THE EVOLUTION OF THE COXA IN MITES AND OTHER GROUPS OF CHELICERATA

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The evolution of the coxa constitutes one of the fundamental problems in arachnology. It is generally assumed that a coxa is present in all Chelicerata, and that in many groups it has lost its movability, extended in ventro-sagittal direction, and fused with the ventral wall of the body.

GRANDJEAN (1934 : 504) criticized this opinion. According to him there is no evidence that, in the course of evolution, the Oribatid epimeres (the ventral sclerites of the podosoma) developed from free coxae. In a subsequent paper (GRANDJEAN, 1936 : 414) he further developed this view ; in his opinion, the reverse hypothesis (i.e. the secondary character of the free coxae) was even more probable. He repeated his view in later papers (e.g. GRANDJEAN, 1952 : 561), and it is now generally accepted (at least by Oribatologists) that the trochanter is the first segment of the Actinotrichid appendages.

Until recently, the Actinotrichida constituted the only group of which the absence of a coxa was known with certainty. In a paper on the mouthparts of Palpigradi (cf. VAN DER HAMMEN, 1969*a*) I demonstrated that the first segment of the Palpigradid chelicera and palp is a trochanter. Although I discovered at the same time that the first segment of the Palpigradid legs represents also a trochanter, this discovery was not yet published. I now return to this problem, and the present paper especially deals with the segmentation of the Palpigradid legs, in comparison with Actinotrichida and other Chelicerata.

Terminology, abbreviations, and methods used here are defined and explained in the Glossary of Acarological Terminology, of which the second volume is now in press (VAN DER HAMMEN, 1976). The classification of mites referred to in the present paper was recently treated by me in detail (VAN DER HAMMEN, 1972). I am very grateful to Dr. Y. COINEAU who, on my request, sent me the material of *Eukoenenia mirabilis* (Grassi).

THE SEGMENTATION OF THE PALPIGRADID APPENDAGES

The homology of the segments of the legs can be established by a study of their topography and of the types of articulation with adjacent segments. One of the most characteristic articulations of the Chelicerate leg is that between trochanter and femur ; it is bicondylar (with two condyles) and bidesmatic (with two tendons), presenting elevator and depressor muscles. A careful study of the Palpigradid appendages (fig. 1E-G) demonstrates that the first segment of all appendages is a trochanter ; its terminal articulation is bicondylar and bidesmatic.

The articulation between the second and third segment of the Palpigradid legs is incompletely developed. It is monocondylar, but an arthrodial membrane is not distinctly differentiated whilst a tendon of flexor muscles is apparently not present. The articulation reminds of the condition in several primitive Actinotrichid mites (fig. 2E) in which there are two femora. In some of these Actinotrichid species, the articulation is completely developed in all legs ; in other species, tendon and muscles of the articulation have disappeared, whilst in the majority of Actinotrichida an entire femur takes the place of the two femora. The presence of two femora appears to be an ancestral character of some Actinotrichida. Evidently segment 2 and 3 of the legs of *Eukoenenia mirabilis* are homologous with femur 1 and femur 2 of Actinotrichida. Considering the variability of the articulation between femur 1 and femur 2 in Actinotrichida, it will be interesting to study it also in different species of Palpigradida, and in the course of postembryonic ontogeny.

After a study of the articulations of all Palpigradid appendages I arrived at the following terminology of the segments. Chelicera : trochanter, body of chelicera, apotele. Palp : trochanter, femur, genu (patella), tibia, tarsus 1-5, apotele. Leg I : trochanter, femur 1, femur 2, genu (patella), tibia, tarsus 1-7, apotele. Legs II-III : trochanter, femur 1, femur 2, genu (patella), tibia, tarsus 1-2, apotele. Leg IV : trochanter, femur 1, femur 2, genu (patella), tibia, tarsus 1-3. apotele. (In fig. 1E I have represented two laterodorsal tendons tg_a and tti_a, at the base of genu and tibia respectively. These tendons should be subject of further studies. Because the articulations in question are monocondylar, the tendons can apparently cause lateral movements only).

The epimeric region

Just as in Actinotrichida the sclerites in the ventral region of the Palpigradid prosoma represent epimeres (fig. 1A). The epimeres of segments *II* and *III* (*ep.P* and *ep.1*) constitute one sclerite. Epimeres 2-4 constitute separate sclerites. Epimeric setae are present on epimere *P* and epimere *1* only.

Supracoxal setae

In my first study of *Eukoenemia mirabilis* (cf. fig. 2I) I pointed to the presence of laterocoxal setae in the regions of chelicera and palp (Van der Hammen, 1969 a) ; it was the first record of these setae outside mites. Laterocoxal (or preferably supracoxal) setae were discovered and named by Oudemans (1931 : 316) and especially studied by Grandjean (e.g. 1962 : 401-404).

Supracoxal setae (the term is based on an incorrect interpretation of the first segment of the Actinotrichid leg : this was named coxa instead of trochanter) are originally prosomatic setae, inserted dorsally or laterodorsally of the base of the trochanter. When a coxal region has developed around the base of the trochanter, the supracoxal seta is found there. In Actinotrichid mites supracoxal setae can be found in the regions of palp, leg I and leg II. The setae can be seti- or spiniform (fig. 2K) or present a different shape. In Actinotrichida a supracoxal seta can be replaced by two setae (fig. 2J, L). This number is also found in several Palpigradi (fig. 2H),

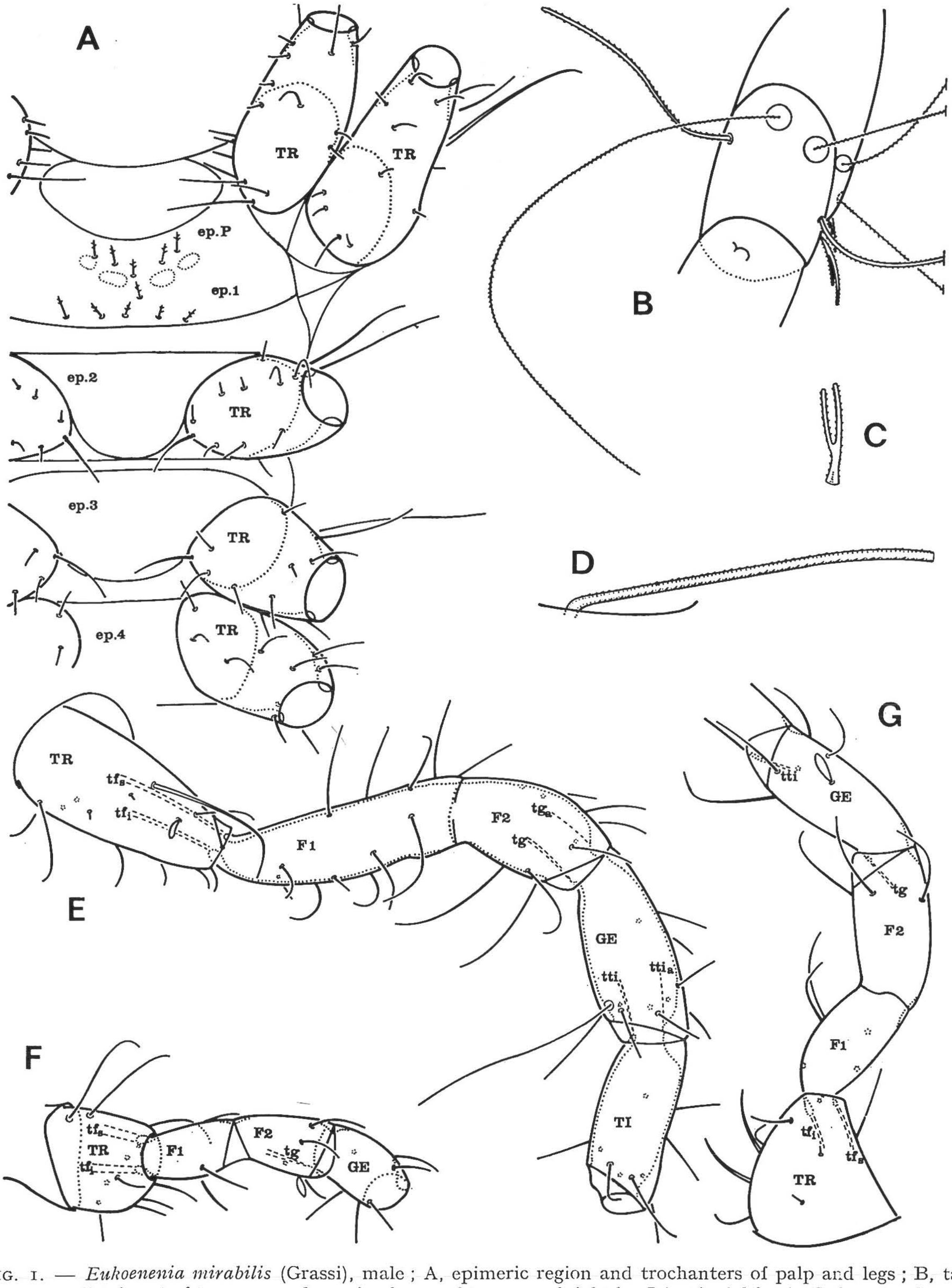

FIG. 1. — *Eukoenenia mirabilis* (Grassi), male ; A, epimeric region and trochanters of palp and legs ; B, tarsus 2, distal part of tarsus 1, and proximal part of tarsus 3 of right leg I (antiaxial face) ; C, furcate phanere of tarsus 7 of right leg I ; D, reclining phanere of tarsus 7 of right leg I ; E, posterior (antiaxial) face of part of right leg I ; F, posterior (antiaxial) face of right leg II ; G, anterior (antiaxial) face of right leg IV ; A, E-G, × 370 ; B, × 710 ; C, D, × 1 315.

although in some species there can be up to five seta (fig. 2F). In the case of the supracoxal setae *eC*, the setae represent a partly fused pair (fig. 2G). Consequently, supracoxal setae are recognizable, because of their position, and sometimes also because of their different shape.

GRANDJEAN (1936) homologized setae of free coxae I and II of *Opilioacarus segmentatus* With with supracoxal setae *eI* and *eII*. I found the same setae in another species of *Opilioacarus* (cf. VAN DER HAMMEN, 1966). In Opilioacarida supracoxal setae are apparently in regression ; they are reduced to their epiostracal layer, but are still distinctly mucronate (fig. 2B, C). Starting from the condition in Opilioacarida, I introduced the hypothesis that regressive supracoxal setae *e* and *eI* are present in some Gamasida (Anactinotrichida). Apparently the regression of supracoxal setae in Anactinotrichida is closely connected with the development of free coxae.

TROCHANTER 1 AND TROCHANTER 2

In Opilioacarida (the most primitive group of Anactinotrichida) legs III and IV present two trochanters (fig. 2D) ; a bicondylar, bidesmatic articulation is present between trochanter 1 and trochanter 2, and between trochanter 2 and femur (the femur is subdivided into a basifemur and a telofemur ; these adesmatic segments are incompletely separated by the basifemoral ring). Trochanter 2 is subject to regression ; its base level is tritonymphal. The presence of two trochanters is apparently an ancestral character, also mentioned for legs III and IV of Ricinulei and Solifugae. Trochanter 2 and femur 1 (although both incorporated in the femur in the course of evolution) are evidently heterologous structures because of their different types of articulation.

CONCLUSIONS

It is now evident that the absence of a coxa constitutes an ancestral character. Coxal evolution starts with the development of a coxal region, and the next stage is the development of free coxae and a sternum (fig. 2A). In many groups of Arachnidea the free coxae have extended in ventrosagittal direction, by which the greater part of the sternum has disappeared ; at the same time the extended coxae have more or less lost their movability.

Palpigradi and Actinotrichida are the only groups of Chelicerata in which coxae are not present. These groups are at the same time characterized by the presence of epimeres and prosomatic supracoxal setae. Palpigradi and Actinotrichida constitute also the only groups in which at least some species present two femora (of about equal length). Other characters found in both groups include the presence of an empodium (homologous with a central claw). It will be very important to make a careful comparative study of phanerotaxy in both groups. The tarsus of Palpigradi presents interesting bifurcate phaneres (fig. 1C), probably hollow at the base, which could be homologous with the famulus of Actinotrichida. It will also be interesting to compare the reclining phaneres (fig. 1D) of Palpigradi with solenidia ; these are hollow, but present four ciliate ribs (unknown from Actinotrichida). The Palpigradid legs present also several trichobothria (fig. 1B).

Summarizing our present knowledge of affinities in Chelicerata, we can now introduce the following hypothetical classification :

1. Merostomata.

2. Scorpionidea. According to ANDERSON (1973) the pattern of postembryonic development in Scorpions is the nearest approximate of the pattern in Xiphosura. The base of the deri-

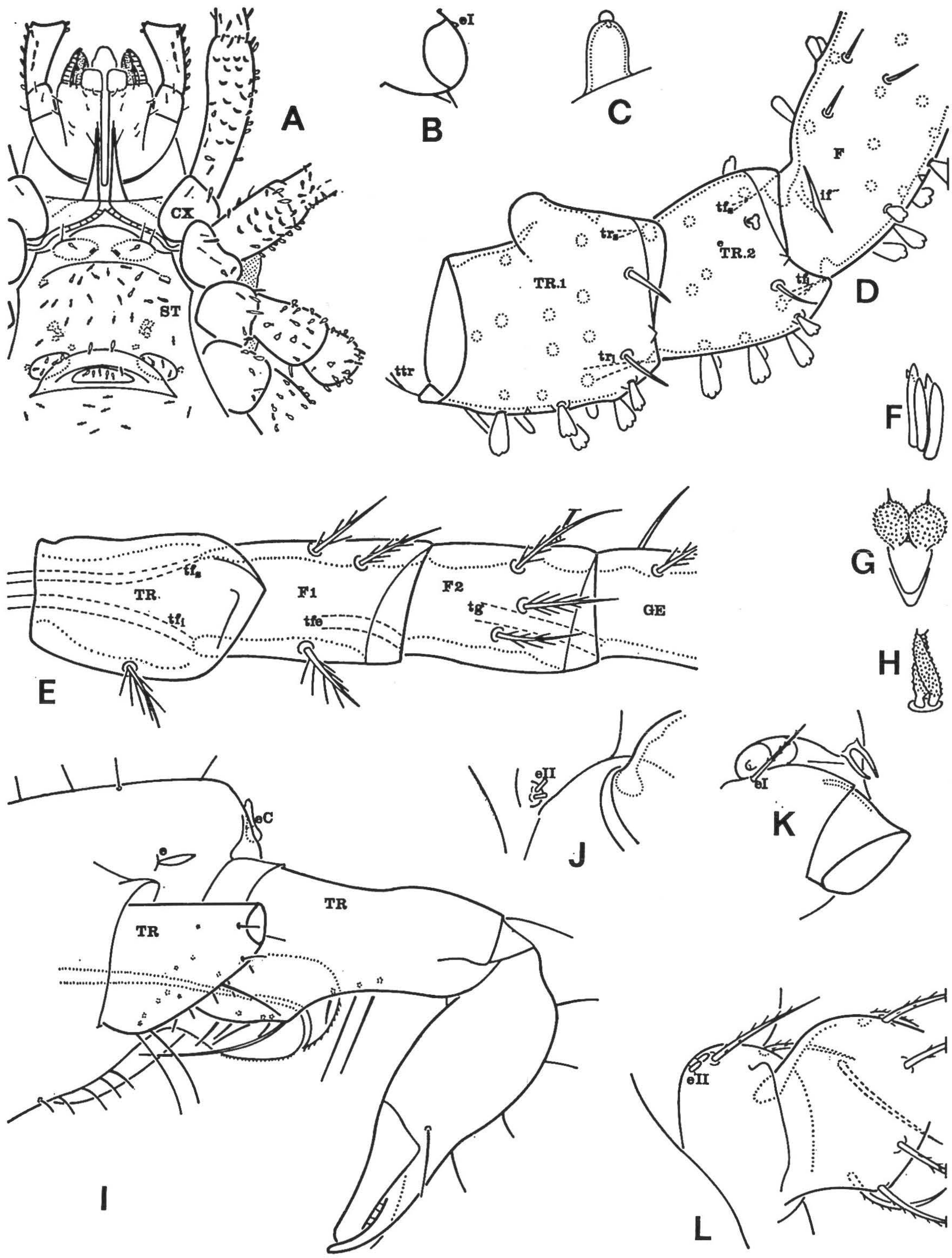

FIG. 2. — A-D, *Opilioacarus texanus* (Chamberlin & Mulaik) (after van der Hammen, 1966) ; A, ventral view of part of female, with sternum and coxae ; B, lateral view of right coxa I, with supracoxal seta *eI* ; C, supracoxal seta *eII* ; D, lateral (paraxial) view of trochanter 1, trochanter 2, and basal part of femur of right leg III of tritonymph ; E, *Alycus roseus* C. L. Koch, lateral (antiaxial) view of trochanter, femur 1, femur 2 and proximal part of genu of left leg IV (after VAN DER HAMMEN, 1969) ; F, *Eukoenenia pyrenaica* (Hansen), supracoxal setae *e* (after HANSEN, 1926) ; G, H, *Leptokoenenia scurra* Monniot (after MONNIOT, 1966) ; G, supracoxal setae *eC* ; H, supracoxal setae *e* ; I, *Eukoenenia mirabilis* (Grassi), lateral view of anterior region of prosoma with mouthparts and supracoxal setae *eC* and *e* (after VAN DER HAMMEN, 1969a) ; J, *Oecosmaris callitricha* Grandjean, supracoxal setae *eII* of larva (redrawn from GRANDJEAN, 1947) ; K, *Fusacarus* spec., lateral view of base of leg I of protonymph, with supracoxal seta *eI* (redrawn from GRANDJEAN, 1953) ; L, *Balaustium florale* Grandjean, coxal region and trochanter of right leg II of deutonymph, with supracoxal setae *eII*, obliquely from above (redrawn from GRANDJEAN, 1959) ; A, B, × 115 ; C, × 1315 ; D, × 370 ; E, × 710 ; F, × 366 ; G, H, much enlarged ; I, × 370 ; J, × 653 ; K, × 950 ; L, × 180.

ved pattern of other Arachnidea could lie in that of the Xiphosura, but not in that of the Scorpions. These data, together with morphological characters (such as the presence of a metasoma), justify the separation of the Scorpionidea from the Arachnidea.

3. Arachnidea s. str. In this class the following groups can provisionally be distinguished (because of lack of space, arguments will be given in a separate paper) : *a*) Anactinotrichida, Ricinulei and Opilionida ; *b*) Schizomida, Uropygi, Solifugae and Pseudoscorpionida ; *c*) Amblypygi and Araneida.

4. Chelicerata Acoxata, comprising Palpigradi and Actinotrichida. Some species of both groups are known as members of the interstitial fauna ; they have been found in soil water (*Leptokoenenia scurra* Monniot ; Nematalycidae). Palpigradi have, moreover, also been found in litoral soil-water. MONNIOT (1966) considered this an argument in favour of the marine origin of Palpigradi. Many Palpigradi and Actinotrichida are members of the soil fauna ; several primitive members of these groups have been found in the deeper layers. The evolution of Palpigradi and Actinotrichida could have passed from marine animals living in the ocean-floor, by way of members of the interstitial fauna, to terrestrial soil animals. In this connection it is interesting to mention SCHALLER's comparative study of mating behaviour in lower terrestrial Arthropods (SCHALLER, 1965) ; he characterized the simple depositing of spermatophores on the substrate (as found in many Actinotrichida) as the most primitive way of sperm transference, and the first stage in the transition from aquatic to terrestrial life.

ALPHABETIC LIST OF NOTATIONS (ABBREVIATIONS) USED IN FIGS. 1-2.

CX, coxa.
e, supracoxal seta of palp.
eC, supracoxal setae of chelicerae.
ep.P, epimere of segment II (segment of palp).
ep. 1-4, epimeres of segments III-VI (segments of legs I-IV).
eI, supracoxal seta of leg I.
eII, supracoxal setae of leg II.
F, femur.
F1, femur 1.
F2, femur 2.
GE, genu (patella).
if", posterior lyrifissure of basifemoral ring.
ST, sternum.
tf_i, inferior tendon of femur.
tf_s, superior tendon of femur.
tfe, tendon of femur 2.
tg, tendon of flexor muscles of genu (patella).
tg_a, laterodorsal tendon of genu (patella).
TI, tibia.
tr_i, inferior tendon of trochanter 2.
tr_s, superior tendon of trochanter 2.
TR, trochanter.
TR.1, trochanter 1.
TR.2, trochanter 2.
tti, tendon of flexor muscles of tibia.
tti_a, laterodorsal tendon of tibia.
ttr, tendon of trochanter (or trochanter 1).

SUMMARY

1. In the present paper it is demonstrated that Actinotrichid mites and Palpigradi are the only Chelicerata in which coxae are absent. Species of these groups present moreover epimeres, prosomatic supracoxal setae, and (primitively) two femora. Both groups are classified here as Chelicerata Acoxata.

2. The evolution of the coxa apparently started with the development of a coxal region. In many groups of Arachnidea the free coxae have extended in ventro-sagittal direction, and secondarily lost their movability.

3. Four groups of Chelicerata are now distinguished : Merostomata, Scorpionidea, Arachnidea s. str., and Chelicerata Acoxata. Two trochanters appear to be present in species of three groups of Arachnidea ; the presence of a second trochanter is considered here an ancestral character.

4. The evolution of the Chelicerata Acoxata could have passed from animals living in the ocean floor, by way of interstitial animals, to terrestrial soil animals.

Résumé

1. Dans le présent travail on a montré que les Acariens Actinotriches et les Palpigrades constituent les seuls groupes de Chélicérates dans lesquels il n'y a pas de coxae. Les espèces de ces groupes présentent en outre, des épimères, des poils supracoxaux prosomatiques, et (primitivement) deux fémurs. On a réuni les deux groupes dans la classe des Chelicerata Acoxata.

2. L'évolution du coxa a apparemment commencé par le développement d'une région coxale. Chez beaucoup d'Arachnides les coxae libres se sont étendus en direction ventro-sagittale, et ont perdu secondairement leur mobilité.

3. Dans le présent travail on distingue quatre groupes de Chélicérates : Merostomata, Scorpionidea, Arachnidea s. str., et Chelicerata Acoxata. Chez trois groupes d'Arachnides on trouve deux trochanters ; on considère cela comme un caractère ancestral.

4. L'évolution des Chelicerata Acoxata pourrait s'être déroulée à partir d'animaux vivant dans le fond de la mer, en passant par des animaux interstitiels, pour aboutir aux animaux terrestres du sol.

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Postcript

The present paper was finished in March 1976. In the meantime my classification of Chelicerata has been further developed in the following publication :

HAMMEN (L. van der), 1977. — A new classification of Chelicerata. — Zool. Meded. Leiden, **51** : 307-319, fig. 1, tab. 1-3.

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