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Eoarthropleura (Arthropoda, Arthropleurida) from the Silurian of Britain and the Devonian of North America

By

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With 12 figures and 1 table in the text

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Abstract: *Eoarthropleura*, previously known only from the Lower Devonian of Germany, is reported here from the Upper Silurian (Přídolí) of Shropshire, England, the Upper Devonian (Frasnian) of New York State, USA, and the Lower Devonian (Emsian) of New Brunswick, Canada. The Shropshire form (*E. ludfordensis* n. sp.) is the earliest representative of the Arthropleurida. The New York species, originally ascribed to a scorpion, *Tiphoscorpio*, becomes *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986). The New Brunswick *Eoarthropleura* is too fragmentary for species level distinction. Within the Class Arthropleurida, *Eoarthropleura* is the type of a family and an order.

Zusammenfassung: *Eoarthropleura* war bisher nur aus dem deutschen Unterdevon bekannt. Weitere Vorkommen werden hier aus dem Obersilur von Shropshire, England, dem Mitteldevon von New York State, USA, und dem Unterdevon von New Brunswick, Canada, beschrieben. Die englische Art, *E. ludfordensis* n. sp., ist der bisher älteste Vertreter der Arthropleurida. Die New Yorker Art, von KJELLESVIG-WAERING (1986) als Skorpion *Tiphoscorpio hueberi* beschrieben, wird zu *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986). Die Stücke von New Brunswick sind zu fragmentarisch für eine artliche Zuordnung. Die Systematik der Klasse Arthropleurida wird diskutiert, wobei *Eoarthropleura* als Typus einer Familie und Ordnung gilt.

Introduction

An exciting and relatively recent development in arthropod palaeontology has been the realisation that the palaeobotanical technique of hydrofluoric acid (HF) maceration of silicate rock can yield abundant arthropod cuticle as well as plant material. It had long been known that intact, organic arthropod cuticle could be present in arthropod fossils (THORELL & LINDSTRÖM 1885) but this observation was limited to a few taxa and preservational situations. HOLM (1898) used dilute hydrochloric and acetic acids to remove cuticle comprising

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nearly complete specimens of the eurypterid *Baltoeurypterus tetragonophthalmus* from limestone, and SELDEN (1981) exploited this technique more fully in work on the functional morphology of that species. WILLS (1925) obtained well preserved cuticle from Triassic scorpion fossils by softenting the silty clay matrix with warm water, and a similar technique enabled BARTRAM, JERAM & SELDEN (1987) to recover scorpion cuticles from coals. ROLFE (1982) and SHEAR et al. (1987) reported that abundant fragments as well as complete specimens of terrestrial arthropods could be obtained from mudstones and shales by completely digesting the matrix in HF, a technique developed by palaeobotanists to obtain spores, plant cuticle and other fragments. JERAM, SELDEN & EDWARDS (1990) provided criteria for recognizing genuine fossils from such residues as opposed to the rare contaminant. Suitable rock treated, and residue evaluated, in this way has yielded unprecedentedly detailed information about the earliest known terrestrial arthropods, from the Ludford Lane locality in Shropshire, England, at the base of the Přídolí Series (about 414 mya; JERAM, SELDEN & EDWARDS 1990). Continued exploration of this locality has yielded a great variety of arthropod remains in addition to those already reported. Among them is a complete K plate from a new species of *Eoarthropleura*. This specimen represents the earliest known occurrence of the atelocerate arthropod class Arthropleurida, whose fossil record now extends from Upper Silurian to Stephanian (ALMOND 1986, HAHN, HAHN & BRAUCKMANN 1986).

In the course of using the HF technique to obtain plant fossils from the Frasnian Onteora formation of New York State, Dr. FRANCIS HUEBER of the Smithsonian Institution encountered a small assortment of arthropod fragments, which he turned over to the late ERIK KJELLESVIG-WAERING. KJELLESVIG-WAERING (1986) described these fragments as parts of an aquatic scorpion, *Tiphoscorpio hueberi*, which species was a linchpin of his argument for a great diversity of respiratory arrangements amongst scorpions. However, a re-examination of this material by SELDEN & SHEAR (1992) revealed that most of the fragments were virtually identical with similar pieces of the Lower Devonian (Emsian) arthropleurid *Eoarthropleura devonica* STØRMER (STØRMER 1976). Other parts originally considered to be pieces of *T. hueberi* are evidently neither scorpion nor arthropleurid. The Onteora formation requires further exploration by the HF technique; potentially, it is rich in terrestrial arthropods.

The Arthropleurida

Arthropleurids are myriapodous arthropods of uncertain phylogenetic position. Heads are known only from one undescribed species, and do not closely resemble the heads of any other known atelocerate arthropods; the head will be described in a forthcoming study by SHEAR & ALMOND. The trunk segments, with the possible exception of 1-3 at the front of the body, are diplosegments, each tergite covering two leg pairs and their associated complex of ventral plates. It is this complex of ventral plates, differing somewhat from genus to genus, that is the most diagnostic feature of the group. Each leg pair is accompanied by a median sternum, while on each side the leg base is buttressed by up to three additional plates (in *Arthropleura*), called, in order from postero-median to anterolateral, K, B, and rosette plates. Complete limbs are known only in a few cases and vary from seven (undescribed species) to eleven (*Arthropleura*) podomeres. The trunk posterior ends are poorly understood except in juvenile *Arthropleura* (ALMOND 1986) where the posterior diplosegments and their associated limbs become smaller and less differentiated and the exact details of the terminus are not clear (ALMOND 1986). Nothing is known of arthropleurid respiratory organs, but the animals are generally believed to have been terrestrial on functional morphological grounds.

Knowledge of the Arthropleurida up to 1967 has been summarized by ROLFE (1969), and references therein. Subsequent developments will be briefly described below.

Arthropleurids first occur in the dark shales above the Ludlow Bone Bed at Ludford Corner, Ludlow, Shropshire, from whence diagnostic fragments are reported in this paper. They are known from three Devonian localities. The Emsian black shales of Alken-an-der-Mosel, Germany (STØRMER 1976), yielded impression fossils of *Eoarthropleura devonica* STØRMER, and we report here an Emsian occurrence from New Brunswick, Canada, of fragments possibly attributable to the same species. A second species, *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986) was macerated from Frasnian shales of the Onteora Formation in New York State (both are discussed in more detail below). Between the Emsian and Frasnian occurrences, a very different species of minute arthropleurid, only about 5 mm long, has been obtained by HF maceration of black shale of the Givetian Panther Mountain formation, also in New York State (see SHEAR et al. 1987, SHEAR 1993 for a general description of this site and its fauna).

About 10 nominal species (the number is undoubtedly fewer) of the gigantic *Arthropleura* have been described from the Pennsylvanian of North America, the British Coal Measures, and the Ruhr Valley of Germany (ROLFE 1969, ALMOND 1986, HAHN, HAHN & BRAUCKMANN 1986). They were the largest known terrestrial arthropods. Extrapolating from complete specimens, fragmentary remains indicate a maximum length of over two metres. Numbers of well preserved trackways attributed to *Arthropleura* establish at the least a partly terrestrial mode of life in coal swamps and mud flats (BRIGGS, ROLFE & BRANNAN 1979, BRIGGS, PLINT & PICKERILL 1984). Their food included the wood and cortical tissue of decaying lycopod trunks (ROLFE & INGHAM 1967). Likely juvenile specimens have been found in Stephanian nodules from Montceau-les-Mines, France (SECRETAN 1980, ALMOND 1986).

We reaffirm the recognition of Arthropleurida as a class of Arthropoda probably, but not with complete certainty, belonging in the subphylum Atelocerata. The divergent morphologies of both described genera justify placing each in a separate order and family.

The order Eoarthropleurida SHEAR & SELDEN, and family Eoarthropleuridae STØRMER, 1976 are the subject of this review, which treats the two previously known species and describes a new one from the upper Silurian. Eoarthropleurids are presently known only from fragments, most of which comprise, however, complete exoskeletal elements. Heads are entirely unknown, and little information is available on the limbs. Each tergite has a trilobate organization, with an axial part which covered the internal organs, and on each side a broad paratergal fold, delimited from the axial part by a distinct suture. These tergal elements were evidently easily separated from one another in moulted cuticles or after death.

STØRMER (1976) interpreted the ventral fragments available to him as shown in Fig. 10, a copy of his text-figure 40. Our study of the ventral plates of *E. hueberi* has led us to slightly different conclusions, as discussed below.

Systematic Descriptions

Class Arthropleurida WATERLOT, 1934
Order Eoarthropleurida SHEAR & SELDEN, new order

Diagnosis: Rosette plates absent, B and K plates present; tergites without nodules or spines and with a suture between the axial portion and the paratergal folds; number of trunk segments unknown, legs unknown. One family, Eoarthropleuridae. Upper Silurian to Middle Devonian of North America and Europe.

Family Eoarthropleuridae STØRMER, 1976

1976 Eoarthropleuridae. – STØRMER, p. 90, type genus *Eoarthropleura* STØRMER, 1976.
1986 Tiphoscorpionoidea and Tiphoscorpionidae. – KJELLESVIG-WAERING, p. 126, type genus *Tiphoscorpio* KJELLESVIG-WAERING, 1986 new synonymy.

Eoarthropleura STØRMER, 1976

Type Species: *Eoarthropleura devonica* STØRMER, 1976, p. 91, text-figs. 1-4, 6-24, 39-41; Pls. 1-4.
Synonym: *Tiphoscorpio* KJELLESVIG-WAERING, 1986, p. 126, type species. *Tiphoscorpio hueberi* KJELLESVIG-WAERING, 1986, text-fig. 50, Pls. 5-8, new synonymy.
Remarks: The genus may be diagnosed by the smooth cuticle of the dorsum, with a distinct suture separating the paratergal folds from the axial plate. K and B plates accompany the cordate sterna, but rosette plates are unknown. The K plates and sterna bear distinctive terrace lines as illustrated in the figures. Heads

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Fig. 1 a - d. *Eoarthropleura ludfordensis* n. sp. from the Downton Castle Sandstone Formation (lowermost Přídolí) at Ludford Lane, Ludlow, Shropshire, UK. a: Holotype [K25082], type 2 (K) plate, x 47; b: Holotype, detail of cuticle pattern, x 330; c: Paratype [K25088]; another plate, x 114; d: Paratype, detail of cuticle pattern, x 275. e, f: *Eoarthropleura* from the Emsian La Garde Formation at Escuminac Bay, New Brunswick, Canada. e:NB-1FB, axial tergal plate with paratergal folds. x 4.8; f: NB-1FA, left paratergal fold, x 4.4. All specimens oriented with presumed anterior to top.

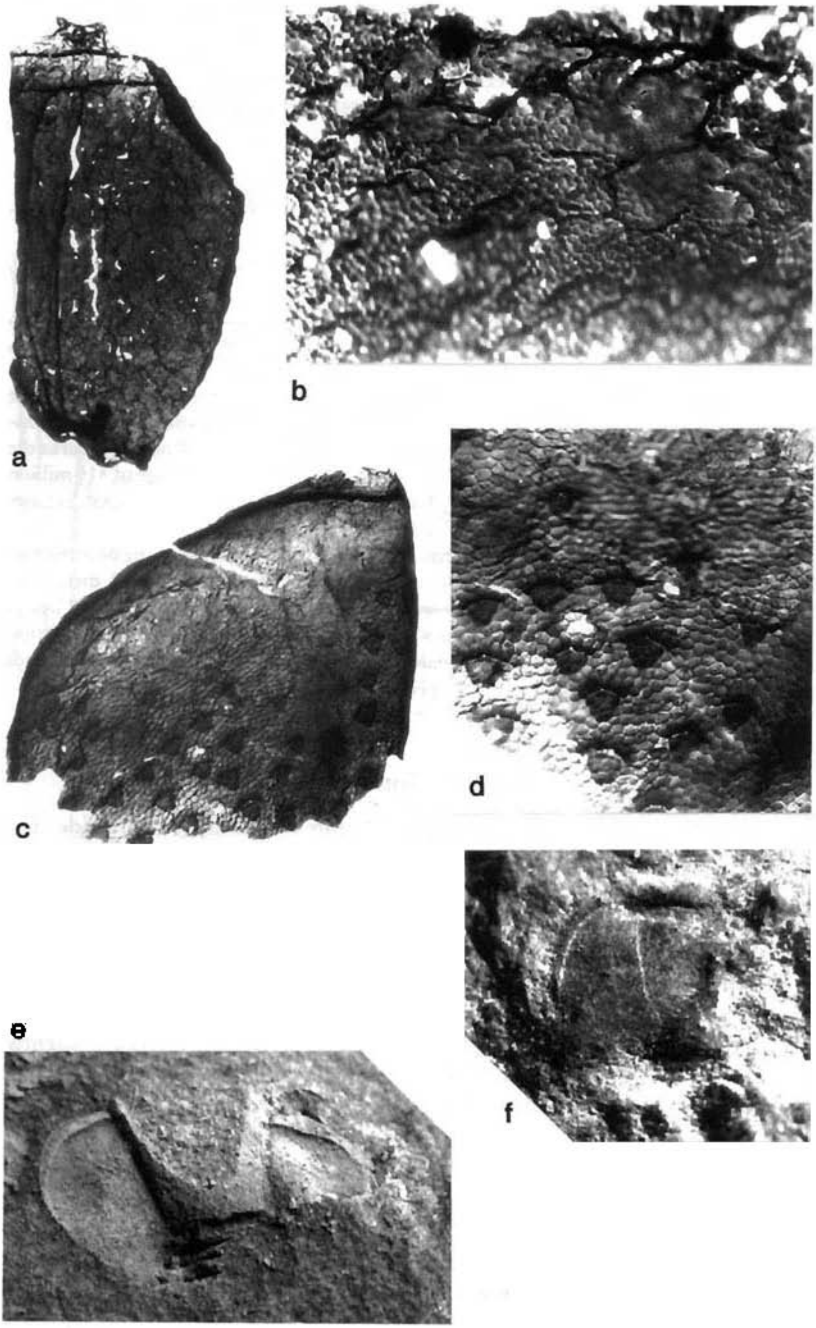

Fig. 1 (Legend see p. 350)

are unknown and very little information is available about the legs. Three species are recognized here, but these may be no more than 'form species' the status of which will have to be reconsidered if and when more complete material becomes available. Geological range is from Přídolí (Upper Silurian) to Frasnian (Middle Devonian).

Eoarthropleura ludfordensis n. sp.
(Figs. 1, 2)

Derivatio nominis: 'of Ludford', the type locality at the corner of Ludford Lane, Ludlow, Shropshire.
Type specimens: Holotype, a K plate, registered as K25082; paratype, another plate, registered as K25088, both in collections of the Ulster Museum, Belfast, Northern Ireland, UK.
Locality and Horizon: Ludlow Bone Bed Member of Downton Castle Sandstone Formation, 0.15 to 0.20 m above the Ludlow Bone Bed, Ludford Lane, Ludlow, Shropshire, England (National Grid Reference SO 5116 7413). The Ludlow Bone Bed marks the base of the Přídolí Series of the Silurian System and has an approximate age of 414 million years. Further details are given in Bassett, Lawson & White (1982) and in Jeram, Selden & Edwards (1990).
Diagnosis: The holotype, a K plate, differs from that of *E. hueberi* in having only the two posteriormost marginal setae (at least four setae present in *E. hueberi*) and a distinctive pattern of terrace lines. The paratype shows that parts of the body of this animal bear a distinctive pattern of raised triangular thickenings. The differing manner of preservation makes comparisons with *E. devonica* difficult, but the preserved terrace lines of *E. devonica* are of a different pattern than the present species.

Description

A large K plate (Figs. 1, 2) measuring 1.25 mm long and 0.65 mm wide. The cuticular ornament (Fig. 1b) is typical of the genus (Fig. 7j, k), consisting of closely set irregular rows of small, jagged tubercles slightly raised disto-posteriorly, superimposed on a polygonal pattern. The cuticle itself is much altered by preservation, has many wrinkled regions and cracks, and is dark brown in colour, with the raised edges of terrace lines black. There are no indications of setal sockets, which occur in *E. hueberi*. The anterior edge of the plate is torn and the lateral margin is folded under; the whole plate is slightly convex ventrally. There are two transverse terrace lines anteriorly, with traces of a third anterior to these. From about the midline of the most posterior transverse terrace line, two lateral marginal terrace lines arise and run posteriorly to the median setal socket. The median socket is separated from the more lateral one by about a diameter. We presume that stout spines were borne in these sockets, as preserved in some specimens of *E. hueberi*.

The paratype [K25088] (Fig. 1c, d) is a plate of uncertain type with a clear cuticular pattern and a single, distinct terrace line preserved. The cuticle (Fig. 1d) bears the same polygonal pattern as the holotype on one surface, but the other surface shows regularly spaced triangular thickenings with a rampart along the presumed anterior edge; a ?setal socket occurs in the middle of each rampart. The pattern of triangular thickenings everywhere except close to the anterior edge of the specimen. The plate has a nearly straight (presumed medial) edge; the anterior edge runs at an angle of 70° from the medial edge, and then curves to produce a lateral edge which is parallel to the medial. The posterior part of the

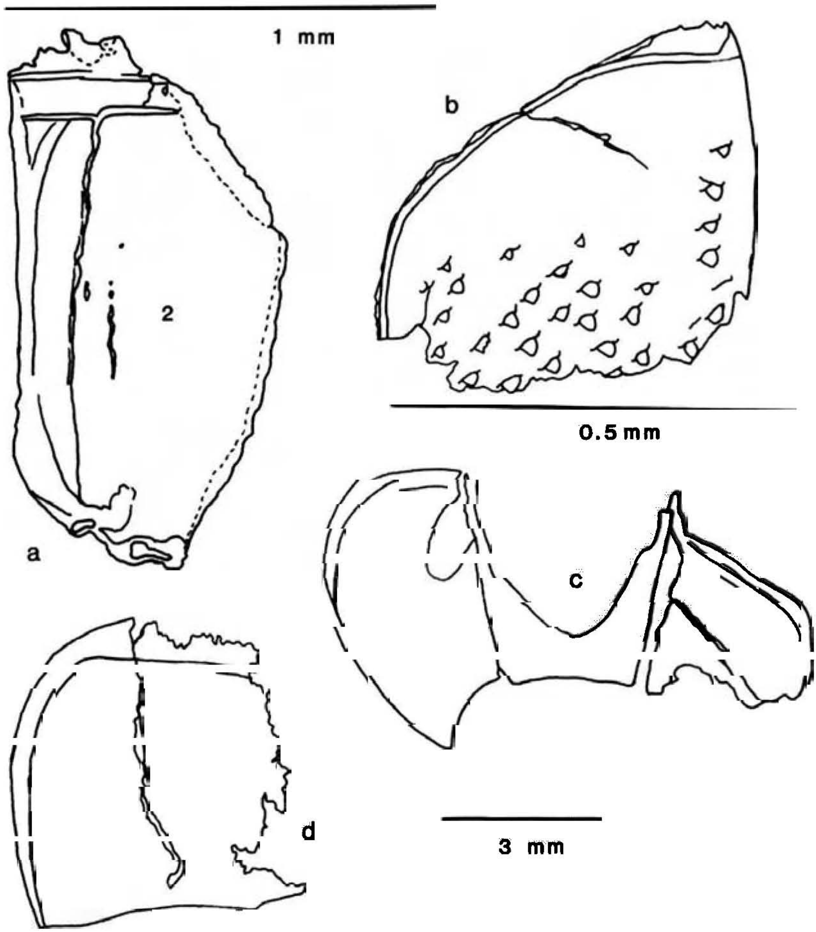

Fig. 2. Camera lucida drawings. **a, b**: *Eoarthropleura ludfordensis* n. sp. from the Downton Castle Sandstone Formation (lowermost Přídolí) at Ludford Lane, Ludlow, Shropshire, UK. **a**: Holotype, type 2 (K plate); note spine follicles at posterior (lower) margin; lateral to right, 1 mm scale bar; **b**: Paratype, 0.5 mm scale bar. **c, d**: *Eoarthropleura* from the Emsian La Garde Formation at Escuminac Bay, New Brunswick, Canada, 3 mm scale bar. **c**: NB-1FB, axial tergal plate with paratergal folds; **d**: NB-1FA, left paratergal fold. All specimens oriented with presumed anterior to top.

specimen is missing. The terrace line starts close to the junction of the medial and anterior edges and then runs along the anterior and lateral edges of the plate. This specimen is clearly the anterior part of an *E. ludfordensis* plate, but of which type is uncertain.

Five additional fragments from the Ludford Lane site may also represent parts of *E. ludfordensis*, but because we are not entirely convinced of this we have not included them as paratypes. They have been deposited in the Ulster Museum; their registration numbers are given in the following discussion together with the original slide numbers. Two of them (DE 3.2.38/147 [K25083] and DE 1.M.4 [K25084]) have an edge which bears the same sculpture of regularly spaced triangular denticles seen in *E. hueberi* B plates. On DE 3.2.38/147, a projecting, damaged piece of cuticle could be the tongue-like process of this plate. These specimens are nearly identical in size and edge curvature and could have come from positions close together on a single animal's body. A third fragment (LL 1.6/12/1 [K25085]) has a series of three poorly preserved podomeres, on at least one of which can be seen a large setal socket. These podomeres bear a resemblance to those of the undescribed Givetian arthropleurid from New York, and could be from *E. ludfordensis*. Two pieces (LL Orig./12 [K25086] and LL 1.6/13.2/34g [K25087]) have edges which are similar to the toothed, incised labrum of the New York species. They, too, may be part of *E. ludfordensis*.

A few pieces have also been recovered from Ludford Lane which are much like the tips of atelocerate mandibles. While these fragments may also be from *E. ludfordensis*, we are far less sure of it.

Remarks

The significance of a diagnostic fragment from an individual of *Eoarthropleura* is an extension of the time range of the genus, and indeed the Class Arthropleurida, into the past by about 15 million years. Arthropleurids may now be recognized as part of the earliest known fauna of terrestrial animals (JERAM, SELDEN & EDWARDS 1990). The structure of this K plate, though differing in what may be minor details, is strikingly similar to the Devonian forms described below, and speaks for a very conservative rate of evolution for this structure over a period of nearly 45 million years.

Eoarthropleura hueberi (KJELLESVIG-WAERING, 1986
(Figs. 3-9)

1986 *Tiphoscorpio hueberi*. – KJELLESVIG-WAERING, p. 126, text-fig. 50, pls. 3-8.

Material: Ten microscope slides bearing cuticular fragments mounted in Canada Balsam, under Registration Numbers USNM 252629 (holotype) and 252630 (paratype), Accession Number 251091, United States National Museum of Natural History, Smithsonian Institution, Washington, DC, USA. In addition to pieces of *E. hueberi*, these slides also carry fragments of plant cuticle and parts of other arthropods. Only the elements described as such in detail below and illustrated in this paper can unequivocally be stated to belong to

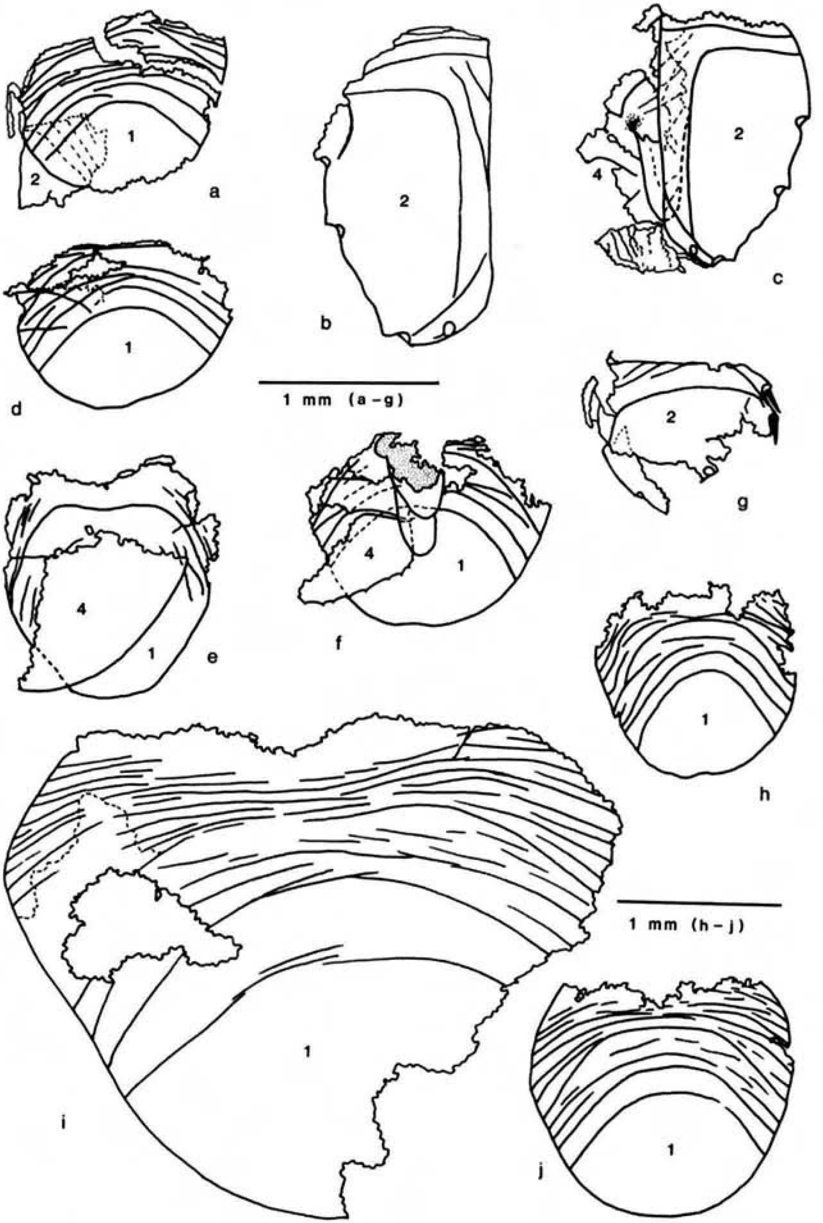

Fig. 3. Camera lucida drawings of *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986), Onteora Formation (lower Frasnian) of South Mountain, Schoharie County, New York State, USA. Numerals refer to plate type. **a**: 1 f & 2 m; **b**: 2 j; **c**: 2 f & 4 a; **d**: 1 g; **e**: 1 d & 4 f; **f**: 1 e & 4 b; **g**: 2 g, note posterior piece (with edge and spine socket) rotated to left; **h**: 1 b; **i**: 1 a; **j**: 1 c. All specimens oriented with presumed anterior to top.

E. hueberi. Our assignments of the pieces and those of KJELLESVIG-WAERING are compared in table 1. KJELLESVIG-WAERING (1976) did not designate any of the individual fragments as holotype because he believed all the pieces except the paratype to have come from the same individual. One fragment, mounted alone on a slide, was selected as a paratype since because of its much larger size, he assumed it to be from another individual; we believe it is simply from a more posterior position on the trunk of the same animal. We agree that all the fragments on the slides probably came from a single animal, so we believe they should all have equal status as parts of holotype individual, except, of couse, for the single piece designated as a paratype by the original author.

Locality and Horizon: Lower Frasnian (lower Upper Devonian), lowermost Onteora Formation, from a dark, fine-grained shale lens in a quarry on the north-west slope of South Mountain, Schoharie County, New York State, USA, 1.1 miles west of the Schoharie-Green County border (on Livingston 7½' quad.) at 74° 16' 30" E, 42° 23' 55" N, collected and macerated from the rock by F. M. HUEBER. This is a well-known locality for fossil plants (e. g. HUEBER 1960). However, in a footnote (p. 129) in KJELLESVIG-WAERING (1986; prepared for posthumous publication by A. S. and K. E. CASTER) initialled K. E. C., it is stated that HARLAN P. BANKS, in a letter, associated the Onteora Formation with the earliest terrestrialization of plants and animals, and that it contained centipeds, 'tarantula-like' arachnids, mites, and machilid insects. ROLFE (1982) is also cited in support of this assertion. The list of supposed fauna and the reference to ROLFE (1982) make it clear that the CASTERS misunderstood, and that what is being discussed in this footnote is not the Frasnian Onteora Formation, but the Givetian Panther Mountain Formation, known informally as the Gilboa locality, first reported on in detail by SHEAR et al. (1984), and the subject of numerous subsequent papers.

Description

We have combined descriptions and remarks on the specimens, comparing our interpretations with those of KJELLESVIG-WAERING (1986) and with *E. devonica* as described by STØRMER (1976). The various plates are categorized into nine 'types' and each individual specimen, if more than one of the type occurs, is given a letter, i. e., 1a, 1b, and so on. Table 1 gives our designation for each specimen, the number of its illustration in KJELLESVIG-WAERING (1986) and STØRMER (1976), and a short interpretation.

Cuticle

The cuticle is light to dark brown in colour, with regions of overlap and heavy terrace lines black. The surface of the cuticle of the ventral plates has a typical microsculpture already described and illustrated for *E. ludfordensis*. The cuticle of the paratergal folds is superficially smooth and featureless, but under high magnification is densely set with minute, dark denticles. Both dorsal and ventral plates are pierced by evenly scattered small, round holes, which are very likely sockets for small setae or hairs. At the edges of Type 2 specimens are four or six large sockets in which stout, black macrosetae are sometimes preserved.

Fig. 4. Camera lucida drawings of *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986), Onteora Formation (lower Frasnian) of South Mountain, Schoharie County, New York State, USA. Numerals refer to plate type. **a**: 2 h & 2i (small upper specimen), note six spine sockets on 2i, 2 spines (one loose) on 2i, and 2 spines in situ on 2h; **b**: 2k & 4e; **c**: 2c; **d**: 2e; **e**: 2d; **f**: 2b; **g**: 2l & 4d; **h**: 2a; **i**: 3g; **j**: 4c. All specimens oriented with presumed anterior to top.

Table 1. Figures of parts of *Eoarthropleura hueberi* and *E. devonica* and their interpretation in this paper, KJELLESVIG-WAERING (1986), and STØRMER (1976).

	This paper *Eoarthropleura hueberi*		KJELLESVIG-WAERING 1986 *Tiphoscorpio hueberi*		STØRMER 1976 *Eoarthropleura devonica*	
Nº	Figure	Interpretation	Plate/figure	Interpretation	Plate/figure	Interpretation
1a	3i, 7g		not figured			
1b	3h, 7a		6/2; 8/5-7		Text-figs. 15	
1c	3j, 7b		6/1		(1a), 16, 17	
1d	3e, 7d	sternite	6/4; 50J	rounded gill	Pl. 2, fig. 7;	labrum
1e	3f, 7e, 7k		8/1; 6/8		Pl. 4, fig. 2;	
1f	3a, 7c		6/3,5		Pl. 8, fig. 2.	
1g	3d, 7c		6/6			
2a	4h, 8d		7/1			
2b	4f, 8i		not figured			
2c	4c, 8b		not figured			
2d	4e, 8c		6/7		Text-fig. 11	
2e	4d		not figured	sub-	(K).	
2f	3c, 8f	K plate	7/4	rectangular		K plate
2g	3g, 8e, 8l		7/2,3; 8/3	gill	Pl. 4, fig.	
2h	4a, 8j		7/6,7		3a, b (right).	
2i	4a, 8j		7/6,7			
2j	3b, 8h		not figured			
2k	4b, 8g		7/5; 8/8			
2l	4g, 7f		not figured			
2m	3a, 7c		6/3,5			
3a	5a, 9c		50I		Text-figs. 6–	
3b	5b, 9b		50D		9, 11 (p.f),	
3c	5c, 9a		50E, F, G		12, 13.	
3d	5e, 9g	paratergum	not figured	tergite	Pl. 1, figs. 1–	paratergum
3e	5d, 9h		50C		3; Pl. 2, figs.	
3f	5g, 9f		50H		1–6; Pl. 3,	
3g	4i, 9d		50K		fig. 2a	
3h	5f, 9e		not figured		(bottom right).	
4a	3c, 8f		7/4		Text-figs. 11	
4b	3f, 7e, 7k		8/1; 6/8		(B), 15 (B),	
4c	4j, 7j		not figured		21, 22	
4d	4g, 7f	B plate	not figured	irregular gill	Pl. 4, figs. 3	B plate
4e	4b, 8g		7/5		(left), 4, 5	
4f	3e, 7d		6/4; 50J		(left).	
5	6e, 8a	uncertain	not figured	–	Text-figs. 15 (mnd?), 23. Pl. 8, fig. 1.	mandible
6	6a, 8k	uncertain	50B	pectine	–	–
7	6c	uncertain	1/9	chelal hand	–	–
8	6f, 7h	spine?	not figured	–	–	–
9	6d, 7i	not scorpion	5/1-3; 50A	carapace	–	–
10	6b	not scorpion	5/4	tarsus	–	–

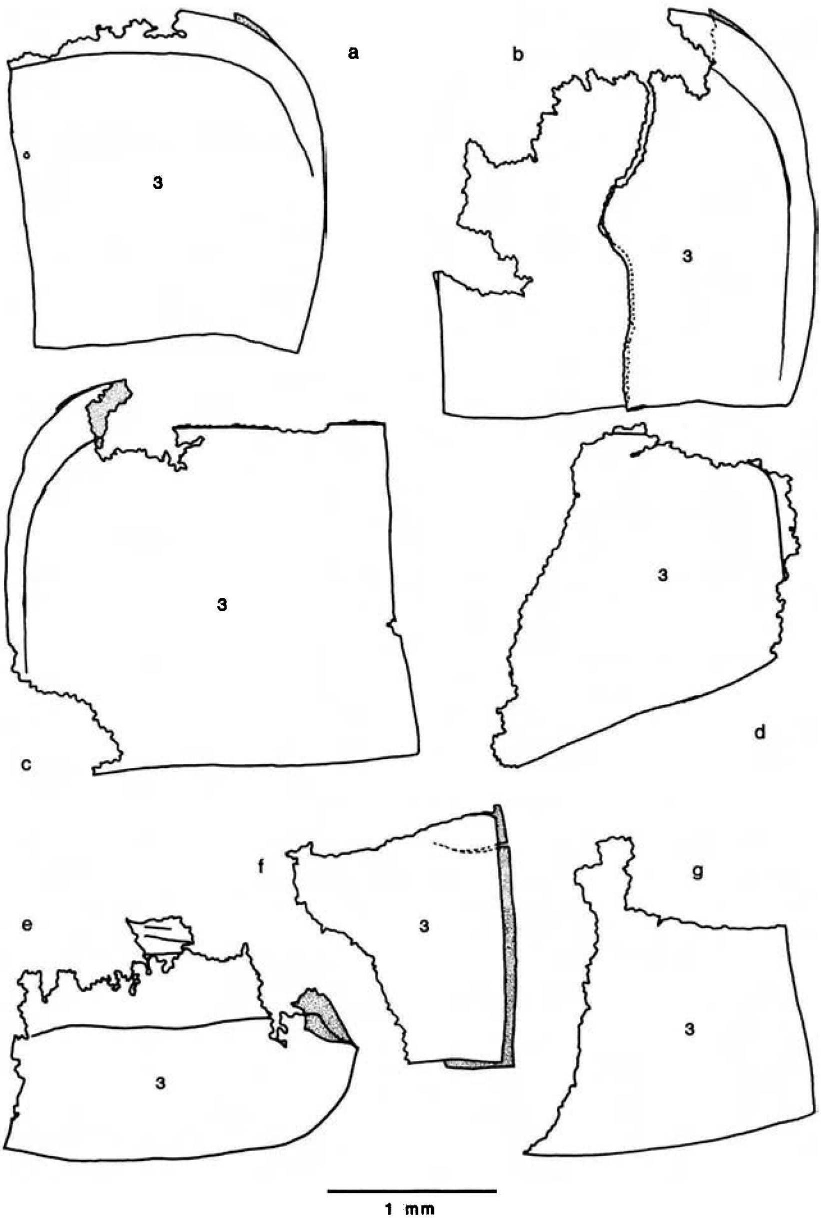

Fig. 5. Camera lucida drawings of *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986), Onteora Formation (lower Frasnian) of South Mountain, Schoharie County, New York State, USA. Numerals refer to plate type. **a**: 3a; **b**: 3b; **c**: 3c; **d**: 3e; **e**: 3d; **f**: 3h; **g**: 3f. All specimens oriented with presumed anterior to top.

Type 1 Plate

Specimens 1 a through 1 g (Table 1), this plate ranges from 3.8 mm wide (incomplete, probably 4 mm in life), 3.125 mm long, in specimen 1 a, to the smallest, 1 d, which measures 1 mm wide and 1.325 mm long. It is symmetrical and suboval, but with slightly straighter edges between the lateral and posterior extremities. The anterior edge is not known, since the margin is always torn, but the tear commonly forms a gently bilobed curve (Figs. 3, 7). The characteristic sculpture of this plate consists of raised lines which curve parabolically, with cusps posterior. The angle between the cusps decreases in more anterior lines, so that the most anterior lines only flex gently along their length. Commonly a slight convex-posterior flexure occurs at the apex of the parabola, and this flexure is more noticeable in anterior lines. The posteriormost two lines are generally fairly complete, as are some others, but most run only for a a short distance. The overall appearance of the sculpture on the plate resembles a fingerprint. The area behind the most posterior, complete line describes an ellipse of dark cuticle. The whole plate consists of two layers of cuticle, and was therefore assumed to be free in life, except for the anterior edge which presumably merged into the body wall.

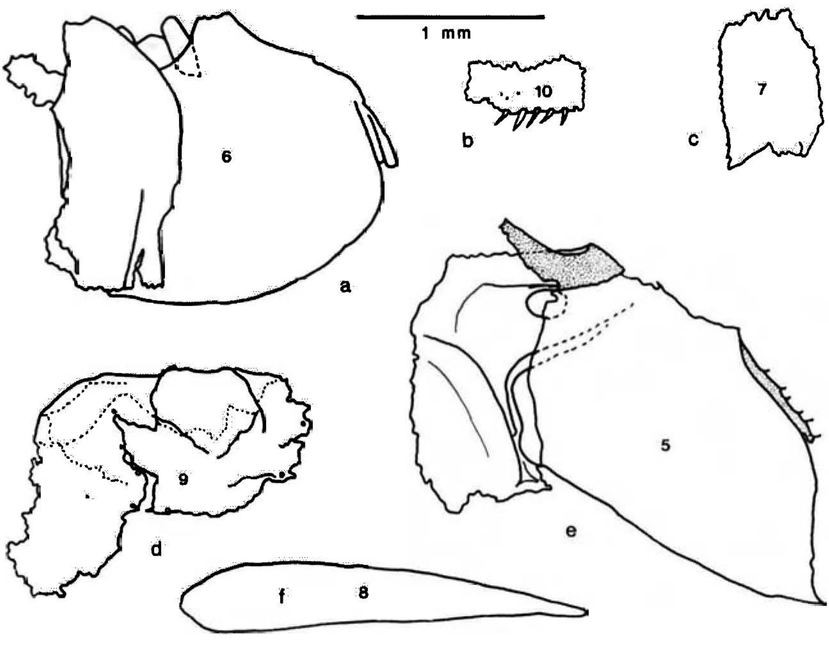

Fig. 6. Camera lucida drawings of *Eoarthropleura hueberi* (Kjellesvig-Waering, 1986), Onteora Formation (lower Frasnian) of South Mountain, Schoharie County, New York State, USA. Numerals refer to plate type. a: 6; b: 10; c: 7; d: 9; e: 5; f: 8.

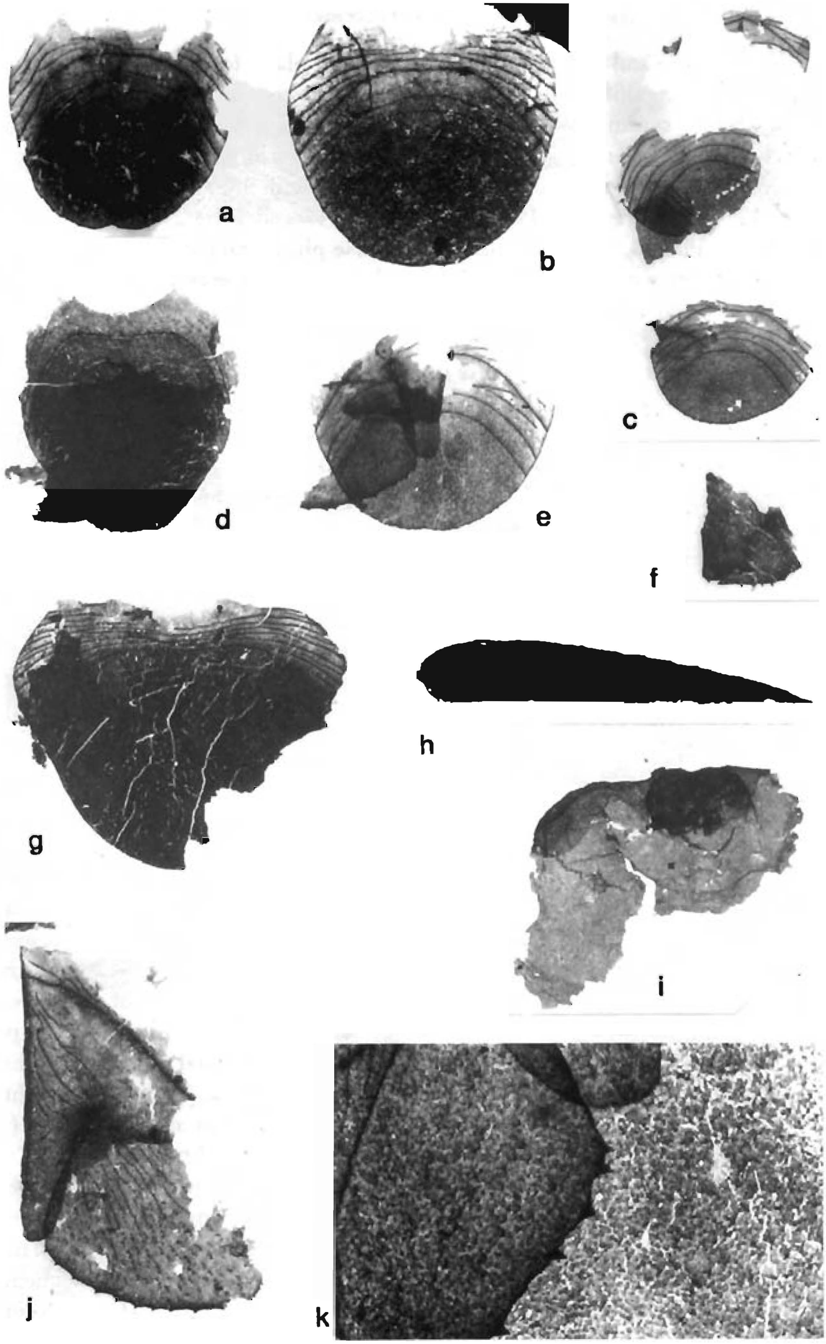

Fig. 7. *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986), Onteora Formation (lower Frasnian) of South Mountain, Schoharie County, New York State, USA. **a**: 1b, x 24; **b**: 1c, x 21; **c**: 1f, 1g, 2 m, x 18; **d**: 1d, 4f, x 23; **e**: 1e, x 23; **f**: 21, 4d, x 24; **g**: 1a, x 11; **h**: 8, x 23; **i**: 9, x 24; **j**: 4c, x 24; **k**: 1e, 4b, x 100. Presumed anterior to top in all specimens, except **h** (orientation unknown) and **k** (anterior to top left).

The number and different sizes of the Type 1 plates found suggests that we are seeing a range of forms of the same structure serially homologous on the body, and the symmetry of the structure suggests it was median in position. It does not resemble a tergite so it was probably ventral in position, and therefore a sternite. This plate is undoubtedly homologous with STØRMER's cordate plate of *E. devonica* (STØRMER 1976, Text-figs. 15-17 and Plate 2, fig. 7; Plate 4, fig. 2; and Plate 8, fig. 2). Inspection of these photographic plates reveals an ovate structure with parabolic sculpture identical in shape and detail with that of '*Tiphoscorpio*' specimen type 1. STØRMER (1976) interpreted this structure as the labrum. The labrum is a head structure forming the front wall of the preoral cavity in atelocerates; among these it is movable (and hence likely to be easily detached) only in insects. It is probably not homologous to the labrum of trilobites, as STØRMER implied in his discussion, who also confused the cucullus of ricinuleid chelicerates with this structure. He also speculated that these 'cordate plates' might close the preoral cavity posteriorly, but finally concluded that they were labra. In any case, the evidence of a great number of specimens in the present material, of two 'labra' in what is probably one specimen (STØRMER's SMF VIII 300), and the structure of the plate which he called the sternite in his material appearing to match more closely that of a tergite (see below), all point to the interpretation given here as that of a sternite.

These are the specimens KJELLESVIG-WAERING (1986) interpreted as 'rounded type gills' of a scorpion. He described them as being composed of 'white, spongy material' but in reality they are the typical buff brown colour of preserved cuticle from this collection.

Type 2 Plate

Specimens 2 a through 2 m (Table 1). This plate is asymmetrical, and on several of the specimens can be seen to consist of two layers of cuticle. The largest is 2 a, which measures 1.725 mm wide and 2.95 mm long. Specimen 2 b is about the same size, but represents only the posterior part. The smallest is 2 i, which differs in some morphological details from the other specimens of this type, measures 0.7 mm wide and 0.525 mm long, and thus, unlike all the others, is wider than long rather than longer than wide. The medial edge is straight throughout its length, except in large specimens (e. g. 2 a, 2 j) where a slight bulge occurs posteriorly. The anterior margin is ragged in all specimens (cf. specimen type 1), which suggests it merged into thin membrane. In all nearly complete specimens the anterior edge occurs at about the same position relative to the other parts, and approximately parallels the anteriormost sculpture line. The junction between the medial and anterior margins is a right angle. The lateral margin curves, and the curvature depends upon the size of the specimen. In the smallest specimen (2 i), the anterior margin is straight, and the rest of the edge nearly describes a circle. In larger specimens, as the anterior border lengthens, so the plate extends backwards at a greater rate. Thus the plate becomes more rectangular in larger specimens, the lateral edge forms a gentle curve, and the posterior border forms a tight curve to meet the medial edge.

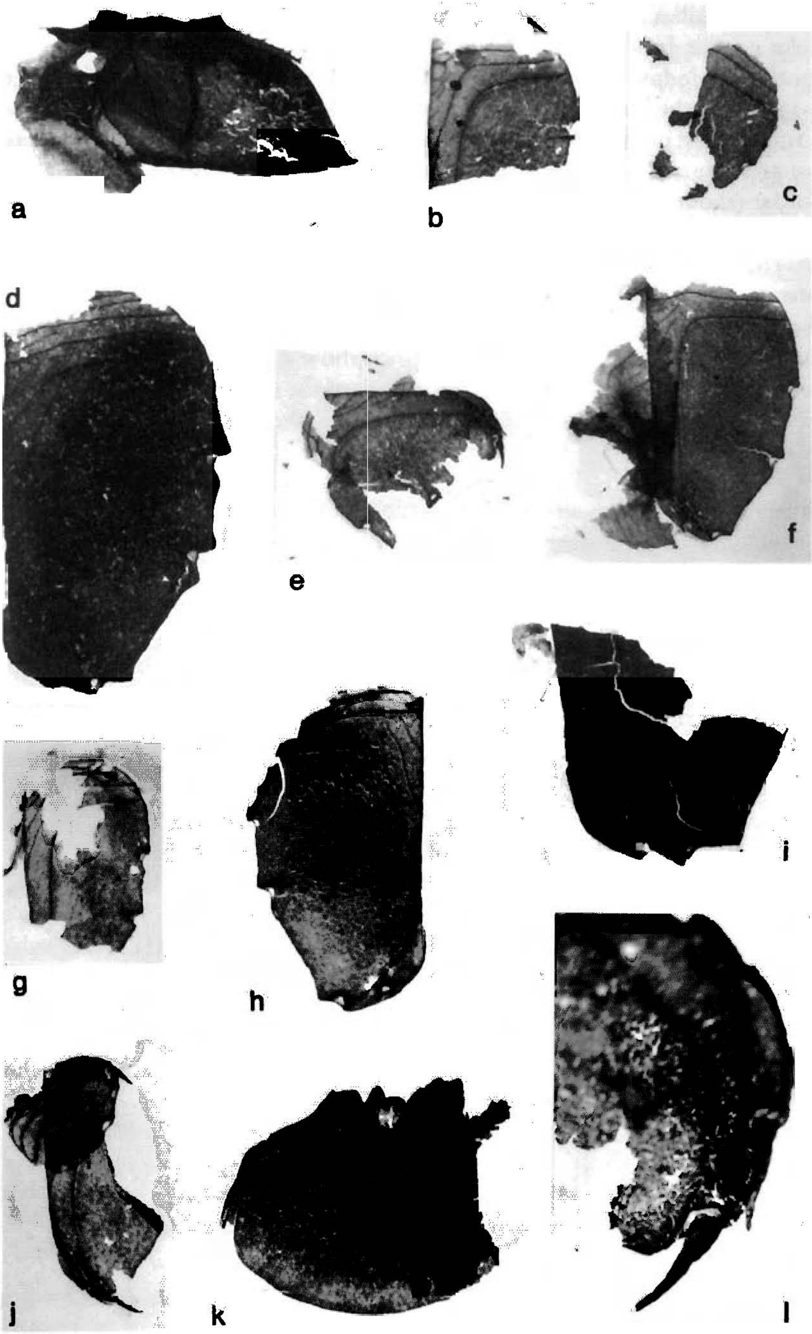

Fig. 8. *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986), Onteora Formation (lower Frasnian) of South Mountain, Schoharie County, New York State, USA. **a**: 5, x 15; **b**: 2c, x 24; **c**: 2d, x 23; **d**: 2a, x 18; **e**: 2g, x 24; **f**: 2f, 4a, x 24; **g**: 2k, 4e, x 23; **h**: 2j, x 23; **i**: 2b, x 17; **j**: 2h, 2i, x 24; **k**: 6, x 19; **l**: 2g, x 100. Presumed anterior to top in all specimens.

The smallest specimen has six spine sockets. These appear as subcircular holes on one lamella of the cuticle, the other (presumably the more dorsal), forming a window behind when the spine is absent. Just anterior to each socket is a tooth on the plate margin. The six spine sockets in specimen 2i run from the posteriormost point to the anterolateral corner. In larger specimens four sockets are present; two near the posterior end, and two, wider apart, on the lateral border (about 1/3 and 2/3 of the distances between the anterolateral corner and the posterolateral point). The spines are short, thick, and gently curved.

The sculpture consists of concentric lines which parallel the anterior and lateral edges of the plate approximately 1/4 of the width of the plate in from the edges. Subsidiary lines occur anterior (3-5) and anterolateral (2-3) to this main line. All except the smallest specimen show a line from the medial edge cutting across close to the posterior terminus of the main concentric line to the posterior border of the plate just at or anterior to the most lateral socket of the posterior socket pair.

These asymmetrical plates are presumed to be paired, ventral structures situated lateral to the sternite. Specimen 2f appears to be associated with specimen 4a, a small fragment of specimen type 2 edge with sockets is attached to specimen 4d, and additionally, there is a small piece of cuticle with sculpture resembling that of specimen type 4 (see below) continuing beyond the medial edge of specimens 2j and 2l. It is therefore concluded that specimen types 2 and 4 were related, and perhaps closely attached, in life.

Specimen type 2 is nearly identical to STØRMER's (1976) K plate of *E. devonica* (his text-figs. 11, 15, 21, 22, and plate 4, figs. 3a, b, 5, 6). It can be seen from STØRMER's photographic illustrations that the specimen type 2 plate resembles the *E. devonica* K plate in nearly every detail, including the positions of the spine sockets with their anterior teeth, the straight medial edge, and the pattern of sculpture lines including a main concentric line. STØRMER's K plate is firmly attached in three of his specimens to another plate, which he called a B plate; we show below that this plate is homologous with type 4 of '*Tiphoscorpio*'.

Type 2 specimens were interpreted by KJELLESVIG-WAERING (1986) as 'subrectangular' and 'irregular' type scorpion gills. Again, we think he was mistaken in referring to them as being composed of 'spongy, white material' and consisting of a 'single lamella'.

SHEAR & ALMOND (in preparation) studied a complete specimen of the minute Givetian arthropleurid from Gilboa and found K plates very similar in form and spination to *E. devonica* and *E. hueberi* K plates. However, their orientation in the Givetian arthropleurid, where they are found in situ, is the reverse of the orientation figured by STØRMER (1976; Text-figs. 40, 46) in his reconstruction of *E. devonica*.

Type 3 Plate

Specimens 3a through 3h (Table 1). These plates are roughly rectangular (except for 3e, see later), with a curved anterolateral corner. Specimens 3b and 3c are both approximately 2.375 mm square, and specimen 3a is 2 mm long and 1.875 mm wide. There is a concentric sculpture line running parallel to the anterior margin about ⅙ of the width of the plate inside the edge, which follows

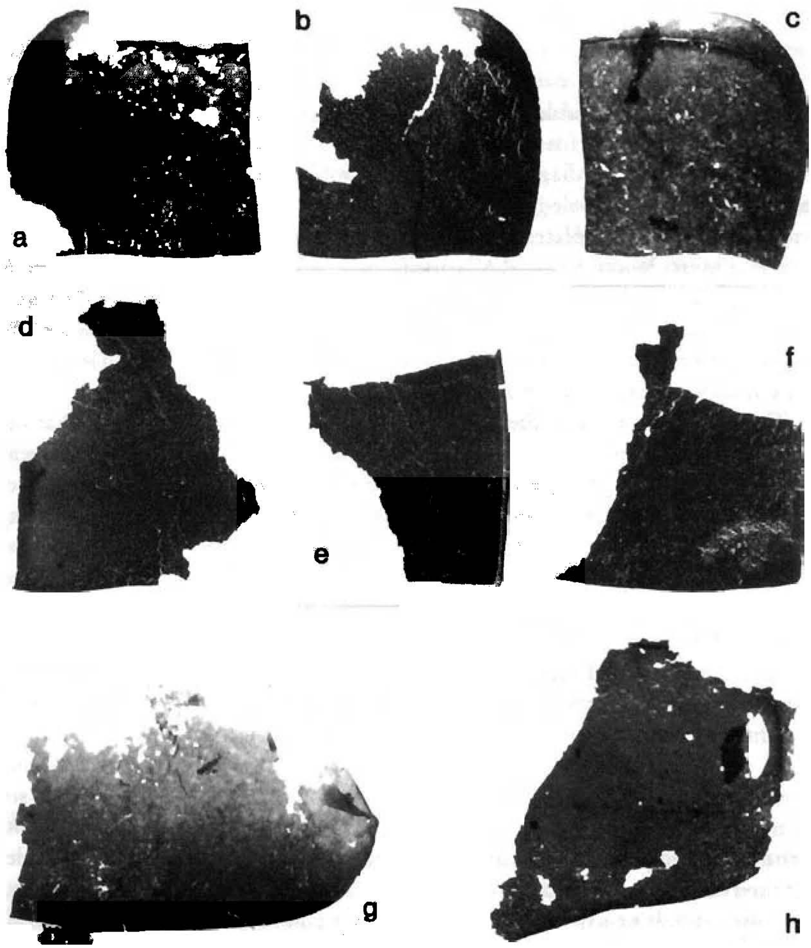

Fig. 9. *Eoarthropleura hueberi* (KJELLESVIG-WAERING, 1986), Onteora Formation (lower Frasnian) of South Mountain, Schoharie County, New York State, USA. **a**: 3c, x 13; **b**: 3b, x 13; **c**: 3a, x 14; **d**: 3g, x 16; **e**: 3h, x 19; **f**: 3f, x 19; **g**: 3d, x 22; **h**: 3e, x 20.

the lateral margin about 1/8 of the plate width inside that edge and gradually disappears just before reaching the posterior border. The cuticle is darker towards the lateral edge of the plate. There is a double thickness of cuticle, which is revealed at the anterolateral corners where the two layers are separated due to compression (see specimens 3a, b, c; Figs. 5, 9).

Specimen 3e bears the same sculpture as the other type 3 specimens, but it is not rectangular; the posterior margin runs at an angle of about 120° to the lateral margin of the plate.

Specimens 3f, g, and h do not show the concentric sculpture line; nevertheless, since they are all double-lamellate they must be paratergal lobes and not true tergal plates, and it is possible to orient them using the shape of the preserved corner and the density of the cuticle.

These plates are the paratergal lobes of an arthropleurid. The sculpture is distinctive, and the double nature of the cuticle indicates that they are true paraterga, outgrowths from the tergites, and not tergal plates. Comparison with STØRMER's (1976) diagrams and photographic illustrations (e.g. plates 1, 2) show that they are homologous with the paratergal folds of *Eoarthropleura*. No true tergal plates (axial plates) are present among the specimens.

KJELLESVIG-WAERING (1986) called these specimens 'abdominal plates' of a scorpion. The abdominal plates of some Palaeozoic scorpions are appendage-derived structures, movable flaps which cover the book gills (JERAM 1990). Because in '*Tiphoscorpio*' they appeared divided (actually the right and left paraterga) he assigned this 'scorpion' to his infraorder Meristosternina.

The smooth cuticle of the dorsum in *Eoarthropleura* is similar to that of the Givetian arthropleurid, but in the latter genus there is no suture line between the paratergal folds and the axial plates, and characteristic marginal setae are present (SHEAR & ALMOND in preparation).

Type 4 Plate

Specimens 4a-4f (Table 1). Specimen 4c is the largest, measuring 1.625 mm along its medial edge; the smaller specimens are incomplete. The medial edge is straight. The anterior border is not known, and is less complete than on specimen types 1 and 2; it is again presumed that the anterior border was the connection to the body wall. The sculpture lines run at an angle of about 50° to the medial edge, so it is likely that the anterior edge was angled by this amount to the medial edge also. Posteriorly, the medial edge turns an abrupt right angle and then curves back to nearly parallel the medial edge, forming a linguoid lobe. The lobe extends nearly half the length of the medial edge, and its anterolateral corner consists of an area of dark cuticle. Arising from this dark cuticle is the medial border of the flange: A plate which forms the posterior part of the type 4 plate. The medial border of the flange is overlapped by the lobe in part; it curves medially and then, at the posterior end of the lobe, laterally to form the posterior border of the flange. The posterior border runs in a wide curve; a tangent to the posterior, starting from the end of the lobe, would subtend an angle of about 130° with the medial border of the lobe. The posterior border is fringed with short spines spaced along its length, with one about every 0.125 mm. The lateral margin of the flange is missing in all specimens, but in 4c the posterior border curves anteriorly from the posterolateral corner. When the direction of curvature is extrapolated forward, it meets the extrapolated anterior sculpture line such that the shape of the whole plate 4 would be a parallelogram. The posterolateral flange is nearly separated from the lobe and anterior area of the type 4 plate by a deep incision at right angles to the long axis of the lobe, extending (presumably) from the lateral margin nearly to the area of dark cuticle at the anterior end of the lobe. The sculpture of the type 4 plate consists of a major line running at an angle of about 50° to the medial edge, parallel to the presumed anterior edge of the plate. There are subsidiary lines subparallel to, but slightly diverging from, the main line at its medial end. Another prominent line runs from the anteromedial area in a posterolateral direction (again at about 50° to the medial edge) to the dark cuticle area at the anterior end of the lobe, where the line bends posteriorly towards the centre of the dark area. Additional lines run subparallel to this line on its medial side, and beyond the lobe, across the flange, in a continuation of the line swarm towards the posterolateral corner. Before reaching the posterior and lateral edges of the flange, the lines break up into series of aligned mucrones (small, broadly V-shaped cuticular thickenings).

Specimen type 4 is presumed to be a lateral, paired structure. Associations of this plate occur with type 2 (2f with 4a; 2n with 4d), and with type 1 (1e with 4b) plates.

Specimen type 4 is homologous with STØRMER's (1976) B plate of *Eoarthropleura*, as shown on his text-figs. 15, 21, 22, and plate 4, figs. 3a, b, 4, 5. The specimens of *Eoarthropleura* B plate shown on STØRMER's Plate 4 are virtually identical with specimen type 4. Additionally they show the lateral edge of the plate, and that it is attached to the K plate, the '*Tiphoscorpio*' type 2.

KJELLESVIG-WAERING (1986) figured only a part of the associated 1e and 4b plates, and described it as an 'irregular type' gill associated with a 'round type'. The remaining examples of type 4 were not figured.

Type 5 Plate

This plate consists of two layers of cuticle: The more extensive has a strong fold which bifurcates, forming a Y-shape, one branch of which runs near a hole. The double-lamellate area is a flange forming over half of the specimen, and resembles the flange of plate Type 4 to some extent. Two pieces at the presumed anterior border appear to be refolded (during fossilization or preparation), the lateral one has a row of short teeth similar to those on the flange of the type 4 plate.

There is only a single specimen of this type of plate; it is asymmetric, and not attached to any other recognizable piece. A connection with the Type 4 plate is suggested, but no more than that. However, a very similar plate occurs in *Eoarthropleura devonica*, as shown in STØRMER's (1976) text-figs. 15, and 23a, b, and plate 8, fig. 1, which he interpreted as a mandible. In STØRMER's photographic illustration (best seen when inverted) a Y-shaped fold can be seen, the lateral (right when inverted) branch of which runs adjacent to a circular area which be could a hole. Lateral to the Y is a flange similar in shape to that seen in specimen Type 5. We consider it unlikely that this is a mandible, but two possibilities are suggested; firstly, that it may be a form of B plate, perhaps from the anterior or posterior end of the animal. Secondly (and less likely), the plate may represent the rosette plate, a feature of arthropleurids which has hitherto not been recognized in *Eoarthropleura*. In the latter possibility, theY-shaped fold would represent the folds between the lobes of the rosette plate as known in Carboniferous arthopleurids) i. e., *Arthropleura armata*), and it was pointed out by ROLFE (1969) that the number of lobes on the rosette plate increases with the size of the animal; *Eoarthropleura*, being small, would be expected to have had only few or no lobes on its rosette plate. Lastly, it is possible that the fragment represents the basal podomeres of an appendage; the distal margins of the appendages of the minute Gilboa arthropleurid have small spines similar to those seen here (SHEAR & ALMOND in preparation).

Type 6 Plate

This fragment undoubtedly belongs to *E. hueberi* because of the distinctive cuticle pattern; however, its position and orientation are not certain. For the convenience of its description, we presume the plate to have been symmetrical and elliptical in life. The left lateral edge is not preserved. The posterior margin follows a gently curve, and at the right lateral side there is fold in cuticle which extends beyond the line of the curve of the ellipse. The presumed anterior edge is deeply indented, with a rounded process midway in the indentation; two layers of cuticle can be made out in this process, and possibly a third layer overlaying it form the main plate. Below this indentation are two small oblong pieces of cuticle which may or may not be attached to the plate. The one on the right side is nearly completely obscured by a large piece of black cuticle which may represent part of the plate edge folded over; in support of this interpretation, a small fold extending beyond the elliptical outline can be seen on the folded piece.

This specimen was regarded by KJELLESVIG-WAERING as a scorpion pectine, which it undoubtedly is not. It is part of *Tiphoscorpio*, but which part is uncertain. Based on analogy with the minute Gilboa arthropleurid, it is possible that this represents at least part of the head, perhaps including the true labrum, which in the Gilboa arthropleurid has three deeply incised teeth.

Type 7 Plate

A single example is present. The cuticular sculpture appears to be an exaggeration of that found on the other genuine pieces of *E. hueberi*, but this specimen does not match anything previously known. The acute point and serrated margin appear to be true edges, but the rest of the margins are torn. The small serrations, figured by KJELLESVIG-WAERING as 'serrations along inner edge of hand and possibly the cheliceara' are simply expressions of the larger teeth of the surface sculpture. We are unable to suggest what part of the animal this represents.

Type 8 Plate

This single specimen is a completely opaque, spine-shaped piece of cuticle. We cannot tell if this is a real macroseta or a fortuitously folded piece of plant or animal cuticle. It was not figured by KJELLESVIG-WAERING.

Type 9 Plate

The cuticle pattern of this single specimen differs considerably from the other pieces, and it appears unlikely that this specimen is a part of *Eoarthropleura*. Our experience with undoubted scorpion cuticle from other, similar conditions of preservation indicates that this piece is not from a scorpion. No median eyes are apparent on the specimen, as KJELLESVIG-WAERING claimed. The area which is folded under is larger than KJELLESVIG-WAERING supposed, and is definitely not a scorpion compound eye. We are quite certain that the piece was once bilaterally symmetrical, with a large central tubercle and a symmetrical pattern of setal sockets on either side. Its interpretation as a scorpion head is most unlikely, nor does it seem to belong with the rest of the pieces.

Type 10 Plate

This single specimen consists of a small piece of fragile cuticle, bearing along one margin five macrosetae and a socket for a sixth. The cuticle matches neither that of *Eoarthropleura*, nor any scorpion cuticle we have seen, not that of Type 9. These latter two types, taken together with the presence of *Eoarthropleura*, seem clearly to indicate that the Onteora Formation preserves a diverse fauna of arthropods, certainly worthy of further study.

Reconstruction

Figures 10 and 11, copied from STØRMER (1976) illustrate the essential features of his reconstruction of *E. devonica*. More recent developments make certain features of this reconstruction obselete. We now know (ALMOND 1986) that the trunk of *Arthropleura* was composed of diplosegements, and it is likely that the same is true for *Eoarthropleura*. STØRMER's reconstruction of two adjacent segments shows the sternites as just touching, but in his ventral view of

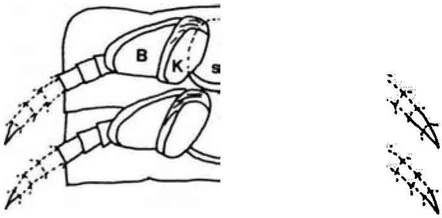

Fig. 10. *Eoarthropleura devonica* STØRMER, 1976, Nellenköpfchen-Schichten (Lower Emsian) of Alken an der Mosel, Germany. Copy of STØRMER's (1976) Text-fig. 40, with legend: 'Reconstruction of two somites of the trunk. – Not drawn to scale. – B = B-plate or ventral extension of the coxa; ... K = K-plate or endite; ... st = sternite'. Notice the relationship between the sternites of succeeding segments, and the relative sizes of the plates compared to the reconstructed lengths of the tergites. Compare with Figures 11 and 12.

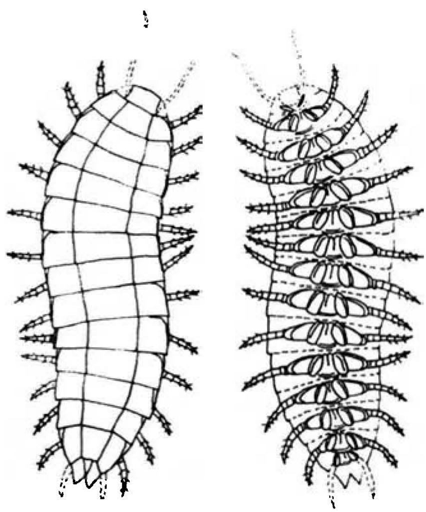

Fig. 11. *Eoarthropleura devonica* STØRMER, 1976, Nellenköpfchen-Schichten (Lower Emsian) of Alken an der Mosel, Germany. Copy of STØRMER's (1976) Text-figs. 45 (left, dorsal view) and 46 (right, ventral view), with legend: 'Reconstruction, about x $^3/_4$. Since the broad doublure indicates a strong horizontal mobility an undulating body is suggested. In the reconstructions the free cheeks, the labrum, antennae and gnathites are hypothetical. The mutual positions of the coxae of the trunk in relation to the sternites are based on structures in *Arthropleura*. The exact number of somites and the presence or absence of tail appendages and a telson are also unknown.' Compare with Figures 10 and 12.

a whole animal, they are widely separated. The latter is unlikely on analogical grounds; in other arthropleurids preserved as whole animals, the sternites overlap. Examples of *E. devonica* showing several plates closely adjacent on the same slab (e. g. STØRMER 1976, Text-fig. 15), the sternites and K plates present are about half the length of the associated tergites, which argues for diplosegments in *E. devonica*. Because all the dorsal and ventral plates are completely separated in *E. hueberi*, we cannot make the same argument for that species. Heads of *Eoarthropleura* remain unknown. It is likely that the plate described by STØRMER as the dorsal surface of the head, with missing 'free cheeks' is in reality the collum, or first tergite. Firstly, there is no basis for an analogy between arthropleurids and trilobites, and secondly, juvenile *Arthropleura* and adults of the minute Gilboa species have first tergites with lateral embayments, similar to the shallow excavations on the sides of STØRMER's supposed head, where he thought the non-existent 'free cheeks' were attached. As STØRMER stated, the number of trunk segments is not known for this genus, but *Arthropleura*, with a probable number of more than 30, contrasts with the 13 shown by STØRMER for *Eoarthropleura*. Extrapolating from the largest paratergal fold fragments of *E. hueberi* we have, the animal was at least 6 mm wide. The legs shown by STØRMER are entirely hypothetical.

STØRMER's (1976) reconstruction of the ventral surface was based on his erroneous identification of probable short, posterior axial tergites as sternites, and of the true sternites as labra. These tergites were turned over to make sternites; the rebordered edge should actually be anterior. The association of the B and K plates is well supported by two sets in apparent organic connection (SMF VIII 303 b). The same association occurs in some of the present material of *E. hueberi*, as described above. However, we question the orientation of the B and K plate complex. It seems unlikely to us, based on experience with living arthropods, that the setae of the K plates would be on the mesal edge and point proximally. (STØRMER did not have the evidence of these setae, which were not preserved in his specimens.) To reorient the B and K plate complex to place the setose margins of the K plates laterally would swing the B plates into a mesal position (Fig. 12), making it unlikely that in *Eoarthropleura* what we have been calling B and K plates are actually homologous to the so-named structures in *Arthropleura*. Thus we are less confident of homologies with *Arthropleura*, from whence the names for the structures are derived, and the reconstruction of which by ROLFE & INGHAM (1967) has strongly influenced subsequent work.

ROLFE & INGHAM (1967) argued that the B, K, and rosette plates were parts of the body wall that had become sclerotized to reinforce the leg-body junction. STØRMER (1976), on the other hand, interpreted them as parts of basal podomeres. He suspected that the B and rosette plates were not really separate structures, and that the B plate of *Eoarthropleura* was in fact homologous to the B plate plus the rosette plate of *Arthropleura*. The K and B plates were considered as extensions of the leg coxae, with the K plate being homologous to the coxal endite. There is little we can add to this debate with the material available to us.

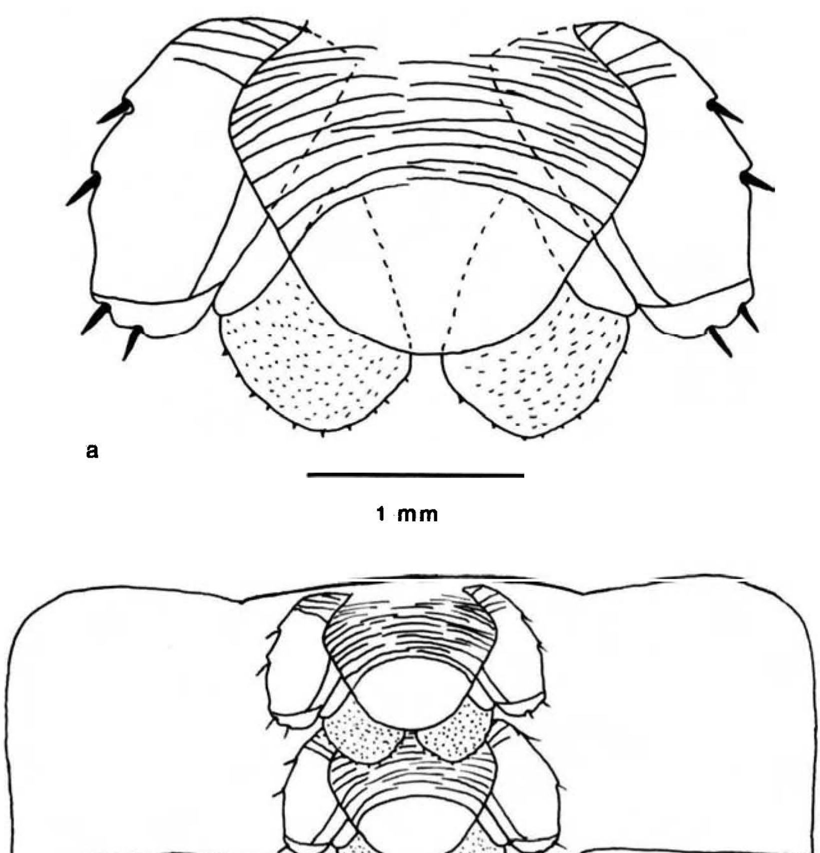

Fig. 12. *Eoarthropleura hueberi* (Kjellesvig-Waering, 1986) possible reconstruction based on re-orientation of B and K plate complex so that setose margin of K plate is lateral in position, and probable diplosegmentation. **a**: relationship between B and K plates and sternite; **b**: position of the complex in relation to tergite.

Figure 12 represents our best attempt at a reconstruction of the relationship between the B and K plates and the sternite on the ventral side of *Eoarthropleura*. The reconstruction is based on the presumption that the setose margin of the K plate should point outwards, and the few examples where the B and K plates are seen to be in a close connection. This arrangement is still unsatisfactory in a number of ways. The strong cuticle patterning at the anterior part of the K plate is covered by the sternite, and no function for the lobe on the B plate can be suggested, particularly in its position in Figure 12a. The function of the B and K plates also remains a mystery, and we have no idea where the legs fitted into this scheme. New specimens are appearing in the fossil record, some of which are described below; it is to be hoped that as more material of *Eoarthropleura* becomes available that a better reconstruction of this enigmatic animal will eventually be possible.

New Brunswick Specimens

Dr. PATRICIA GENSEL of the University of North Carolina, Chapel Hill, USA, has loaned us specimens from the shore of Escuminac Bay, in New Brunswick, Canada, which are undoubtedly *Eoarthropleura*. The specimens were collected by WILLIAM GENSEL about 1/2 mile west of Dalhousie Junction, New Brunswick; there is no formal description of the strata in this region, but P. GENSEL (1982, 1986) has tentatively included them in the Emsian La Garde Formation in descriptions of the included plants. Like the *Eoarthropleura* material from Alken an der Mosel, these are impression fossils. However, black, coalified cuticle is present over the impressions. The specimen (Fig. 1f, 2d) designated NB-1 FA is a left paratergal fold about 5 mm in both dimensions; the rebordered anterior and lateral margins are clearly preserved. Specimen NB-1 FB consists of an axial tergal plate and its two associated paratergal folds (Fig. 1e, 2c). The entire complex is about 8 mm wide and 3.5 mm long. The anterior portion of the axial plate is missing, and the right paratergal fold is somewhat crumpled. The condition of the matrix suggests that the crumpling did not take place after fossilization, as a result of tectonic distortions, but instead probably occurred when the specimen settled into the soft mud, providing further evidence of possible weak sclerotization in *Eoarthropleura*. The left paratergal fold is complete except for a small notch along its inner margin. The shape and arrangement of the axial plate and paratergal fold suggests (by comparison with *E. devonica*) that this specimen represents a segment near the posterior end of the body. A formal description must wait for more material; arthropod cuticle fragments, including scorpion remains, are relatively common in this formation. Most of the plants are still undescribed, but the genera *Drepanophycus*, *Psilophyton* and *Leclerqia* have been identified (P. GENSEL, pers. comm.). The animals from this deposit, together with older fossils of millipeds from further east on the Gaspé Peninsula, constitute the oldest records of land animals known from North America and will be reported on in detail in forthcoming studies (see also LABANDEIRA, BEALL & HUEBER (1989)).

Acknowledgements

We thank Mr. Fred Collier, formerly of the Smithsonian Institution, Washington, DC, USA, for the loan of the type material of *Tiphoscorpio hueberi*. We thank Dr. Patricia Gensel for bringing the Gaspé material to our attention. Dr. Francis Hueber of the Smithsonian and Dr. Harlan Banks of Cornell University, Ithaca, NY, USA are thanked for correspondence on the Onteora Formation. Messrs Philip Manning and Neil Dubé provided technical assistance in Manchester.

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