Arthropods from the Lower Devonian (Lower Emsian) of Alken an der Mosel, Germany.

Part 1:
Arachnida.

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With 5 plates and 8 text-figures.

Abstract.

A rich fauna of chelicerates from the Lower Devonian (late Lower Emsian) has been collected by Mr. Josef Hefter, Koblenz. The arachnids described in the present paper include a scorpion *Waeringoscorpio hefteri* n. g. et n. sp. representing a new family, *Alkenia mirabilis* n. g. et n. sp. of the order Trigonotarbida, and *Archaeomartus levis* n. g. et n. sp., and *Archaeomartus tuberculatus* n. sp. which probably belong to the same order. The scorpion displays very primitive structures in the development of the coxo-sternal region, and paired filamentous structures probably represent branchial organs signifying an aquatic mode of life. The morphology of the other arachnids indicates that they were terrestrial arachnids, the oldest ones hitherto known.

Übersicht.

Aus einer reichen Cheliceraten-Fauna der unter-devonischen Nellenköpfchen-Schichten (spätes Unter-Emsium) des Steinbruchs im Alkener Bach-Tal bei Alken an der Mosel, gesammelt von Josef Hefter (Koblenz), werden in vorliegender Arbeit die Arachniden dargestellt. Sie umfassen einen Skorpion aus der neuen Familie Waeringoscorpionidae, *Waeringoscorpio hefteri* n. g. et n. sp., und einen Vertreter der Ordnung Trigonotarbida, *Alkenia mirabilis* n. g. et n. sp., außerdem die wahrscheinlich ebenfalls zu den Trigonotarbida gehörigen *Archaeomartus levis* n. g. et n. sp. und *Archaeomartus tuberculatus* n. sp. — Der Skorpion zeigt im Bau des coxo-sternalen Bereiches sehr altertümliche Züge; paarige, filamentöse Strukturen dürften als Kiemen-Organe zu deuten sein und weisen auf eine aquatische Lebensweise von *Waeringoscorpio* hin. Die übrigen Arachniden von Alken hatten nach Ausweis ihres Körperbaus eine terrestrische Lebensweise.

Introduction.

In 1956 Mr. Josef Hefter (Koblenz) kindly asked me to determine a collection of Lower Devonian (late Lower Emsian) eurypterids collected by him in the Nellenköpf-chen-Schichten exposed in a quarry in the Alkener Bach-Tal near the village of Alken at the Mosel river. I was pleased to be invited to describe this material, particularly

because eurypterids of that age are not too common. During the following years and up to the present Mr. HEFTER has made very valuable additional collections which he generously has offered me to describe. A preliminary description of the fossil occurrence has been given by FAHLBUSCH (1966: 166) and quite recently SOLLE (1970) has completed a more detailed study of the quarry in the "Alkener Bach-Tal".

The fossils which are preserved in a dark, sometimes black shale, may be considerably compressed and distorted. However, many fine details may be preserved which are not seen in fossil specimens from arenaceous sediments. Besides many arthropods belonging to the Subphylum Chelicerata, the fossils include numerous plants (see: KRÄUSEL & WEYLAND 1962; SCHAARSCHMIDT 1970), one ostracoderm, particular brachiopods such as "Lingula", and a few gastropods, pelecypods, and tentaculitids (FAHLBUSCH 1966: 166). Only one chelicerate (a scorpion erroneously interpreted as an eurypterid) has been described STØRMER (1960). The scorpion was found by HEFTER in 1956. It occurred together with fragments of Pteraspis (Rhinopteraspis) dunensis (FERD. ROEMER). Meanwhile a considerable number of eurypterids have been described from the Lower Devonian in the Rhine area, particularly from Willwerath and Overath (65 km N. of Koblenz) by JAEKEL (1914), GROSS (1933), STØRMER (1934, 1936, 1969a).

General description of the arachnids.

Arachnids are extremely scarce in the large arthropod material from Alken. Only one scorpion and five specimens of other arachnids have been recorded. All non-scorpionid specimens represent the dorsal surface of the animals; the ventral structures are unknown. Like other fossil arthropods from the dark shale of Alken, the arachnids are difficult to photograph. The best results are obtained when the specimen is embedded in alcohol or some other liquid. In order to get good contrasts the light should be either at low angle from "NW", or at highest possible angle. In the latter case the specimen should be slightly tilted so that light is reflected from the shining surface of the specimen into the camera (pls. 1-2, pl. 3 fig. 1, pl. 4 fig. 1). One has to bear in mind that impressions of structures not having the reflecting skin or shell preserved, do not show up in the photograph.

The scorpion from Alken.

Family **Waeringoscorpionidae** n. fam.

Type genus: *Waeringoscorpio* n. g.

Diagnosis: Small Scorpionida with the coxae of all four pairs of walking legs adjoining a large pear shaped sternum.

Taxonomic relations.

PETRUNKEVITCH's major division of the scorpions into two suborders, based on the presence or absence of the first (pregenital) segment, is based on erroneous

observations and cannot be maintained (KJELLESVIG-WAERING 1969). However, his stressing of the importance of the development of the coxo-sternal region (PETRUNKEVITCH 1952, 1955) is supported by present finds (see below). The primitive structures in *Waeringoscorpio*, not observed in any other known genera, justify the establishment of a new family. It might be mentioned that WILLS (1959: 266) is not much in favour of a taxonomy based on the coxo-sternal features which are seldom seen and can rarely be related to dorsal features. It is to be hoped, however, that future finds will extend our knowledge to a degree that will prove the coxo-sternal features useful in the taxonomy of Paleozoic scorpions.

Waeringoscorpio n. g.

Type species: *Waeringoscorpio hefteri* n. sp.

Derivation of name: Named after ERIK KJELLESVIG-WAERING.

Diagnosis: Waeringoscorpionids with long and slender postabdomen (tail); dorsal side of prosoma and preabdomen little known; chelicers powerful; pedipalps with slender hand and fingers, inner edges cultrate; walking legs scorpionid, rather long; labrum (?) directly in front of sternum; opercular plates ovate, combs relatively small with 20-25 (?) teeth, median appendage present; ventral abdominal plates moderately lobostern (?), ovate filamentous areas probably attached to ventral plates; postabdomen with long segments, each with close set longitudinal ridges; telson triangular in outline.

Waeringoscorpio hefteri n. sp.
Pl. 1, pl. 2, pl. 5 figs. 7-8; text-figs 1-2, 5a-a', 6a.

1960 scorpion-like eurypterid ? gen. et spec. indet. — STØRMER, a scorpion-like eurypterid from the Lower Devonian of Germany: text-fig. 1.

Derivation of name: Named after JOSEF HEFTER (Koblenz).
Holotype: The specimen figured on pl. 1, pl. 2, pl. 5 figs. 7-8, and in text-figs. 1-2, SMF VIII 31, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main. Only specimen known. — Type horizon: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten. — Type locality: Quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Diagnosis: The same as for the genus.

General description.

Since the preliminary description (STØRMER 1960) the specimen has been subject to further cleaning. The two pedipalps have been uncovered and more details have been obtained regarding the other appendages and the filamentous structures. The holotype shows the ventral surface and certain imprints of the dorsal surface. The preabdominal segments are somewhat telescoped but otherwise the different parts have maintained their original position. The specimen is preserved in a dark fine-grained shale which permitted the preservation of minute morphological details. The body is flattened but a slight relief is yet preserved. The distal portions of the pedipalps are preserved at a lower level than the rest of the scorpion, and as mentioned below the presumed gill tracts are also preserved at different levels. Because of the compression of the specimen the portions of the tergites are visible on the ventral surface.

The p r o s o m a l d o r s a l s h i e l d is not exposed but since there is little variation in the outline of the prosoma in other Paleozoic scorpions, there is reason to believe the prosoma of the present form also was more or less subquadrate in outline.

5 mm
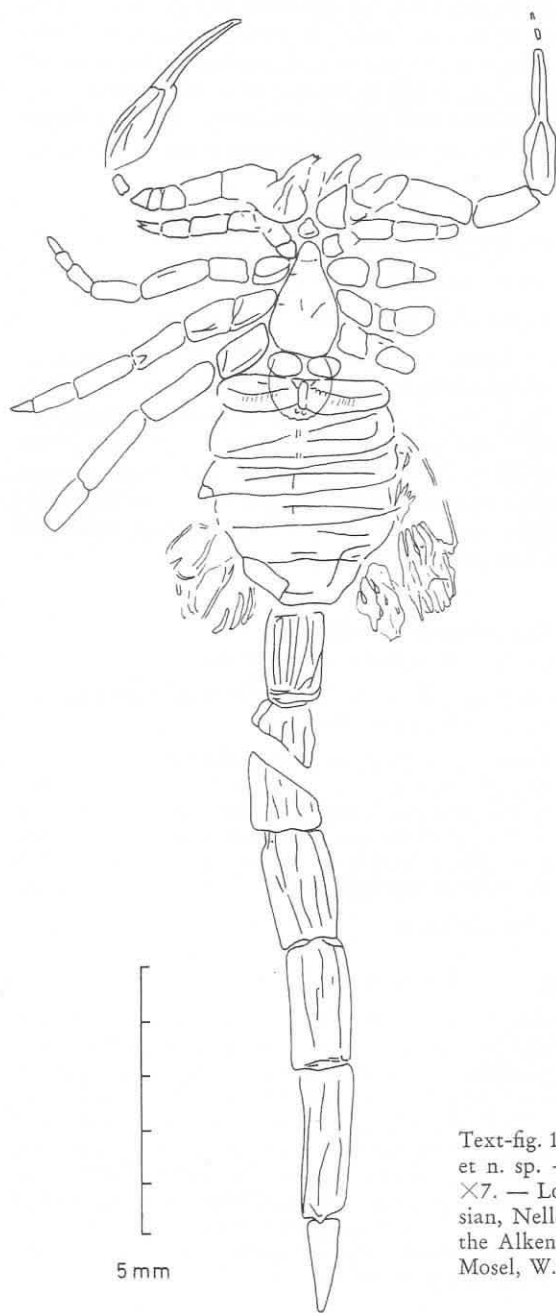
Text-fig. 1. *Waeringoscorpio hefteri* n. g. et n. sp. — H o l o t y p e, SMF VIII 31; ×7. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Ventral structures of the prosoma.

Labrum:

A small subtriangular mound in front of the large sternum has a length and width of 0·4 mm. Just in front of the slightly convex posterior margin a faint transverse furrow is present (text-fig. 3b). The structures resemble those in the Palpigrada (text-fig. 3a) where an anterior mound represents both the upper lip or labrum, and the lower lip or labium. The mouth is represented by a transverse slit between the two. In the Araneida a similar mouth between the labrum and labium is present (text-fig. 3c). The labium which forms the floor in the mouth is formed by the anterior portion of the prosomal sternites, in the Palpigrada possibly by the first sternite, in the Araneida by the second or third.

The correspondence in structure in *Waeringoscorpio* and the Recent Palpigrada and Araneida indicates that *the anterior subtriangular mound with the transverse furrow represents the labrum, mouth, and labium.*

Sternum:

The large median plate behind the labrum evidently represents the sternum (or fused prosomal sterna). The prominent plate is narrow, pear-shaped with a well rounded anterior portion and the gently curved posterior margin partly broken off. The plate has a length of 2·2 mm, and greatest width of 1·3 mm. The lateral margins of the sternum show only very slight emarginations where the coxae of the walking legs abut to it. However, the lateral margins seem to be independent of the coxal margins, not continuing around the coxae. Moreover the surface of the sternum, at least in the posterior part, seems to a lie at a lower (more ventral) level than the proximal portions of adjoining coxae. This gives the impression that the sternum forms a separate plate independent of the coxal bases. The ventral surface of the sternum is smooth except for a few very faint crossing furrows. One transverse furrow separates an anterior narrow portion from the rest of the sternum. Other faint furrows extending inwards from the lateral margins might suggest a further transverse division of the sternum. These structures are, however, too indistinct to be interpreted as true division lines between trito-, tetra- and pentasterna such as in the Palpigrada (text-fig. 3a), Architarbida (PETRUNKEVITCH 1955: text-fig. 58/4b) or in the broad sternum of the Amblypygii (KÄSTNER 1932: text-fig. 2). The development and nature of the prosomal sternum is discussed below (p. 344).

Chelicera (I):

The structures of the most anterior portions of the specimen are difficult to interprete. The chelicera are evidently partly covered (in ventral view) by the coxae of the pedipalps. The portions preserved in front represent the segment with the fixed finger. A denticular margin is indicated, a common structure also found in Recent species.

Pedipalps (II):

These appendages have been exposed during a recent cleaning of the specimen. Both appendages are preserved in a position characteristic of scorpions in general. The coxae are short with a rounded median margin resembling the coxae of the walking legs. In Recent scorpions the coxae of the pedipalps are directed forward, forming the lateral walls of the preoral chamber. In *Waeringoscorpio* on the other hand, the coxae have an anteriolateral direction like the coxae of the first walking legs. The exact outline of the pedipalp coxa is not exposed, but the length may be a little less than the width at the distal border. The trochanter has twice the length of the coxa, and the width seems slightly smaller. The left trochanter has a crossing furrow like in some Recent forms (e. g., *Scorpio maurus*, MILLOT & VACHON 1949: text-fig. 158). The nearly rectangular prefemur has a length a little more than twice the width, whereas the femur has a length twice the width and has a moderately curved outer margin. The chela or hand, formed by the tibia and tarsus, is slender with a curved outer margin; the surface

has striae more or less parallel to the margins. The right pedipalp has a well preserved, slightly curved finger. A narrow ridge or carina runs along the concave margin indicating that this is the biting margin such as in Silurian forms, which also are cultrate and without denticles. Although the basal point-line is not well demonstrated, the finger evidently represents the movable one or posttarsus. The left appendage also has a curved finger, but in this case the ridge, a little broader than on the right appendage, runs along the convex margin suggesting that this finger represents the fixed one.

Walking legs (III-VI):

The first pair of walking legs (III) is not well preserved. The coxae of which only the convex median portions are preserved, abut the lateral margins of the narrow anterior portion of the sternum. This, evidently primitive feature, is unknown in other scorpions. The coxae have an anteriolateral, whereas the more distal joints have a transverse direction.

The second pair of walking legs (IV) is better preserved. The coxae, transversally directed, have a rounded outline and a more straight distal margin. A furrow running parallel to the posterior margin may correspond to the furrow marking the internal ridge in the coxae of Recent scorpions (KÄSTNER 1940: text-figs. 94, 127, 128). The trochanter is shorter than the prefemur which has a length three times the width. The femur marking the bend of the appendage, is shorter than the prefemur. The tibia and basitarsus are indicated, but the joint-lines are not distinct. The posttarsus is not preserved.

The third pair of walking legs (V) is similar to the second one, but the coxae have a more rhombic outline. A furrow along the posterior margin may correspond to the one on the coxae of the first walking legs. The separate joints of the legs are not well distinguished. The femur seems to be relatively longer than in the first legs.

The fourth pair of walking legs (VI) has long joints but the size relations between the joints are largely the same as in the other legs. The hind legs have a postlateral direction. The coxae have a rhombic outline with a furrow parallel to the posterior margin. Only four segments of the posterior legs are preserved.

The four pair of walking legs are slender and increase in size backwards. They resemble the legs of Carboniferous and Recent scorpions, but are more primitive particularly in lacking maxillary lobes. The Silurian *Palaeophonus* (THORELL & LINDSTRÖM 1885) has more stout and short legs, but the legs of *Proscorpius* and *Archaeophonus* (KJELLESVIG-WAERING 1966), also of Silurian age, have similar long and slender legs. *Proscorpius* differs by probably having a double trochanter on the last walking legs (KJELLESVIG-WAERING 1966: 373).

Operculum:

These plates are not visible when the specimen is embedded in alcohol (pls. 1-2). The reason is that the reflecting integument is not preserved. The dry specimen, on the other hand, shows the impressions of two opercular plates just behind the posterior border of the sternum (pl. 5 fig. 7). The plates (text-fig. 2) measuring 5·0 mm in length and 0·6 mm in width, have an ovate, nearly circular outline. In the specimen the plates are well separated, but in life they were probably more closely together such as in other scorpions with similar opercular plates (comp. PETRUNKEVICH 1955: text-fig. 40).

Pectines or combs:

These structures are but slightly indicated in the specimens. Just behind the opercular plates a pair of elongate transverse lobes is suggested. On the right side the lobe has traces of filaments with a width of 0·08 mm. At their base a row of fulcra is indicated. The filaments or teeth have a posteriolateral direction as shown in text-fig. 2. Since striae of about the same direction, probably of tectonic origin, occur on the abdomen, I have been in doubt whether or not the observed teeth are genuine or of tectonic

origin. However, a minute study of the structures indicates that traces of true teeth are present. Judging from the density of teeth and the probable length of the comb margin, the number of teeth may have been from 20-25.

Traces of a median appendage or lobe with small triangular areas on either side in front may belong to the comb segment (IX). The appendage (right margin distinct, left one faintly marked) has a length of 0·4 mm and a width of 0·15 mm. The median
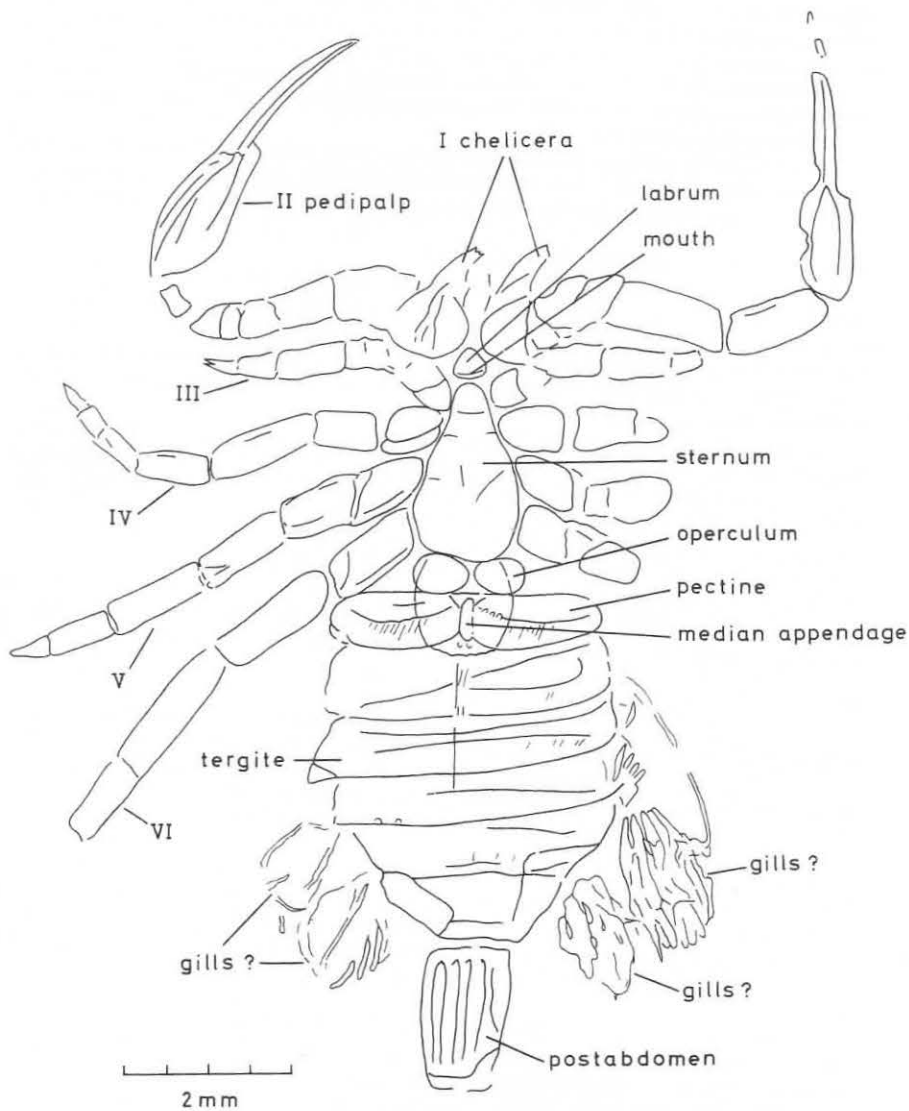
Text-fig. 2. *Waeringoscorpio hefteri* n. g. et n. sp. — Holotype, details of anterior portion; SMF VIII 31; ×5·5. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

appendage or lobe is reminiscent of the structure in *Gigantoscorpio* (STØRMER 1963: text-figs. 19, 40) and in *Cyclophthalmus* (?) (NOVOJILOV & STØRMNER 1963: pl. 1).

On either side of the median lobe, and posterior to the combs are two transverse flat lobes which may represent the first plate-shaped abdominal appendages. However, the structures are not quite clear. The median appendage seems to belong to the same segment as the transverse lobes and in that case the lobes would belong to the comb-segment (modified precoxae or coxae). The lobes are of the lobostern type. Curiously enough the structures are not unlike the operculum (VIII) of the Carboniferous *Mazoniscorpio mazonensis* (WILLS 1960: 298, text-fig. 13). It is not impossible that the development of the comb-segment might have had structures in common with the primitive operculum in *Mazoniscorpio*.

In the posterior emargination between the two lobes parts of a plate with a convex posterior border are exposed. From the lateral points of the plate a faint curved line runs forward to the opercular plates bordering an ovate area around the median appendage.

Ventral plates of abdomen (X-XIII):

The overlapping ventral plates in Paleozoic scorpions are evidently homologous with the plate-shaped abdominal appendages in *Limulus* and eurypterids (comp. PoCOCK 1911: 15, WILLS 1925: 94-96, 1959: 277, and STØRMER 1963: 110). As mentioned above the lateral lobes above and behind the combs may represent the first pair (X) of ventral plates. In that case the well rounded posteriolateral corners indicate that the plates are lobostern, at least to a certain extent.

Further back the structures are difficult to interprete in details. Transverse lines seem to mark the posterior margins of the dorsal tergites. The coarser chitinous and to some extent granulated plates hardly represent the ventral plates which are generally relatively thin and smooth. Probably the lateral lobes of the ventral plates were pressed into the concave ventral side of the tergites. The posterior margins of the ventral plates are not distinct, nor are the outlines of the tergites well demonstrated. Of the seven tergites present in the preabdomen of the scorpion the fourth one apparently had a trapezoid outline with acute posteriolateral corners. In the sixth and seventh tergites the lateral margins converge backwards toward the narrow tail or postabdomen.

Branchial organs:

Of particular interest, and unique among all known fossil scorpions are the filamentous structures present on both sides of the posterior portion of the preabdomen. These structures were mentioned in my preliminary description of the specimen (STØRMER 1960) and were than interpreted as possible parasitic fungi developed during the decay of the animal. Meanwhile new preparations and a minute study of the structures have led to another interpretation.

The filaments are preserved in a similar way on both sides of the preabdomen. It is important to notice that the four clusters are mutually rather alike in outline, and that they form two pairs of filamentous areas on either sides of the body. Remains of a third pair is indicated on the left side of the scorpion. The two pairs of filamentous areas have their antemedian portion in the direction of the two last plate-shaped ventral appendages.

The best preserved area of filaments is found on the left side of the specimen (right side in ventral view). It has a subovate outline measuring 1·8 mm in length and about 1 mm in width. In the antemedian portion five filaments (or ridges in an area) converge toward the abdomen. In the middle of the ovate area separate filaments cannot be well distinguished, a certain anastomosing of ribbons is suggest, but in the postlateral portion the single filaments or ribs are again visible. The structures are best studied in reflected light when the specimen is embedded in alcohol (pl. 2).

In each of the two clusters of filaments, the filaments or ribs appear to be preserved at one level, and this level is different in the two subsequent areas. If the filaments are

remains of fungi or algae one would not expect them to be restricted to certain definite levels. The preservation rather suggests the filaments or ribs belong strictly to the ovate areas or tracts.

Of the two areas mentioned the posterior one is less well preserved, but resembles the one in front of it, and was probably a little smaller. In front of the two areas, scattered filamentous structures, probably belonging to a third area are preserved.

On the right side (left in pl. 2 and text-fig. 2) of the abdomen the two succeeding areas are less well preserved, but they seem to correspond in size and position to the two posterior ones on the left side.

Because of their symmetric position, ovate outline, and preservation at distinct levels, the filamentous areas or tracts probably belong to the scorpion itself rather than representing fungi or algae. As discussed below the structures observed may be interpreted as branchiae or gills, or rather dislocated gill-tracts normally situated above the ventral plates of the abdomen. Similar structures are described in *Eurypterus* by HOLM (1898) and WILLS (1965).

Postabdomen:

The long and slender tail has the usual five segments and a telson spine. The separate segments were evidently cylindrical provided with distinct longitudinal ridges and furrows. The distance between the close set ridges is 0·3-0·4 mm. The dimensions (in mm) of the five postabdominal segments are:

	1	2	3	4	5	telson
length	1·4	2·1	2·1	2·3	2·6	1·9
width	1·3	1·1	1·1	1·0	0·9	

The complete length of the postabdomen is 12·5 mm. The original length of the body is difficult to determine because of the telescoping of the preabdominal segments. KJEL-LESVIG-WAERING has pointed out to me that the long fifth segment of the tail may indicate that the scorpion represents a male. In dorsal view the telson has a lanceolate triangular outline.

Taxonomic relations.

Only ten specimens of Silurian and early Devonian scorpions are known up to present time (KJELLESVIG-WAERING 1966: 361). As pointed out by several authors the classification and taxonomic relation of the rare fossil scorpions are hampered by the fact that one species is known from the dorsal side only, while another is known from the ventral. Rarely it has been possible to refer both sides to one and the same species.

As pointed out above the present species deviates from all previously described by the large prosomal sternum to which all four pairs of walking legs abut. This is evidently a major taxonomic feature which justifies the establishment of a new family as mentioned above. The closest relative of *Waeringoscorpio* is apparently the Silurian *Proscorpius osborni* (WHITFIELD 1885) recently redescribed by KJELLESVIG-WAERING (1966: text-figs. 16-17). The general features including the walking legs and the ribbed postabdominal segments are similar. *Proscorpius* also has a large prosomal sternum but still smaller than in the present species. *Palaeoscorpius devonicus* (LEHMANN 1944) and *Archaeophonus* (KJELLESVIG-WAERING 1966: 373) are practically unknown as far as the ventral side is concerned; the legs, however, differ from those in the present species. In the former genus the legs are rather stout, more like in *Palaeophonus* (THORELL & LINDSTRÖM 1885; PETRUNKEVITCH 1953); in the latter they are long and slender but diviate from our species by probably having a double trochanter.

The development of the prosomal sternum in scorpions.

In Recent scorpions the morphology of the prosomal sternum is one of the main characters used in scorpionid taxonomy. In living species, and even in forms as far back as in the Carboniferous, the sternum forms but a small plate behind the maxillary lobes of the second pair of walking legs, and in front of the operculum. PETRUNKEVITCH (1952) has rightly stressed the phylogenetic importance of the coxo-sternal region in Palaeozoic scorpions. A trend of development is suggested by "the disappearance of a portion of the sternum and the shifting into the vacated place of 1 or 2 pairs of coxae".

This assumed trend of development was demonstrated by him in various Carboniferous genera of scorpions. *Archaeoctonus* represents the most primitive features by having a large sternum and indications of only one pair of auxillary lobes in front (comp. text-fig. 5c). More recently KJELLESVIG-WAERING (1966) has described a slightly more primitive stage in the Silurian *Proscorpius* (text-fig. 5b). Here the sternum reaches a little further forward, and the coxae in front have no forward extending maxillary lobes. *Waeringoscorpio*, although it is younger than *Proscorpius*, presents a stage which is even more primitive. In this genus the sternum is still larger reaching forward between the coxae of the first walking legs, more or less to the mouth (text-fig. 5a).

The recent find thus confirms and illustrates the assumed trend of development in the sternum of scorpions: A large elongate sternum reaching forward to the mouth becomes gradually reduced in front where one or two pairs of coxae take over the vacated place.

The prosomal sternum in scorpions is generally regarded as a true sternum or a composite structure including sterna of several segments. However, MILLOT & VACHON (1949: 390) are inclined to interpret the prosomal sternum in Recent scorpions as a fused pair of modified appendages of the seventh or pregenital segment, homologous to the chilaria in *Limulus*. Since the metastoma in eurypterids also are regarded as homologous with the xiphosuran chilaria, it would mean that the sternum of the scorpions is homologous with the metastoma in eurypterids.

KJELLESVIG-WAERING (1966: 367, text-fig. 17; text-fig. 5b of the present paper) points out that the large sternum of Silurian *Proscorpius osborni* is reminiscent of the metastoma in eurypterids. This is even more so the case in *Waeringoscorpio hefteri*. The size and position of the sternum, as well as its appearance as a separate plate might favour the assumption of a homology. However, in contrast to the scorpionid sternum the eurypterid metastoma has a distinct marginal doublure (comp. HOLM 1898: pl. 1 fig. 5) which allows the plate to cover (in ventral view) a major portion of the large coxae of the hind legs. In *Waeringoscorpio* and in *Proscorpius* the sternum does not cover parts of the coxae.

The embryology of scorpions shows that a pregenital or seventh segment was present in certain embryological stages, and then was quite reduced. The same was the case with the buds of appendages belonging to the same segment. The preabdominal "sternites" which evidently are modified appendages (comp. STØRMER 1963: 110) left their "fingerprints" in the more advanced embryo in the form of broad plates (KÄSTNER 1940: text-fig. 182,

after BRAUER). If the scorpionid sternum (so prominent in early forms), should be interpreted as modified appendages one would expect the structures not to be completely reduced in late embryological stages.

If the sternum is interpreted as modified appendages the similar sternum in the Araneida, and the broad sternum in the Amblypygii have to be interpreted in the same way. This is unlikely since these sterna do not appear as a separate plate, and because the former has an anterior segment functioning as a labium and the latter has a sternum with transverse ridges suggesting separate segments (to some extent also suggested in *Waeringoscorpio*). Moreover a distinct segmentation of the sternum is demonstrated in the Recent Palpigrada and in the Carboniferous Architarbida.

The rather common development of the labrum, mouth, labium, and large composite sternum in the Palpigrada, Araneida, and *Waeringoscorpio* may give us a clue to the structures of the ancestral archaic arachnid [the primitive *Sternarthron* from the Jurassic (HAASE 1890) is not considered since the preservation may not be good enough for a detailed comparison]. The archaic arachnid may have had a well segmented prosoma with the six pairs of coxae forming two rows on either side of a segmented sternum, the first sternal segment forming the labium.
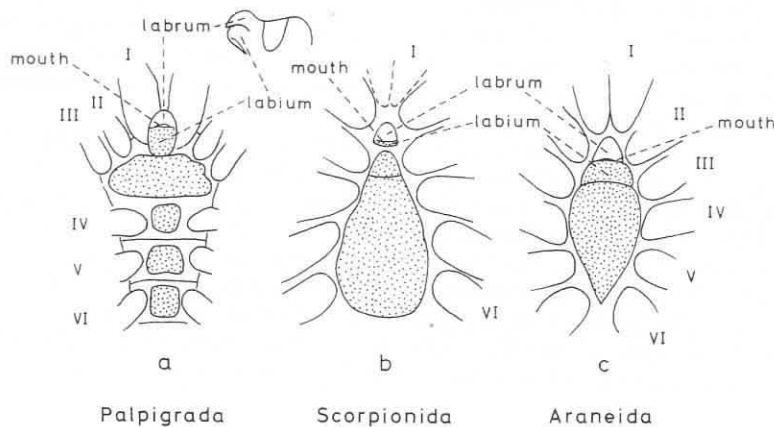
Text-fig. 3. Archaic arachnid structures demonstrated in the coxo-sternal region of three main groups of arachnids. Sternites dotted. Lateral view of mouth in Palpigrada shown above a-b. (3a after KÄSTNER 1932; 3b-c after PETRUNKEVITCH 1955.)

The development of the preoral chamber.

Text-fig. 4 illustrates two important stages in the embryology of arachnids. In the early germ band (4a) the segments which are mutually alike, enclose the globular yolk. At a later stage (4b) the germ band becomes straightened out and the area in front of the mouth is bent strongly upwards and slightly backwards. The chelicerae with their segment attain a dorsal position and the pedipalps and mouth become frontal. This is diagrammatically illustrated in text-figs. 5a'-d'.

In this development the arachnids deviate fundamentally from the mero-stomes including the xiphosurans and eurypterids. In these groups a bending of the anterior portion of the prosoma has not taken place, the chelicerae and pedi-palps remain on the ventral surface (text-figs. 5e-e′, f-f′). In *Limulus* in parti-cular the mouth has migrated somewhat backwards (or the anterior appendages correspondingly forward).

Since the characteristic arachnid position of the chelicerae and pedipalps apparently occurs already in Silurian scorpions (text-fig. 5b-b′) this important development must have taken place in very early Paleozoic time.

A special scorpionid morphological feature is the development of a preoral chamber or preoral cavity in the frontal portion of the prosoma. The chamber opens forward; the ceiling is formed by the chelicerae reaching forward, the floor by the maxillary lobes of the coxae of the two first pairs of walking legs, the back wall by the narrow labrum, the two lateral walls by the coxae of the pedi-palps. The mouth is situated near the floor at the base of the labrum. The struc-ture is shown diagrammatically in text-fig. 5d-d′. A preoral chamber was present already in Carboniferous scorpions as shown by the presence of maxillary lobes on the coxa in front of the sternum.

The present fossil material may to some extent elucidate the formation of a preoral chamber in the scorpions. One has to bear in mind that different evo-lutionary stages occur side by side and even more primitive forms may occur in beds younger than those with primitive forms.

In *Waeringoscorpio* (text-fig. 5a-a′) the sternum reaches far forward, no maxillary lobes are present, and the labrum suggests that the mouth had a ventral position. The chelicerae, the coxae of the pedipalps, and the labrum may have sheltered the mouth to some extent, but no chamber was evidently formed. In *Proscorpius* (text-fig. 5b-b′) the mouth was probably slightly more frontal, yet no maxillary lobes were developed. The coxae of the first walking legs united, taking over some of the protecting functions of the reducing sternum.

A first indication of maxillary lobes is found in *Archaeoctonus* (text-fig. 5c-c′)[1]. This suggests an initial stage in the formation of a preoral chamber. Later
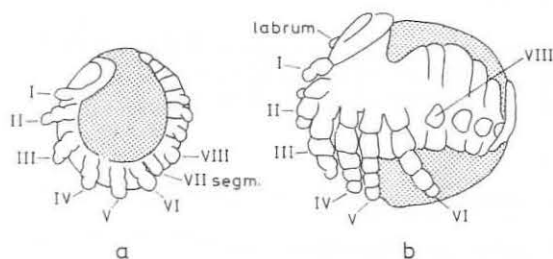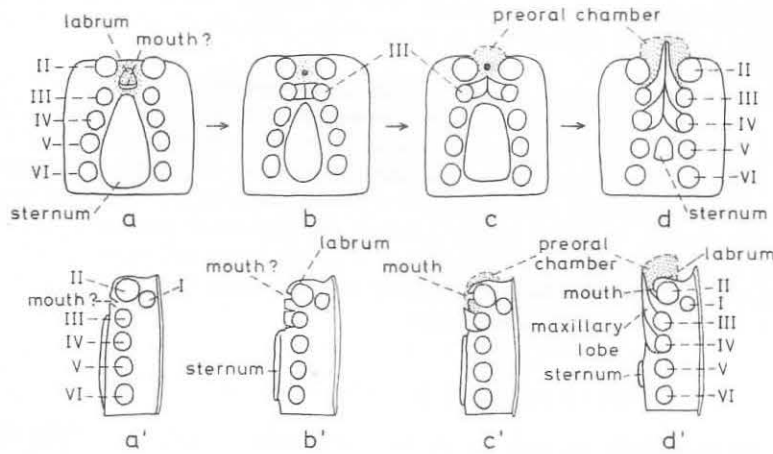

Text-fig. 4. Embryology of Araneida. (After KÄSTNER 1940a). — a) Early stage at which the embryo surrounds the yolk. — b) Later stage at which the anterior portion of the prosoma is bent upwards and backwards.
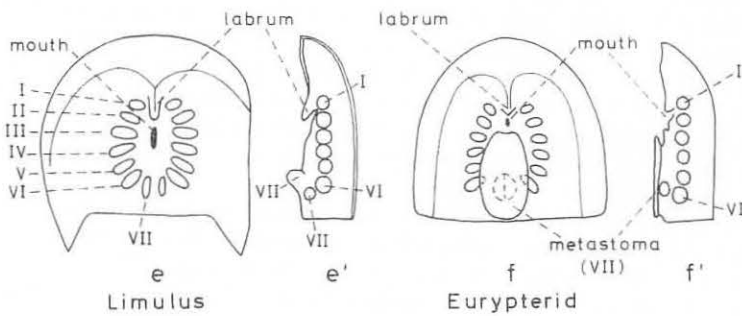
[1] Mr. KJELLESVIG-WAERING has now examined the type specimen, and informs me that the maxillary lobes are hardly present; only a curved anterior margin of the coxae is indicated.

on, distinct maxillary lobes develop on the coxae of both pairs of anterior walking legs and a complete chamber is eventually formed.

Characteristic of the scorpions is the external digestion of the prey. The prey is grasped by the pedipalps, if necessary stung and killed by the telson, and

Text-fig. 5. Diagrams of scorpions and merostomes, showing locations of prosomal appendages in relation to mouth and sternum. — a–f) Ventral views. — a'–f') Lateral views, partly as median sections.

a-a') *Waeringoscorpio*; Lower Devonian. c-c') *Archaeoctonus*; Carboniferous.
b-b') *Proscorpius*; Silurian. d-d') *Isobuthus*; Carboniferous.

The scorpions indicate a trend of development characterized by a gradual reduction of the prosomal sternum (or sternites), and the formation of maxillary lobes taking part in the formation of a preoral chamber.

e-e') *Limulus* (Xiphosuran). f-f') Eurypterid.

The xiphosurans and eurypterids differ from the arachnids by not having the upwards bend of the anterior portion of the prosoma, a bend causing a dorsal position of the chelicerae.

then mashed by the chelicers. Digestive enzymes are injected into the body of the prey, and when the soft parts of the prey have become fluid by the action of the enzymes, they are sucked in by the aid of the pharynx which serves as a pump.

There is reason to believe that the soft parts of a prey could more easily be made liquid in an aquatic environment, and the sucking process would also be easier. As a Recent example may be mentioned the sucking out of the soft parts of pelecypods by starfishes.

Since the early scorpions evidently lived in an aquatic environment an external consumption directly from the mouth would have been easy. In terrestrial scorpions on the other hand, the fluid parts of the prey would tend to dry up and the sucking would need some extra moisture to serve efficiently. This might be the main reason for the development of a preoral chamber in terrestrial forms. *When the aquatic scorpions of the Silurian and Devonian gradually became adapted to an amphibious, and further to a purely terrestrial mode of life, a preoral chamber probably had to be formed in order to keep sufficient moisture around the prey during its consumption.*

The presumed branchial organs.

As mentioned above I was first inclined (STØRMER 1960) to regard the filamentous structures along the abdomen in *Waeringoscorpio* as parasitic fungi of some kind. However, a more detailed examination of the structures seems to favour another interpretation. Since the filaments or ribs appear to be restricted to more or less distinct ovate areas, and since these areas are preserved at different levels, the observed structures hardly represent clusters of individual filaments. More likely the filaments or ribs belong to more disc-like areas. Two or perhaps three pairs of discs are indicated on the left side of the specimen (right in text-fig. 2 and on pl. 2 and pl. 5 fig. 8) and two on the right side. The shape, arrangement, and mode of preservation indicate that the structures belong to the scorpion, are parts of its anatomy.

If we regard the evidently delicate discs with filaments or ribs as part of the scorpion, there is reason to assume that the structures were located above the ventral, probably lobostern plates. In text-fig. 6a the larger discs are placed in position between the ventral plates and the body wall, either representing leaf-
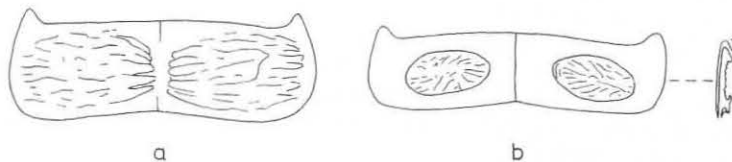
Text-fig. 6. The possible position of gills above the ventral preabdominal plates in (a) *Waeringoscorpio*, compared with the conditions in (b) the eurypterid *Eurypterus trigonophthalmus* [= *Eurypterus fischeri*]. The section to the right shows the gill tracts at the ventral surface of the body (simplified after WILLS 1965).

like structures between them, or representing the ventral surface of the body wall or the dorsal surface of the plates. The shape and size of the ventral plates are not known, but might have been as suggested in text-fig. 6a. If the ventral plates were exceptionally long, the ovate discs might have had a longitudinal, rather than a transverse direction.

If the filamentous discs had this protected position above the ventral plates *they probably represent branchial structures.* The gills or branchiae in *Limulus* and eurypterids have a similar position. As a result of a detailed study of GER-HARD HOLM's specimens of *Eurypterus* from Esthonia, WILLS (1965) concludes that the ovoid areas or gill-tracts on the body wall had a branchial surface composed of ridges and "valleys" with minute spinules. The surface and outline of the gill-tracts (text-fig. 6b) are not unlike the areas in *Waeringoscorpio* which, however, have broader ridges resembling filaments. Compared with the gill-tracts in *Eurypterus* the corresponding areas in the scorpion are relatively much bigger, occupying almost all the space above the ventral plate. In spite of a larger size of the discs and although the details of the presumed gill discs are less similar, a comparison with the eurypterids rather supports the idea that *the filamentous discs in Waeringoscorpio represent true gills and thus confirm the assumption of the early scorpions being aquatic.* The comparatively large gill-tracts in the scorpion might perhaps be explained as due to a small oxygen contents in the swamps producing the dark shale in which the scorpion from Alken is preserved.

Were the early scorpions aquatic forms?

This problem has been subject to much discussion ever since the Silurian scorpions were discovered in the eighties. Since the structures revealed in *Waeringoscorpio* have some bearing on the problem it may be useful to consider some of the main morphological characters which have been applied in assessing the habitat of the Paleozoic scorpions. The subject has recently been discussed by KJELLESVIG-WAERING (1966: 360) who points out that although most paleontologists working with fossil scorpions (LAURIE, POCOCK, CLARKE, RUEDEMANN, and WILLS) have assumed an aquatic habitat, most textbooks regard the early scorpions as representatives of the earliest terrestrial arthropods. The reason for the latter view is chiefly the close resemblance of Paleozoic and Recent forms, but also the evidently erroneous observation of stigmata in the Silurian *Palaeophonus* (THORELL & LINDSTRÖM 1885; PEACH 1885). In recent time only PETRUNKEVITCH (1949: 134; 1953: 6) has advocated the view that the Silurian scorpions were air-breathing. However, his chief argument is a negative one: "The Silurian scorpions were air-breathing because (1) no Recent or fossil Arachnida of any order are known to possess respiratory organs other than book-lungs or tracheal tubes". Naturally the delicate gill-structures would be rarely preserved, but their presence might be indirectly indicated by other morphological characters. His second argument: The "tarsi ending in a claw-like point or having a simple claw are known in many Recent terrestrial Arthropoda", is simplifying the problem too much (comp. below). Strangely enough PETRUNKE-VITCH admits that the early scorpions might have led a marine life, but in his opinion with aerial respiration by means of lungs.

The features speaking in favour of an aquatic habitat, implying a respiration by gills, are mainly expressed in the development of the following morphological characters: (1) the abdominal ventral plates and possible respiratory structures, (2) the walking legs, (3) the sensory setae, (4) the general resemblance of eurypterids and early scorpions, and (5) the faunal assemblages.

(1) The abdominal plates and possible respiratory structures.

In Recent scorpions the ventral surface of the abdomen is segmentally covered by chitinous plates usually called sternites although they probably represent the modified basal portions of appendages (comp. STØRMER 1963a: 110). The "sterna" of segments X-XIII have a pair of stigmata or spiracula leading into the book-lungs. The oldest known scorpion with stigmata, *Palaeopisthacanthus schucherti* PETRUNKEVITCH from the Carboniferous, was described by VOGEL & DURDON (1966), who noted for the first time round stigmata very similar to those present in some living Chactidae.

All other scorpions, the well preserved ones included, show no trace of stigmata on the ventral plates. Moreover, the plates at least in many forms, appear to be attached at the anterior margin only, and overlapping each other backwards just as in eurypterids. The shape of the plates vary from distinctly bilobed (Lobosterni of POCOCK 1911) to rectangular (Orthosterni). From his excellent studies of Carboniferous scorpions WILLS (1960: 329) concluded that the lobostern scorpion would have "room for gills above the laminate sternites". He infers that they were gill-breathers, and that they were capable, like *Limulus*, of spending part of their life on land. Regarding the orthosterns he is inclined to regard them as terrestrial, chiefly because he finds the slightly overlapping plates too small to house gills, and because these forms are so like the Recent forms (buthids). Since stigmata are missing WILLS mentions a possible respiration by direct oxidation through the skin, or by some other openings leading into the book-lungs. However, in the orthostern *Mazoniscorpio* (WILLS 1930: 299) he finds a doublure at the posterior margin of the ventral plates, a structure very similar to that in the ventral plates of *Eurypterus*. Although the ventral plates of the Orthosterni are shorter than those of the Lobosterni they, too, might possibly have had gills.

The possible gill-tracts in *Waeringoscorpio* fit in very well with our assumption of gills above the ventral plates. Anyhow the smooth overlapping ventral plates, very similar to the structures in the eurypterids (and *Limulus*), present a strong argument in favour of branchial respiration.

(2) The walking legs.

The stout legs with a single powerful claw in the Silurian *Palaeophonus* was regarded by POCOCK as indicative of an aquatic environment. WILLS (1960: 329) states that particularly the claws and spurs of the lobostern forms were better adapted for an aquatic than for a terrestrial life. STØRMER (1963: 90) points out that one might distinguish between "digitigrade" and "plantigrade" types of tarsi. In the former only the posttarsus touches the ground, in the latter both the tarsus and posttarsus. The "digitigrade" foot occurring in some Paleozoic scorpions might be derived from the basic eurypterid foot with three terminal claws of which only the two lateral ones remain in typical terrestrial arachnids.

Although two terminal claws occur already in Silurian scorpions (KJELLES-VIG-WAERING 1966), the generally more eurypterid-like feet of several Paleozoic scorpions (particularly lobostern forms) suggest an aquatic environment. Some "plantigrade" forms with well developed spurs (like *Gigantoscorpio*, STØRMER 1963: text-fig. 17) might have been amphibious, living in softbottom swamps.

(3) Sensory setae.

The characteristic trichobothria, forming long and flexible sensory setae or hairs are placed in cups on the pedipalps in particular. These flexible structures would hardly be useful in an aquatic environment, at least not when the animal moved about. WILLS (1960: 295, 305) refers to the presence of trichobothrial bristles in the Carboniferous *Mazoniscorpio* and *Buthiscorpius*, and KJELLESVIG-WAERING (1969: 180) mentions possible ones in *Mazonia*. It is, however, difficult to decide whether or not true trichobothria were present although the bristles in *Mazoniscorpio* appear to have been flexible (WILLS 1960: pl. 50 fig. 3).

In the well preserved pedipalp of *Gigantoscorpio* trichobothria are not present. Instead of these, numerous short and stiff movable setae have taken over the sensory functions. These setae are apparently identical with the sensory setae in *Eurypterus*. These conditions indicate that this scorpion chiefly lived in the water (indicated also by the large size).

The structure of the sensory setae may thus to some extent support the assumption of an aquatic environment.

(4) The general resemblance of eurypterids and early scorpions.

This has already been emphasized under (1)-(3). In addition to the characters discussed, one might mention the presence of composite eyes (KJELLESVIG-WAE-RING 1966: 365) quite similar to the eyes of eurypterids, and indication of a median appendage on the comb-segment (STØRMER 1963; NOVOJILOV & STØR-MER 1963; present paper). A similarity which, however, might be due to convergent development, is the large size of the postoral sternum and metastoma.

In general the early scorpions are more eurypterid-like than the later ones. This is due to a closer relationship, both being more primitive chelicerates, but the common features may also suggest a common mode of life.

(5) The faunal assemblages.

KJELLESVIG-WAERING (1966: 361) points out that all the Silurian and Lower Devonian scorpions have been found in association with eurypterids and few, if any, other fossils. A common habitat for scorpions and eurypterids he therefore finds strongly indicated. If those scorpions had been terrestrial the occurrence would hardly have been restricted to eurypterid faunas, scattered specimens would just as well have been washed out in the sea, later to be found in ordinary marine faunas. The Carboniferous forms are relatively common in sediments deposited in "coal swamps". The rare occurrence of scorpions in Mesozoic and Tertiary sediments is interpreted by KJELLESVIG-WAERING as possibly due to the presence of terrestrial rather than aquatic scorpions in these younger times as it would be a rare event for a cryptozoic, solitary organism to be washed out to the seas and to be preserved.

The fossil record, including several morphological characters as well as the geological occurrence, indicate an aquatic mode of life of the early scorpions.

Like the eurypterids they probably inhabited coastal waters of variable salinity. In the later part of the Paleozoic some of the scorpions became able to spend a certain time on land, and already in Carboniferous time some scorpions became air-breathers and adapted to a fully terrestrial mode of life.

The trigonotarbid arachnids from Alken.

Order **Trigonotarbida** PETRUNKEVITCH 1949.

The rich fossil material from Alken also contains specimens of evidently terrestrial arachnids. Since these forms are of Lower Emsian age they represent the oldest land arachnids hitherto known. As such they deserve particular interest, and a preliminary report of the find was published in "Science" (STØRMER 1969b: 1276). As pointed out in this article the arachnids are related to minute species occurring in the well known Rhynie Chert in the Old Red of Scotland, the age of which has previously been regarded as Middle Devonian, but more recently possibly as Emsian, i. e., about the age of the Nellenköpfchen-Schichten or slightly younger.

Representatives of the order Trigonotarbida are known from the Devonian and Carboniferous. Characteristic of the group is the araneid configuration of the coxo-sternal region (PETRUNKEVITCH 1955: 107), probably a primitive arachnid structure (comp. page 344).

The Palaeocharinidae, known only from the Devonian, differ from the other trigonotarbids by having eleven instead of ten abdominal segments a number which, however, may be uncertain (comp. page 355). The two last segments form a "pygidium" situated on the ventral side of the abdomen. Members of the family apparently had compound eyes similar to those in certain fossil scorpions.

Family **Palaeocharinidae** HIRST 1923.

Alkenia n. g.

Type species: *Alkenia mirabilis* n. sp.

Diagnosis: Large Palaeocharinidae; prosoma subtriangular with inflated ovate median portion with bifurcating median furrow, flat sickle-shaped flanks, and a posterior transverse rib; four posterior pairs of legs uniform with blunt tarsus; body surface coarsely tuberculated.

Taxonomic relations: See discussion on page 355.

Alkenia mirabilis n. sp.
Pl. 3, pl. 4, pl. 5 fig. 1; text-fig. 7.

1969 Arachnid. — STØRMER, oldest known terrestrial arachnids: 1276, text-figs. 1-2.

Derivation of name: mirabilis (Lat.) = amazing, surprising.
Holotype: The specimen figured on pl. 3-4 and in text-fig. 7, SMF VIII 30a, b (counterpart), Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main.

— Type horizon: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten.
— Type locality: Quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.

Paratype: The specimen figured on pl. 5 fig. 1, SMF 26029, from type horizon and type locality.

Diagnosis: The same as for the genus.

Description.

Both holotype and paratype show the dorsal surface of the body; in the former also parts of the ventral surface are exposed along the margin of the opisthosoma.

The elongate body measuring 12·5 mm in length, has a large subtriangular prosoma attached to the opisthosoma along a broad juncture. The prosoma is divided into four parts, a median inflated portion, two broad sickle-shaped lateral rims, and a posterior transverse rib. The median portion has an elongate ovate outline with a well rounded
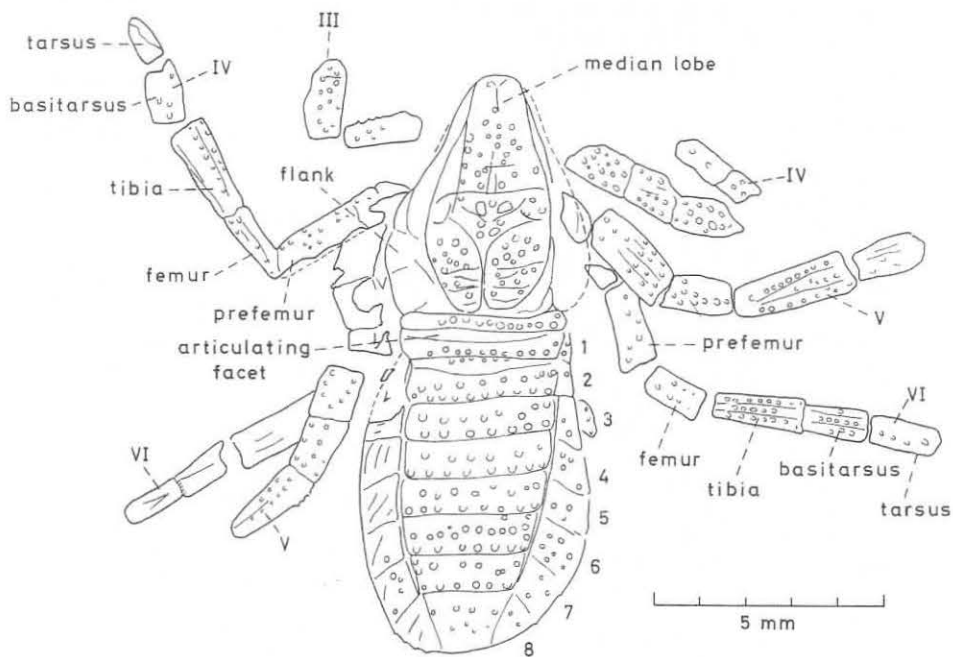
Text-fig. 7. *Alkenia mirabilis* n. g. et n. sp. — Composite figuration based on h o l o t y p e and counterpart; SMF VIII 30a-b; ×6. — III-VI = walking legs of prosoma. 1-8 = segments of opisthosoma or abdomen. The transverse, tuberculated rim in front of segment 1 is regarded as belonging to the prosoma, but might possibly represent the abdomen making a total of 9 instead of 8 abdominal segments on the dorsal surface. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

anterior and posterior. The largest width, 2·7 mm, occurs about ³/₅ the length from the anterior to the posterior border of the median portion. A transverse furrow divides the median portion into two equally long parts. The anterior one is flat in front; farther back five more or less distinct longitudinal rows of tubercles, partly mounted on ridges are suggested. The posterior part is somewhat distorted. A median furrow runs forward from the posterior border; midway it bifurcates forming a pair of diverging furrows becoming nearly transverse toward the lateral borders. Because of some deformation the furrow is less distinct on the left side. On the right side the oblique furrow seems to bifurcate again with one branch reaching the transverse furrow bordering the posterior portion in front. A bifurcation of a median furrow is also present in the Carboniferous *Trigonomarthus* (PETRUNKEVITCH 1955: text.-fig. 80/1). Posterior to the bifurcation two or three transverse lines or furrows indicate a segmentation of the posterior portion of prosoma, a feature indicated also in some other fossil arachnids. The coarse tubercles are to some extent arranged parallel to the furrows. If median ocelli were present they would have been present in the middle of the v-shaped area in front. Lateral to this, and just behind the transverse furrow, a curved line on the left side may indicate the outline of a lateral eye.

The flat sickle-shaped flanks of the prosoma are narrow in front and increase in width backwards to the posterior margin of the prosoma. The surface has longitudinal ridges or edges in front, and certain less distinct transverse lines suggesting a segmentation, in the posterior part, a feature present also in several other trigonotarbids.

A transverse rib or segment provided with one row of about 14 tubercles, forms the posterior margin of the prosoma. From the prosomal structures preserved it is not possible to decide whether the rib belongs to the prosoma representing a neck-segment, or represents a first tergite of the mesosoma. However, since the sickle-shaped lateral rims reach so far backwards, and since a distinct articulating facet (half-ring) is present on the following segment, the rim probably belongs to the prosoma.

Of the six pairs of p r o s o m a l   a p p e n d a g e s the four posterior ones (III-VI) are more or less preserved. These walking legs are mutually very similar in shape and size. Each leg is evidently composed of a coxa (not exposed), trochanter, prefemur, femur, tibia, basitarsus, tarsus, and posttarsus (not preserved). Some of the legs show a flexure between the prefemur and femur, the femur being shorter than the prefemur and tibia. The separate joints or segments of the legs were probably cylindrical. The exposed part of each joint has about four longitudinal ridges with tubercles smaller than those present on the dorsal surface of the prosoma (pl. 4 figs. 1-2). The tarsus has about the same width as the other joints, a feature which is characteristic of most terrestrial arachnids, but which is not found in typical aquatic chelicerates such as the merostomes and the early Paleozoic scorpions with short and stump legs. In the Devonian *Paleocharinoides* (HIRST 1923: pl. 12 fig. C) the tarsus ends in two minute and slender claws which hardly could be expected to be preserved in *Alkenia*. The two claws in the Rhynie forms are characteristic of terrestrial not of aquatic forms unless they were parasitic or commensal on other organisms. Although the claws are not preserved in *Alkenia* the similar blunt tarsus indicates that also this form lived on land. In the eurypterids and some of the early scorpions the distal portion of the walking legs has a posttarsus developed as a powerful median claw or spine flanked by two lateral spines (sometimes reduced). In later scorpions and most other arachnids these lateral spines remained as the two distal claws whereas the median spine, the posttarsus, became reduced into a heel or talon, or completely lost (STØRMER 1963: 86).

The oblong opisthosoma measuring 7·1 mm in length and 5 mm in width, is connected with the prosoma by a broad juncture. In the holotype the opisthosoma is divided by two longitudinal furrows into one median and two lateral portions. In the paratype, however, (pl. 5 fig. 1) this feature is less significant; a longitudinal furrow is only suggested on the right side.

The opisthosomal shield is transversally divided into eight segments, each representing a tergite. The tergites are separated from each other by a thin furrow or line which is transverse in the middle portion and more posteriorly directed in the lateral areas. In the paratype the suture or division lines between the tergites are gently curved. The first tergite has a length of 1 mm whereas the six following ones have a length of about 0·8 mm, and the last one of 1·3 mm. The first tergite has the posterior part of the shell broken off, a feature giving the appearance of two tergites rather than one. The first tergite differs from the others by having a well developed articulation facet or articulating half-ring (text-fig. 7) on which the posterior border of the prosoma could slide when the opisthosoma was moved up and down. Each tergite has two rows of tubercles, one at the posterior margin. In the paratype a third row is suggested between the two in parts of the tergites. The lateral portions of the opisthosoma also have tubercles, less typical in the paratype. On the left side, and partly on the right, the ventral surface of the lateral portions are exposed as impressions. The pleurae show posteriorly directed wrinkles but also tubercles. The posterior and postlateral margins of the opisthosoma are well demonstrated in the counterpart (pl. 4 fig. 4) where they are slightly denticulate.

Taxonomic relations.

The elongate body with the broad juncture between the prosoma and opisthosoma places the present species in order Trigonotarbida. The Devonian, Old Red species belong to a separate family Palaeocharinidae (HIRST 1923). PETRUNKEVITCH (1955: 107) states that members of the family have eleven opisthosomal segments, the two last ones being reduced and visible almost only on the ventral side. However, judging from HIRST's (1923) good descriptions and illustrations only eight tergites seem to be present on the dorsal surface. Probably PETRUNKEVITCH visualized an extra tergite in front of a structure which I am inclined to interprete as part of the prosoma. *Alkenia* has several general characters in common with the Scottish genera from Rhynie. Of more special characters might be mentioned the crest and ridges in front of the prosoma in the palaeocharinids, which may be compared with the anterior ridges in *Alkenia*. The backwards diverging sides of the median portion of the prosoma seem also to be common to both. On the other hand the German species differs from the Scottish ones chiefly by having a coarse tuberculation and a different shape of the prosoma. These differences evidently justify the establishment of a new genus the diagnosis of which is given above.

Remarks: Because of its Lower Devonian age this early terrestrial arachnid deserves particular interest. Together with the Scottish forms of the same or slightly younger age, it represents the earliest terrestrial arachnids known (the Silurian and early Devonian scorpions being regarded as aquatic). It is interesting to ascertain that these early species appear to be well developed and well established forms which must have had a long and extensive development before they appear in the Lower Devonian. The fact that these early terrestrial arachnids are similar to Carboniferous forms — they have a Carboniferous aspect — confirms the impression that the group was well established and settled already in the Lower Devonian.

Family **Trigonotarbidae** PETRUNKEVITCH 1949.

Archaeomartus n. g.

Type species: *Archaeomartus levis* n. sp.

Diagnosis: Medium sized Trigonotarbidae; opisthosoma circular in outline, composed of eight segments, axis distinct, not reaching posterior border, axial furrows diverging near anterior border. Integument smooth or provided with few tubercles.

Archaeomartus levis n. sp.
Pl. 5 figs. 2-5; text-figs. 8a-b.

1969 Arachnid. — STØRMER, oldest known terrestrial arachnids: 1277, text-figs. 3a-b.

Derivation of name: levis (Lat.) = smooth.
Holotype: The specimen figured on pl. 5 figs. 2-3 and in text-fig. 8b, SMF VIII 32, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main. — Type horizon: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten. — Type locality: Quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münstermaifeld r 03800 : h 68670, W. Germany.
Paratypes: The specimens figured on pl. 5 figs. 4-5 and in text-fig. 8a, SMF VIII 33a-b, from type horizon and type locality.

Diagnosis: A species of *Archaeomartus* devoid of tubercles along the margin of opisthosoma.

Description.

The holotype (pl. 5 figs. 2-3; text-fig. 8b) is a moderately inflated opisthosoma with a subcircular outline measuring 4·4 mm in length and 4·6 mm in width. A median axis (portion of median plates) with seven segments of about equal length, is marked off by
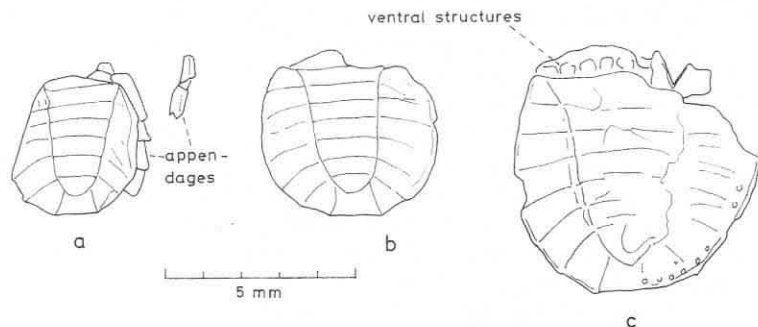
Text-fig. 8. Abdominal shields of *Archaeomartus*; ×5. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

a-b) *Archaeomartus levis* n. g. et n. sp. — a) Paratype, SMF VIII 33a. — b) Holotype, SMF VIII 32a.
c) *Archaeomartus tuberculatus* n. sp. — Holotype, SMF VIII 34.

distinct longitudinal furrows or lines. The axis expands in front so that the first segment or tergite is broader than the following. In front the first segment has an articulation facet. The last, double segment has a rounded hind portion not reaching the posterior margin of the opisthosoma. The lateral or pleural areas of the opisthosoma are divided into eight pairs of plates of which the last one forms a single plate behind the axis. A narrow marginal rim is indicated on the right side of the shield. The surface of the opisthosoma is smooth.

The paratype SMF VIII 33a (pl. 5 fig. 4, and text-fig. 8a) is less complete but shows parts of two of the walking legs. The legs have powerful joints of which the distal one to the right has a terminal cleft.

Taxonomic relations.

Archaeomartus levis has the eight opisthosomal segments characteristic of the family Trigonotarbidae. However, with its subcircular outline of the opis-thosoma and an axis not reaching the posterior border, the species does not fit into the previously described genera. The shape of the opisthosoma recalls that of the Carboniferous Order Anthracomartida, but members of this group have an extra row of pleural plates outside the proximal ones. The Lower Devonian *Archaeomartus* may possibly be related to ancestors of the Anthracomartida.

Archaeomartus tuberculatus n. sp.
Pl. 5 fig. 6; text-fig. 8c.

1969 Arachnid. — STØRMER, oldest known terrestrial arachnids: 1277, text-fig. 3c.

Derivation of name: tuberculatus (Lat.) = tubercular.
Holotype: The specimen figured on pl. 5 fig. 6 and in text-fig. 8c, SMF VIII 34, Natur-Museum und Forschungs-Institut Senckenberg, Frankfurt am Main. — Type horizon: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten. — Type locality: Quarry in the Alkener Bach-Tal E. of Alken an der Mosel, MTB Münster-maifeld r 03800 : h 68670, W. Germany.

Diagnosis: A large species of *Archaeomartus* with one row of tubercles along a narrow marginal rim of the opisthosoma.

Description.

The inflated opisthosoma has a length of 6 mm and a width of 6·5 mm. The axis which has seven segments, the last one double, has an expanded frontal portion and a rounded hind portion which does not reach the posterior margin of the shield. The lateral or pleural areas have eight segments or plates of which the last ones unite into a single posterior plate. On the right side a row of tubercles is present just inside the narrow marginal rim. In front some of the ventral structures are indicated. A row of cavities is suggested, the nature of which is unknown.

Taxonomic relations.

The present species differs from *Archaeomartus levis* by the larger size and the presence of tubercles along the margin.

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Plate 1.

Waeringoscorpio hefteri n. g. et n. sp. — Holotype, the scorpion exposed from the ventral side with impressions of dorsal tergites; SMF VIII 31; specimen photographed in alcohol, ×5 (scale in mm). — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

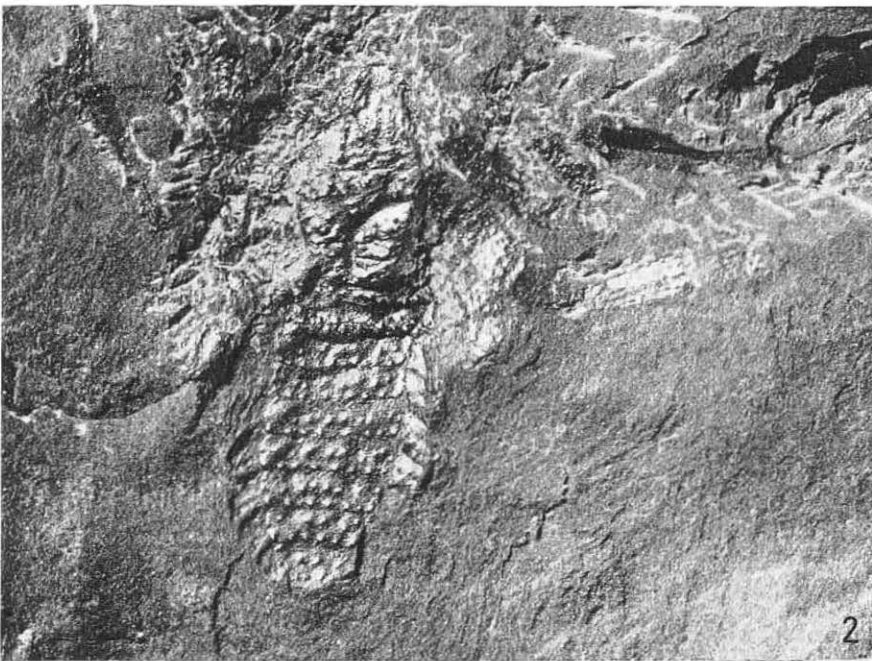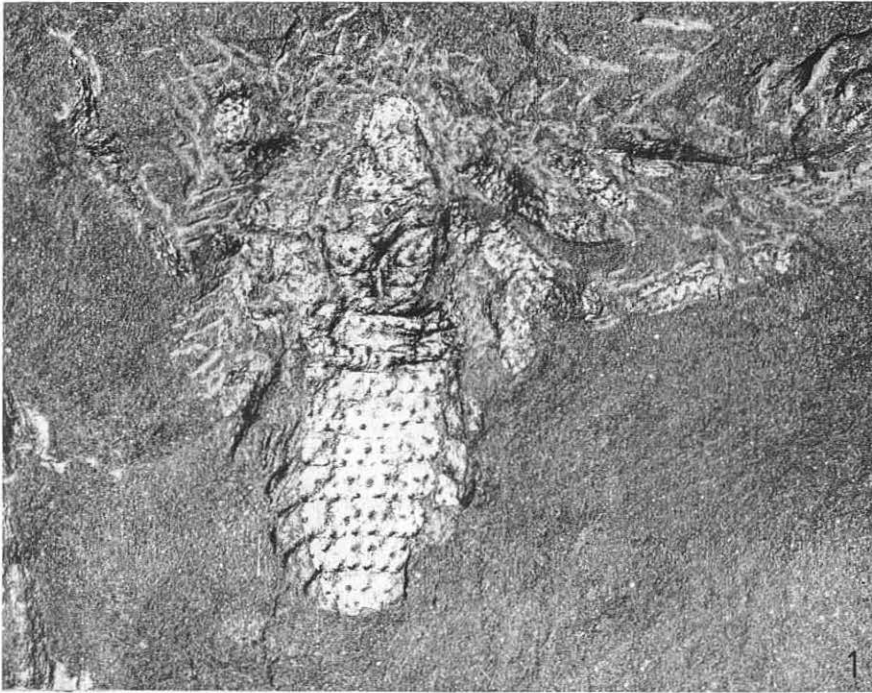L. Størmer: Arachnida from the Lower Devonian of Alken an der Mosel.

Plate 2.

Waeringoscorpio hefteri n. g. et n. sp. — H o l o t y p e, details of anterior portion of the scorpion from the ventral side; SMF VIII 31; specimen photographed in alcohol, ×8·6. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

L. STØRMER: Arachnida from the Lower Devonian of Alken an der Mosel.

Plate 3.

Alkenia mirabilis n. g. et n. sp. — H o l o t y p e , dorsal view; SMF VIII 30a; ×5·5. —
Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener
Bach-Tal E. of Alken an der Mosel, W. Germany.

Fig. 1. Specimen photographed in alcohol in reflected light.
Fig. 2. Dry specimen photographed with light from NW.

L. Størmer: Arachnida from the Lower Devonian of Alken an der Mosel.

Plate 4.

Alkenia mirabilis n. g. et n. sp. — H o l o t y p e , specimen (fig. 1) and counterpart (figs. 2-4); SMF VIII 30a-b. — Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.
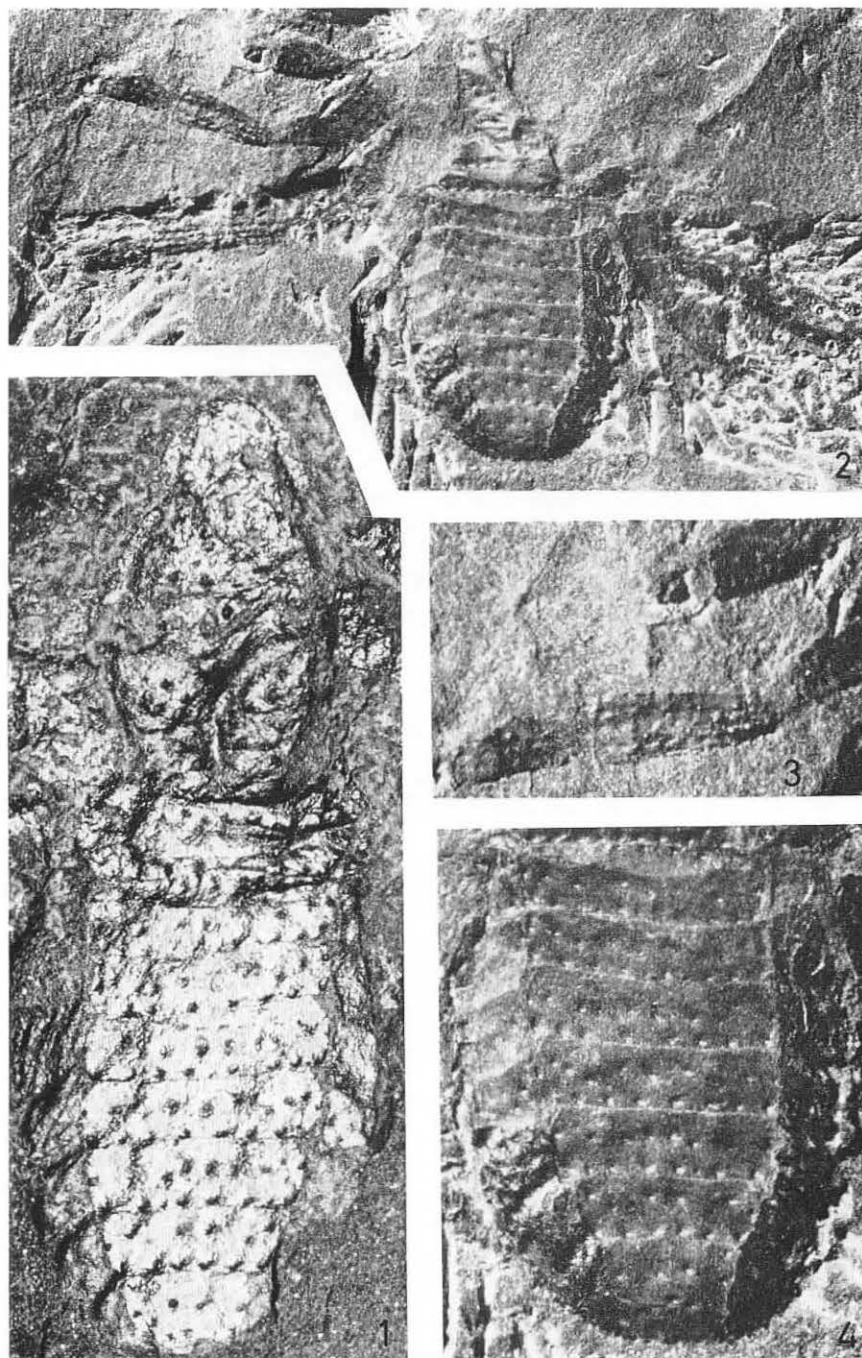
Fig. 1.   Details of specimen; photographed in alcohol, ×10.
Fig. 2.   Impression of dorsal surface of abdomen and surface of walking legs; ×5·2.
Fig. 3.   Detail of walking leg; ×10.
Fig. 4.   Detail of abdomen; ×10.

L. Størmer: Arachnida from the Lower Devonian of Alken an der Mosel.

Plate 5.

All specimens from: Lower Devonian, late Lower Emsian, Nellenköpfchen-Schichten; quarry in the Alkener Bach-Tal E. of Alken an der Mosel, W. Germany.

Fig. 1.   *Alkenia mirabilis* n. g. et n. sp. — Paratype, segments of abdomen; SMF 26029; ×16.

Fig. 2-5. *Archaeomartus levis* n. g. et n. sp.
         2-3. Holotype; SMF VIII 32. — 2: Abdomen, photographed in alcohol; ×5·5. — 3: Abdomen, whitened; ×5·5.
         4. Paratype, abdomen; SMF VIII 33a; photographed in alcohol; ×8.
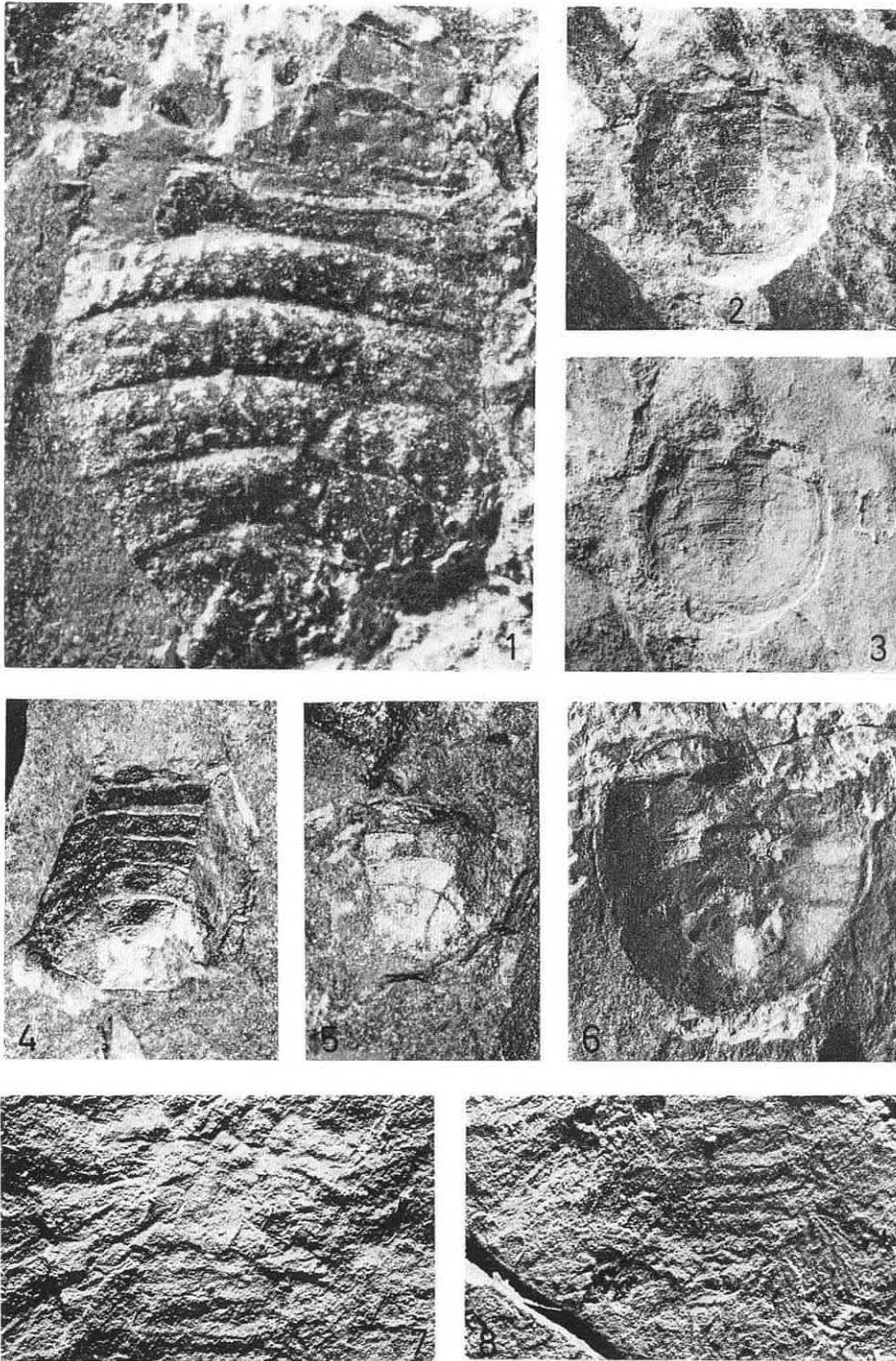   5. Paratype, parts of abdomen; SMF VIII 33b; photographed in alcohol; ×8.

Fig. 6.   *Archaeomartus tuberculatus* n. sp. — Holotype, abdomen; SMF VIII 34; photographed in alcohol; ×5·5.

Fig. 7-8. *Waeringoscorpio hefteri* n. g. et n. sp. — Holotype, details of specimen; SMF VIII 31; whitened.
         7. Coxo-sternal area; behind the sternum impressions of opercular plates, and pectines; ×5·8.
         8. Posterior part of preabdomen with gill tracts (?) preserved at different levels on the right side in the photograph; ×8·6.

L. STØRMER: Arachnida from the Lower Devonian of Alken an der Mosel.