been described in great detail in a series of papers by PEREIRA and his co-workers. PEREIRA *et al.* (1995) used the number of basiconic sensilla, which they termed claviform sensory setae, on antennomere XIV and the nature of the cuticle around the so-called specialised setae on II, V, IX and XIII, the homologies of which are not always clear, to differentiate *Schendylurus marchantariae* PEREIRA, MINELLI and BARBIERI and *S. andesicola* CHAMBERLIN and the sensilla of antennomeres IX and XIII to differentiate *Schendylurus janauarius* from *S. iguapensis* VERHOEFF. FODDAI & MINELLI (1999) used basiconic sensilla of antennomere XIV in grooves or not as a character separating species of *Geophilus*.

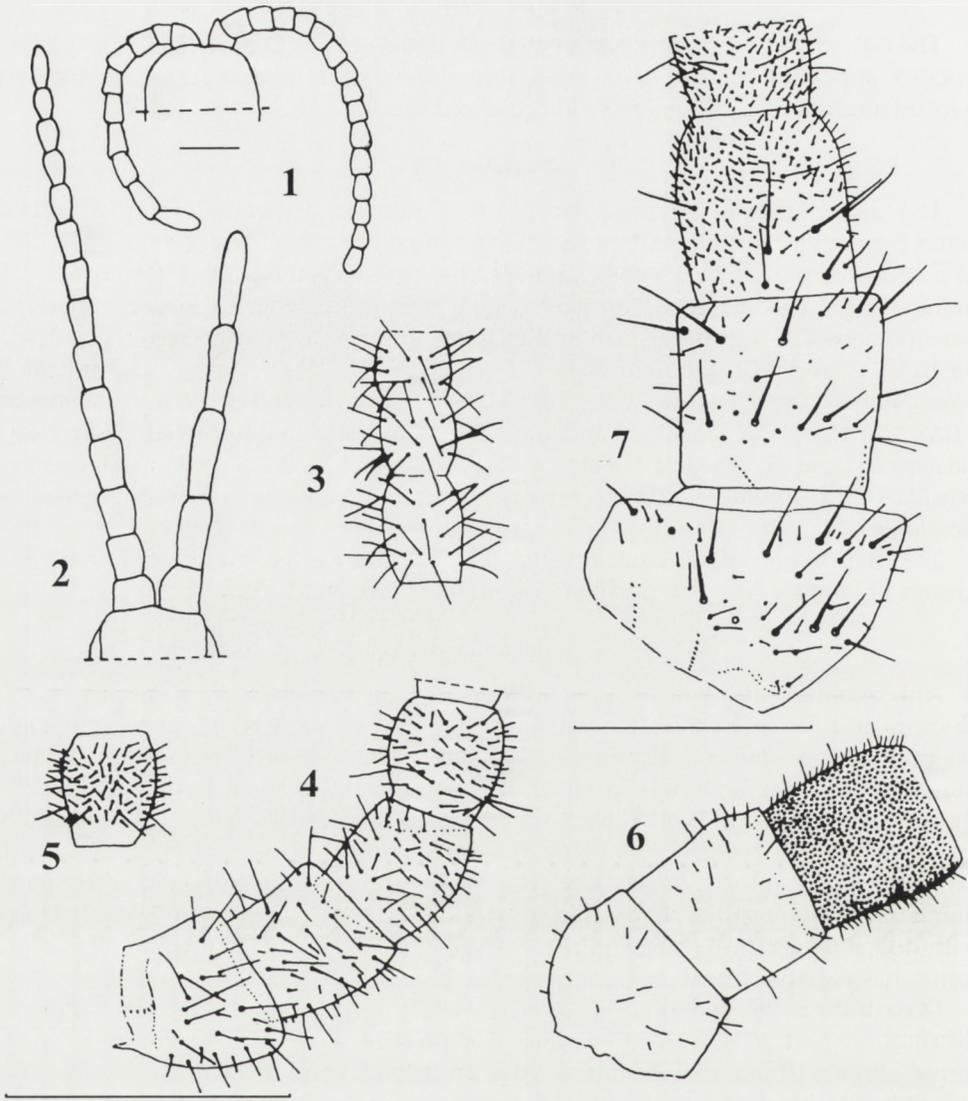
The distribution of basiconic sensilla also characterises geophilomorph families or groups of families (FODDAI, personal communication).

Scolopendromorpha

Antennomere number. In some scolopendromorph genera, for example *Asanada*, *Cryptops* and *Scolopocryptops*, the antennomere number is always 17. Other genera, for example *Scolopendra* and *Otostigmus*, contain some species in which antennomere number is fixed at 17, others in which it is variable. Data taken from ATTEMS (1930) show that in the New World there are 10 *Scolopendra* species with 17 antennomeres and these all have dorsal spines on the prefemora of some of legs 1-20 with the exception of *S. robusta* KRAEPELIN. The seven species with variable antennomere number lack these spines. In the Old World there is only one species, *S. valida* LUCAS, with dorsal prefemoral spines on some of legs 1-20. It, in contrast to the New World forms, has variable antennomere number (19-27).

Distribution of sensilla. KRAEPELIN (1903) noted that there were different distribution patterns of antennal setae. He pointed out that *Cryptops* and "related forms" show a similar distribution of setae on the basal and distal antennomeres (Figs 4 & 5) but in most genera the basal segments were bereft of these (in fact a few are present) and there was often a sharp distinction between these and the distal setose antennomeres (Fig. 6).

In *Cryptops* typically the basal three antennomeres bear long setae and an increasing number of short setae, antennomere 4 is clothed in short setae with the long setae reduced to a basal whorl, subsequent antennomeres showing this arrangement. A similar arrangement to that found in *Cryptops* was described for *Thalkephops* by CRABILL (1960) and is here shown for *Newportia* (Fig. 7).



Figs 1-7: 1 - Head and antennae of holotype of *Cryptops melanotypus*. 2 - Anterior region of clypeus and antennae of *Schendyllops pampeanus* after PEREIRA (1999). 3 - Dorsal view of antennomeres 34-36 of *Lithobius variegatus* with 42 antennomeres. Somerset, U.K. 4 - Dorsal view of basal four antennomeres of *Cryptops hortensis* LEACH. Bournemouth, U.K. 5 - Antennomere 7 of the same specimen. 6 - Dorsal view of basal three antennomeres of *Scolopocryptops ferrugineus* BROLEMANN. Loma Mts., Sierra Leone. 7 - Dorsal view of basal three and a half antennomeres of *Newportia longitarsis virginensis* LEWIS. U.S. Virgin Isles; Scale line =0.5mm.

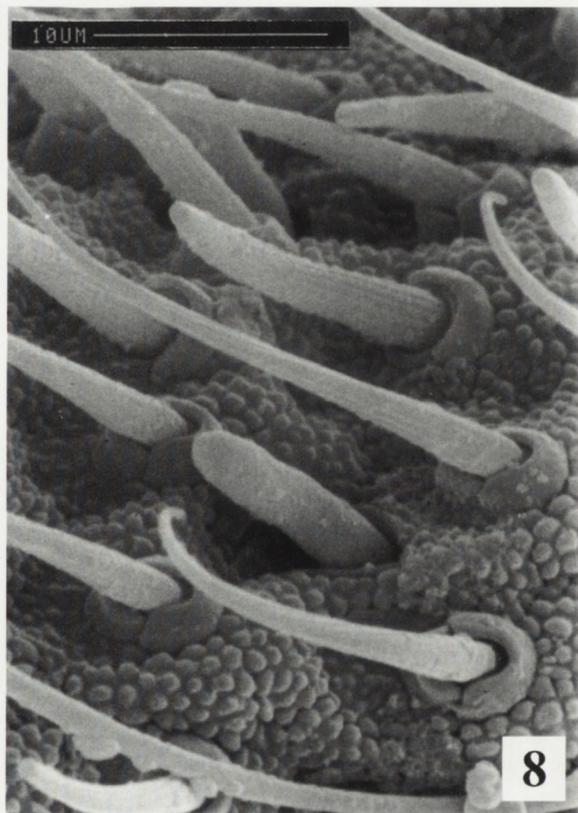


Fig. 8. SEM detail of cuticle and sensilla of terminal antennomere of *Scolopendra morsitans*, Zaria, Nigeria.

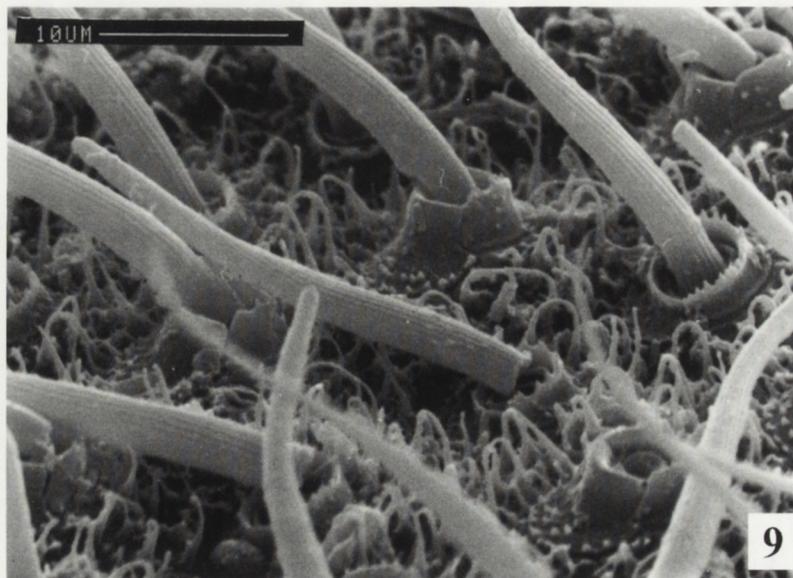
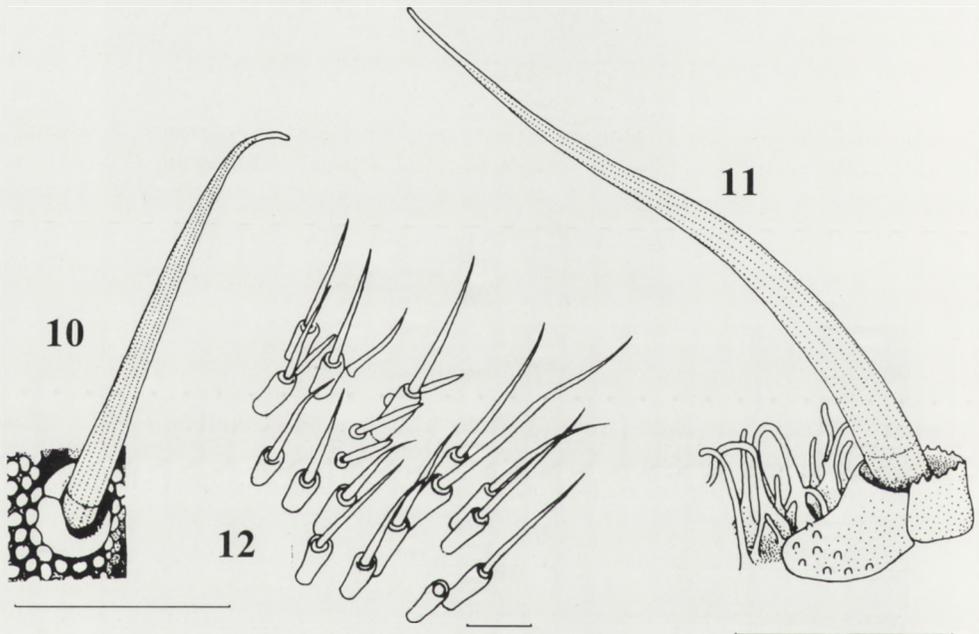


Fig. 9. SEM detail of cuticle and sensilla of antennomere 9 of *Otostigmus multidentis* HAASE, Kalimantan.

In some Scolopendridae there is a sharp distinction between proximal glabrous antennomeres and densely setose distal ones. The basal $2\frac{1}{2}$ to 3 are glabrous in *Otostigmus* and *Rhysida*, the basal 4 in *Ethmostigmus*. In other genera such as *Scolopendra* and *Cormocephalus* the distinction between glabrous and setose antennomeres is less distinct and adults have more glabrous antennomeres than young specimens. In *Asanada socotrana* POCOCK there is a gradual transition from relatively sparsely setose basal, to densely setose distal antennomeres. The number of glabrous basal antennomeres is sometimes used to distinguish species.

More detailed data on the distribution of antennal sensilla in *Scolopendra morsitans* L. were given by FUHRMANN (1922). The basal six antennomeres do not bear socketed trichoid sensilla (*massiven Borsten*): there are a few hollow setae (*hohle Borsten*), the homology of which is uncertain, and short cones (*hertzförmiger Sinneskegel*). The distal antennomeres bear typical trichoid sensilla in which the shaft is bent and tapers to a point and a socket in the form of a tubercle (Figs 8 & 10).



Figs 10–12. 10 – Antennal trichoid sensillum of *Scolopendra morsitans*. 11 – Antennal trichoid sensilla of *Otostigmus multidens*. 12 – Group of antennal sensilla of *Scolopocryptops ferrugineus*. Scale line = 20µm.

Structure of trichoid sensilla. The trichoid sensilla of *Scolopendra* are described above. In *Otostigmus* the sockets are in the form of an "upright" collar with a more or less tuberculate edge and with a tuberculate plate anteriorly (Figs 9 and 11).

In *Cryptops* the setae are mostly short but similar to those of *Scolopendra*.

ATTEMS (1930) wrote of *Otocryptops* (= *Scolopocryptops*) that the seta-bearing tubercle is higher (than in *Scolopendra*), so that it appears two-segmented. The setae in

Dinocryptops are similar. These structures (Fig. 12) are remarkable and as far as I am aware, quite unlike the setae of any other centipedes.

Structure and distribution of other sensilla. Lack of information precludes any conclusions about other sensilla but their distribution may well be significant and would reward investigation.

Cuticular sculpturing. FUHRMANN (1922) reported that whereas the cuticle of the basal antennomeres exhibits a pattern of polygonal areas characteristic of many chilopods, this *Felderung* is absent from the distal antennomeres, the surface of which is covered with many small granules (*Körnchen*). Scanning electron micrographs confirm this and also show that the cuticle is thrown into a series of ridges (Fig. 8).

Most surprising is the cuticle of the distal antennomeres of *Otostigmus* which is covered not with tubercles but with loops and digitate processes (Fig. 9).

In *Cryptops* the cuticle of the distal antennomeres exhibits polygonal fields as it does in *Asanada*.

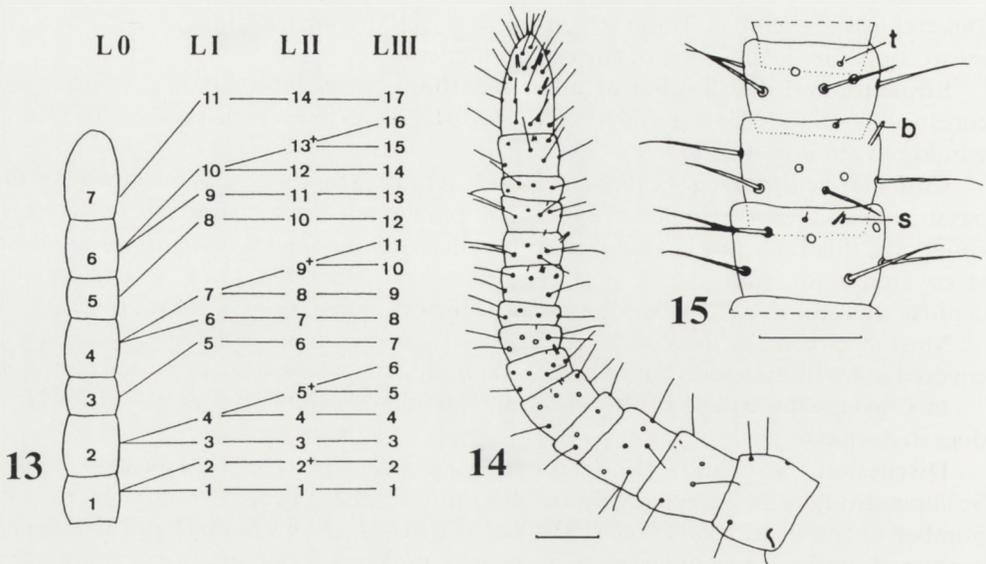
Discussion. SCHILEYKO (1992) proposed a radically new classification of the Scolopendromorpha based largely on the number of leg-bearing segments and the number of spiracles. KRAEPELIN (1903) noted that the genera *Rhysida* and *Otostigmus* contained similar forms differentiated solely by the presence or absence of spiracles on segment 7. In this new classification these genera are placed in different subfamilies. A comparative study of antennal characters could well serve to resolve these differences of opinion.

POSSIBLE COMMON DEVELOPMENTAL PATTERN IN ANTENNAE OF THE PLEUROSTIGMOMORPHA

The fact that the lowest antennomere number in Craterostigmomorpha, Scolopendromorpha and epimorphic stadia of the Lithobiomorpha is 17 suggests that a common developmental pattern may be involved. The Geophilomorpha, however, have only 14 antennomeres.

Accurate data on antennal development are available for the Lithobiomorpha as antennomere number increases through the anamorphic stadia and in some or all of the epimorphic stadia as well. SCHEFFEL (1969) described antennal development in larval *Lithobius forficatus* (L.). He designated the larval stadia 1–5. In stadium 1 larva there are seven antennomeres (Fig. 13), in stadium 2, 11, in stadium 3, 14 (the number seen in the Geophilomorpha) and in stadium 4, 17 antennomeres (the lowest number seen in Scolopendromorpha and Craterostigmomorpha). Stadium 5 has 22.

ANDERSSON (1979) recorded the data for nine species of European Lithobiidae, two species of Henicopidae and five Japanese species, the latter investigated by MURAKAMI. He designated the larval stadia L0 or foetus (the same as SCHEFFEL's (1969) stadium I larva) and LI to LIV. Almost all species investigated had 7 antennomeres in L0 and 11 in LI. In all species LII has 14 antennomeres and in LIII numbers are 14 or 17 or between 14 and 17 except *Esastigmatobius longitarsis* VERHOEFF with 20–24. Generally, therefore, the pattern is 7, 11, 14, 17.



Figs 13–15. 13 – Pattern of antennomere division in *Lithobius forficatus* based on SCHEFFEL (1969). + - antennomeres with specialised sensory setae in geophilomorphs. 14 – Dorsal view left antenna of larva II of *Lithobius microps*. 15 – Details of antennomeres 5, 6, and 7 of the same. s - specialised sensory seta, b - basiconic sensillum. t - very short seta. Scale line = 50µm.

That all lithobiomorphs so far investigated go through a stage with 14 antennomeres (the number in all Geophilomorpha) and most through a stage with 17 (the basic number in Scolopendromorpha) may be a coincidence but there is another condition that appears to link the antennae of lithobiomorphs and geophilomorphs. DEMANGE (1943) described small specialised setae (microchètes) on the anterior border of antennomeres 5, 9 and 13 in the geophilomorph *Hydroschendyla submarina* (GRUBE). PEREIRA & COSCARON (1976) described small groups of trifid setae on the end of the apical antennomere and on antennomeres 2, 5, 9 and 13 in *Pectiniunguis pampeanus* PEREIRA and COSCARON & PEREIRA (1984) described short simple specialised setae on the terminal antennomere and on 2, 5, 9 and 13 in *Dinogeophilus oligopodus* PEREIRA. In subsequent papers the same distribution of specialised sensory setae has been described in other genera and species, for example *Ityphilus*, *Ribautia* and *Schendylurus* (PEREIRA *et al.* 1995). This pattern is obviously widespread in geophilomorphs.

Examination of SCHEFFEL's data on *L. forficatus* shows that in his larval stadium 3 with 14 antennomeres, antennomeres 2, 5, 9 and 13 also share a common character, they are each the distal antennomere of a group that have arisen by the division of antennomeres 1, 2, 4, and 6 of the antenna of his stadium 1. The terminal antennomere does not divide (Fig. 13).

A single specimen of a larva II *Lithobius microps* MEINERT examined had specialised sensory setae, probably brachyconic sensilla, on antennomeres 2, 5, 9 and 13 (Figs 14 & 15 (s)), and larger ones at the apex of 14 as in geophilomorphs. Basiconic sensilla were present on 6, 10 and 14 (Figs 14 & 15 (b)). Very short setae were present, on most

antennomeres (Figs 14 & 15 (t)). These appear to be situated at the base of the antennomere on that region telescoped into the preceding one. The sensilla are very small and difficult to see and the observations should be repeated, preferably with a scanning electron microscope.

These data suggest a common developmental pattern in the antennae of pleurostigmomorphs. Precise data on antennomere number in the embryonic stadia of geophilomorphs and scolopendromorphs and *Craterostigmus* would shed further light on this subject.

SUMMARY

Scolopendromorph species which increase the number of antennomeres during post-embryonic development can regenerate damaged antennae by the division of the distal antennomeres. Species in which antennomere number is fixed at 17 can only increase the length of a damaged antenna by elongating the remaining antennomeres. The Geophilomorpha are likewise unable to increase antennomere number after loss.

Antennomere number has taxonomic significance in lithobiomorphs and scolopendromorphs as does the distribution of sensilla in the Scolopendromorpha and Geophilomorpha. The hitherto unrecognised variation in antennal cuticular sculpturing in scolopendromorphs may prove to be very important taxonomically.

The basic number of 17 antennomeres found in *Craterostigmus*, the lithobiomorphs and scolopendromorphs suggests a common underlying developmental pattern. In geophilomorphs there are only 14 antennomeres but all lithobiomorphs pass through a 14 antennomere stage. A further similarity is that in the 14 antennomere stage in *Lithobius* antennomeres 2, 5, 9 and 13 are each the distal mere of a group that have arisen by division of the initial seven antennomeres. In geophilomorphs specialised sensory setae are located on antennomeres 2, 5, 9 and 13. These also occur on the same antennomeres in larva II *Lithobius microps* which has 14 antennomeres.

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