PHYLOGENETIC PATHWAYS IN THE CHILOPODA

by

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ABSTRACT

The phylogenetic relationships of the chilopod orders are discussed on the basis of cladistic principles. The autapomorphies of the five orders (Scutigeromorpha, Lithobiomorpha, Craterostigmomorpha, Scolopendromorpha, and Geophilomorpha) are summarized. The monophyly of the Epimorpha is established. *Craterostigmus* is tentatively regarded as belonging to the epimorph branch. The Lithobiomorpha are united with the Epimorpha on the ground of a great number of common characters which must be classified as synapomorphies. A detailed phylogenetic tree is proposed. The probable characteristics of the chilopod ancestor are worked out.

INTRODUCTION

In his book "The biology of centipedes", J. G. E. Lewis stated while discussing the relationships of the chilopod orders, that "no study of their relationships based on cladistic phylogenies has yet been made" (Lewis, 1981: 424). This deficiency is to my mind also responsible for the fact that an old question has remained unsolved up to the present time: Was the ancestor of the chilopods a *Geophilus*- or a *Scolopendra*-like creature which was long and slender and had many homonomous segments, which inhabited the crevices of the soil and which gave rise to shorter animals like *Lithobius* and finally to fleet rushing beasts like *Scutigera*? Or was the ancestor rather an animal resembling a *Scutigera*, with only 15 pairs of legs, with dome-shaped head, compound eyes, organs of Tömösváry, from which evolved longer forms with numerous segments? If this assumption is right the Geophilomorpha have to be regarded as the most derived centipedes. As evolution has followed only one pathway, at least one of the two assumptions must be false. A brief discussion of the methods which will enable us to decide between the alternatives seems to be necessary.

METHODS

Although it is three decades ago since Hennig (1950, 1966) and others pointed out the necessity of employing a consistent and well-founded method when judging evolutionary events, yet many biologists and especially myriapodologists still try to rely on their intuition. They have arranged recent species in evolutionary series on the basis of supposed phylogenetic laws (e. g. tachygenesis, elongation) or of ascribed functional value or advantage. Groups were founded according to determination keys or mere summing up of similar characters. Other groups were split up and the subgroups isolated or combined with others based upon "personal and perhaps subconscious values in character weighting" (Hoffman, 1980: 15).

All these approaches led to contradictory results and were not in accordance with modern evolutionary theory. With regard to the Chilopoda and especially the theoretical background of the work of Brölemann (1921, 1930), Manton (1965, 1977) and Fahlander (1938) the present author has submitted a detailed discussion (Dohle, 1980). Only some major points will be considered here.

Evolution includes two very essential phenomena:
— The alteration of specific characters within a species in the course of time during many generations.
— The splitting and isolation of populations of a species, which gain different characters
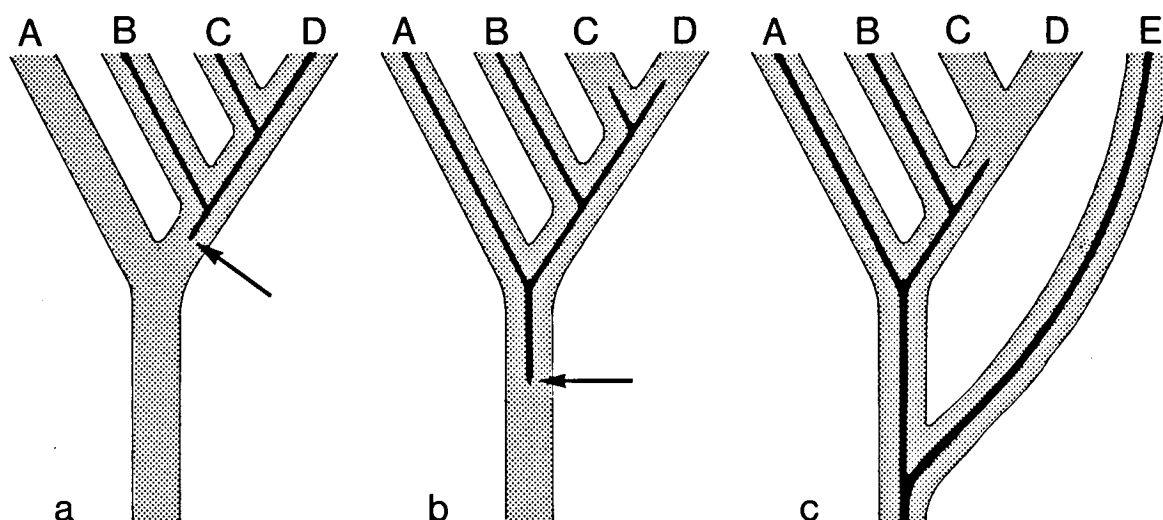
Fig. 1. Three possibilities of appearance and loss of characters in the course of evolution. A-E: different taxa. Arrow: appearance of a new character.

that prevent (after a certain threshold) the mixing and interbreeding of the individuals of the different populations.

After the splitting of a species into two different species, which thus have the relation of sister-species, one of these sister-species may acquire a new character which eventually becomes a species-specific character. If this species splits up further, the new character can only be inherited by the daughter-species and cannot be transferred to the offspring of the other sister-group. In our attempt to unite monophyletic groups we are thus looking for specific characters which are characteristic only of a certain number of species. If these characters were most probably acquired only by the ancestor-species of this group they can be designated as synapomorphies (fig. 1a).

If new characters did not alter or disappear during evolution, it would be quite easy to reconstruct a phylogenetic tree. But a character can be lost or completely altered, so that only some of the descendant species retain this character, whereas others do not. In fig. 1b the taxa A and B share a character, but this does not prove a monophyletic relationship between A and B; the character was acquired by the ancestor of A-D and was lost in C and D.

Sometimes rudiments of such a character are still found in taxa C and D or are recapitulated in early ontogenetic stadia.

If a character which only unites A and B is in reality a very old heritage, it can be detected by an out-group comparison with taxa only remotely related to the group in question (fig. 1c). If it is found there, it is most probably a symplesiomorphic character and thus without significance for the establishment of closer phylogenetic relationships within the taxa A-D.

So our task with regard to the chilopods is to reconstruct the sequence of splitting of ancestor-species into the different groups, or — in other words — to establish the sister-group relationships by detecting the synapomorphies for each group.

THE MONOPHYLY OF THE CHILOPOD ORDERS

When discussing the relationships of the chilopod orders, two important assumptions have to be made. One assumption is that the Chilopoda constitute a monophyletic group, which means that all species which are classified as chilopods have one common ancestor. This

ancestral chilopod species is not likewise the ancestor of other myriapod groups, e.g. millipedes or symphylans. The monophyly of the Chilopoda has never been in doubt, though there are only few derived characters shared by all chilopod groups:

— The first trunk appendages have been transformed into poison-claws.

— An egg-tooth on the embryonic cuticle of the second maxilla is formed in the embryo.

— The spermatozoa have a very special structure with a spiral ridge on the nucleus, a striated cylinder around the axoneme and a helicoidal "mantle" (Horstmann, 1968; Descamps, 1972; Camatini et al., 1974, 1977; Camatini & Franchi, 1979; Franchi et al., 1977; Cotelli et al., 1978).

The other assumption is that each of the five orders of chilopods is monophyletic.

The Scutigeromorpha comprise only one family. This already indicates that the genera and species are very similar, not only in their general aspect, but also in many detailed characters down to the spinulation of legs and tergal plates. Some of the common derived characters are: annulation of antennal flagellum and tarsi, the strange maxillary organ, and the formation of one large tergal plate over trunk segments 7-9.

The Lithobiomorpha do not have many common characters that could be designated as synapomorphic. Probably the unpaired tubular testis in connection with the pair of large seminal vesicles in the male, and the female gonopods, with a basal article with spines and a terminal article with a broad claw, are synapomorphies.

The order Craterostigmomorpha has been erected by Pocock (1902) for the species *Craterostigmus tasmanianus* Pocock. This species, though incompletely known, does not share synapomorphies with any other order. Thus its separate treatment is justified.

The Scolopendromorpha have bean-shaped spermatophores with a tough envelope. The poison-claw segment is without a separate tergite.

The Geophilomorpha show the greatest diversity of features and families. Their monophyly can be established by the divided tergites and sternites, by the female's habit of coiling dorsally around the egg-cluster, and by the fixed number of 14 antennal articles. Another derived character, though not conclusive in itself, is the lack of eyes in all members of this order.

THE EPIMORPHA

There is almost general agreement that Scolopendromorpha and Geophilomorpha are very closely related and share a recent common ancestor. There are strong arguments for this, as for instance:

— Epimorphosis. Although they have a higher number of segments than the other three chilopod orders, both Scolopendromorpha and Geophilomorpha hatch with the full complement of segments. For geophilomorph species with a variable number of segments, postembryonic addition of new segments has been suspected several times (Verhoeff, 1902-25; Misioch, 1978), but this has not been confirmed by recent investigations (Eason, 1979; Horneland & Meidell, in press; Minelli, 1985).

— Brood-care. This need not necessarily be combined with epimorphosis or vice versa. Not only is the egg-cluster guarded until hatching, but also the first two postembryonic stadia (peripatoid and foetoid stadium), which are very incomplete and show only restricted movements, remain under the protection of the mother.

— The testes, of which there are two to many pairs in the Scolopendromorpha and only one pair in the Geophilomorpha, are spindle-shaped in both orders. Vasa efferentia issue from both tapering ends.

— Anastomoses are found between the tracheal branches of different segments.

— The direct articulation between the 1st and 4th article of the telopodite of the poison-claw which leaves the 2nd and 3rd article incomplete is a very peculiar feature.

THE POSITION OF *CRATEROSTIGMUS*

Craterostigmus tasmanianus is still an enigmatic species. None of its hitherto known features can clearly be regarded as synapomorphic with one of the other orders. *Craterostigmus* has been brought into close connection with the Lithobiomorpha because of the 15 pairs of walking legs and the distribution of spiracles. But the 15 pairs of walking legs are also shared by the Scutigeromorpha, and the distribution of the spiracles is found in equivalent form in the Scolopendromorpha.

Manton (1965) believed that the affinities of *Craterostigmus* lie rather with the Epimorpha. One character which speaks in favour of this is brood-care. The female lies humped over the egg-mass like a scolopender, the first stadium has 12 pairs of legs and gains the final number of 15 after only one moult, so that anamorphosis is almost suppressed. Because of the brood-care I would also join *Craterostigmus* with the epimorph branch and regard it as the sister-group of the Epimorpha, but would like to put a question mark until more information is available.

THE PLEUROSTIGMOPHORA

Having united Scolopendromorpha and Geophilomorpha as Epimorpha and regarding the Craterostigmomorpha tentatively as the sister-group of the Epimorpha there remains only one alternative to be solved: Did the Lithobiomorpha split off from the branch leading to the Epimorpha (fig. 2, right), or did they share a part of their evolution with the Scutigeromorpha (fig. 2, left)?

The question seems to be very simple, but actually it is very complex. Generations of myriapodologists have tried to solve it the one way or the other. The difficulty arises as there seem to be arguments for both alternatives. There are characters which Scutigeromorpha and Lithobiomorpha have in common and which are lacking in the Epimorpha. There are other characters which Lithobiomorpha and
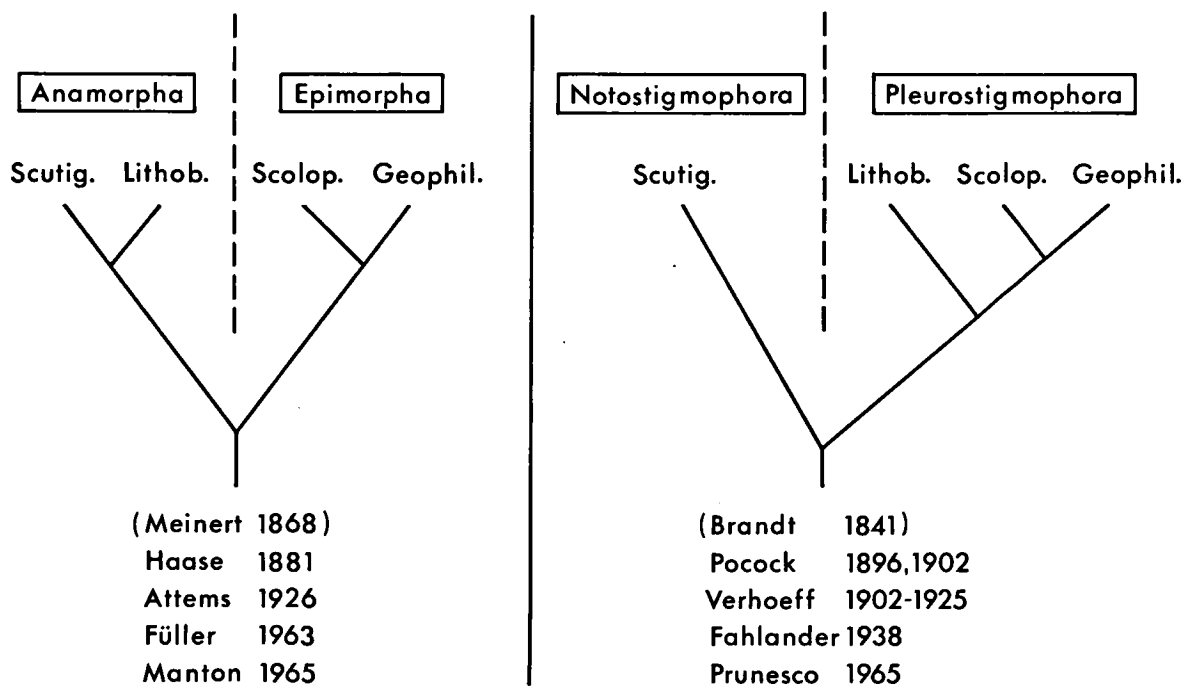

Fig. 2. Alternative views regarding classification and evolution of the chilopod orders. In parentheses: classifications from pre-phylogenetic times (after Dohle, 1980).

Scutigeromorpha	Lithobiomorpha	Epimorpha

- maxillary nephridia	- flattened head-capsule
- organs of Tömösvåry	- moniliform antennae
- heterotergy	- single eyes or none
- gonopods	- form of tentorium
- hemianamorphosis	- coxae of 2nd maxillae fused
- 15 pairs of walking	- coxosternal plate of poison-claw
legs	- pleurostigmophoran state
	- coxal organs
	- spermatophore web,"Spinngriffel"

Fig. 3. Homologous structures common to Scutigeromorpha and Lithobiomorpha (absent in Epimorpha) are listed on the left, those common to Lithobiomorpha and Epimorpha (absent in Scutigeromorpha) on the right.

Epimorpha have in common and which are not found in the Scutigeromorpha (fig. 3).

This is a dilemma, but this is at the same time an opportunity. For if only two or three characters of one side are clearly derived characters, which were not already characters of the common chilopod ancestor and have only been acquired after the first splitting event in the Chilopoda (as in fig. 1a), then all the characters of the other side must be regarded as ancestral characters (as in fig. 1b or 1c)*. This is a logical conclusion inferred from the fact that a derived character can only be inherited by the direct descendants and cannot be transferred to another line. It is impossible that there are derived characters or synapomorphies for the solution of the above-named alternative on both sides. With this inevitable postulate in mind the characters which are common to Lithobiomorpha and Epimorpha will be discussed first.

Characters common to Lithobiomorpha and Epimorpha

— Flattened head-capsule. Whereas the head of the Scutigeromorpha has a dome-shaped form, the head-capsule of Lithobiomorpha and Epimorpha is very much flattened. But it is not only this more superficial feature

* Another possible explanation could be, that these characters have evolved convergently. This possibility has to be excluded first. One is obliged to discuss in this context only homologous characters. Apart from the character: single eyes or none, the other characters enumerated have not been suspected to be the result of convergent evolution within the chilopods.

which could be regarded as a common derived character. It is rather the fact that the whole clypeal or epistomal region has been bent ventrally, so that a line drawn between the bases of the antennae assumes the most anterior position of the head; the bases of the antennae lie very close together, so that there is only a narrow bridge of sclerotized cuticle left between them (or even none in Geophilomorpha). This is an unusual solution for flattening a head. In Symphyla and Diplura the clypeal region is not bent ventrally and backwards, and the mouth is at the most anterior part of the head.

— Moniliform antennae. The articles of the antennae are like beads on a string. Every article has its own muscles and can be moved independently of the others. The articles are very much alike and thus have a primitive aspect. This question will be discussed further below.

— There are single eyes, not quite correctly named ocelli, at the lateral margins of the head (if there are eyes at all). The Scutigeromorpha, by contrast, have large compound eyes.

— When the tentorium of Lithobiomorpha and Scolopendromorpha is compared with a tentorium of the Scutigeromorpha (Fahlander, 1938: fig. 6), it becomes quite obvious that the tentoria of the former two orders are very similar, while the tentorium of the Scutigeromorpha has a different aspect.

— The coxae of the second maxillae of Lithobiomorpha and Epimorpha are fused in

the midline and thus form a transverse band. The telopodite has only 3 articles.

— The so-called coxosternal plates of the poison-claws are fused, whereas in Scutigeromorpha the coxae are still independent. It would be very difficult to assume that the fused coxae are more primitive than the independent ones. There are only four articles of the telopodite, whereas the fang in Scutigeromorpha is subdivided.

— Pleurostigmophoran state. The lateral stigmata in Lithobiomorpha and Epimorpha as well as the branched tubular tracheae closely resemble the tracheae in Hexapoda. This state could in principle be a heritage from the common ancestor of all Antennata (= Tracheata) and thus a symplesiomorphy. This point will be discussed further below.

— Coxal organs. Until recently the structure of the organs associated with the coxal pores was insufficiently known. In a series of investigations, Rosenberg (1982; 1983a, b) showed that these organs are nearly identical in their fine structure. There is a main transport epithelium, there are junctional cells and distal glands with gland cells, additional cells and canal cells. Coxal organs and the similar anal organs are completely lacking in the Scutigeromorpha.

— Spermatophore web. In *Lithobius* as well as in *Scolopendra* and *Geophilus* (= *Necrophloeophagus*) a web is spun for the deposition of the spermatophore, as Klingel (1959; 1960a, b) has described. In this connection a device, the so-called "Spinngriffel", has been developed. It was thought to be a penis by the older naturalists.

Whereas the structure of antennae and tracheae may at a first glance be original, all the other characters enumerated, which Lithobiomorpha and Epimorpha have in common, are most certainly derived, as they cannot be found in their special form in the Scutigeromorpha or in another group of myriapods or insects. This corroborates the idea that these characters evolved only after the Scutigeromorpha split off

from the common chilopod branch (cf. right hand side of fig. 2).

Characters common to Lithobiomorpha and Scutigeromorpha

The above discussion led to the conclusion that Lithobiomorpha and Epimorpha form a monophyletic group. Are then all the characters common to Lithobiomorpha and Scutigeromorpha original characters of the chilopod ancestor which have been lost on the branch leading to the Epimorpha?

To investigate this question it is fruitful to make an out-group comparison and take into consideration other myriapods and the Hexapoda.

— The maxillary nephridia of Scutigeromorpha and Lithobiomorpha can be looked upon as the fused nephridia of the first and second maxillary segment. This was the view of Fahlander (1938), who first described them in detail, and has fully been accepted by Gabe (1972). Unfortunately Knoll (1974), in his investigation on the embryology of *Scutigera*, does not describe the formation of the maxillary nephridia. But as maxillary nephridia are present in many arthropods, within the myriapods in Symphyla, Diplopoda and Pauropoda, within the Hexapoda in their original form in the "Thysanura", their existence is clearly an ancestral character. The fusion may have been an acquisition of the chilopod ancestor, the nonexistence in the Epimorpha is certainly a secondary loss.

— Organs of Tömösváry. Haupt (1979) has pointed out that the organs of Tömösváry or postantennal organs may be homologous in all Antennata (= Tracheata) and hence be a common heritage. The fine structure of the organs of Tömösváry in *Scutigera* is not known. Whether *Craterostigmus* has these organs is unclear (Lewis, 1981). But it seems that the chilopod ancestor had such organs and that they have been lost in the Epimorpha.

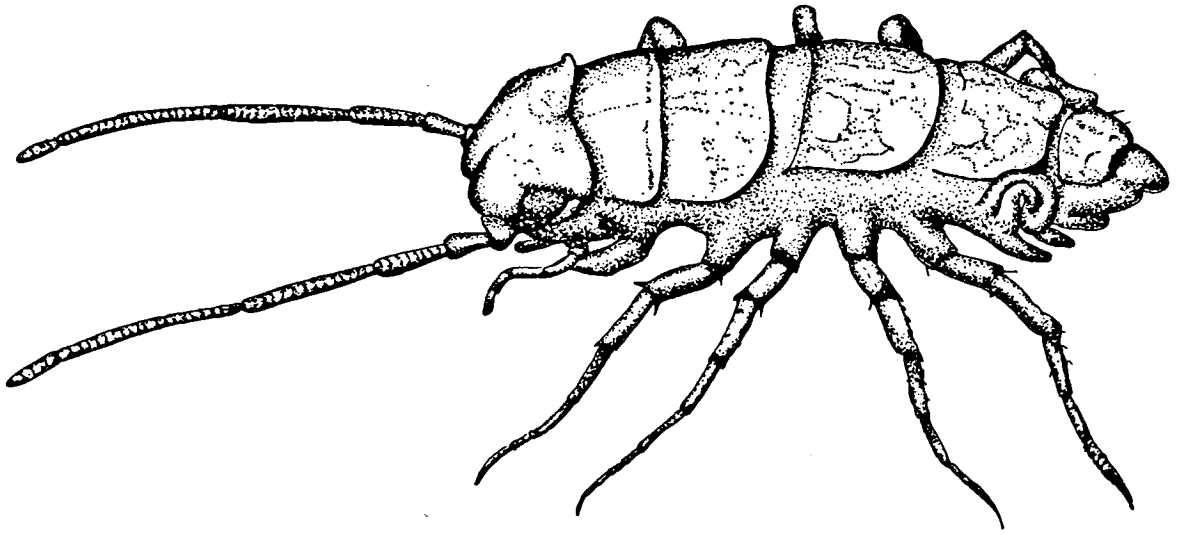— Heterotergy. This is not a feature only com-

Fig. 4. First postembryonic stadium of *Scutigera coleoptrata* (Linnaeus).

mon to Scutigeromorpha and Lithobiomorpha, but is found in less pronounced form in *Craterostigmus* and in Scolopendromorpha as well. The tergal plates covering the trunk segments 8 and 9 are long ones. That there is in Scutigeromorpha only one large tergal plate covering these segments is clearly a derived character.

— Gonopods. Rudiments of gonopods are present in Scolopendromorpha and Geophilomorpha, so the presence of well-developed gonopods must be ancestral. In the female of *Lithobius* and *Scutigera* they are involved in egg-laying, the egg being held by them for some time, so that it can be coated with soil and becomes well camouflaged (Dohle, 1970; Brocher, 1930; Demange, 1945, 1956). Only males of Scutigeromorpha have two pairs of gonopods. This is apparently the original number. In *Scolopendra* Heymons (1901) described in the first postembryonic stadium two pairs of limb buds behind the last pair of walking legs.

— Hemianamorphosis. The first stadium hatching from the egg-shell has a limited number of legs and segments in Scutigeromorpha and Lithobiomorpha. In Scutigero-

morpha the number is four pairs of walking legs (fig. 4), in Lithobiomorpha the number is generally seven, exceptionally six (*Lamyctinus*) or eight (*Esastigmatobius*). If we have a look at early embryonic stages of *Lithobius* with the developing germ-band, we see that (when the leg buds are at first clearly visible) there are four pairs of them behind the buds of the poison-claws (fig. 5). Therefore, I suppose that four pairs of walking legs is the original number of the first stadium.

— The course of anamorphosis is not exactly the same in Scutigeromorpha and Lithobiomorpha. It is difficult to decide which of these was characteristic of the ancestor. But adults of Scutigeromorpha and Lithobiomorpha have 15 pairs of walking legs. Whereas it is easy to show that the above-named characters are original characters, this character seems to be more troubling. Are there arguments which could speak in favour of the assumption that 15 pairs of walking legs were also a feature of the ancestor of the centipedes? Scolopendromorpha have mostly 21, some have 23 pairs of walking legs; but *Craterostigmus* has still 15 pairs of legs though it has nearly completely lost the anamorphosis.
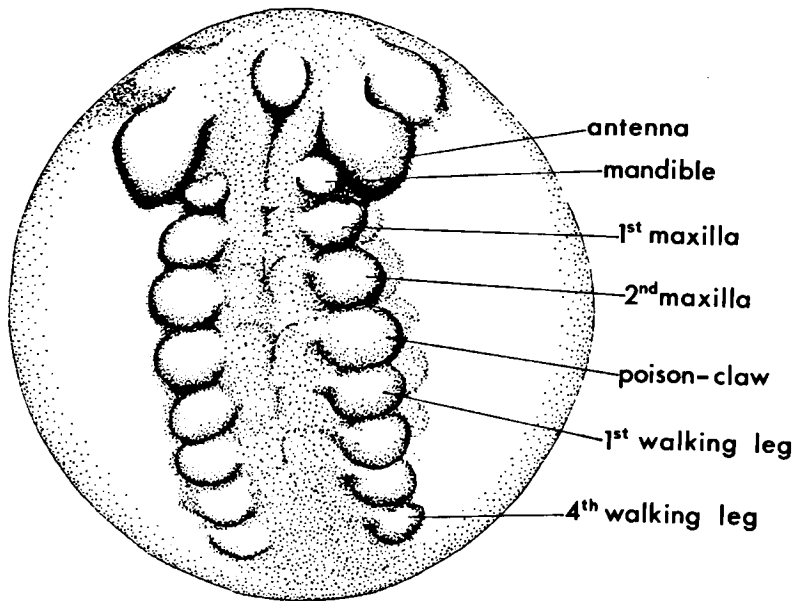
Fig. 5. Germ-band of *Lithobius forficatus* (Linnaeus) with rudiments of four pairs of walking legs (compare similar germ bands of *Scutigera* in Dohle, 1970, and Knoll, 1974).

If the position which I ascribed tentatively to the Craterostigmomorpha is correct, then it is quite obvious that the chilopod ancestor must have had 15 pairs of walking legs and that this number has been augmented on the way to the Epimorpha. If we take the opposite point of view, namely that the number of 15 pairs of legs is a synapomorphy for Scutigeromorpha and Lithobiomorpha (and Craterostigmomorpha), then we decide that all the characters which Lithobiomorpha and Epimorpha have in common are either original characters or have been evolved convergently in these two groups. Both assumptions are highly improbable.

Therefore we conclude that many of the characters which Lithobiomorpha and Epimorpha have in common are derived, synapomorphic characters. On the other hand all the characters which Lithobiomorpha and Scutigeromorpha have in common are most certainly original, symplesiomorphic characters which have been lost or altered in the Epimorpha.

The logical conclusion is: Lithobiomorpha and Epimorpha constitute a monophyletic group. The ancestor of the chilopods must have had the characters of the anamorphic side.

Characters of uncertain state

There are three characters which do not fit well into our scheme and which have been left to be discussed separately:
— the form of the antennae,
— the structure of the eyes,
— the tracheal system in Noto- and Pleurostigmophora.

There is general agreement that the annulation of the antennal flagellum in Scutigeromorpha is a derived character. But do the antennae of the Pleurostigmophora then represent a primitive, ancestral state? I would like to throw doubt on this assumption. The proximal articles of the antennae of most Antennata which do not live in crevices of the soil are differentiated and can be bent downwards so that the tip of the antennae can touch the soil surface from above. Only animals extremely flattened and adapted for living in small crevices have antennae pointing straightly forwards, the ar-

ticles having the form of beads on a string, as in Symphyla, Diplura, or Pleurostigmophora. I assume that the antennae of *Scutigera* are more original though their annulation is derived. In the first stadium the annulation is scarcely visible and the four original articles of the flagellum are pronounced (fig. 4).

Many investigators pointed out the great resemblance in morphology and fine structure of compound eyes and ommatidia in Crustacea and Hexapoda. This leads to the conclusion that compound eyes were a feature of the ancestor of these groups and hence existed also in the common ancestor of myriapods and Hexapoda. The Scutigeromorpha are the only recent myriapods with compound eyes, but the structure of their ommatidia is not the same as in Hexapoda, as Bähr (1975) and Paulus (1979) have shown, and so they do not represent the ancestral state. The question arises: Did the ancestor of the chilopods have lateral fields of single eyes as in Lithobiomorpha and Scolopendromorpha which —under the selection pressure of hunting and catching swift prey— united to form the complex eye of *Scutigera*? This assumption would be probable if the eye of *Scutigera* had an essential function in perceiving and hunting the prey. Manton laid stress on the fact that "the hunting habits of *Scutigera* are dependent upon acute vision and great fleetness" (Manton, 1965: 350). But there are no observations or experiments which could clearly demonstrate that the conspicuous eyes had a function in discerning or hunting the prey. On the contrary, according to observations of Klingel (1960b) and myself, the eyes play no obvious role in discerning form or movements of the prey. One can hold an actively buzzing fly with a forceps in front of the eyes of *Scutigera* without any apparent reaction of the animal. But as soon as the fly touches the antennae or tarsi of the legs, *Scutigera* at once pounces on the prey. One can produce the same effect when touching the antennae with a cotton ball dipped into fly sap.

Thus the evolutionary conclusion would rather be that the compound eye of *Scutigera* has

lost its former function in movement detection or pattern recognition which it had in the antennate ancestor; that the structure of the ommatidia has been altered, but that it has not disintegrated as much as the eye of Lithobiomorpha or Scolopendromorpha.

No comment must be made on the fact that blindness is a derived character in the chilopods. Geophilomorpha and Cryptopidae all lack ocelli, but also some genera and species of the Lithobiomorpha have lost the eyes secondarily and convergently.

Whereas the tracheal system is completely different in the Notostigmophora on the one hand and the Pleurostigmophora on the other hand, the circulatory system is of striking uniformity. According to the descriptions of Herbst (1891), Duboscq (1898) and Fahlander (1938) the circulatory system is very complex, having especially in the anterior part of the body an elaborate system of arteries and a pair of "aortic arches" leading to the supraneural artery.

Without doubt there is in most arthropods a close correlation between the respiratory and the circulatory systems. When the respiratory tissue is confined to small regions of the body, as in the gills of many crustaceans (e. g. Eucarida or Peracarida) or in the "lungs" of many arachnids (e. g. Pedipalpi or Araneae), then there is an elaborate system of arteries forcing the course of the aerated blood in certain directions and being responsible for a good oxygen supply to the brain, the ventral nerve chain, the muscles and the digestive glands.

When on the other hand there is, in terrestrial arthropods, a complicated tracheal system bringing the air directly to the oxygen-consuming organs, as in Hexapoda or in Solifugae, then the circulatory sytem is greatly reduced leaving only the dorsal heart for a circulation of the blood without exact arterial pathways.

It follows that in an animal as *Scolopendra* or *Lithobius* one would rather expect a very simplified circulatory system. The complexity and the striking similarity with the system of
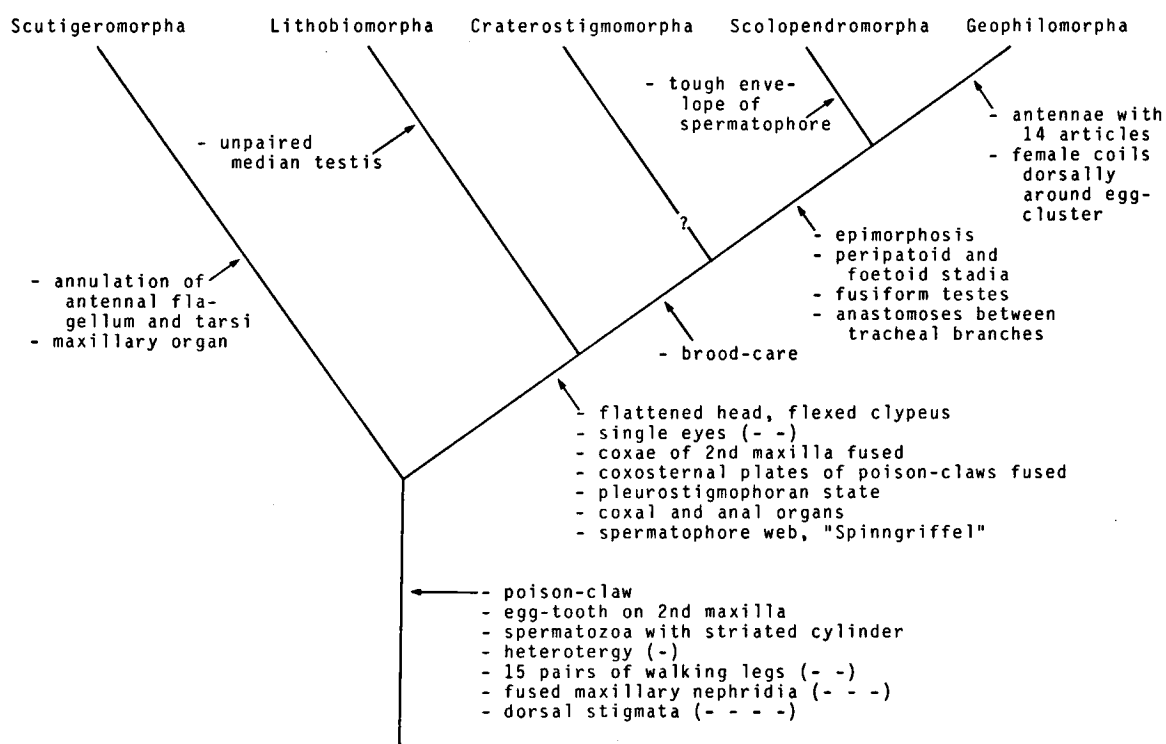
Fig. 6. Proposed phylogenetic tree of the Chilopoda with assumed appearance of characters during evolution. Characters without a mark are shared by all descendants after their appearance (as far as known); characters with - have been lost in one -, two - -, or more orders.

Scutigeromorpha points to another conclusion: The ancestor of the chilopods had a localized system with small tracheae aerating only the blood in the pericardial sinus, as in *Scutigera*. The pleural stigmata and the elaborate tracheal system of the Pleurostigmophora were a more recent acquisition which has not yet led to a profound alteration of the circulatory system, even though the latter no longer has the same functional value as in *Scutigera*. This means that the pleurostigmophoran state is regarded as a derived character and as convergent to the insect condition.

If this appears to be improbable at first sight, one should remember that the Diplopoda have ventral stigmata and the Symphyla one pair of stigmata in the mandible region, so that at least in these two classes tracheae have been evolved independently from the Hexapoda and the Chilopoda. Even in the Collembola tracheae have been lost and then been regained in the

Symphyopleona with a pair of stigmata in the neck region. Similar forms of branched tubular tracheae have been acquired several times convergently not only in the Antennata (= Tracheata), but in the Arachnida as well (Ripper, 1931).

As a result of the foregoing discussion, a phylogenetic tree of the chilopods is proposed, which indicates the appearance of the different characters during evolution (fig. 6).

THE CHARACTERISTICS OF THE CHILOPOD ANCESTOR

If we review all the probably original characters which could have made up the aspect of the common ancestor of all chilopods, we come to the conclusion that this ancestor must have looked very much like a *Scutigera*. Its head was dome-shaped, not flattened; it had compound

eyes with ommatidia, which were probably more similar to an insect ommatidium than in recent scutigerids; organs of Tömösváry were present; the antennae had two differentiated basal articles and a flagellum with four articles, but were not as annulated as in recent species. The second maxillae had independent coxae. The poison-claws, which were rather leg-like and could be moved in all directions had free coxae as well. The tergites were heteronomous, with an alternation of short and long ones, except the 8th and 9th, which were both long. There were 15 pairs of walking legs in the adult, the tarsi most certainly without annulation. The females had gonopods which held the singly laid eggs after deposition. The males had two pairs of gonopods. The juveniles hatched with four pairs of walking legs and developed by hemianamorphosis.

Fused maxillary nephridia were present, the sacculus most certainly had a wide lumen and not a compact meshwork as in *Scutigera*. The blood vascular system was complex, with an elaborate system of arteries and with "aortic arches" to a supraneural artery. The blood was aerated by localized, short tracheae only reaching into the pericardial sinus.

In contrast to this, the annulation of the tarsi and the antennal flagellum, the extreme heterotergy with only one tergal plate covering trunk segments 7-9, the maxillary organ, the compact sacculus, and the fused bases of the female gonopods are regarded as derived characters of the recent Scutigeromorpha.

It is highly improbable that a species having retained all original characters and thus resembling in all its features the ancestor of a whole group has survived in competition with its sister-groups. It is much more likely that every recent species represents a mosaic of original and derived characters. By focusing on the probabilities of certain characters being derived or original, we find a species with more ancestral characters which therefore most closely resembles the ancestor. If the result is surprising, at least we have displayed the logical steps which must be refuted if an alternative hypothesis is to be proposed.

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