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A NEW CLASSIFICATION OF CHELICERATA

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With 1 text-figure and 3 tables

Progress in classification of Chelicerata has been thwarted especially by two factors, viz., the concept of mites as one monophyletic group, and the opinion that this group consists of species with a highly modified plan of construction and without any trace of true segmentation.

The only characters which are generally shared by all groups of mites refer to the presence of a gnathosoma (i.e. the cone-shaped, movable structure comprizing the mouthparts), and the occurrence of a larva with only three pairs of legs (the last-mentioned character is also found in Ricinulei).

A comparative morphological study of the gnathosoma (Van der Hammen, 1970b, 1972) has, however, demonstrated that two fundamentally different types can be distinguished, which must be the result of parallel evolution. Two groups of mites (Actinotrichida and Anactinotrichida) are now distinguished, each characterized by a great number of special characters, for instance, with reference to chaetotaxy, sternal structure, leg segmentation, respiratory organs, etc. (Van der Hammen, 1972: 275-277). In each of the two groups, very primitive, segmented representatives are known (Van der Hammen, 1966, 1969, 1970a), some of which can be characterized as living fossils and which are very important for our knowledge of primitive Chelicerata.

The two groups of mites differ in their affinities with other groups of Chelicerata. Because of this, a revaluation of chelicerate affinities, and a new study of phylogeny and classification were indispensable.

It might be useful to recall in this connection that, according to recent investigations by Mrs. Manton (1972, 1973) and Anderson (1973), Arthropods do not constitute a monophyletic group. On the contrary, at least three phyla should now be distinguished, viz., Crustacea, Chelicerata and

Uniramia (comprising Onychophora, Myriapoda and Insecta). Arthropoda must now be regarded as a grade of advancement which has been reached independently by Chelicerata, Crustacea and Uniramia (Manton, 1972: 381).

The phylum Chelicerata has arisen from an unknown phylum of marine animals. Just as in the phylum Crustacea, locomotory organs certainly arose in the sea, especially as an adaptation to walking and creeping on the bottom, and burrowing. In this respect they differ from the phylum Uniramia in which the evolution of locomotory organs has certainly been terrestrial.

Just as modern Xiphosura, the marine ancestors of Chelicerata were certainly characterized by internal digestion, and by the absence of stigmata and tracheae. Fertilization must have been external, sperm being transported by the water.

We now know that terrestrial life was not yet possible before the Silurian period. Indeed, marine Merostomata only are known from the Cambrium, whilst terrestrial Chelicerata (i.e. Scorpions) first occurred in the Silurian period. The first terrestrial Chelicerata have certainly been members of the soil fauna.

Adaptation of Chelicerata to terrestrial life included the evolution of external digestion, the evolution of stigmata and tracheae, and the evolution of sperm transfer. The great variety of respiratory organs suggests that in many groups the respiratory system arose independently from that in other groups.

Many groups of modern Chelicerata certainly arose from ancestral marine groups which were already separated by distinct gaps. Adaptation to terrestrial life must have evolved from earlier adaptations to special types of marine life. For this reason a study of chelicerate affinities should start with those structures which arose in the marine period as adaptations to various ways of marine life. The best instance of these structures is constituted by the walking legs.

1. The jointed legs

Chelicerate legs consist of segments separated by various types of joints. Just as in Uniramia, these segmented legs probably arose (by partial thickening of the cuticle and the evolution of joints) from muscular-walled structures of which the rigidity was controlled by hydrostatic pressure working against the tension of muscles (Manton, 1973).

It is generally assumed that all chelicerate legs can be derived from one primitive type of leg with some seven segments. A set of seven terms is indeed sufficient as base of a general terminology, but it is doubtful whether this terminology is based on homology.

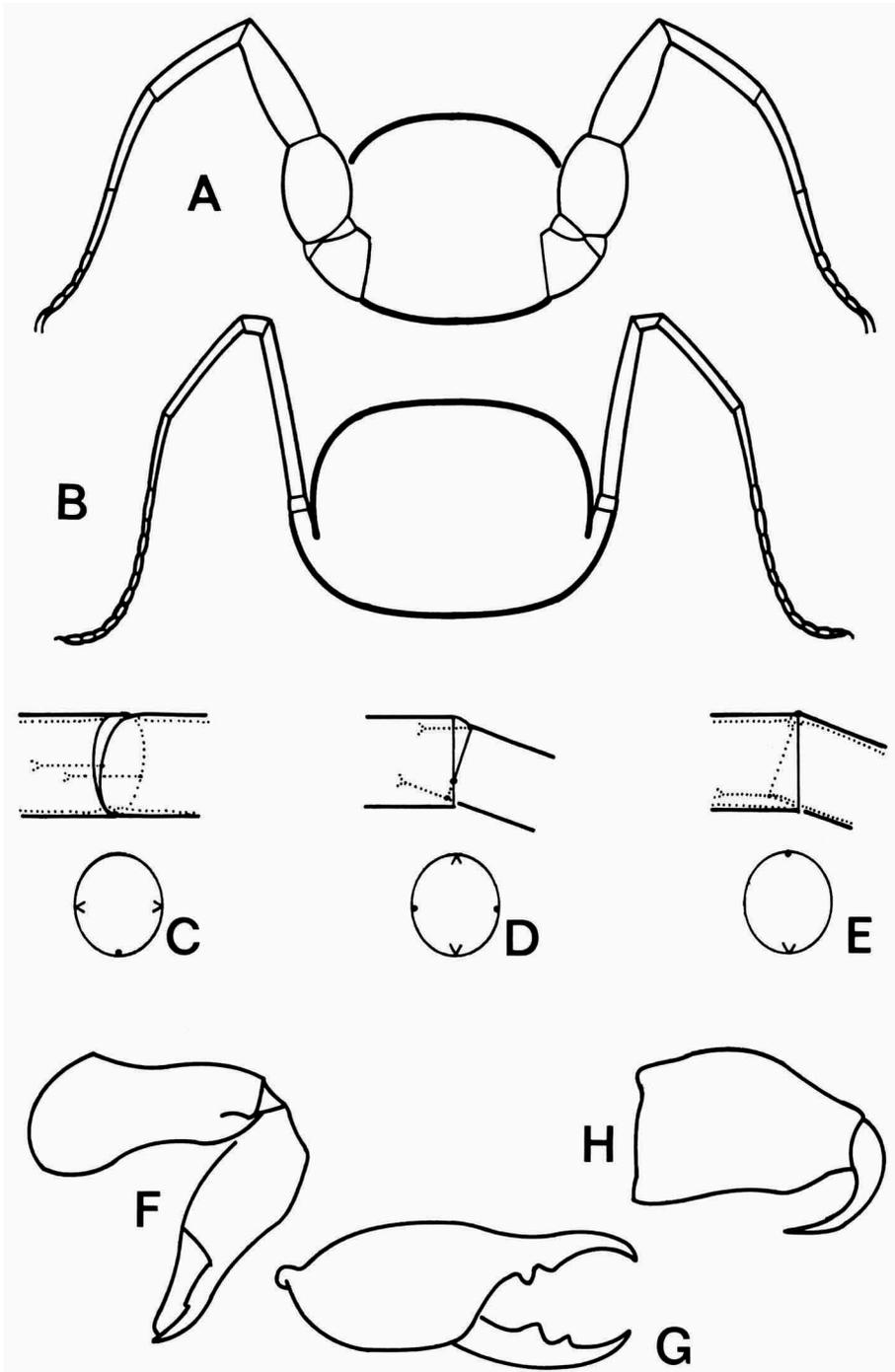


Fig. 1. Schematic representation of chelicerate appendages and joints. A, B, transverse piece of body bearing one pair of walking-legs; A, with knee-joint; B, with knee-segment. C-E, types of joints (in the schematic section, a dot represents the articulation, a v-shaped symbol represents the insertion of muscles or tendons); C, rocking joint; D, pivot joint; E, hinge joint. F-H, three types of chelicerae; F, prehensile type; G, raptorial type; H, pocket-knife type.

A comparative study of the position of the legs, the stance, in various groups of Chelicerata demonstrates some fundamental necessities. Because Chelicerata hang down from their legs (fig. 1A, B), the basal part of the leg must rise rather steeply, whilst the terminal part must go down.

Another fundamental necessity is, of course, constituted by the adaptation to stepping movements.

Generally, three types of eudesmatic joints (i.e. joints with one or more tendons attached at the base of the distal segment) are present in the chelicerate leg: pivot joints, hinge joints and rocking joints (fig. 1C-E). Besides, a number of adesmatic joints (i.e. joints without tendon attachments at the base of the distal segment) can also be present.

The distribution of these types of joints in the individual legs of various groups of Chelicerata presents a degree of diversity not found in other Arthropod groups. A general survey of this diversity is represented in table 1. In this table, the terminology of the segments is based on topographical and functional criteria.

A close examination of this diversity enables us to distinguish the following seven types of chelicerate legs, which are apparently not reducible to a general primitive type of leg. In the course of evolution these types probably arose independently of each other.

(1) The first type, present in Palpigradi and Actinotrichid mites is characterized by the absence of a coxa and (in primitive species) the presence of two femora. In these two groups the sternal region still presents the original segmented structure.

(2) The second type, present in Anactinotrichid mites and Ricinulei, is (in primitive species) characterized by the presence of two trochanters in legs III and IV.

(3) In Opilionida a third type of leg is found, characterized by the presence of rocking joints between trochanter and femur, and between patella and tibia.

(4) A fourth type, present in Solifugae and Pseudoscorpions is characterized by the absence of a patella, and by the presence of two femora. Solifugae present, moreover, a second trochanter which is absent in Pseudoscorpions.

(5) A fifth type is characterized by the presence of a specialized rocking joint between patella and tibia, and a specialized rocking joint (with an intercalary sclerite) between coxa and trochanter. It is found in Schizomids, Uropygi, Amblypygi and Spiders.

(6) In Xiphosura a sixth type is found. In this group a rocking joint is

Table 1	BD/CX	CX/TR (GB/TR)	TR.1/TR.2	TR/F	F.1/F.2	F/PA	PA/TI (F.2/TI)	T1/TA	TA/AP
Palpigradi									
Actinotrichida									
Anactinotrichida									
Ricinulei									
Opiliona									
Solifugae									
Pseudoscorpionida									
Schizonida									
Uropygi									
Amblypygi									
Araneida									
Xiphosura									
Scorpionida									

Table 1. Schematic representation of the joints on the chelicerate legs. Each joint is viewed distally, with the anterior face on the right. Fixed (or nearly fixed) coxae are represented by their ventral outline. The symbols are those used in fig. 1C-E (dots represent articulations, v-shaped symbols represent muscle- and tendon-insertions). The representation is provisional and simplified; generally, adesmatic segments (especially those of the tarsus) are not included. Compartments of the scheme presenting important characters are shown by a heavy black border. The continuation of the inferior tendon t_1 of the apotele in the tibia, has not been drawn. The coxa/trochanter joint of Schizonida, Uropygi, Amblypygi and Spiders presents a sclerite, represented here by a short line passing a dot. The joint between patella and tibia in Amblypygi, permits very little movement. The schematic representation is prepared after the following material: *Eukoenia mirabilis* (Grassi) (Palpigradi); *Alycus roseus* C. L. Koch (Actinotrichida) (based on Van der Hammen, 1969); *Opilioacarus texanus* (Chamberlin & Mulaik) (Anactinotrichida) (based on Van der Hammen, 1966); *Ricinoides* spec. (Gaboon) (Ricinulei); *Siro rubens* Latreille (Opiliona); *Galeodes* spec. (Turkey) (Solifugae); *Chthonius* (*Chthonius*) *tenuis* L. Koch (Pseudoscorpionida); unidentified Schizonida, Uropygi and Amblypygi (Surinam); *Tegenaria atrica* C. L. Koch (Araneida); *Limulus polyphemus* (L.) (Xiphosura); *Euscorpium flavicaudes* (De Geer) (Scorpionida) (based on Couzijn, 1976). Abbreviations: AP, apotele; BD, body; CX, coxa; F, femur; F. 1, femur 1; F. 2, femur 2; PA, patella (genu); TA, tarsus; TI, tibia; TR, trochanter; TR. 1, trochanter 1; TR. 2, trochanter 2. (The table is based on right leg IV).

present between coxa and body, just as in Spiders. The type is especially characterized by the absence of the characteristics of the other types.

(7) In Scorpions a seventh type is found, especially characterized by the presence of a pivot joint between patella and tibia.

The evolution of the coxa in the chelicerate leg constitutes an important problem recently dealt with in a separate paper (Van der Hammen, 1977).

2. Embryological data

A detailed comparative study of the embryonic development of Chelicerata was recently published by Anderson (1973). According to him, the Xiphosura retain the most generalized pattern of embryonic development among modern Chelicerata, whilst the pattern of embryonic development in Scorpions is the nearest approximate of the pattern in Xiphosura. The base of the derived pattern of other Chelicerata could lie in that of the Xiphosura, but not in that of the Scorpions. Among these Arachnids, Opilionida and Mites present the more generalized pattern, Spiders, Uropygi, Amblypygi, Solifugae and Pseudoscorpions more modified patterns with forwardly flexed opisthosoma.

There are, however, many important gaps in our knowledge of the embryonic development of Chelicerata. The embryonic development is, for instance, not yet studied in Palpigradi, primitive Actinotrichid mites, Opilioacarids and Holothyrids (i.e. primitive Anactinotrichid mites), Ricinulei and Schizomids.

3. Mouthparts and ingestion

The marine ancestors of modern Chelicerata were certainly characterized by internal digestion, and the possession of organs for seizing food and for manducation. Terrestrial feeding-habits certainly arose from earlier marine habits.

Ingestion of solid food and internal digestion are still found in Xiphosura, in many Actinotrichid mites, and also in some Anactinotrichid mites (e.g. Opilioacarids). In the case of mites, it probably concerns an ancestral condition. As far as known, external digestion is now found in most other groups of Chelicerata.

The feeding organs now include the chelicerae, the palps and often one or more pairs of endites of the prosomatic appendages.

In some groups, such as Palpigradi, Opilioacarids and Opilionida, the chelicerae present a large trochanter, and have a distinct prehensile function (fig. 1F).

In other groups, such as Spiders and Amblypygi, the chelicerae resemble a pocket-knife, lack the trochanter, and are especially adapted to holding and kneading (fig. 1H). Transitions between the prehensile and the "pocket-knife" type are also found (e.g. the "raptorial" type of Solifugae) (fig. 1G). The prehensile type possibly represents the ancestral condition.

The original function of the palp probably was ambulatory, as still found in Xiphosura and Palpigradi. In many groups of Mites the palp has become an appendage with sensory function, a "feeler". In most groups of Chelicerata the palp has developed a more or less pronounced prehensile function; in several groups distinct chelae are present and in this case the palp can have taken over the original function of the chelicera.

Endites of the appendages can also form part of the feeding organs: e.g. in prosomatic appendages 2-6 in Xiphosura. In Scorpions and Opilionida several appendages present endites participating in feeding. In many groups of Chelicerata endites of the palps form part of the feeding organs.

A very successful evolution is constituted by the development of the so-called gnathosoma in mites. As mentioned above, a gnathosoma is found in both groups of mites and certainly is the result of parallel evolution. The gnathosoma has enabled mites to develop a great variety of feeding habits, ranging from external to internal digestion, from grinding to sucking, from carnivorous to herbivorous habits, and including ecto- and endoparasitism. In this way both groups of mites present a greater variety in feeding habits than in all the remaining Chelicerata together.

4. Respiratory organs

Among the adaptations to terrestrial life, the development of respiratory organs has been of particular importance. Part of the marine ancestors were probably characterized by the possession of gills. In other marine groups the (soft) cuticle was probably associated with the exchange of oxygen and carbon dioxide.

Gills are still found in Xiphosura. In this group the opisthosomatic appendages of segments IX-XIII are carrying the gills.

Some groups of terrestrial Chelicerata and also the immature forms of some other groups, are apparently characterized by respiration through the cuticle. This is the case in Palpigradi, several groups of Actinotrichid mites and the immature forms of several other groups of Actinotrichid mites.

In several groups of terrestrial Chelicerata respiratory organs are found which are apparently homologous with opisthosomatic appendages. This condition is found in: Scorpions (in segments X-XIII); Spiders, Amblypygi, Uropygi, Schizomids and Pseudoscorpions (in segments IX and X; in

Schizomids in IX only). Part of the respiratory organs of Solifugae are possibly also homologous with opisthosomatic appendages (viz., those in segments IX, X, and sometimes XI).

In other cases the morphological interpretation of the respiratory organs is more complicated. Solifugae have also ventral prosomatic respiratory organs, of which the stigma is situated behind coxa II. Ricinulei possess a pair of prosomatic stigmata above coxa IV. Opilionida possess a pair of ventral stigmata behind coxa IV.

The respiratory organs of Anactinotrichid mites can theoretically be derived from the series of opisthosomatic respiratory organs with laterodorsal stigmata in Opilioacarids, with the exception of the respiratory organs of Ixodid ticks, which could be homologous with a pair of opisthosomatic appendages (other hypotheses, however, are also possible).

In Actinotrichid mites there are many types of respiratory organs starting from various parts of body and appendages. In some isolated cases genital tracheae are present.

The great variety of respiratory organs in Chelicerata points to an independent origin in several groups. It appears that in Actinotrichid mites respiratory organs even arose independently in the main groups. There could, on the contrary, be closer affinities between a number of groups with respiratory organs homologous with opisthosomatic appendages. In view of this, a general survey of structures homologous with opisthosomatic appendages in various groups of Chelicerata is perhaps interesting. For this reason our present knowledge on the subject is represented in table 2.

5. Sperm transfer

One of the important problems during the transition from aquatic to terrestrial life was constituted by sperm transfer. Fertilization had certainly been external in the ancestors of modern Chelicerata (as it is still external in Xiphosura). Just as in other primitive terrestrial Arthropods, the transition to terrestrial life involved the transfer of sperm cells in spermatophores, the first stage of internal fertilization (cf. Schaller, 1965, 1971). In many cases this type of indirect sperm transfer involves courtship behaviour.

Generally, the formation of spermatophores is restricted to members of the fauna of the soil and similar biotopes. The evolution of other ways of internal fertilization opened up new possibilities, and demonstrates again the great diversity among terrestrial Chelicerata.

Nearly direct sperm transfer with gonopods is found in three groups. In Solifugae and some groups of Anactinotrichid mites, the chelicera is functioning as a gonopod; in Spiders the palp; and in Ricinulei leg III. There is

a gradual transition from the transfer of spermatophores by the appendages to the transition of a sperm drop by a gonopod.

Direct sperm transfer through copulation is found in Opilionida and some groups of Actinotrichid mites, although in some of these mites the receptaculum seminis or bursa copulatrix can have a separate opening.

Table 2	Opisthosomatic segments:												
	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX
Palpigradi		●	●	●	●	●							
Actinotrichida		●	●	●									
Anactinotrichida		●											
Ricinulei													
Opilionida													
Solifugae		●	⊙	⊙	⊙								
Pseudoscorpionida			○	○									
Schizomida			○										
Uropygi			○	○									
Amblypygi			○	○									
Araneida			○	○	●	●							
Xiphosura	●	●	*	*	*	*	*						
Scorpionida		●	●	○	○	○	○						

● = homologues of opisthosomatic appendages.

⊙ = homologues of opisthosomatic appendages with endites and exites.

○ = respiratory organs homologous with opisthosomatic appendages.

* = opisthosomatic appendages carrying gills.

Table 2. Homologues of opisthosomatic appendages in Chelicerata. (In the case of Actinotrichida, the table is based on Endeostigmata and Oribatida; in the case of Anactinotrichida the table is based on Opilioacarida).

6. Evolution and diversity

Some groups of Chelicerata are characterized by a marked degree of variation in body form, by the adaptation to various types of environments, and by a striking numerousness. Other groups of Chelicerata present less diversity and are mainly restricted to the soil fauna.

Among the very successful groups mention must be made of Spiders, both groups of Mites, and Opilionida. The development of a gnathosoma (in Mites), and the development of direct or nearly direct sperm transfer are closely associated with this successful evolution. Numerous representatives of the four groups have left the soil fauna and have colonized many new niches.

Spiders have certainly reached the highest stage of development, partly because of visual faculties and spinning behaviour. Actinotrichid mites undoubtedly present the greatest diversity.

7. Classification

Until recently Chelicerata have been subdivided into two groups: Merostomata and Arachnidea. A summary of the present views on chelicerate affinities results in a new classification in which Chelicerata are subdivided into seven groups (table 3). The following concise diagnoses of these groups (classes) can be given.

(1) Epimerata class. nov. No coxae. Legs originally with two femora. Although the tarsus can present adesmatic segments, no separate basitarsus can be distinguished. Sternal region with epimera. Supracoxal setae often present. Ambulacra originally with a central claw (or empodium) homonomous with the lateral claws. Respiration originally through the cuticle. Ingestion of solid food and internal digestion is found in many Actinotrichid mites and could be present in Palpigradi. (Palpigradi, Actinotrichida).

(2) Cryptognomae class. nov. Legs III and IV originally with two trochanters (in Anactinotrichid mites trochanter 2 is present in tritonymphs and adults of Opilioacarids only). Larva with three pairs of legs; leg IV vestigial in the larva of Opilioacarida and Ricinulei. Tarsus I often with sunken sensory organs. Segment III originally presenting a pair of sternapophyses. Chelicerae often with a ventral oncophysis. Mucronate setae present in Ricinulei and Opilioacarids. (Anactinotrichida, Ricinulei).

(3) Opilionidea nom. transl. Legs with rocking joints between trochanter and femur, and between patella and tibia. Direct sperm transfer by copulation. Chelicerae (and sometimes also the palps) belonging to the prehensile type. (Opilionida).

(4) Apatellata class. nov. Legs without patella. Chelicerae of raptorial

Table 3. Classification of Chelicerata	
1. Epimerata	Palpigradi Actinotrichida
2. Cryptognomae	Anactinotrichida Ricinulei ?Architarbi
3. Opilionea	Opilionida
4. Apatellata	Solifugae ?Kustarachnae Pseudoscorpionida
5. Arachnidea	Schizomida Uropygi Amblypygi Araneida Trigonotarbi
?	Haptopoda Anthracomarti
6. Merostomata	Xiphosura Eurypterida
7. Scorpionidea	Scorpionida

Table 3. Classification of Chelicerata.

type. Respiratory organs probably partly homologous with opisthosomatic appendages. (Solifugae, Pseudoscorpionida).

(5) Arachnidea nom. transl. Legs with a specialized rocking joint between patella and tibia. Chelicerae of pocket-knife type. Respiratory organs homologous with opisthosomatic appendages. Pseudonychial claw often present (not homonomous with the lateral claws). (Schizomida, Uropygi, Amblypygi, Araneida).

(6) Merostomata. Segments IX-XIII with gills carried by opisthosomatic appendages. External fertilization. Internal digestion. Generalized pattern of embryonic development. (Xiphosura, Eurypterida).

(7) Scorpionidea nom. transl. Legs with pivot joint between patella and tibia. Pattern of embryonic development the nearest approximate of the pattern in Xiphosura, but different from other groups of Chelicerata. (Scorpionida).

Probably these diagnoses can be extended by detailed comparative studies. A series of standard descriptions should preferably be prepared, just as these now exist in acarology (Van der Hammen, 1961, 1964, 1966, 1969,

1970). Terminology should preferably be based on the standardized terminology defined in the Glossary of acarological terminology (van der Hammen, 1976).

The present classification should be regarded as a model containing our general knowledge on the groups, together with a number of hypotheses. The model should now be tested against new observational data.

Extinct groups (cf. Petrunkevitch, 1955) add little to this new classification because the joints of the legs cannot be studied in detail. It seems that Architarbi should be classified with Cryptognomae, because in Opiliotarbiidae legs III and IV present 2 trochanters. Trigonotarbi certainly belong to Arachnidea s. str. Haptopoda and Anthracomarti present prehensile chelicerae; they are perhaps related to Arachnidea s. str. (because of the respiratory organs) or to Merostomata (because of the sternal structure); probably, they constitute a separate, extinct group. Kustarachnae are probably related to Apatellata (all legs with two trochanters, eyes as in Solifugae). All extinct groups now known are highly developed and specialised when compared with such primitive living groups as Palpigradi, primitive Actinotrichid mites and Opilioacarids.

8. Transition from aquatic to terrestrial life

The biology of modern terrestrial Chelicerata is a transformation and an adaptation of earlier marine ways of life. Practically nothing is known about these marine ancestors, but some hypotheses could be formulated, starting from living species.

Some species of both groups of Epimerata appear to belong to the interstitial fauna, viz., representatives of the genus *Leptokoenenia* (cf. Monniot, 1966) and the family Nematalycidae (cf. Coineau, Fize & Delamare Deboutteville, 1967). Palpigradi have, moreover, also been found in the sea (in sand not far from the coast). Monniot (1966) considered this an argument in favour of the marine origin of Palpigradi. Many Epimerata belong to the soil fauna; several primitive representatives of the group are found in the deeper layers of the soil. The evolution of Epimerata could have passed from species living in the ocean-floor, by way of members of the interstitial fauna, to terrestrial soil-animals.

The biology of modern Xiphosura suggests that the ancestors of several other groups of Chelicerata lived near the coast in shallow water, walking on the bottom, burrowing, and temporarily leaving the water. This could, for instance, have been the biology of the ancestors of modern Scorpions and Arachnidea s. str.

Studies in the functional morphology of Chelicerata, especially of walking-legs and feeding organs could perhaps yield further indications.

One of the most important problems concerns the relation between biology and plan of construction, considered in historical perspective, i.e. the recognition of several plans of construction ranked in a hierarchy. The fascinating study of this problem is still in its initial stage.

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