Senckenbergiana lethaea	**84**	(1/2)	173 – 193	13 text-figs	Frankfurt am Main, 30. 12. 2004

On the Emsian (Early Devonian) arthropods of the Rhenish Slate Mountains: 4. The eurypterids *Alkenopterus* and *Vinetopterus* n. gen. (Arthropoda: Chelicerata)

With 13 Text-figures

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Abstract

Recently collected material of Early Devonian eurypterids (Chelicerata: Eurypterida) from the Rhenish Slate Mountains is described and compared to the reexamined type material of *Drepanopterus struvei* STØRMER, 1974 and *Alkenopterus brevitelson* STØRMER, 1974, both from the Emsian of Alken an der Mosel. *Vinetopterus martini* n. gen., n. sp., from Siegenian strata of the newly detected eurypterid localities Burglahr and Hombach in the Westerwald, is described. *D. struvei* is transferred to *Vinetopterus* n. gen. *Vinetopterus* n. gen. is diagnosed as having short prosomal appendage VI of *Drepanopterus*-type A, and a first order opisthosomal differentiation. A second species from the Siegenian of Burglahr is described as *Alkenopterus burglahrensis* n. sp. The new family Alkenopteridae, diagnosed by possessing at least two pairs of non-spiniferous legs, V of *Drepanopterus*-type B and VI of *Alkenopterus*-type, is proposed to accomodate *Alkenopterus*. The palaeoecology of Burglahr and Hombach is briefly discussed and the habitat of these eurypterids is interpreted as representing a shallow water environment in a deltaic setting with marine or brackish influence.

Key words: Eurypterida, Stylonuroidea, Drepanopteridae, Alkenopteridae, morphology, taxonomy, palaeoecology, deltaic setting, Early Devonian, Rhenish Slate Mountains, Germany.

Kurzfassung

[Über Arthropoden des Emsiums (Unter-Devon) aus dem Rheinischen Schiefergebirge: 4. Die Eurypteriden *Alkenopterus* und *Vinetopterus* n. gen. (Arthropoda: Chelicerata).] - Neu aufgefundene Eurypteriden aus dem Unterdevon des Rheinischen Schiefergebirges werden beschrieben und mit dem Typusmaterial zu *Drepanopterus struvei* STØRMER, 1974 and *Alkenopterus brevitelson* STØRMER, 1974 aus dem Emsium von Alken an der Mosel verglichen. *Vinetopterus martini* n. gen., n. sp. aus dem Siegenium von Burglahr und Hombach im Westerwald wird beschrieben. *D. struvei* wird zu der Gattung *Vinetopterus* n. gen. gestellt, die durch folgende Merkmale diagnostiziert wird: Eine kurze prosomale Extremität VI vom *Drepanopterus*-Typ A und eine opisthosomale Differenzierung ersten Grades. Eine zweite Art, ebenfalls aus dem Siegenium von Burglahr, wird als *Alkenopterus burglahrensis* n. sp. beschrieben. Die hinteren prosomalen Beinpaare (V-VI) von *Alkenopterus* sind unbestachelt, aber so unterschiedlich gebaut, dass sie sich zwei getrennten Typen zuordnen lassen. Die neue Familie Alkenopteridae, diagnostiziert durch den Besitz einer 5. prosomalen Extremität vom *Drepanopterus*-Typ B und einer 6. Extremität vom *Alkenopterus*-Typ, wird vorgeschlagen. Paläoökologische Aspekte hinsichtlich der beiden neu entdeckten Eurypteriden-Fundpunkte werden kurz andiskutiert und der Lebensraum dieser Eurypteriden als ein Flachwasser-Habitat innerhalb eines Delta-Komplexes, mit marinem oder brackischem Einfluss, interpretiert.

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Introduction

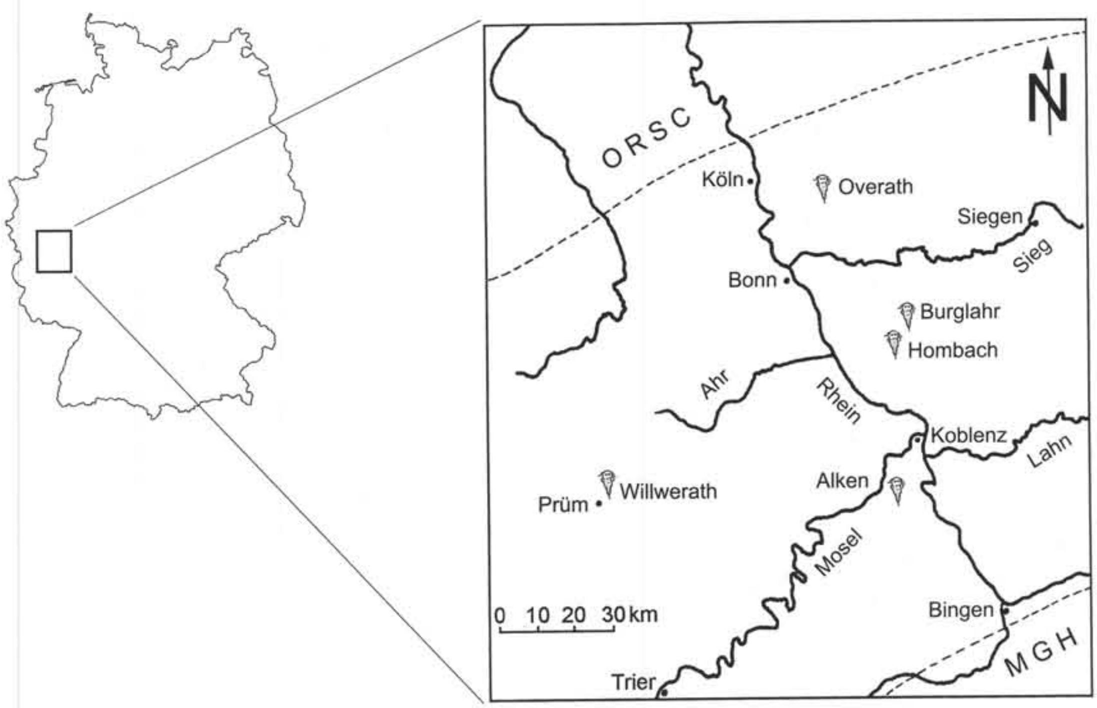
Eurypterids are a monophyletic group of predatory Palaeozoic chelicerate arthropods attaining maximum diversity and abundance in the Late Silurian and Early Devonian. They occupied a wide variety of ecological niches from fairly deep marine to brackish and lacustrine/fluviatile settings (Plotnick 1999, BRADDY 2001). Eurypterids from Early Devonian strata of the Rhenish Slate Mountains have been described from a number of different localities, including Overath (lowermost Emisan) (GROSS 1933; DUNLOP et al. 2002), Willwerath (uppermost Lower Emsian) (STØRMER 1936, 1969) and Alken an der Mosel (uppermost Lower Emsian) (STØRMER 1973, 1974). As part of an on-going reevaluation of Early Devonian chelicerate arthropods of the Rhenish Slate Mountains, we report here the results of our investigation of some important eurypterid finds collected after the publication of STØRMER's (1973, 1974) comprehensive papers on the Alken fossils.

Geological setting and stratigraphy

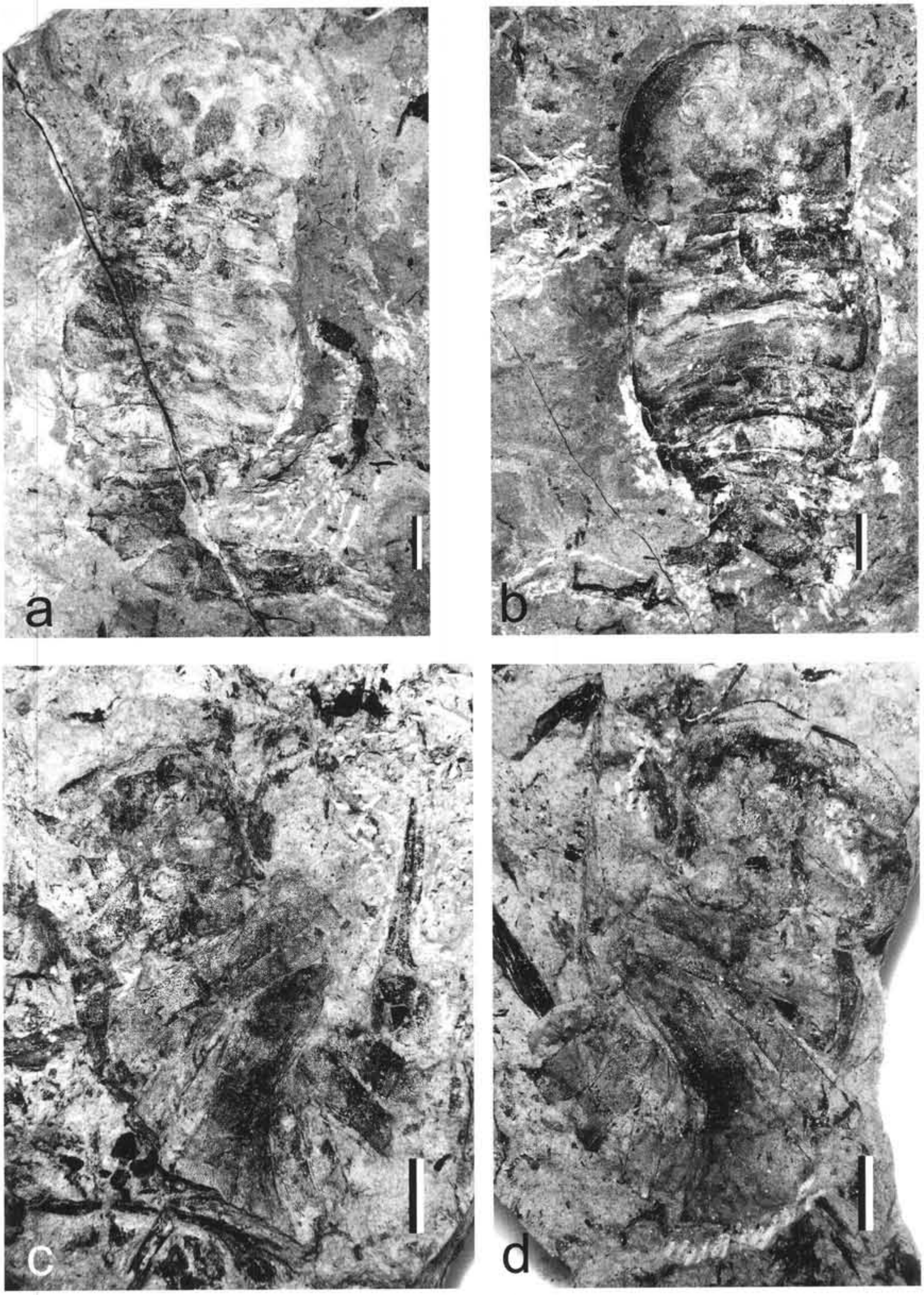
The newly collected specimens partly originate from the so-called „Oberbank“ deposit from Alken (Nellenköpfchen Formation, upper Vallendar Group, uppermost Lower Emsian) (for locality information see e.g. SOLLE 1970, STØRMER 1976, BRAUN et al. 1997, DUNLOP et al. 2001, BROCKE et al. 2002). Now we can add two newly discovered sites in Siegenian strata of the Westerwald area that yielded representatives of stylonurid eurypterids. Both localities are situated north of the Siegen Main Thrust, a prominent tectonic lineament traversing the Eifel and Westerwald area in SW-NE direction. Here, on the footwall block of the Siegen Main Thrust, siliciclastic sediments of Siegenian age form the Hönningen-Seifen Anticline (HENKE 1933). These sediments, developed in "Rhenish Normal Facies" as defined by ERBEN (1962), are derived from the Old Red Sandstone Continent and reflect a wide variety of shallow water environmental conditions in a deltaic depositional setting (WALLISER & MICHELS 1983). Huge fluvial mud flats, flood plains and low relief deltas developed in the Northern Facies belt of the Rhenohercynian Basin (STETS & SCHÄFER 2002). Constant subsidence was compensated by detrital input and thus, depending on sea-level stand and amount of clastic material delivered, the facies changes several times from fully marine to brackish and freshwater. Even dry areas must have existed allowing terrestrial arthropods, e.g. trigonotarbid and phalangiotarbid arachnids, to flourish (POSCHMANN & JANSEN 2003).

One of these sites is situated near the village of Hombach (MTB sheet 5410 Waldbreitbach R: [26]03 855, H: [56]06 220) and was temporarily exposed in 1999 during works for a new ICE highspeed train route from Cologne to the Rhine/Main area. POSCHMANN & JANSEN (2003) described the lithological log of the sequence exposed and gave preliminary listings of the faunal associations. Due to its tectonic setting in the core of the Hönningen-Seifen Anticline (see HENKE 1933), these authors considered the eurypterid-bearing strata as being older than a brachiopod fauna of typical middle Siegenian aspect characterized by e.g. *Acrospirifer primaevus* (STEININGER, 1853), *Boucotstrophia herculea* (DREVERMANN, 1904) and *Multispirifer solitarius* (KRANTZ, 1857), which has been recorded in a sequence on the southeastern flank of the Hönningen-Seifen Anticline (POSCHMANN & JANSEN 2002, 2003).

The second newly discovered locality lies approximately 300 m south of the village of Burglahr in the Wied valley, around 40 m east of the old entrance to the so-called Alvensleben-Stollen, part of the abandoned Louise Mine (MTB



Text-fig. 1. Approximate geographical position of major Early Devonian eurypterid localities in the central Rhenish Slate Mountains. Palaeogeographical position of Old Red Sandstone Continent (ORSC) and Mid-German High (MGH) indicated.



Text-fig. 2. a-b. *Alkenopterus brevitelson* STØRMER, 1974, holotype SMF VIII 150, Emsian of Alken, part and counterpart. – c-d. *Vinetopterus struvei* (STØRMER, 1974) n. gen., holotype SMF VIII 191, Emsian of Alken, part and counterpart. Alcohol immersion and polarized light. Scale bars = 5 mm.

sheet 5311 Altenkirchen R: ^{33}93 900, H: ^{56}09 920). This site, situated roughly 4.6 km northeast of Hombach on the northwestern flank of the Hönningen-Seifen Anticline, is also Siegenian in age, but any further discussion concerning its detailed stratigraphic position would be premature. These two localities are probably of approximately the same age.

It should be noted here, that we prefer to retain the local stratigraphic term "Siegenian", because a reliable correlation of the deltaic facies developed in the type region of the Rhenish stages with the international chronostratigraphic standard scale is problematic. The fully marine, probably mid-shelf level-bottom brachiopod communities reported by POSCHMANN & JANSEN (2003), that originate from younger strata, suggest a latest Pragian to early Early Emsian age in terms of the redefined standard stages for the eurypterid localities Hombach and Burglahr (see BRICE et al. 2000).

Preservation

In less weathered rocks the arthropod compression fossils occur as dark, somewhat shiny and sometimes silvery films on the dark grey matrix of silty mudstone to muddy siltstone. In the case of Alken the fossils occur in grey silt- to fine sandstone (DUNLOP et al. 2001). The presence of organic material, probably coalified remains of the highly sclerotized and therefore recalcitrant exocuticle (cf. e.g. BUTTERFIELD 1990, BRAUN 1997), is evidenced by the use of polarized light which often greatly enhances contrast. The sediment from Hombach layer 4 and most of the Burglahr material is strongly weathered changing the colour of the fossils into various kinds of brown, grey, reddish or white. In heavily weathered specimens the organic substance has completely vanished, leaving only a slight relief of the fossil. As STØRMER (1973, 1976) pointed out with respect to the Alken material the fossils probably represent shed exuviae. This might have contributed to their preservation in as much as empty exuviae do not attract scavengers as do decaying carcasses (e.g. STØRMER 1976; MP, own observations in notostracan branchiopods). Furthermore it excludes rapid enzymatic degradation of organic structures, which would be expected in a dead animal (cf. BUTTERFIELD 1990, 1995).

Another factor contributing to the preservation of unmineralized arthropod cuticle in eurypterid Lagerstätten of the Rhenish Slate Mountains (and elsewhere) is rapid burial induced e.g. by storm-events and enclosing of the potential fossils in an oxygen-poor sediment (cf. STØRMER 1976, ANDERSON et al. 1998, POSCHMANN & JANSEN 2003). Plant material and associated arthropod exuviae that accumulated along the "shoreline" may thus have been transported into a hypautochthonous setting (cf. BRAUN 1997). This interpretation seems likely with respect to layers in which arthropod cuticles occur immediately above or in the upper part of a layer filled with plant material, but is less likely for arthropod remains that do not occur in close association with plants, as observed in the stylonurid occurrences at Alken. It is within the bounds of probability that these accumulations are due to synchronized moulting of eurypterids in sheltered areas (cf. BRADDY & DUNLOP 1997; BRADDY 2001). BRAUN (1997) pointed out that pyrite is often associated with the Alken fossils, in both plants and arthropods. Pyrite has also been observed in the Hombach (POSCHMANN & JANSEN 2003) and Burglahr sediments, but it is as yet unclear if it significantly contributed to the preservation of fossil cuticle. However, detailed studies of taphonomic processes leading to the formation of Lagerstätten in Early Devonian marginal marine settings of the Rhenish Slate Mountains are needed.

Material and methods

For study purposes and photographs, the fossils were immersed in alcohol using both normal reflecting light and polarized light. Photographs in both reflecting and polarized light are reproduced here if both reveal information. The photographs and *camera lucida* drawings have been scanned, processed and arranged as figures using Photoshop 5.0. In the application of morphological terms and systematics we follow TOLLERTON (1989).

All specimens with repository numbers prefixed by PWL will be deposited in the Landessammlung für Naturkunde Rheinland-Pfalz, housed at the Naturhistorisches Museum Mainz (the original collector's numbers are retained in brakkets where appropriate). STØRMER's type material, prefixed by SMF, is housed in the Senckenberg Museum Frankfurt am Main. The remaining specimens are deposited either in the private collection of PETER MÜLLER (Langenhahn, prefixed by M) or in the reference collection of one of the authors (MP, specimens with suffix –D), which is open to public study for scientific reasons.

Abbreviations used in the drawings: cx = coxa, ep = epimera, gb = gnathobase of coxa, le = lateral eye, me = median eye tubercle, mr = marginal rim, or = ornament, tl = telson. Opisthosomal segments and individual podomeres of appendages are numbered in arabic numerals, the prosomal appendages in roman numerals.

Systematic Palaeontology

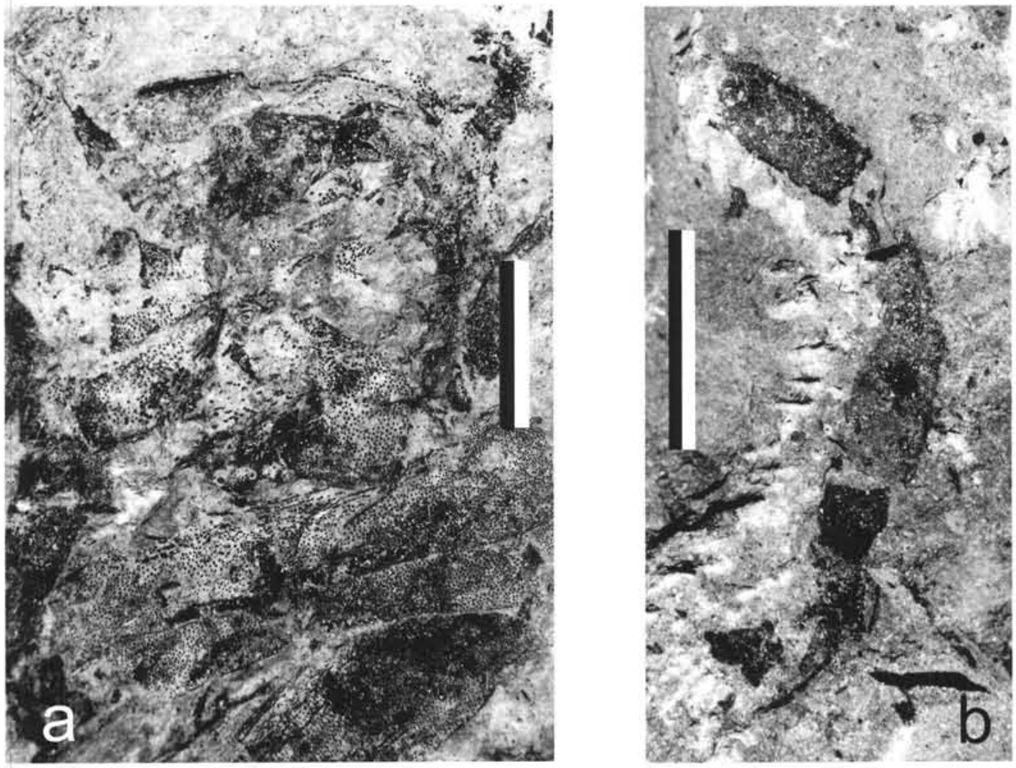
Order Eurypterida BURMEISTER, 1843
Suborder Eurypterina BURMEISTER, 1843
(nom. trans. CASTER & KJELLESVIG-WAERING, 1964)
Superfamily Stylonuroidea DIENER, 1924
(= Drepanopteroidea KJELLESVIG-WAERING, 1966)

Diagnosis: Legs II-IV spiniferous, *Hughmilleria*-type; legs V-VI non-spiniferous (emended after TOLLERTON 1989).

Remarks: The diagnosis of the superfamily Stylonuroidea is slightly modified here to accomodate the newly diagnosed family Drepanopteridae (see below), which possesses non-spiniferous legs V and VI of different types. This configuration has been observed in at least *Vinetopterus* n. gen. and *Drepanopterus bembycoides* LAURIE, 1898, and is possibly also present in *Moselopterus*.

Family Drepanopteridae KJELLESVIG-WAERING, 1966

Diagnosis: Legs II-IV spiniferous, *Hughmilleria*-type; legs V-VI non-spiniferous, V of *Drepanopterus*-type B, VI of *Drepanopterus*-type A (emended after TOLLERTON 1989).



Text-fig. 3. a. *Vinetopterus struvei* (STØRMER, 1974) n. gen., holotype SMF VIII 191a, Emsian of Alken, detail of prosomal and anterior preabdominal region in ventral view. – b. *Alkenopterus brevitelson* STØRMER, 1974, holotype SMF VIII 150a, Emsian of Alken, detail of prosomal appendage VI. Alcohol immersion and polarized light. Scale bars = 5 mm.

Remarks: Following a suggestion by Victor P. TOLLERTON, Jr. (New York; pers. comm.) leg V of *Drepanopterus* may be designated *Drepanopterus*-type B, in contrast to *Drepanopterus*-type A, which possesses podomere 7a. It has to be noted that A and B does not imply a sexual dimorphism, as it does in the designation of genital appendage types.

Genus ***Vinetopterus*** n. gen.

Etymology: vinetus (Lat.) = vineyard; named after the occurrence of the type species in this famous vineyard region.

Diagnosis: Small to moderately sized drepanopterid with a relatively large horseshoe-shaped prosoma, postero-lateral corners rounded, narrow marginal rim decreasing in width posteriorly, prosomal margin crenulate; centrimesially positioned eyes ovocrescentric, of moderate size; prosomal appendages short; metastoma circular with shallow anterior notch; genital appendage type B obpyriform; opisthosoma with slight first order differentiation and posterior second order differentiation; anterior and posterior margins of tergites crenulated; postabdominal tergites ornamented with longitudinal ridges; telson lanceolate; ventral integument covered with small pustules.

Stratigraphic range: Early Devonian.

Type species: *Vinetopterus struvei* (STØRMER, 1974) n. gen.

Included species: *Vinetopterus martini* n. sp.

Remarks: *Vinetopterus* n. gen. can be differentiated from *Drepanopterus* in possessing an ornament consisting of longitudinal ridges on the postabdominal segments, a slight first order differentiation of the opisthosoma, shorter appendages, and possibly also the shape of podomere 7a of appendage VI, which seems to be more slender and rectangular in *Drepanopterus* and *Moselopterus*.

The little known species *Stylonurella*? *arnoldi* (EHLERS, 1935) from the Late Devonian of Pennsylvania also shows a crenulate prosomal margin (EHLERS 1935: pl. 1, fig. 3), but can easily be distinguished from *Vinetopterus* by the more parabolic shape of the prosoma, the slender preabdomen, and the very large, prominent lateral eyes. Judging from the shape of the prosoma, the dorsal ornamentation of the integument and the likely presence of an obturbinate metastoma (EHLERS 1935: pl. 1, figs. 2, 4), the affinities of *Stylonurella*? *arnoldi* more probably lie with the family Rhenopteridae STØRMER, 1951.

Vinetopterus struvei (STØRMER, 1974) n. gen.

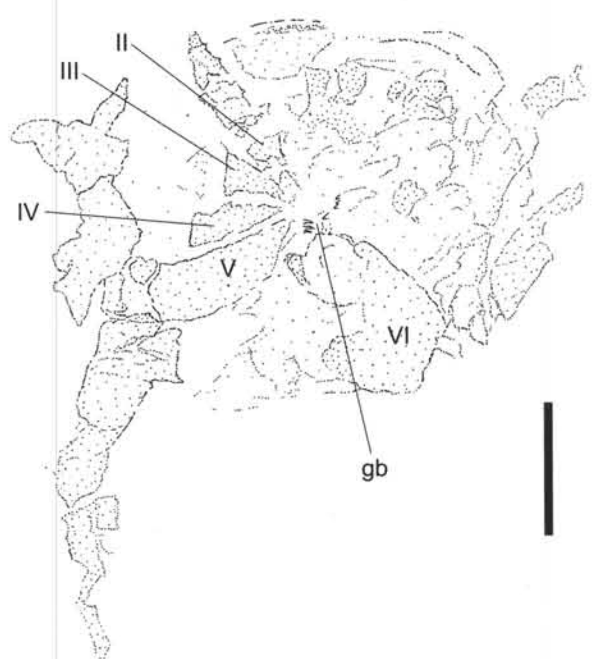
Text-figs. 2c,d, 3a, 4, 5a-d, 6a-d, 13a

1974 *Drepanopterus struvei* n. sp. - STØRMER: 383-386, text-figs. 18-20, pl. 1 figs. 2-4.

1976 *Drepanopterus struvei* STØRMER 1974. - STØRMER: tab. 2.

Diagnosis: Small to moderately sized *Vinetopterus* n. gen. possessing a relatively long pretelson and telson.

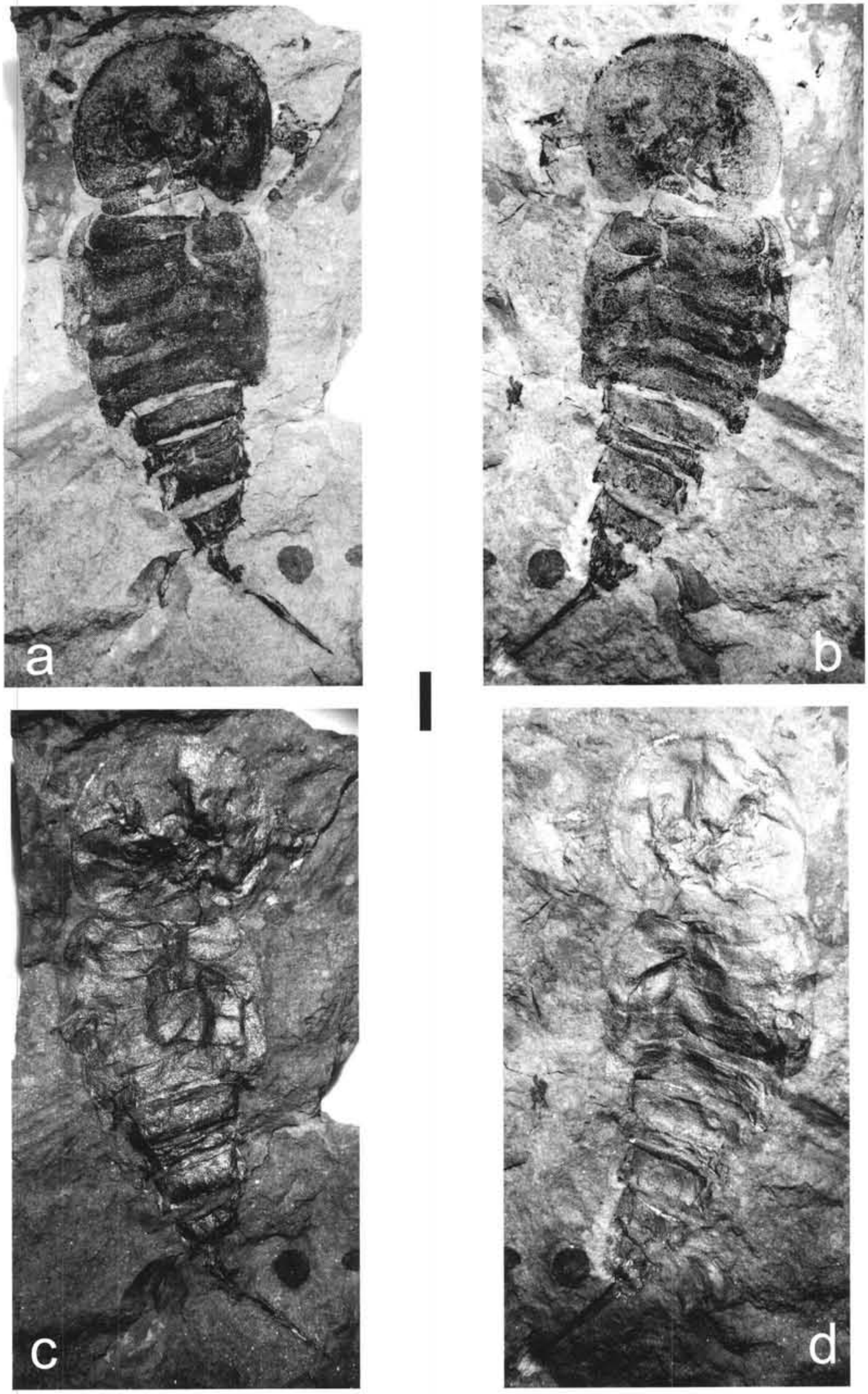
Description: The holotype of this species (SMF VIII 191a/b) (figs. 2c,d, 3a, 4) is unfortunately rather faint with weak contrast to the matrix. Furthermore a lot of fragmented plant material obscurs details of the eurypterid cuticle. The exact outlines of many morphological features are thus difficult to identify. Here we only provide additional evidence that serves to complement STØRMER's original description. SMF VIII 191a shows ventral structures in the prosomal area that



Text-fig. 4. *Vinetopterus struvei* (STØRMER, 1974) n. gen., holotype SMF VIII 191a, Emsian of Alken, interpretative drawing of prosomal region in ventral view (cf. text-fig. 3a). Scale bar = 5 mm.

were not described by STØRMER (1974) (fig. 3a, 4). The arrangement of the coxae of appendages II-V is clearly visible on the left side of the specimen. All these coxae are slender and roughly triangular in outline. Some teeth of the gnathobases are seen in the central area of the prosoma. Remains of the coxa of appendage VI are preserved to the posterior right side of the prosoma, showing that this structure was very massive and powerful with a more rectangular outline. In the left postero-lateral portion of the prosoma there is a prominent structure that we interpret as the displaced remains of appendage V or VI. At least three podomeres (the exact numbering is unsure, possibly 4-6) can be identified. The most proximal is 2.1 mm long and 2.7 mm wide, the second 1.8 mm long and 2.8 mm wide, the third 3.0 mm long and 2.3 mm wide. The remaining part of the appendage is insufficiently preserved. In the more anterior portion of the prosoma, appendage II is also preserved, but a detailed description of individual podomeres is not possible. We can only state that this appendage is approximately 5.0 mm long and 1.2 mm wide, tapering distally. The structures that are shown in STØRMER's drawing (1974: text-fig. 18) to the right side of the prosoma cannot be confirmed as representing remains of appendages by the present study. The same is true for the seemingly triangular area in the anterior portion of the prosoma that reminded STØRMER of a similar structure in *Limulus*. In the opisthosoma the only feature not recognized by STØRMER are the prolonged lateral epimera of the postabdominal segments, which are indicated in the fourth postabdominal segment of the counterpart specimen SMF VIII 191b. The small pustules covering the ventral integument in this species are wonderfully demonstrated in the holotype specimen (fig. 3a).

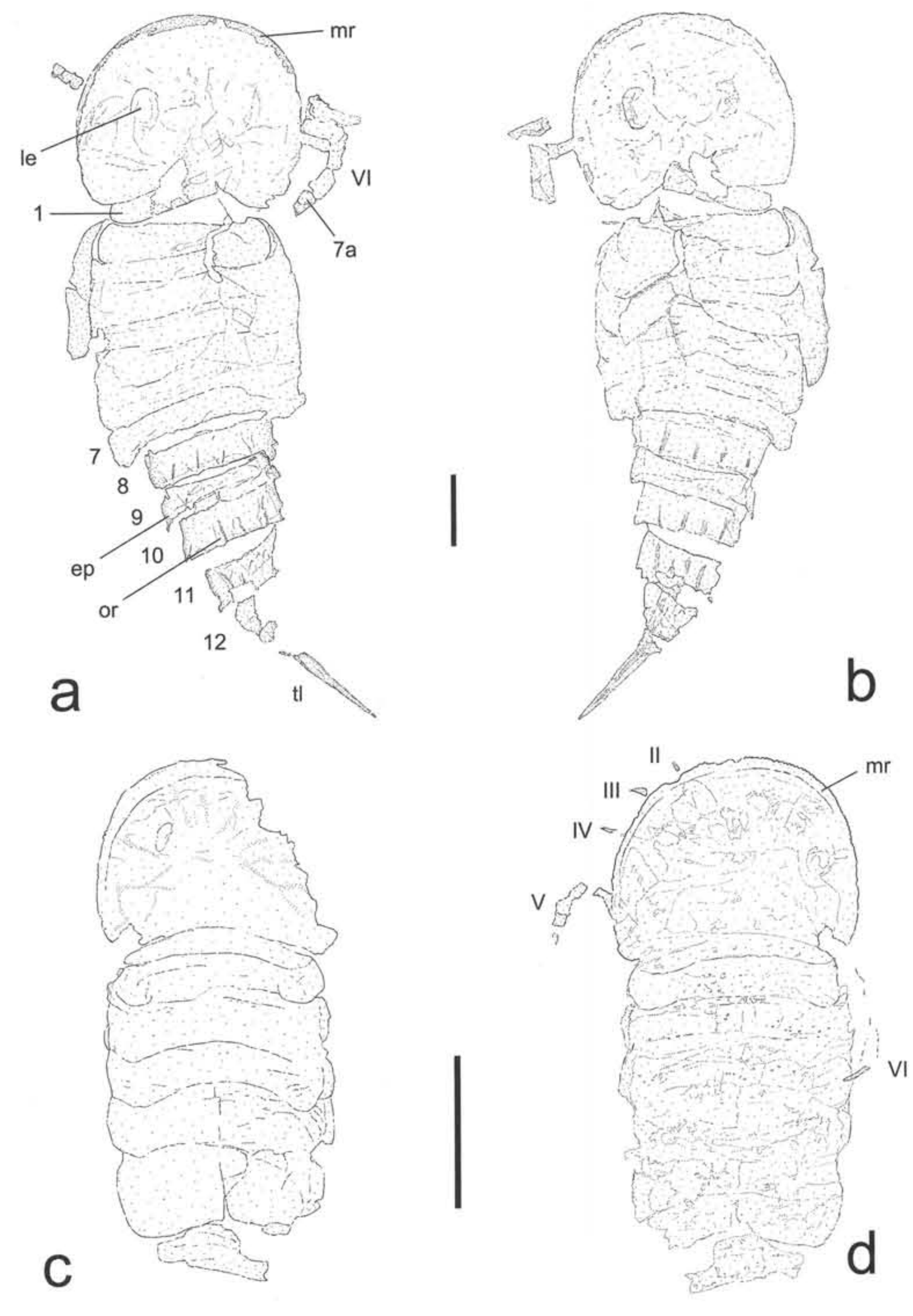
614-Da/b: This specimen (figs. 5a-d, 6a,b) represents the best preserved example of this species from Alken. The total length, including the telson, is 49 mm. The horseshoe-shaped prosoma is well rounded with slightly convex lateral margins and rounded postero-lateral corners. It is widest in the region posterior to the lateral eyes. A truncated median anterior border, as mentioned by STØRMER (1974: 384), is not present (see also description of the holotype). In the anterior portion a narrow marginal rim is visible. The margins of the carapace are distinctly crenulate, the crenulation decreasing postero-laterally. The length of the prosoma is not clearly demonstrated due to its posterior border being damaged by the action of some burrowing organism and compression. It is about 26 mm long, with a maximum width of 33 mm. Thus, the length/width ratio is 0.79. The position of the ovocrescentric lateral eyes, about 2.9 mm long and 1.9 mm wide, is centrimesial. Two median ocelli seem to be present about midway between the lateral eyes. Traces of the posterior prosomal appendages are preserved. They probably belong to appendages V and VI, but the exact shape of individual podomeres is hardly recognizeable. However, in appendage VI five relatively short podomeres can be discerned, including an apparently flat, lobate projection at the penultimate podomere. The opisthosoma shows a slight first order differentiation into pre- and postabdomen and a posterior second order differentiation, indicated by the presence of prolonged lateral epimera in the postabdomen. The preabdomen has a subrectangular outline, being approximately as wide as the prosoma and about 33 mm long. As usual in these compression fossils the borders of the slightly displaced tergites and sternites are superimposed. The first tergite is apparently slightly reduced, squeezed beneath the posterior prosomal margin and broken. The seventh and last preabdominal tergite possesses slightly prolonged but blunt postero-lateral corners. There is a marked decrease in segment width from the preabdomen to the postabdomen, the postabdomen further tapering gradually posteriorly. The first postabdominal tergite is approximately 3.3 mm long and 9.5 mm wide, the pretelson of about the same length and 4.3 mm wide. In their posterior portions the postabdominal segments show a distinct ornament consisting of longitudinal ridges terminating at the posterior border of the segments. Four of these ridges are found in the first four postabdominal segments. There might be only two ridges in the pretelson. The postabdominal segments possess a narrow anterior band representing the portion, which was overlapped by the anteriorly situated segment. In the anteriormost postabdominal segment this band is about 0.4 mm long. The telson is styliform, 8.1 mm long and 1.9 mm wide at its triangular base. The ventral integument of the whole animal is cover-



Text-fig. 5. *Vinetopterus struvei* (STØRMER, 1974) n. gen., Emsian of Alken. Large individual, 614-D, part and counterpart. – a-b. Alcohol immersion and polarized light. – c-d. Alcohol immersion and normal light. Scale bar = 5 mm.

ed with small pustules, as in STØRMER's type material of this species. All margins of segments, at least of the tergites, are crenulated, although more delicate than in the prosomal margin.

615-Da/b is a small specimen (figs. 6c,d, 11c,d), consisting of prosoma, the entire preabdomen and remains of the appendages. The total preserved length is 17.3 mm. The prosoma is well-rounded, about 5.8 mm long, 8.0 mm wide, making a length/width ratio of 0.73. A narrow marginal rim and a distinctly crenulated carapace margin can be observed (fig. 11d). The postero-lateral corners of the prosoma are rounded, the posterior margin being slightly concave. The lateral eye, approximately 0.9 mm long, is in a centrimesial position. In 615-Da traces of nearly all prosomal appendages



Text-fig. 6. *Vinetopterus struvei* (STØRMER, 1974) n. gen., Emsian of Alken, interpretative drawings. – a-b. Large individual, 614-D, part and counterpart. – c-d. Small individual, 615-D, part and counterpart. Scale bars = 5 mm.

are recognizeable, but the exact shape of individual podomeres remains obscure. Appendage VI terminates in a powerful spine, 0.9 mm long. The preabdomen is subrectangular in outline, about 10.0 mm long and 7.6 mm wide. The first preabdominal tergite is slightly reduced.

Remarks: The horseshoe-shaped prosoma and the recognizeable features of the prosomal appendages, especially the expanded podomere 7a in appendage VI, verify STØRMER's (1974) placement of this species in the family Drepanopteridae. Additionally the new material shows that there is both a slight first and second order differentiation of the opisthosoma. The ornamentation on the dorsal side of the postabdominal segments consisting of longitudinal ridges as well as the presence of lateral epimera on these segments are also newly recognized features of *V. struvei*. Unfortunately many characters, namely the organization of the anterior prosomal appendages and of the genital appendage type A, remain unknown. The metastoma and the genital appendage type B are only known from one of STØRMER's paratypes (SMF VIII 145). We concur with this author's statement that this specimen can properly be assigned to *Drepanopterus* [=*Vinetopterus*] *struvei* with respect to its dense ventral pustulation, which is unique among the Alken eurypterids.

Vinetopterus martini n. gen., n. sp.

Text-figs. 7a-d, 8d, 9a-e, 10a-e, 13b

Etymology: To honour the son of PETER MÜLLER (Langenhahn), MARTIN MÜLLER, who found the holotype specimen.

Holotype: PWL 2002/5010a,b LS.

Type horizon and type locality: Early Devonian, Siegenian. Near the old entrance of the Alvensleben-Stollen, south of Burglahr in the Wied valley, Westerwald (MTB sheet 5311 Altenkirchen R: [33]93 900, H: [56]09 920).

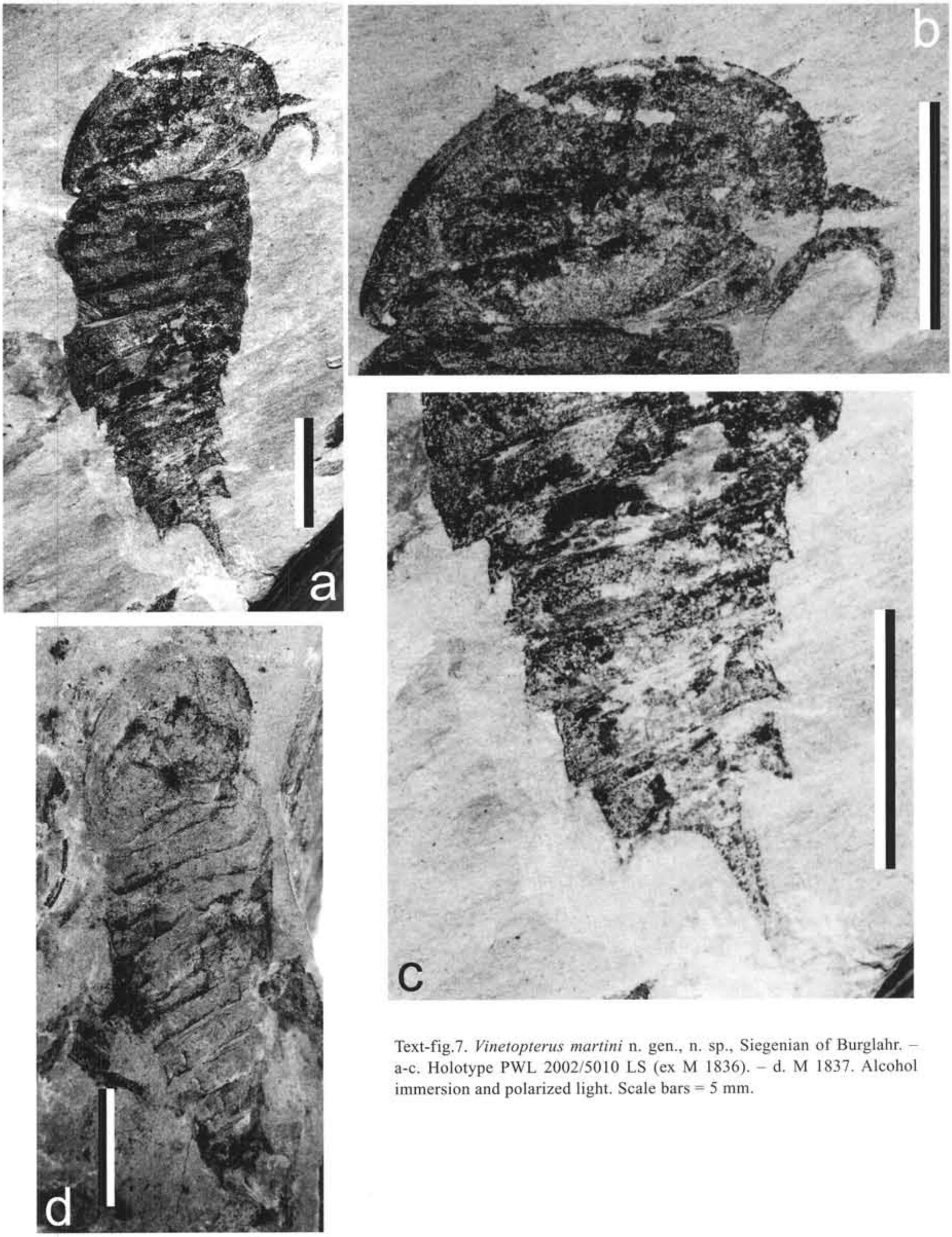
Additional material: Specimen M 1837 from the same horizon and locality as the holotype. Specimens PWL 2000/5015a,b LS; PWL 2000/5016 LS; PWL 2000/5021 LS; 694-D; 695-D. All from the Early Devonian (Siegenian) of Hombach. Roughly 0.5 km SSE of the centre of the small village of Hombach/Westerwald (near Neustadt/Wied-Fernthal) (MTB sheet 5410 Waldbreitbach R: [26]03 855, H: [56]06 220).

Diagnosis: Small *Vinetopterus* n. gen. with prosomal postero-lateral corners truncated and rounded; prosomal appendages very short; pretelson not elongated; telson short lanceolate.

Description: The holotype PWL 2002/5010a,b LS (ex M 1836) (figs. 7a-c, 8d) is the most completely preserved specimen of this species. The horseshoe-shaped prosoma, 5.3 mm long and 8.9 mm wide, has a length/width ratio of 0.60 (distorted!). A narrow marginal rim, widest anteriorly and slowly tapering towards the rounded postero-lateral corners, and a crenulate prosomal margin is present. The posterior prosomal margin, hidden by the first preabdominal tergite, seems to be nearly straight. Eyes cannot confidently be recognized. The distal portions of what we interpret as representing the prosomal appendages III-VI are preserved. They are relatively small and slender in comparison to other members of the family. The anterior appendages III-V terminate in a spine. Leg V is nonspiniferous, whereas in leg IV there is weak evidence of a spinelike projection in the ?penultimate podomere. However, individual podomeres can only be identified in appendage VI. These are nonspiniferous and relatively short with a length/width ratio of around two, and the appendage terminates in a spine. The subrectangular preabdomen is 7.6 mm long and 7.8 mm wide. The first slightly reduced tergite is 0.9 mm long, the remaining tergites being of subequal length, approximately 1.1 mm long with rounded postero-lateral corners, except the last one which seems to possess slightly prolonged postero-lateral corners. The postabdominal segments clearly show prolonged lateral epimera and are all about 1.1 mm long. The first postabdominal segment is 6.0, the second 5.1, the third 4.8, the fourth 4.1, and the pretelson 3.3 mm wide. They possess a narrow anterior band, most clearly demonstrated in the pretelson where it measures 0.3 mm in length. A sculpturing with longitudinal ridges is only very weakly exposed. The telson shows a preserved length of 3.3 mm. Proximally it is at least 2.2 mm wide, but the triangular base tapers rapidly. The integument of this specimen is ornamented with small pustules.

M 1837 (figs. 7d, 10e) is a less well preserved and slightly laterally compressed specimen, 21.8 mm long. The prosoma is roughly 5.5 mm long and 6.8 mm wide. The length/width ratio of 0.81 is obviously due to distortion. The genal regions are rounded, the posterior margin is slightly concave. Traces of pustules covering the integument are present. Traces of the lateral eyes, in approximately centrimesial position, show up as dark spots in polarized light. The preabdomen has a maximum width of 6.8 mm. There is a very weakly developed contraction from the pre- to the postabdomen. The postabdomen is slightly but evenly tapering, showing clearly prolonged lateral epimera of individual segments. An ornamentation consisting of up to 4 longitudinal ridges on tergites 8 to 11 is weakly indicated. The preserved length of the telson is 1.8 mm.

694-D (figs. 9a, 10a) is a relatively complete specimen, approximately 27 mm long, lacking only prosomal appendages I-V. The rock matrix is heavily influenced by weathering, leaving only a whitish impression of the fossil. However, the outline of the little distorted horseshoe-shaped prosoma (TOLLERTON 1989) is beautifully preserved. It is 8.0 mm long and 11.3 mm wide, giving a length/width ratio of 0.71, and the lateral angle lies between 70° and 80°. The posterior margin is slightly concave, the postero-lateral corners appear somewhat truncated and thus are not so evenly rounded as in *V. struvei*. A narrow marginal rim can be best observed on the left side of the specimen. In the anteriormost region the crenulate prosomal margin is preserved. The remains of the last prosomal appendage (VI) show no details, but the short and slender form terminating in a spine is recognizeable. The subrectangular preabdomen is approximately 8.0 mm long and 10.5 mm wide. On the left side the rounded lateral portions of the sternites are exposed. In the tapering postabdomen the tenth to twelfth tergites are reasonably well preserved, showing the ornament of longitudinal ridges, four on the tenth and two on the pretelson. The presence of only three ridges on the eleventh tergite might be preservational. The eleventh segment and the pretelson show the anterior narrow band, approximately 0.3 mm long in the pretelson. The pre-



Text-fig.7. *Vinetopterus martini* n. gen., n. sp., Siegenian of Burglahr. – a-c. Holotype PWL 2002/5010 LS (ex M 1836). – d. M 1837. Alcohol immersion and polarized light. Scale bars = 5 mm.

telson is 1.8 mm long and 4.1 mm wide. The telson with its triangular base has a preserved length of 3.5 mm.

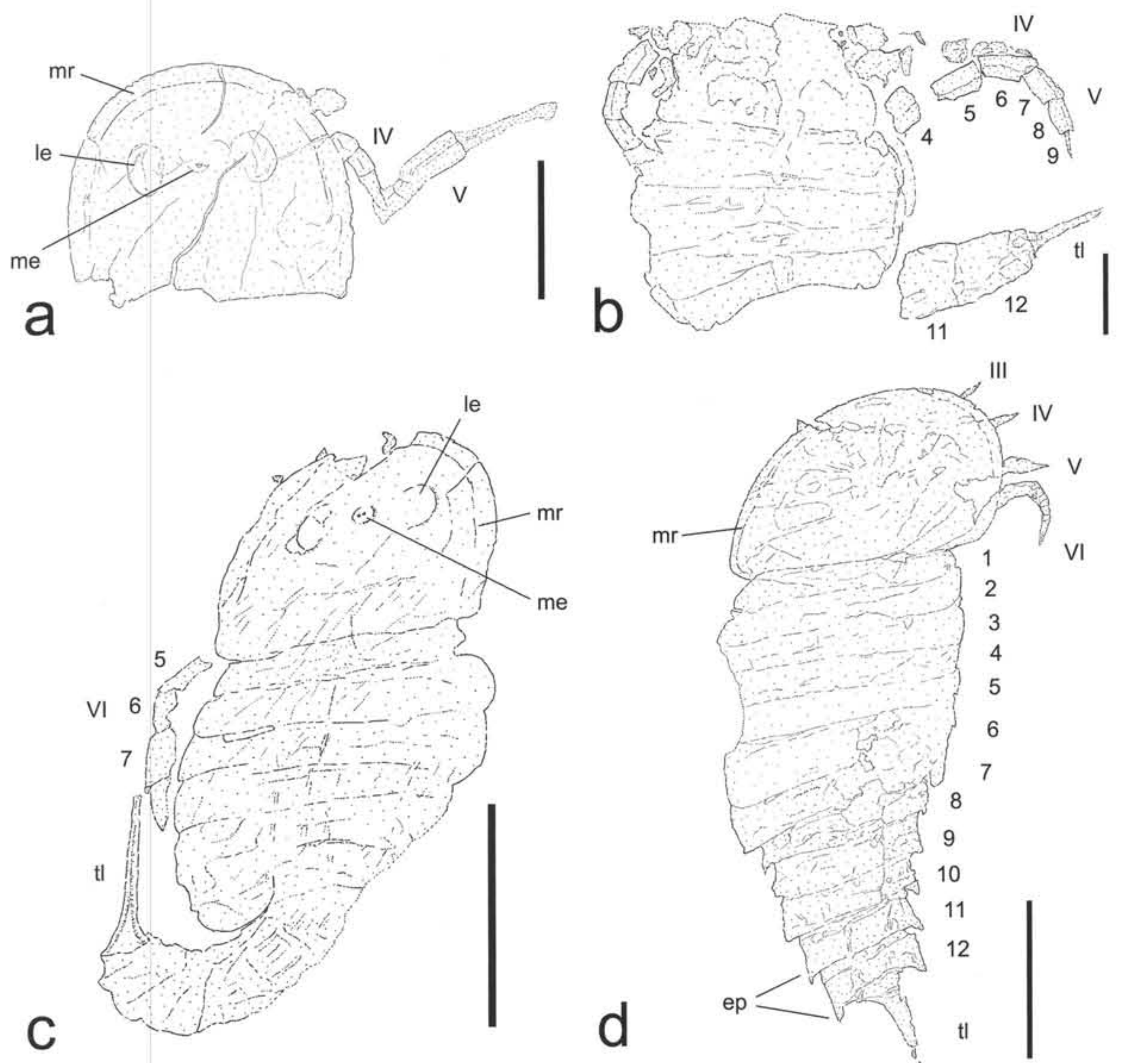
Specimen PWL 2000/5015a,b LS (figs. 9b, 10b) is small, strongly telescoped and somewhat distorted. The total preserved length is 20.7 mm. The prosoma is 5.6 mm long and 9.4 mm wide, but the resulting length/width ratio of 0.60 is due to compression in the longitudinal axis. On the right side of the animal remains of prosomal appendages II-V are preserved, but again no detailed description is possible, except that these legs are short and slender, possessing short podomeres and a spine-like distal podomere. The single structure on the right side of the fossil may represent appendage V or VI. The opisthosoma is strongly telescoped and shows little detail, except the prolonged lateral epimera of the postabdomen. The telson is 3.8 mm long and possesses a median ridge.

PWL 2000/5021 LS (figs. 9c,d, 10c) consists of a prosoma and preabdomen. The posterior part of the fossil is strongly weathered and morphological details are obscured. Thus, only the prosomal region is figured. The prosoma is 6.9 mm long and 10.0 mm wide, the length/width ratio being 0.69. The crenulated prosomal margin and the narrow marginal rim, about 0.5 mm wide anteriorly, are clearly exhibited. The distal podomeres of an appendage, probably VI, are visible. Podomeres 6 and 7 are subquadrate in outline, approximately 0.7 mm long and wide. The penultimate podomere is 1.3 mm long and 0.6 mm wide proximally. The distal-most podomere is slender and pointed, approximately 0.7 mm long and 0.2 mm wide proximally. Both of these podomeres taper distally. In the centre of the prosoma the teeth of some of the coxal gnathobases are preserved. No further details can be observed.

PWL 2000/5016 LS (figs. 9e, 10d) is a relatively large but poorly preserved specimen showing portions of the prosoma, opisthosoma and telson. The maximum preserved length is 34.6 mm. The prosoma shows the typically rounded genal region. Ornamentation on the gradually tapering postabdominal segments is visible. The telson is 5.0 mm long.

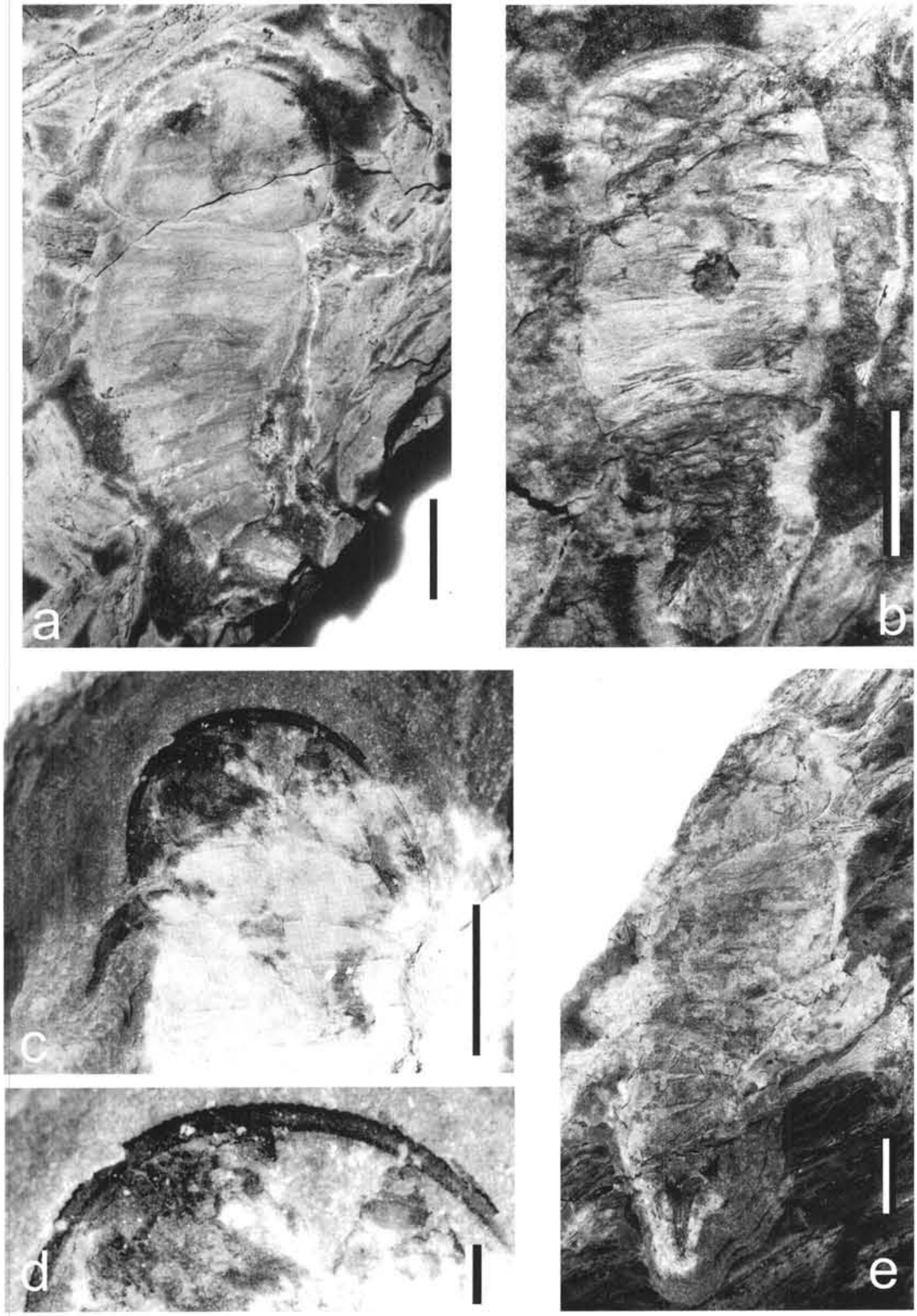
Remarks: *V. martini* n. gen., n. sp. is similar to *V. struvei* n. gen. in overall body form with a slight first and second order differentiation of the opisthosoma. Both species show a reduced first preabdominal tergite, an ornament of longitudinal ridges on the postabdomen, crenulate prosomal and tergite margins, and a ventral integument covered with small pustules.

The main features that serve to distinguish *V. martini* from *V. struvei* are the following: The slightly broader prosoma with somewhat more truncated genal regions, the shorter prosomal appendages, the relatively shorter pretelson, and the shorter telson. However, it should be noted that the prosomal appendages, especially the anterior ones, are insufficiently



Text-fig. 8. Interpretative drawings. – a-b. *Alkenopterus brevitelson* STØRMER, 1974, Emsian of Alken. – a. 624-Da. – b. 697-Da. – c. *Alkenopterus burglahrensis* n. sp., holotype PWL 2002/5011 LS (ex 616-D), Siegenian of Burglahr. – d. *Vinetopterus martini* n. gen., n. sp., holotype PWL 2002/5010 LS (ex M 1836), Siegenian of Burglahr. Scale bars = 5 mm.

known from the material and some other important morphological features such as the metastoma and genital appendages are totally unknown. With the material at hand the presence of an expanded podomere 7a in prosomal appendage VI cannot be substantiated in *V. martini*. However, we think this is due to preservation and prefer to assign it to *Vinetopterus* n. gen.



Text-fig. 9. *Vinetopterus martini* n. gen., n. sp., Siegenian of Hombach. – a. 694-D. – b. PWL 2000/5015b LS. – c. PWL 2000/5021b LS. – d. PWL 2000/5021b LS, detail of anterior prosoma showing crenulate prosomal margin and marginal rim. – e. PWL 2000/5016 LS. Alcohol immersion and polarized light. Scale bars = 5 mm, except in d = 1 mm.

Superfamily inc. sed.
Family Alkenopteridae n. fam.

Etymology: The name of the family is derived from the type genus.

Type and only genus: *Alkenopterus* STØRMER, 1974.

Diagnosis: Leg V non-spiniferous, *Drepanopterus*-type B; leg VI non-spiniferous, *Alkenopterus*-type.
Secondary characters: Opisthosoma shows a first order differentiation into a pre- and postabdomen.

Stratigraphic range: Early Devonian.

Remarks: Since *Alkenopterus* obviously possesses no podomere 7a in prosomal appendage VI it cannot be placed in family Drepanopteridae. The morphologies of the non-spiniferous appendages V and VI differ from all nine standard types of non-spiniferous legs suggested by TOLLERTON (1989). The *Alkenopterus* leg V is of the *Drepanopterus*-type B (as defined above) (fig. 12d). Although leg VI resembles the non-spiniferous *Dolichopterus*-type, there is no close comparison, as this represents appendage V in *Dolichopterus*. The individual podomeres (except the distal spine) of the *Alkenopterus*-type leg are of subequal length, moderately flattened, and a lobate penultimate podomere, as expressed in the *Dolichopterus*-type, is lacking. The length/width ratios of individual podomeres do not exceed 2. The *Alkenopterus*-type of leg is most clearly expressed in the holotype specimen of *A. burglahrensis* n. sp. (fig. 12a). With all the available evidence at hand, we feel justified in formally proposing a new monogeneric family to accomodate *Alkenopterus*. Without known anterior walking legs II-IV, this family is poorly known and to place it in a superfamily would be speculative. We hope that future finds may elucidate the morphology of the anterior walking legs and the higher systematic placement of Alkenopteridae n. fam.

Genus ***Alkenopterus*** STØRMER, 1974

Diagnosis: Small to moderately sized eurypterid with large horseshoe-shaped prosoma with broad marginal rim; ovolunate and prominent centrimesially positioned lateral eyes; opisthosomal segments without lateral epimera; preabdomen short and broad; postabdomen slender; telson styliform; integument without ornamentation (emended from STØRMER 1974).

Stratigraphic range: Early Devonian.

Type species: *Alkenopterus brevitelson* Størmer, 1974.

Included species: *Alkenopterus burglahrensis* n. sp.

Alkenopterus brevitelson STØRMER, 1974

Text-figs. 2a-b, 3b, 8a-b, 11a-b,e, 12b-d, 13c

1974 *Alkenopterus brevitelson* n. gen., n.sp. - STØRMER: 386-388, text-figs. 21-22, pl. 1 fig. 1.

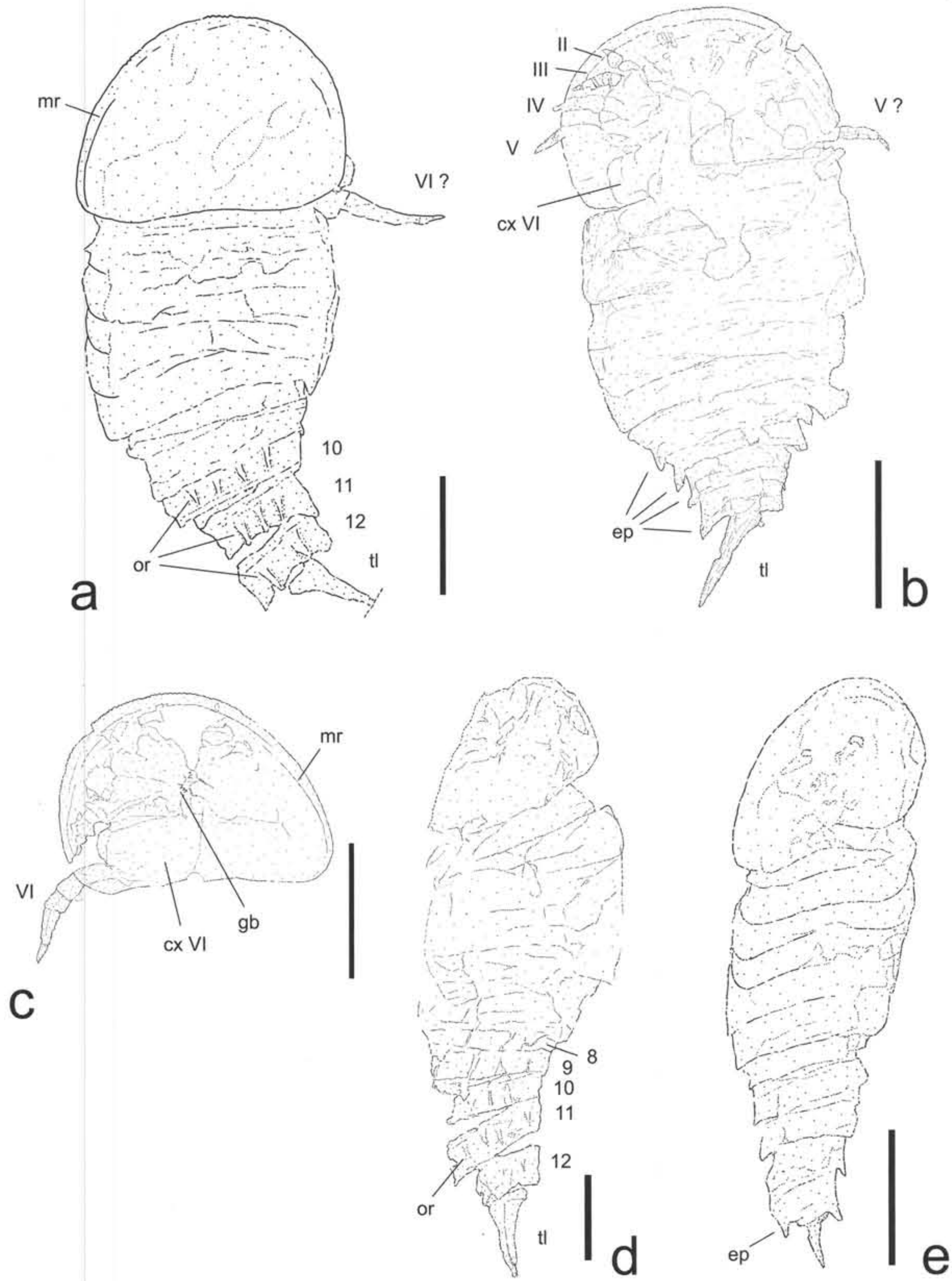
1976 ? *Alkenopterus brevitelson* STØRMER, 1974. - STØRMER: 117, tab. 2, pl. 5 fig. 4.

Diagnosis: *Alkenopterus* with short styliform telson.

Description: Besides a reevaluation of the holotype specimen there are only two newly collected specimens of this species sufficiently preserved to allow description.

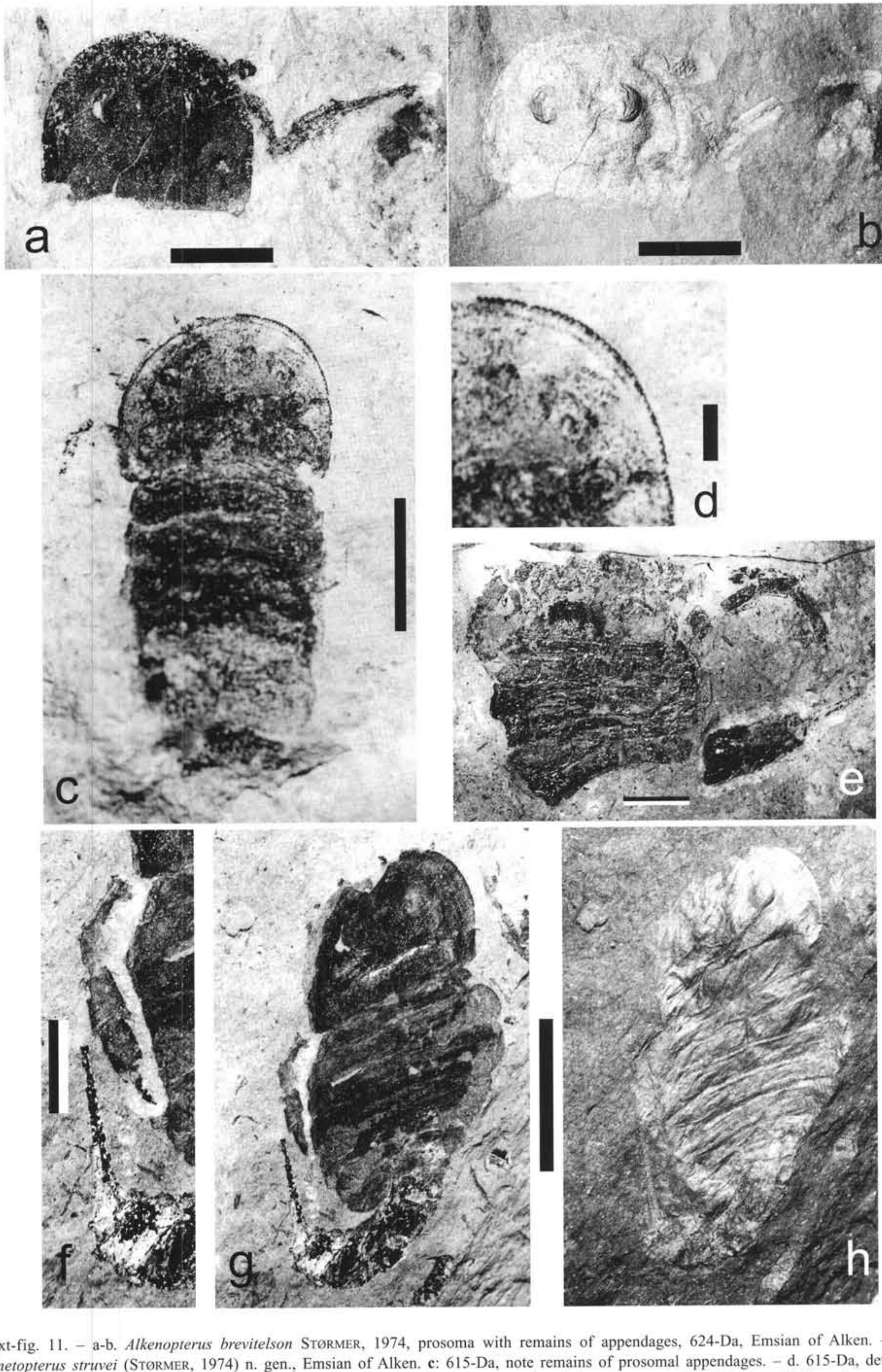
STØRMER's description of the holotype specimen SMF VIII 150a/b (fig. 2a,b in the present paper) is generally accurate and comprehensive. However, some of our observations differ from those made by the original author. As evident on the counterpart specimen SMF VIII 150b the maximum width of the preabdomen exceeds that of the prosoma. In the opisthosoma there is, in contrast to STØRMER'S observations, a more-or-less abrupt contraction in the transition from the pre- to the postabdomen. Thus the opisthosoma shows a moderate first order differentiation. STØRMER described the fourth postabdominal segment as being triangular in outline, which cannot be sustantiated by the present study. This segment is, like the neighbouring ones, subrectangular in outline (see also STØRMER 1974: text-fig. 21a). The longitudinal furrows and ridges that STØRMER noted in the posterior postabdominal segments might be a preservational feature. Concerning the prosomal appendages preserved in the holotype (figs. 3b, 12b,c) we think they more probably represent VI rather than V, because there are slight differences in the morphology of individual podomeres, especially the most distal ones, when compared to the posteriormost prosomal appendage preserved in specimen 697-Da which we interpret as appendage V (fig. 12d). The following approximate measurements of individual podomeres can be given: In the appendage preserved on the left side of the part, only the shape of the most distal podomeres is clear. The basitarsus is at least 3.0 mm long and 2.2 mm wide at its distal end. The tarsus is 2.8 mm long and 1.7 mm wide distally. The posttarsus or distal spine is well preserved, 3.0 mm long and 0.5 mm wide at its base, tapering evenly distally and slightly curved. On the right side of the same specimen the five distal podomeres of appendage VI are evident. The femur is 3.7 mm long and 1.8 mm wide, the tibia 3.4 mm long and 1.6 mm wide, the basitarsus 3.3 mm long and 2.2 mm wide, and the tarsus 3.0 mm long and 1.8 mm wide. The preserved length of the distal spine is 2.7 mm with its base being 0.7 mm wide. These are only approximate values because measurements are amenable to postmortem alterations and other preservational factors, which is demonstrated in the slightly different measurements of corresponding podomeres. However, the length/width ratios of individual podomeres range from 1.5 – 2.1.

624-D is a beautifully preserved prosoma (figs. 8a, 11a,b), 8.5 mm long and 10.3 mm wide, well-rounded anteriorly with slightly convex lateral margins and distinctly cornered postero-lateral regions. The length/width ratio is 0.83, the lateral angle measuring between 70° and 80°. A relatively broad marginal rim is present, approximately 0.6 mm wide anteriorly and 0.8 mm wide laterally. Two prominent, ovocrescentric to ovolunate lateral eyes are present in a centrimesial position, each about 1.8 mm long and 1.3 mm wide. Midway between them a median eye tubercle is positioned. The symmetrical arrangement of the lateral eyes shows that the prosoma has not been subject to strong postmortem alterations (TOLLERTON 1987). Remains of two of the appendages are preserved, probably IV and V. The recognizeable podomeres of appendage IV are short, only slightly longer



Text-fig. 10. – a-e. *Vinetopterus martini* n. gen., n. sp., Siegenian, interpretative drawings. – a. 694-D, Hombach. – b. PWL 2000/5015b LS, Hombach. – c. PWL 2000/5021 LS, Hombach. – d. PWL 2000/5016 LS, Hombach. – e. M 1837, Burglahr. Scale bars = 5 mm.

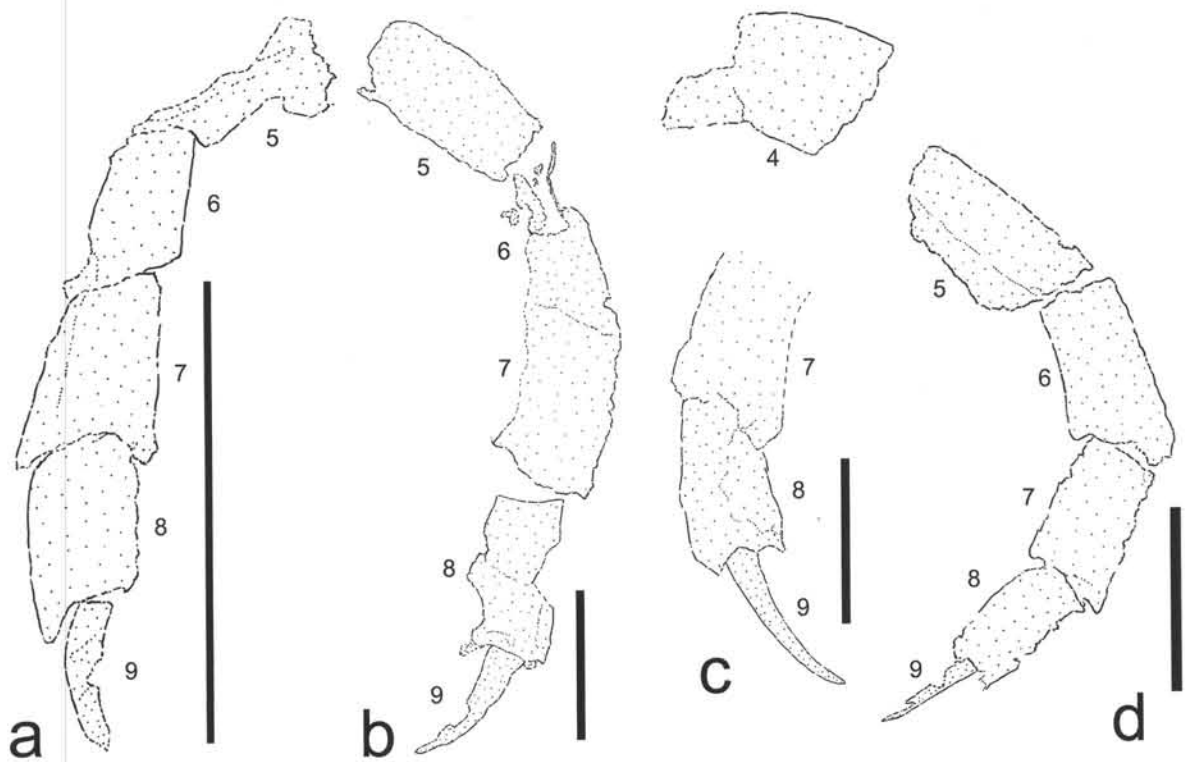
than wide. In appendage V one of the podomeres (probably the fifth) is 2.3 mm long and 1.1 mm wide. The more distal podomeres are poorly preserved and their shape cannot be determined. However, the appendage is similar in size to that



Text-fig. 11. – a-b. *Alkenopterus brevitelson* STØRMER, 1974, prosoma with remains of appendages, 624-Da, Emsian of Alken. – c-d. *Vinetopterus struvei* (STØRMER, 1974) n. gen., Emsian of Alken. **c**: 615-Da, note remains of prosomal appendages. – d. 615-Da, detail of prosoma showing crenulate prosomal margin and marginal rim. – e. *Alkenopterus brevitelson* STØRMER, 1974, Emsian of Alken, fragmentary specimen showing remains of prosomal appendages, preabdomen, and posterior part of postabdomen including telson. – f-h. *Alkenopterus burglahrensis* n. sp., holotype PWL 2002/5011 LS (ex 616-D), Siegenian of Burglahr. – f. Detail of prosomal appendage VI after preparation. – g-h. Entire specimen prior to preparation of appendage VI. Alcohol immersion and polarized light, except b and h photographed in normal preserved in the holotype specimen. All podomeres show the presence of a longitudinal furrow.

697-Da is a fragmentary specimen (figs. 8b, 11e). The exact shape of the prosoma remains obscure. There are remains of three prosomal appendages on the right side, probably belonging to appendages III-V. In appendages III and IV the individual podomeres are rather fragmentary and only the two distal spurs can be described as narrow and pointed, being 0.9 and 1.3 mm long respectively. In appendage V the six most distal podomeres are preserved. The fourth is of uncertain length and 2.4 mm wide, the femur approximately 3.0 mm long and at least 1.7 mm wide, the tibia 3.5 mm long and 1.7 mm wide, the basitarsus 2.6 mm long and 1.5 mm wide, the tarsus 2.2 mm long and 1.2 mm wide, resulting in length/width ratios between 1.7 and 2.1. The podomeres show a longitudinal furrow. The distal spur is 1.7 mm long, slender and sharply pointed. The preabdomen shows convex lateral margins, its central portion being wider than the posterior margin of the prosoma. Only the two distal segments of the postabdomen and the telson are preserved. Segment 11 is of uncertain length and approximately 4.4 mm wide. The pretelson is about 5.2 mm long and 3.7 mm wide. The preserved length of the telson is 5.1 mm.

Remarks: The newly collected material of *Alkenopterus brevitelson* essentially confirms STØRMER's (1974) observations. However, the postabdomen seems to be more strongly contracted relative to the preabdomen than described (and diagnosed) by the original author, and also stronger than in *Vinetopterus struvei* n. gen. Thus, there is a first order differentiation of the opisthosoma of *A. brevitelson*. STØRMER (1974) described one pair of prosomal appendages preserved in the holotype specimen, thought to represent either appendage V or VI. By comparison with specimen 697-D we are convinced that the appendages preserved in the holotype represent appendage VI. A comparison of length/width (L/W) ratios of individual podomeres in appendages V and VI of different stylonurids supports our interpretation. Although stylonurid legs are highly variable, supporting evidence can be seen especially in the distal podomeres. All stylonurids except *Rhenopterus diensti* STØRMER, 1936 show a higher L/W ratio in the distal podomeres of appendage V than in the distal podomeres of VI. The appendage in the holotype of *A. brevitelson* has a distal spine with a L/W ratio of around 5.5 while the distal spine of the appendage preserved in 697-D has a higher L/W ratio of about 7.0 and is less strongly curved. Neither in the holotype nor in specimen 697-D has any podomere 7a been observed.



Text-fig. 12. Interpretative drawings of prosomal appendages with individual podomeres numbered. – a. *Alkenopterus burglahrensis* n. sp., left appendage VI (*Alkenopterus*-type) of holotype PWL 2002/5011 LS (ex 616-Db), Siegenian of Burglahr. – b-d. *Alkenopterus brevitelson* STØRMER, 1974, Emsian of Alken. – b. Right appendage VI (*Alkenopterus*-type) of holotype SMF VIII 150a. **c**: Distal portion of left appendage VI of holotype SMF VIII 150a. – d. Right appendage V (*Drepanopterus*-type B) of specimen 697-Da. Scale bars = 3 mm.

Alkenopterus burglahrensis n. sp.

Text-figs. 8c, 11f-h, 12a, 13d

Etymology: After the village of Burglahr close to the type locality of this species.

Holotype (and only known specimen): PWL 2002/5011a,b LS.

Type horizon and type locality: Early Devonian, Siegenian. Near the old entrance of the Alvensleben-Stollen south of Burglahr in the Wied valley, Westerwald (MTB sheet 5311 Altenkirchen R: [33]93 900, H: [56]09 920).

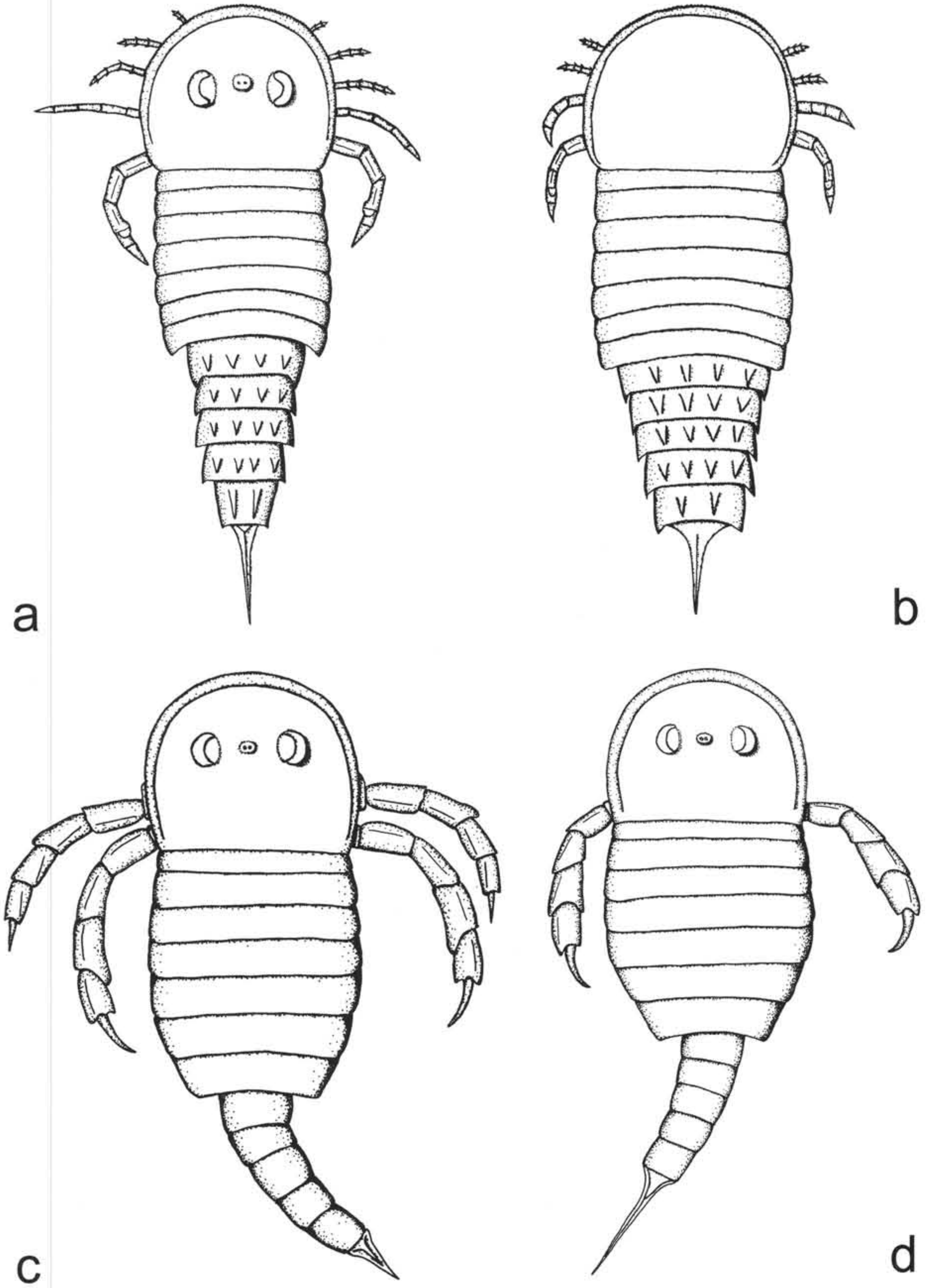
Diagnosis: *Alkenopterus* with moderately long, styliform telson.

Description: The holotype PWL 2002/5011a,b LS (ex 616-Da,b) (figs. 8c, 11f-h) is a nearly complete, somewhat distorted but otherwise well preserved small specimen, representing the only find of this new species. The fossil is approximately 20.3 mm long if outstretched. The prosoma, with slightly convex lateral margins, is 4.4 mm long and 6.4 mm wide, making a length/width ratio of 0.69. The prominent lateral eyes are positioned centrimesially. The better preserved right lateral eye is 0.8 mm long. A median eye tubercle, about 0.5 mm wide, is situated midway between the lateral eyes. Furthermore, the prosoma shows a relatively broad marginal rim (approximately 0.5 mm wide) and an angular genal region. In the anterior region of the prosoma the distal tips of some of the anterior prosomal appendages are preserved, but no further details can be observed. After photographing and drawing the specimen, five distal podomeres of the last prosomal appendage (VI), which were partially hidden beneath the preabdomen, were revealed by careful preparation (figs. 11f, 12a). The femur is poorly preserved, the tibia is approximately 1.0 mm long and 0.6 mm wide, with its lateral margins slightly diverging distally. The basitarsus has a maximum length of 1.2 mm and diverges distally where it is 0.9 mm wide. The tarsus measures 1.2 mm along its outer margin and is 0.7 mm wide. The lateral corners at the distal edges of at least podomeres 7 and 8 are somewhat prolonged. All of the preserved podomeres, except the distal spine, show length/width ratios roughly between 1.3 and 1.7. The preserved length of the distal spine is 1.0 mm, its base being 0.2 mm wide. This spine is slightly curved and probably ended in a pointed tip. The preabdomen shows convex lateral margins and is widest in its central portion, approximately 5.8 mm long and 7.0 mm wide. The first tergite seems to be slightly reduced, at least in width. The postabdomen is rather narrow implying an abrupt to moderate first order differentiation of the opisthosoma. There are no prolonged lateral epimera present in either the pre- or postabdomen. The postabdomen shows a fairly constant width of about 1.9 mm. Individual segments are hardly recognizeable; a faint ornamentation consisting of longitudinal ridges or furrows might be due to postmortem wrinkling of the cuticle. The telson is fairly long with a preserved length of 3.5 mm and a triangular base being 1.2 mm wide proximally.

Remarks: *A. burglahrensis* n. sp. shows a remarkable set of characters that indicate a close relationship to *A. brevitelson* from the younger Alken assemblage. Among these are the general shape of the prosoma, its wide marginal rim, the position and shape of the prominent lateral eyes, and the clear first order, but no second order differentiation of the opisthosoma. The present species can easily be distinguished from *A. brevitelson* by possessing a relatively long telson and slightly broader, more strongly expanded distal podomeres in prosomal appendage VI. Plotnick (1983: 71) discovered that the telson of *Eurypterus remipes* became relatively wider and shorter during ontogeny. This trend is also observable when comparing total body length to telson length in the two available specimens of *A. brevitelson*. In the larger holotype (75 mm) this ratio is roughly 13.6, whereas in the smaller paratype (50 mm) it is around 10. The holotype of *A. burglahrensis* n. sp. is rather small (20.3 mm) and shows a ratio of body length to telson length of 5.8. Although the difference compared to *A. brevitelson* is very large we cannot exclude the possibility that this is due to negative allometric growth of the telson. However, also taking into account the differences in prosomal appendage VI and the different stratigraphic ages of the fossils, the hypothesis that they represent different ontogenetic stages is considered unlikely.

Palaeoecology and taphonomy

General information concerning the Alken fossil associations can be found in SOLLE (1970), STØRMER (1976), BRAUN (1997) and DUNLOP et al. (2001). All of the newly collected stylonurid material from Alken originates from the so-called "Oberbank" deposit (SOLLE 1970) and was collected from the spoil dump. Thus, its exact position in the lithological log provided by BRAUN (1997) is uncertain. STØRMER's material probably came from the same layers, as the sediment containing his originals is the same as the host sediment of the newly collected specimens (see also SOLLE 1970). By far the most common eurypterid at Alken is *Parahughmilleria hefteri* (STØRMER 1973, 1976; MP, own observations), which is commonly associated on the same bedding planes with abundant and well preserved remains of early land plants, including sporangia (DUNLOP et al. 2001). A large number of remains of trigonotarbid arachnids has also been recorded in a single layer within this plant-rich facies by one of us (MP, unpublished). However, it must be noted that the larger stylonurids and *Alkenopterus* are preferentially found in somewhat coarser lithologies (silt to fine sand) devoid of well-preserved plant material (DUNLOP et al. 2001), but containing plant hash. These slabs often show bioturbation in the form of burrows, which were possibly made by endobenthic bivalves. These are a few to over 10 mm in diameter and filled with sediment finer and darker as the surrounding matrix (see the dark spots near the pretelson of the eurypterid in fig. 5). The chasmataspid *Diploaspis casteri* STØRMER, 1972 has also been recorded in this rock type. It is conspicuous that individual slabs sometimes contain more than one specimen of the generally rare stylonurids or *Alkenopterus*, usually representing one taxon. But on the slab containing the paratype of *Alkenopterus brevitelson* two additional specimens referable to *Moselopterus* have been observed. Specimen 697-Da (*A. brevitelson*) is associated with remains of four additional but less well-preserved specimens, probably all representing the



Text-fig. 13. Attempted reconstructions of the dorsal aspect of the eurypterid species discussed in the present paper. – a. *Vinetopterus struvei* (STØRMER, 1974) n. gen., Emsian of Alken. – b. *Vinetopterus martini* n. gen., n. sp., Siegenian of Hombach and Burglahr; eyes omitted. – c. *Alkenopterus brevitelson* STØRMER, 1974, Emsian of Alken. – d. *Alkenopterus burglahrensis* n. sp., Siegenian of Burglahr. Drawings not to scale.

same species. In their analysis of the functional morphology of mating in *Baltoeurypterus*, BRADDY & DUNLOP (1997) and BRADDY (2001) considered it likely that eurypterids were able to synchronize their moulting and mating behaviour. This would be an effective way to diminish losses by predators in the vulnerable phases in their life cycle and may have happened in particularly sheltered habitats, possibly a lagoon or pond. The layers within the Alken "Oberbank" succession yielding the stylonurid and *Alkenopterus* finds may well represent such an environment.

According to POSCHMANN & JANSEN (2003) the stylonurids from Hombach are associated with relatively abundant *Parahughmilleria* specimens, rare pterygotid remains and as yet undetermined eurypterid remains. Trigonotarbid and phalangiotarbid arachnids and the chasmataspid *Diploaspis* sp. have also been recorded, as well as rare remains of vertebrates, e.g. *Rhinopteraspis dunensis* (ROEMER, 1855), and the brachiopods "*Lingula*", *Orbiculoidea* and *Rhenorensselaeria*, the latter not occurring on the same bedding planes as the eurypterids. The fossil host sediment is filled with stems of early land plants. On some bedding planes sporangia of *Taeniocrada*-like habitus are abundant.

At the Burglahr site the fossil-bearing rock is again filled with the remains of early land plants and *Taeniocrada*-like sporangia. Bioturbation in the form of burrows, similar to those occurring at Alken, is frequent. The associated fauna comprises inarticulate brachiopods, abundant but as yet undetermined eurypterids (cf. *Parahughmilleria* sp.), trigonotarbid arachnids and the chasmataspid *Diploaspis* sp., the latter two being rare.

In spite of the different stratigraphical ages of Alken and the Westerwald sites respectively, the eurypterid associations of all three localities bear a striking similarity, which we interpret to reflect similar ecological conditions. They might be described as adelophthalmid-stylonurid-*Alkenopterus*-associations (according to the systematics of TOLLERTON (1989)) or Hughmilleriidae-Drepanopteridae-Stylonuroidea associations in the sense of STØRMER (1974, 1976), thus corresponding to biofacies 3 of KJELLESVIG-WAERING (1961). Interestingly, *Diploaspis* always occurs in association with the eurypterids *Parahughmilleria*, *Vinetopterus* n. gen., and probably *Alkenopterus* (there is only a doubtful record of this genus from Hombach). In associations where pterygotids are more abundant (e.g. Overath or Willwerath), *Diploaspis* and the above mentioned eurypterids are either lacking or rare. Both STØRMER (1976) and BRADDY (2001) discussed some 'inter-phase mixing' of eurypterid ecological phases (see these authors for a definition and discussion) with respect to Alken. However, it must be noted here, that pterygotids are very rare in the Alken assemblage and that inter-phase mixing, although it might actually be present to a very limited extent, seems to be largely due to a sampling of different levels in the succession. As BRAUN (1997) and DUNLOP et al. (2001) remarked, there are considerable ecological changes present within the Oberbank deposit and the sequence cannot be treated as a unit in terms of palaeoecology. The pterygotids (and carcinosomatids) may have entered the Alken palaeoenvironment at times of increased marine influence, which is also documented by layers yielding e.g. bivalves, articulate brachiopods, and tentaculites. Thus, the relative abundance of arthropods given by STØRMER (1976: p.126) is only true if the Alken fauna is considered as a whole. Even the very rare trigonotarbids may dominate an association if only a single layer of a few mm of thickness is evaluated (MP, unpublished observations). Only a layer by layer excavation of the Alken "Oberbank" deposit would be suitable to reveal more natural associations and diminish the effects of a stratigraphic collecting bias that may result in a seeming inter-phase mixing. The same is true for Hombach, where pterygotid remains occur very rarely together with *Parahughmilleria* and the stylonurids. Here pterygotids preferentially are associated with remains of jawless vertebrates (layer 0, sensu POSCHMANN & JANSEN 2003). This cooccurrence of pterygotids and jawless vertebrates is also known from a number of other localities in the Rhenish Slate Mountains, e.g. Overath (GROSS 1933), Oberlahr (DAHMER 1934), Aegidienberg near Bonn (BRAUN 2001, SCHINDLER et al. 2001), and Willwerath (ANDERSON et al. 1998). It probably reflects deposition in a deeper water setting (cf. PLOTNICK 1999), which is further substantiated by the observation that there seems to be a negative correlation in the relative abundance of pterygotids and terrestrial arachnids. At Burglahr, where a layer of only about 15 cm of thickness with a uniform lithology and fossil content has been sampled, pterygotids and vertebrates are lacking.

In accordance with the results of STETS & SCHÄFER (2002) and POSCHMANN & JANSEN (2003) we envisage the habitat of the eurypterids discussed here as being situated in a low relief deltaic complex. Detrital input from the Old Red Sandstone Continent was more or less in balance with basin subsidence. Due to sea level changes and amount of siliciclastic detritus delivered the environmental conditions were rapidly changing. *Parahughmilleria*, the stylonurids, *Alkenopterus* and *Diploaspis* may well have lived in shallow pools or lakes in between fluvial channels and in close proximity to tidal flats. Subaerially exposed areas along the margins of pools and channels were vegetated with early land plants, providing shelter for the terrestrial trigonotarbids. On the other hand, pterygotids and jawless vertebrates may generally have preferred more open, relatively deeper water settings.

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