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POST-EMBRYONIC DEVELOPMENT AND THE PHYLOGENY OF GEOPHILOMORPH CENTIPEDES (CHILOPODA)

by

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ABSTRACT

The post-embryonic development of six geophilomorph species is investigated using histology, biometry and field observations. No instance of anamorphosis was observed. Sexual maturity is reached at the 5th post-foetal stage in *Schendyla nemorensis*, *Dicellophilus carniolensis*, *Henia* (*Chaetechelyne*) *vesuviana*; at the 6th in *Geophilus carpophagus*, *Strigamia crassipes*; at the 8th in *Stigmatogaster gracilis*, suggesting that the Himantariidae differ from the remaining more advanced families. Post-maturational moults are less numerous in the more specialized mecistocephalids, schendylids and linotaeniids. Another derived character state (the appearance of the first coxal pore in the foetus) occurs in the mecistocephalid *D. carniolensis*.

INTRODUCTION

Since Haase's (1880) work, developmental patterns have been used from time to time to provide taxonomic characters for the classification of centipedes. An instance of this is the distinction between the subclasses Epimorpha and Anamorpha.

Until now, however, the main interest in developmental stages for taxonomic purposes has been restricted to classification at the species level. The valuable papers by Andersson exemplify this in an outstanding way (Andersson, 1979, 1981).

As yet, no attempt has been made to review classification at the genus and family levels on the basis of developmental patterns. It is obvious that these patterns are important, because we may be able to identify within them plesiomorphic vs. apomorphic character states.

From a technical point of view, the study of post-embryonic development is difficult and lengthy, because it generally requires serial investigation of developmental stages. This task may be simplified, however, as soon as a method is devised of easily and correctly assigning a given specimen to its developmental stage, i.e. identifying the number of post-foetal moults.

Andersson has demonstrated that morphometric traits commonly allow for a correct identification of epimorphic stages in lithobiids, but this requires extensive work on species reared in the laboratory. Moreover, a distinct set of numerical values has to be obtained for each species and any generalization may not be valid for a widespread and variable species throughout its range.

Some authors adopted the same method when studying geophilomorphs, e.g. Verhoeff (1902-1925), Lewis (1961) and Eason (1964), but this method is not sufficiently sensitive to recognize the full number of stages in this group. As a result, most authors recognize only four adolescent stages. On the other hand, Weil (1958), when studying *Necrophloeophagus longicornis* Leach (= *Geophilus flavus* Degeer) and *Geophilus brevicornis* C. L. Koch (= "*Clinopodes*" *linearis* C. L. Koch) developing under laboratory conditions, was able to identify not less than five or six stages before maturity.

A single, easy and reliable method of stage identification is, nevertheless, available for all geophilomorph species. It rests on an anatomical feature well illustrated by Füller (1960) and subsequently substantiated by Manton (1965): the tracheal branches originating at the two sides of the body anastomize dorsally in the so-called median atria, with obvious conse-

quences for the mechanics of moulting. The cuticular lining of the tracheae breaks apart at both sides of each median atrium, where a small section of the old lining is retained when the exuvium is shed. Therefore, at the level of the median atrium the new cuticle is formed around the old one and, in due course, it also breaks off from the main exuvium, and is retained in situ. The number of tracheal fragments included within each other also increases at each moult. Their number is easily counted on histological sections that may be cut through some segments of the middle part of the body, saving the foremost and hindmost ones for other investigations.

The first two post-embryonic stages, i.e. the peripatoid and the foetus, do not possess a tracheal system, which develops from the first post-foetal stage onwards. Therefore, the total number of post-embryonic stages is obtained by adding two to the number of cuticular rings found in the median atria.

A similar criterion has been proposed by Lewis (1961, 1981), with reference to cuticular linings of seminal vesicles and the number of sperm whorls included within them. The disadvantage of this method is, that it applies only to female specimens and possibly not to all species. Moreover, it is still uncertain at which stage cuticular linings are first retained within seminal vesicles. Possibly it is different in different species. With regard to the tracheal system there are no similar doubts.

MATERIALS AND METHODS

In this preliminary study on developmental patterns of geophilomorphs, I have investigated the following species, as representatives of different families:

Stigmatogaster gracilis (Meinert) (Himantariidae)
Schendyla nemorensis (C. L. Koch) (Schendylidae)
Dicellophilus carniolensis (C. L. Koch) (Mecistocephalidae)
Geophilus carpophagus Leach (Geophilidae)
Henia (*Chaetechelyne*) *vesuviana* (Newport) (Dignathodontidae)
Strigamia crassipes (C. L. Koch) (Linotaeniidae)

For each species, 10 to 20 specimens of both sexes have been employed for histological research, and 60 to 150 for biometry, all from sites in northeastern Italy. Additional data have been obtained for many other species, but on fewer specimens.

Sagittal sections cut at 10 µm and stained with haematoxylin-eosin have been studied to establish sexual maturity and to count the number of tracheal exuvia in the median atria. Microscopic preparations have also been examined for indications of the existence of anamorphosis, the primitive method of development in centipedes, the rudimentary persistence of which has been repeatedly claimed for geophilomorphs, even in recent work (Misioch, 1978).

RESULTS AND DISCUSSION

Anamorphosis

Anamorphosis can be excluded with certainty for all species investigated. There is no correlation between the number of leg-bearing segments and the developmental stage as identified through tracheal rings. Neither is there any difference between the segment number of brood-caring mothers and their daughters, as recorded for other species by Prunesco & Capuşe (1971). There are no traces of a proliferating zone near the caudal extremity of the body.

Misioch's (1978) apparently opposite findings, which show a positive correlation between segment number and age, can be explained when it is taken into account that she estimates age by simply measuring body length, a character already depending on segment number irrespective of age. It is no wonder, therefore, that she finds a correlation between segment number and body length. That this is not a demonstration of anamorphosis, is shown in the model population in fig. 1.

Summing up, Geophilomorpha (plus Scolopendromorpha) may still be regarded as truly epimorphic centipedes, epimorphosis having been achieved early on and definitively in their evolutionary history.

Number of stages preceding sexual maturity

We can reasonably assume a long, perhaps not strictly fixed sequence of moults preceding sex-

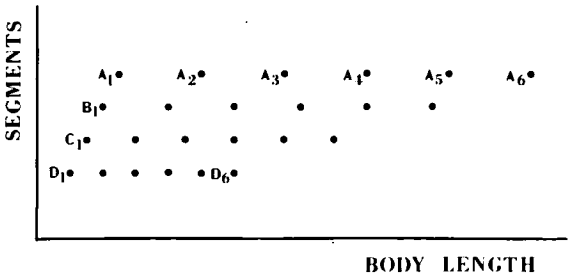

Fig. 1. Correlation between segment number and body length in the absence of a correlation between segment number and age. The diagram refers to a hypothetical population, made up of epimorphic individuals with different segment numbers (A, B, C, D), all developing through stages 1 to 6. A roughly fixed mean length for each body segment at a given developmental stage is assumed, i.e. a longer body for a specimen with more segments, at each stage (e.g. $A_1 > B_1$), the difference increasing with age (compare the difference A_1 vs. B_1 with the difference A_6 vs. B_6). A random sample from such a population shows a significant correlation between segment number and body length, simulating anamorphic development.

ual maturity as the primitive condition among centipedes, as among other classes of arthropods. Therefore, a reduction and stabilization of the number of moults may be regarded as a derived character state. From this point of view, it is difficult to exclude parallelisms, even between closely related taxa, but, at any rate, the direction of this evolutionary change cannot be misinterpreted.

I have found four to seven post-foetal stages before maturity (table I and figs. 2-4), the higher figure being that of *Stigmatogaster gracilis*. This is well in accordance with the primitiveness of the Himantariidae, already suggested by some morphological character states, such as their high and often very variable segment number or the structure of labrum and mandibles.

Number of mature stages

Primitive arthropods still undergo moults after their first sexually mature stage. This faculty, which has been lost in insects and in other groups, is commonly assumed to occur in all centipede orders, but detailed data are still very few. The most accurate record for a geophilomorph species has been provided by Lewis (1961) for *Strigamia maritima* (Leach), where some old females appear to have moulted three times after the onset of maturity.

In my material, four mature stages do occur at least in *Geophilus carpophagus* and in *Henia* (*Chaetechelyne*) *vesuviana*, whereas I could not find more than three in *Strigamia crassipes* and in *Dicellophilus carniolensis*, without any difference between the sexes. The lowest number of mature stages, i.e. two, occurs in *Schendyla nemorensis*, whereas I still lack conclusive evidence for *Stigmatogaster gracilis*.

TABLE I

Number of post-foetal stages.

	before maturity	mature	total
Stigmatogaster gracilis	7	2?	9?
Schendyla nemorensis	4	2	6
Dicellophilus carniolensis	4	4	8
Geophilus carpophagus	5	4	9
Henia vesuviana	4	4	8
Strigamia crassipes	5	3	8

It is tempting to see in the reduced number of post-maturational moults an advanced character state of schendylid geophilomorphs, well matching other specializations of the family, e.g. the structure of the coxal glands.

A reduction of the number of mature stages is also possibly a peculiarity of mecistocephalids, matching their curiously fixed segment number and several advanced morphological traits.

For *Strigamia*, where my findings in *S. crassipes* do not match those by Lewis on *S. maritima*, further investigations are needed.

Developmental schedules of somatic characters

The first appearance or differentiation of given somatic characters may be anticipated or

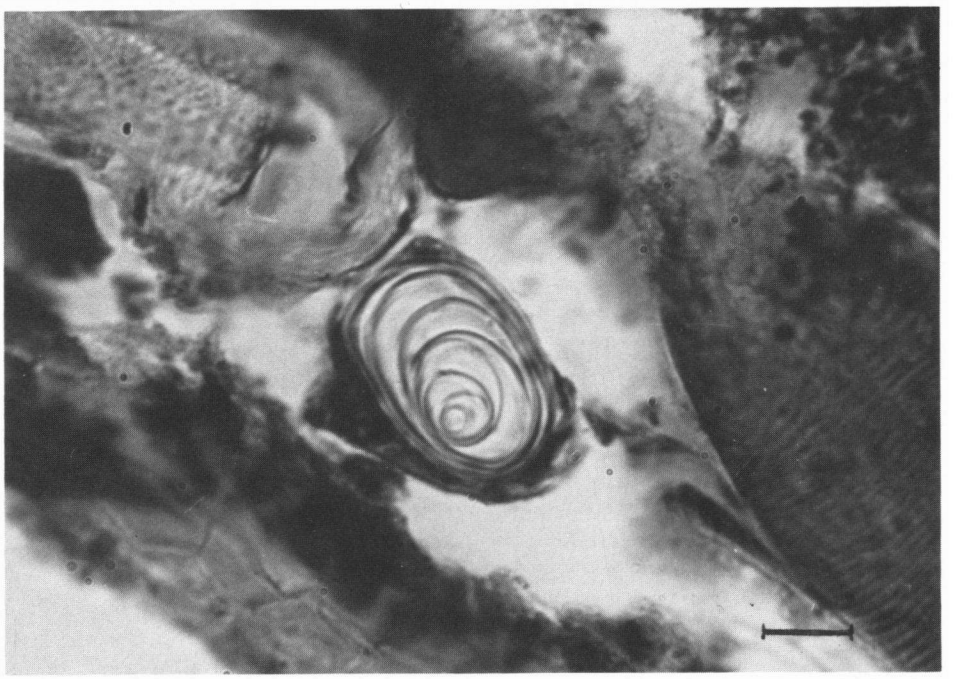

Fig. 2. Cuticular rings in a median atrium of *Dicellophilus carniolensis* (sagittal section). Scale = 10 μm.

Fig. 3. Cuticular rings in a median atrium of *Henia vesuviana* (sagittal section). Scale = 100 μm.

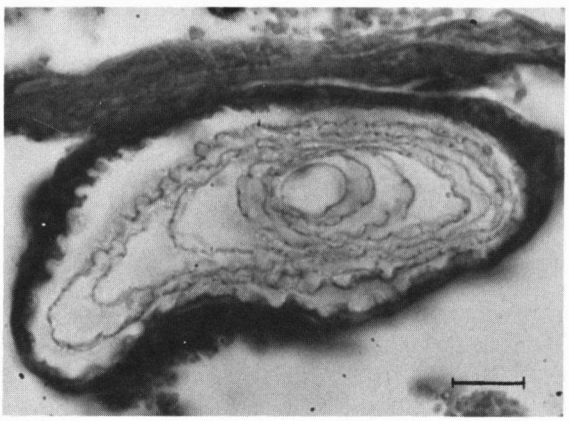

Fig. 4. Cuticular rings in a median atrium of *Strigamia crassipes* (sagittal section). Scale = 10 μm.

delayed in the development of single species with respect to the schedule of others.

I only quote here the case of *Dicellophilus carniolensis*, where the first coxal pore appears in the foetus, whereas it only appears in the first post-foetal stage in *Geophilus*, *Strigamia*, etc. This is again a possibly derived character state for a mecistocephalid.

CONCLUSIONS

In spite of their preliminary character, these investigations on the post-embryonic development of geophilomorph centipedes have provided some new information and confirm the value of developmental studies in revising phylogeny and taxonomy of the group.

At present, we can only suggest some evolutionary trends, e.g. towards the reduction of developmental stages or towards the disappearance of post-maturational moults.

At any rate, it can be seen that developmental characters confirm the primitivity of the Himantariidae, the generalized condition of the Geophilidae and the advanced position of the Schendylidae and the Mecistocephalidae, obviously along divergent evolutionary pathways.

As far as *Henia* and *Strigamia* are concerned, they both seem to be at an evolutionary level similar to that of *Geophilus*, but this does not imply that they must be retained within the Geophilidae (Attems, 1929), or both included in a single family Dignathodontidae, as customary. They are possibly widely separated from each other in the system, as Cook (1895) foresaw.

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