

THE RESPIRATORY ORGANS OF EURYPTERIDS

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ABSTRACT. Cuticle fragments from the upper Silurian (Přidolí Series) of south Shropshire, England, are described and interpreted as the respiratory organs of eurypterids. These fragments, combined with whole body evidence, suggest a dual respiratory system: lamellate book-gills, homologous with those of modern xiphosurans and arachnid book lungs, and an additional Kiemenplatten on the true sternite, the roof of the branchial chamber. Kiemenplatten is used in preference to gill-tract, because it is a more 'neutral' term, without functional implications. Eurypterids may have been partially terrestrial: the Kiemenplatten is interpreted as an accessory aerial respiratory organ, most closely analogous to the branchial 'lungs' of certain terrestrial crabs. Cuticular projections from the Kiemenplatten are interpreted as having held a layer of water to keep the structure moist during excursions onto land. A new reconstruction of the eurypterid respiratory system is presented.

EURYPTERID respiratory organs were first described by Laurie (1893) from a specimen of *Slimonia* as 'branchial lamellae,' and were interpreted as being located on the dorsal surface of the abdominal plates (Blatfüsse). The Blatfüsse consist of five pairs of plate-like appendages (Clarke and Ruedemann 1912, pl. 26, fig. 2; Waterston 1975, fig. 4a) which are ventral to the true sternites (ventral body wall) of the opisthosoma, and they enclose a series of five pairs of branchial chambers (Waterston 1975) between themselves and the true sternites. It is these branchial chambers which contain the respiratory organs, which were described subsequently from *Baltoeurypterus* as five pairs of oval respiratory areas termed 'Kiemenplatten' (Holm 1898); these are areas of raised, conical 'spinules' covered in microscopic cuticular projections, arranged hexagonally as 'rosettes' (Holm 1898; Wills 1965). They were later re-interpreted as being on the ventral surface of the true sternite (the roof of the branchial chamber), not on the Blatfüsse (Moore 1941), and were subsequently renamed 'gill tracts' (Wills 1965). Their position within the branchial chamber of *Tarsopterella* was reconstructed in detail by Waterston (1975).

Some eurypterids may have been capable of terrestrial activity (Størmer 1976; Rolfe 1980) and the Kiemenplatten (gill tracts) have been interpreted variously as having aquatic and/or aerial respiratory functions (Størmer 1976; Rolfe 1980; Selden 1985), comparable with isopod pseudotracheae (Størmer 1976). A possible osmoregulatory function was suggested by Waterston (1979) and by Selden (1985), and plastron respiration by Rolfe (1980), with the microscopic cuticular projections acting like plastron hairs. Palaeophysiological calculations suggested that the respiratory surface area (RSA) alone of the gill tract was inadequate to supply a eurypterid's energy requirements (Selden 1985). From this, it was inferred that the gill tract acted primarily as an accessory aerial 'lung', and that eurypterids possessed additional true gills which had yet to be found (Selden 1985).

Taugourdeau (1967) figured gill tract material from the Sahara in micropalaeontological preparations, but did not recognize its significance. During an investigation into the earliest demonstrably terrestrial biota, from the late Silurian of Ludford Lane (Jeram *et al.* 1990), a number of unusual fragments of arthropod cuticle were recovered. These authors figured gill tract material and interpreted it as the posterior end of an unknown arthropod. New discoveries of these cuticle fragments are described here, and interpreted as representing fragments of the respiratory organs of eurypterids.

GEOLOGICAL SETTING

The fossils came from the Platyschisma Shale Member of the Downton Castle Sandstone Formation, above the Ludlow Bone Bed at its type locality in Ludford Lane, Ludlow, Shropshire (SO 5116 7413), and are of late Silurian (Prídolí Epoch) age (see Bassett *et al.* 1982 for details). This sequence is interpreted as a nearshore deposit (Smith and Ainsworth 1989), and work by one of us (PLM, unpublished) and by Maquaker (1994) suggests that the Ludlow Bone Bed represents a deepening event, with the overlying Platyschisma Shale Member being deposits reworked in a shallowing sequence. The best preserved material was collected from organic-rich horizons within the Platyschisma Shale Member, capping reworked, storm-generated deposits, which are characterized by hummocky cross-stratification. These organic-rich horizons are probably the result of the argillaceous and organic elements of the sediment load settling out after a severe storm. The high quality of preservation of these delicate arthropod fragments may be related to the small grain size of the sediments.

Schmitz (1992) recognized within the Ludlow Bone Bed a high concentration of iridium (0.49 ppb) compared with background (0.040 ppb), which he suggested was precipitated from sea water. Although he did not exclude a relation of the anomaly initially with an asteroid impact event, there is little evidence (such as tektites and shocked quartz) for this at the time of deposition of the Ludlow Bone Bed, and Antia (1979) suggested a volcanic origin for some of its constituents. The evidence for such an origin for part of the bone bed is supported by the high percentage of quartz grains which have highly patchy extinction patterns and contain abundant inclusions (Schmitz 1992). We suggest that the high concentrations of iridium (Schmitz 1992) relate directly to the sedimentary environments prevailing at the time of deposition (Manning 1993; Maquaker 1994). The deepening event, which resulted in sediment by-pass and the subsequent build-up of vertebrate sands, would also allow a concentration of iridium to accumulate, precipitated from the sea water.

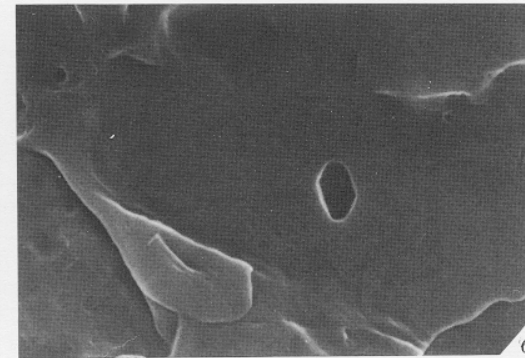
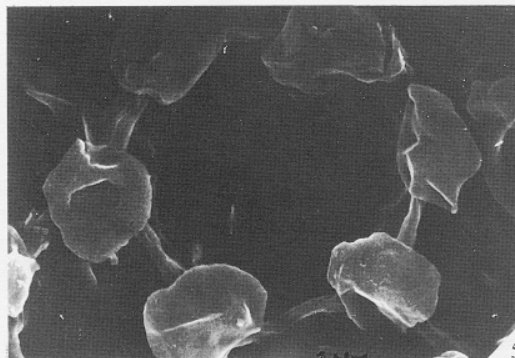
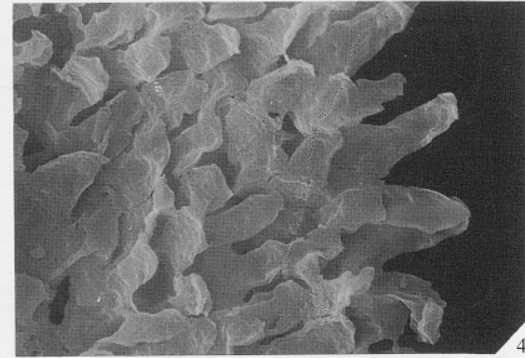
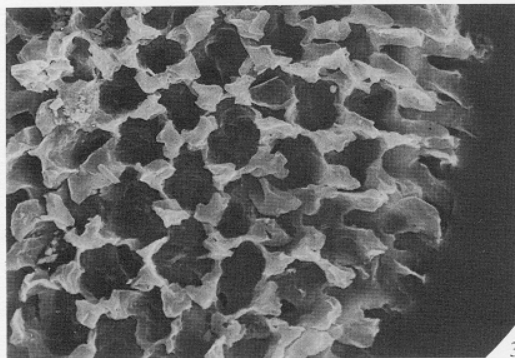
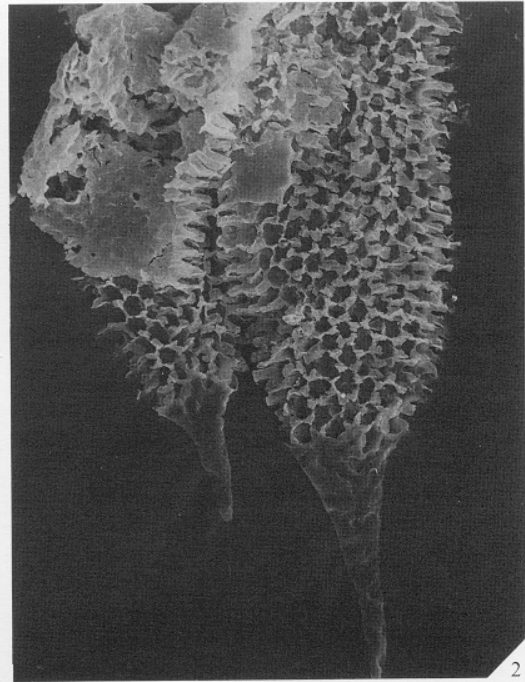
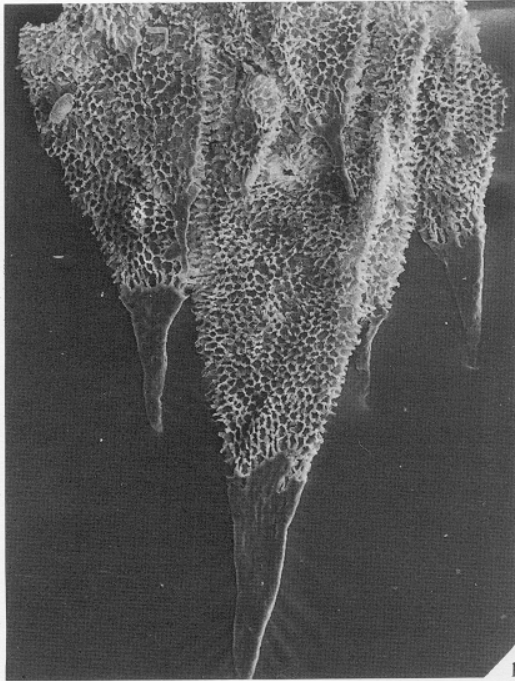
The uncertain report of the crustacean *Ceratiocaris* sp. from this sequence (Bassett *et al.* 1982, fig. 6, p. 13) could not be substantiated in this present study. The eurypterids which have been recognized from it by the senior author are as follows: *Pterygotus* sp.; *Pterygotus* (*Pterygotus*) *denticulatus*; *Eurypterus* sp.; *Eurypterus cephalaspis*; *Hughmilleria* sp.; *Hughmilleria banksi*; *Nanahughmilleria* sp.; *Parahughmilleria* sp.; *Errepterus* (*Truncatiramus*) *gigas gigas* and *Stylonurus* sp. The respiratory material described here is too fragmentary to ascribe to any of these taxa.

MATERIALS AND METHODS

Fragments of arthropod and plant cuticle were recovered by hydrofluoric acid (60 per cent.) maceration of samples of sediment following the method of Shear *et al.* (1987). The resulting

EXPLANATION OF PLATE 1

Figs 1–6. Scanning electron micrographs of cuticular material which represents fragments of eurypterid Kiemenplatten; Upper Silurian (Prídolí), Ludford Lane, Shropshire. 1, LL1119.1; group of seven spinules in assumed life orientation, showing the basic conical shape, terminal spine, surface sculpture and size variation; $\times 170$. 2, LL1119.2; pair of spinules, showing the shape, sculpture and the smooth inner surface where the cuticle is folded over (at the top left); $\times 350$. 3, LL1119.2; detail of cuticular projections ornamenting the spinules, showing the polygonal arrangement extending out from the surface; $\times 790$. 4, LL1121; detail of the cuticular projections, here more densely packed and no longer polygonally oriented; $\times 1200$. 5, LL1117; detail of a single regular 'rosette' of projections from the surface of the Kiemenplatten, showing their approximately circular cross-sectional area; $\times 4500$. 6, LL1117; detail of Kiemenplatten near the base of the spinules, where the cuticular projections have merged into smooth cuticle and which shows a single pore of approximately $1.0 \mu\text{m}$ in diameter; $\times 5000$.



MANNING and DUNLOP, Eurypterid Kiemenplatten

residues were picked for cuticle under both transmitted and incident light. Eurypterid cuticle represents the most common arthropod fragments and was identified by its distinctive morphology and ornamentation (Tollerton 1989; Manning 1993). Material interpreted as eurypterid respiratory organs was dried, mounted on aluminium stubs and gold-coated. It was examined using a Jeol 2020 scanning electron microscope (SEM). All figured material is held in the Department of Geology, Manchester Museum, University of Manchester, numbers LL1117–LL1123. A specimen of a eurypterid, *Rhenopterus?* sp. (Hunterian Museum, Glasgow, no. A23113), believed to show respiratory structures (Selden 1985, p. 223, who referred to it by its Hunterian Museum loan number, G807), was studied under incident light. Preserved specimens of the extant xiphosuran *Limulus polyphemus* were examined for comparative purposes.

RESULTS

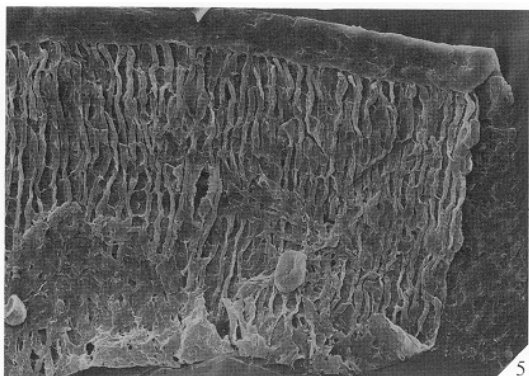
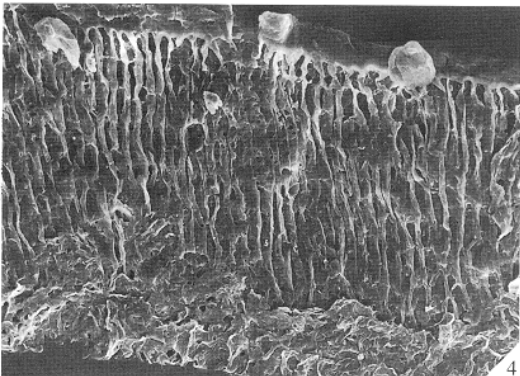
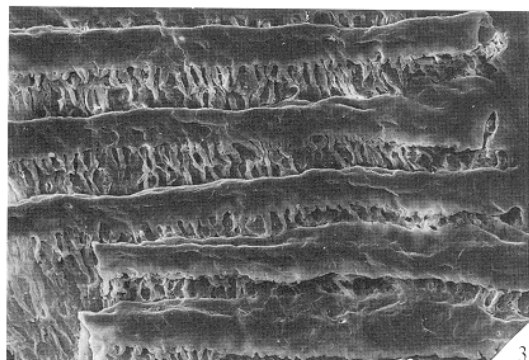
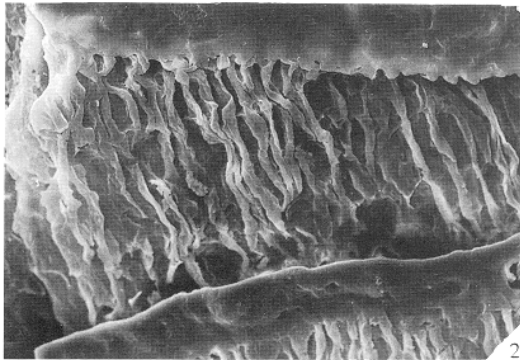
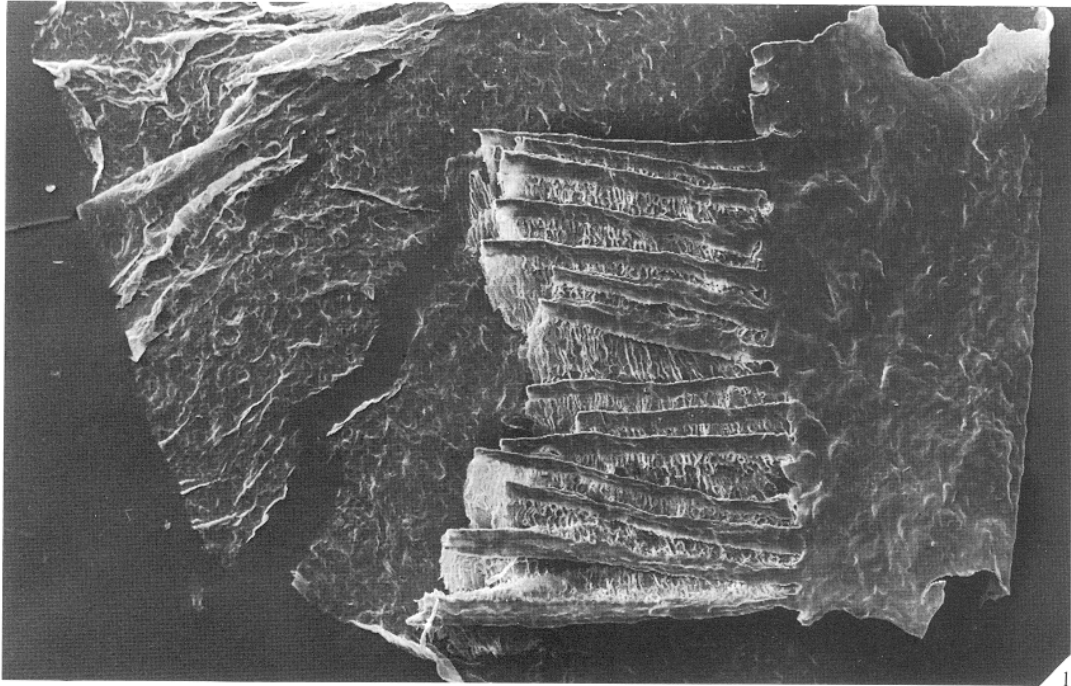
Kiemenplatten (gill tract)

The material includes highly ornamented, conical, cuticular structures (Pl. 1, figs 1–2). These are sometimes found isolated, sometimes grouped, and occasionally attached to larger sheets of cuticle. These cones have a total length of 0.5–2.0 mm and have a basal width of 50–200 μm . The tips of the cones are drawn out into long, tapering spines, typically between 30–150 μm long, which have no surface sculpture (Pl. 1, figs 1–2). The rest of each cone has a dense sculpture of microscopic cuticular projections which stand proud of the surface by approximately 10–15 μm (Pl. 1, figs 3–4). These projections are 2–3 μm wide and give the impression of originally having been cylindrical, and perhaps hollow, but having subsequently become compressed (Pl. 1, fig. 4). However, the internal surface of the *Kiemenplatten*, where visible (Pl. 1, fig. 2), does not show corresponding pores leading into these cuticular projections, suggesting that they may be composed of solid cuticle.

When compared with the material figured by Holm (1898) and Wills (1965) it is clear that these conical structures represent eurypterid *Kiemenplatten*. The latter term is used in preference to gill tract as discussed below. The term spinule was introduced by Wills (1965) for the cones (conical structures) covering the surface of the *Kiemenplatten*. When examined in detail, the polygonal arrangement of the cuticular projections noted by the previous authors is apparent (Pl. 1, fig. 3) including the 'rosettes' (Pl. 1, fig. 5) of Wills (1965), which have a diameter of approximately 20 μm , with the cuticular projections spaced approximately 2 μm apart. However, these projections are less regular and more densely distributed closer to the tip of the spinule, where they lose the 'rosette' arrangement (Pl. 1, fig. 4). Pores were found sparsely distributed in the cuticle between these projections, especially close to the base of the spinules where the projections are less dense (Pl. 1, fig. 6). These pores have smooth margins, which suggests that they are not artefacts, and have a consistent diameter of between 0.5–1.0 μm .

EXPLANATION OF PLATE 2

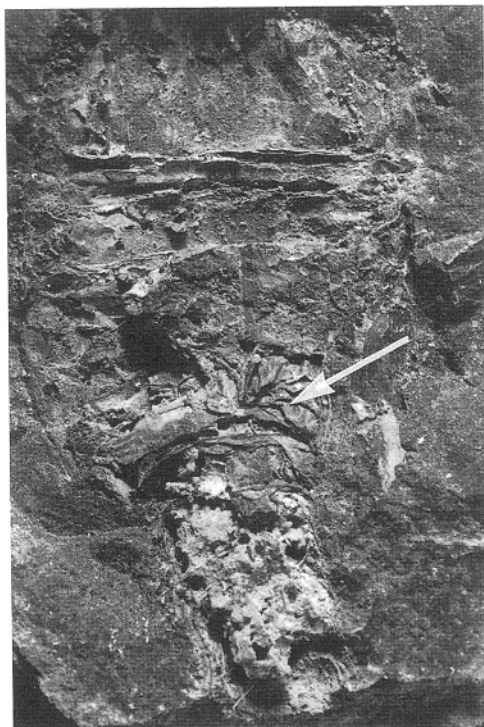
Figs 1–5. Scanning electron micrographs of lamellate cuticular material interpreted as fragments of eurypterid book-gills, from Ludford Lane, Shropshire. 1, LL1118; parts of eighteen lamellae attached to a large fragment of cuticle, which may represent the dorsal surface of the Blatfuss; $\times 115$. 2, LL1118; detail of lamella from figure 1 showing the thickened supporting bar with the ribbed surfaces of the lamella hanging from and continuous with it; $\times 490$. 3, LL1118; detail of lamellae from figure 1 showing them overlapping like the lamellae of modern *Limulus* book gills; $\times 230$. 4, LL1123; fragment of a single lamella, showing a wider, ribbed surface; $\times 230$. 5, LL1122; fragment of a single lamella, showing a broken edge revealing the cross sectional shape of the supporting bar and the two sheets of the lamellae hanging from it, and the smooth inner surface of the lamellae; $\times 230$.



Lamellate gills

Other fragments recovered consist of small thickened cuticular bars (Pl. 2, figs 1–5) up to 7 mm long and approximately 20 μm wide. These bars are ovate in cross section, but with a concave interior surface and support two sheets of thin cuticle (Pl. 2, fig. 5). These cuticle sheets are estimated to have been 20 μm apart, and less than 0.5 μm thick where there is no surface sculpture. The cuticle sheets are fragmentary, at most 3 mm wide but usually much narrower. The two sheets suggest that they once formed an enclosed structure with a smooth interior surface and an exterior surface ornamented with a series of solid, cuticular 'ribs' lying perpendicular to the supporting bar (Pl. 2, figs 1–3). These ribs are approximately 2–3 μm wide, with a spacing of 2–5 μm and stand proud of the surface by approximately 5 μm . There are cross-bars, approximately 0.1–0.5 μm wide, between the cuticular ribs (Pl. 2, figs 1–5) which do not appear to be artefacts. The spacing of these cross-bars is irregular and they occur more commonly towards the thickened cuticular bars.

These supporting bars and their cuticle sheets are usually found isolated, but occasionally up to eighteen overlapping sheets, connected to fragmentary sheets of cuticle (Pl. 2, fig. 1), are found. These structures are interpreted as fragments of the marginal edges of lamellate gills, using the book-gills of *Limulus* as a comparison. Longer fragments show that the supporting bars were curved, suggesting that the whole structure may have been semicircular in life, as are the gill lamellae of *Limulus*.



TEXT-FIG. 1. Phosphatized eurypterid in ventral view. *Rhenopterus?* sp., Lower Carboniferous, Montagne Noire region, France; HM A23113; $\times 1.5$. Specimen interpreted as showing book-gills (arrowed) in life position, consisting of stacked, overlapping lamellae within a branchial chamber.

Whole body evidence

An undescribed specimen of *Rhenopterus?* sp. (Text-fig. 1) is interpreted as showing a single, open branchial chamber which contains at least seven phosphatized, overlapping, lamellate structures. These structures are interpreted as the gills of a single branchial chamber approximately in life position. This specimen provides strong supportive evidence for the presence of lamellate gills in

eurypterids and further suggests that the individual lamellae have an approximately semicircular shape and also that they attach obliquely, close to the midline of the body as in *Limulus*.

DISCUSSION

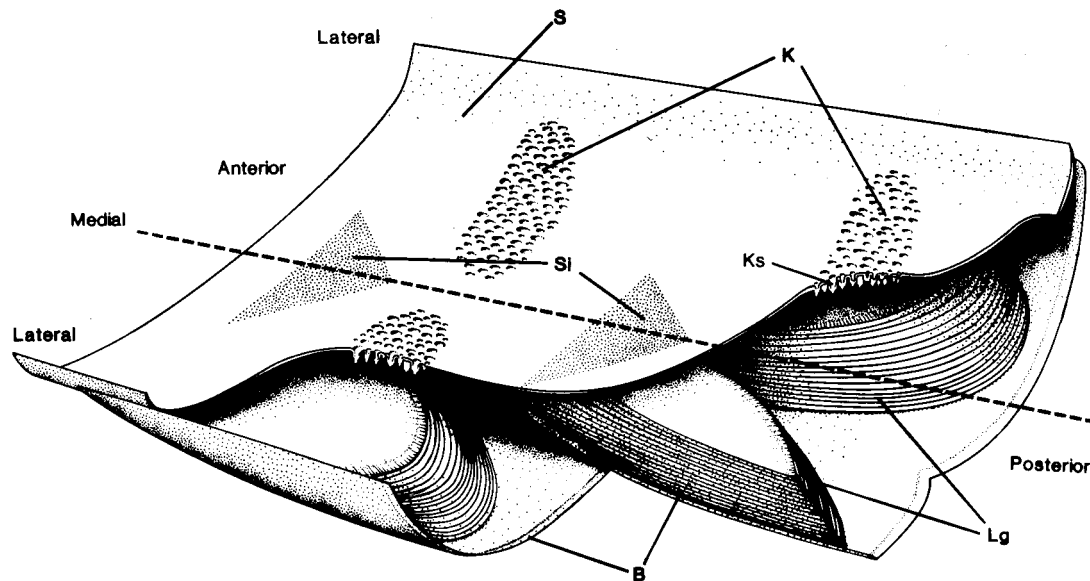
Interpretation of the Kiemenplatten (gill tract)

We are confident that these dissociated fragments of Kiemenplatten belong to eurypterids because their structure matches the material described and figured by Holm (1898) and Wills (1965) from whole body specimens. Also, some fragments show the margins of the Kiemenplatten where it merges with sternite cuticle which matches recognizable fragments of eurypterid cuticle (see Manning 1993 for a discussion of cuticle form and structure). Kiemenplatten material is reasonably common in macerates containing large quantities of eurypterid fragments, and has not been demonstrated to occur in any other arthropod group. Material superficially similar to the spinules described here, but lacking obvious cuticular projections arranged in 'rosettes', has been described as scorpion gill tract from the Upper Carboniferous (Kjellesvig-Waering 1986). This interpretation is probably incorrect because these structures originate from the scorpion abdominal plate, not from the true sternite (A. Jeram, pers. comm.). The fragments recovered during this study can be regarded as being part of a larger, oval area of Kiemenplatten, as noted by previous authors (e.g. Holm 1898). In fragments attached to sternite cuticle the spinules tend to be small, suggesting that the Kiemenplatten is most developed in its centre. The fragmentary nature of this material does not allow the size of the whole Kiemenplatten area to be determined.

The Kiemenplatten bears all the hallmarks of a respiratory structure with its increased surface area formed by the spinules (Pl. 1, figs 1–2). If the projections from the spinules (Pl. 1, figs 3–5) were hollow, this would also increase the respiratory surface area (RSA). It seems likely that the cuticle of the spinules was backed by a blood sinus and provided a surface for gas exchange. There seems no reason to doubt that the Kiemenplatten could have functioned as an accessory 'gill' in water, but what is more interesting is the suggestion that it is a structure which evolved primarily for respiration in air. The structure of the Kiemenplatten suggests that the downward-hanging spinules (Pl. 1, figs 1–2) would not have collapsed in air, leading to a reduction in RSA, in the same way as a lamellate gill. The presence of downward projecting Kiemenplatten spinules could also have maintained a cavity above the lamellae by preventing them from being compressed against the roof of the branchial chamber (A. Jeram, pers. comm.). The suggested primary respiratory function of the highly vascularized regions of the eurypterid sternite, is contradicted by the use of the term gill tract (Wills 1965). Because of its functional implications the term gill tract is rejected and the term Kiemenplatten (Holm 1898) is preferred here as a more 'neutral' term.

The overall morphology of the eurypterids shows that they were clearly primarily aquatic animals (Selden 1985). However, by closing the Blatfüsse during excursions onto land they could have reduced water loss over the gills, in the same way that a narrow book-lung spiracle prevents water loss in arachnids, while relying on gas exchange with air over the gill tract. Since air has a higher partial pressure of oxygen than water, the RSA of the Kiemenplatten may not have needed to be as great as that of the lamellate gills in order to support metabolically the animal in air. The respiratory evidence therefore suggests that at least some eurypterids could have ventured onto land, but the degree to which these animals could have been terrestrial can only be answered in a fuller account of Kiemenplatten palaeophysiology and corroborative evidence from eurypterid palaeoecology.

The small pores described in the Kiemenplatten (Pl. 1, fig. 6) could be interpreted as spiracles leading into some sort of tracheal system (as the figures of Størmer 1976 appear to suggest), but no such tracheae backing them were observed in any of the specimens. An alternative hypothesis is that they were backed by osmoregulatory cells, although this is mere conjecture at this stage. The spines at the tips of the spinules (Pl. 1, figs 1–2) could possibly have been a protective device against haematophagous parasites.



TEXT-FIG. 2. Interpretative reconstruction of two branchial chambers of a generalized eurypterid. The lamellate book-gills (Lg) originate from the dorsal surface of the Blatfüsse (B) and occupy most of the branchial chamber. Blood entered a Blatfuss from a hypothetical blood sinus (Si) and from here entered the lamellae, probably by tidal flow. The Kiemenplatten (K) is a well vascularized oval area of the sternite (S), comprising a series of spinules (Ks) and located above the lamellae within the branchial chamber.

Kiemenplatten have also been found in association with eurypterid fragments in macerates from older horizons at Monterrey, Virginia (Silurian, Llandovery) and younger ones at Hudwick Dingle, Shropshire (Devonian, Lochkovian) and Gilboa, New York (Devonian, Givetian) (unpublished observations). Initial examination of this material suggests some minor, but potentially significant differences, from the material described here.

Interpretation of the lamellate gills

We are confident that these lamellate structures belong to eurypterids and are not the gills of xiphosurans or crustaceans since, like the Kiemenplatten, the lamellae are occasionally found attached to recognizable eurypterid cuticle (Manning 1993). Xiphosurans and non-ostracode crustaceans were not found in the Ludford sequence either as recognizable fragments in macerates, macrospecimens or trace fossils. Also, the lamellae are reasonably common in macerates containing large amounts of eurypterid fragments. Scorpion cuticle fragments have been recorded, and these lamellae could represent the gills of aquatic forms; however scorpion cuticle was rare, rarer even than the lamellate structures within the macerates.

Comb-like structures have been described as the pectinated appendages of the eurypterid *Cyrtoctenus* (Størmer and Waterston 1968). These were subsequently interpreted as modified spines of the distal limb podomeres with a sweep-feeding function (Waterston *et al.* 1985). Detailed examination of the lamellate structures found in this present study has shown that they display two ribbed surfaces, not individual filaments attached to a supporting bar as in *Cyrtoctenus*. Based on these characters we are confident that the lamellate structures from Ludford Corner are not appendicular sweep-feeding devices.

The eurypterid book-gills resemble those of *Limulus* in having a marginal thickening (Pl. 2, figs 1–5), but differ from those of living xiphosurans in having the ribs on the surface of the lamellae (Pl. 2, figs 1–4). These ribs may have strengthened and supported the lamellae, but the fragmentary

evidence does not show if the whole lamella was ribbed or only the margins, which have therefore been preferentially preserved. All the fragments of lamellae found in this study were ribbed, regardless of size. The ribs are not obviously homologous, or functionally analogous, with the struts separating the air spaces between the lamellae of arachnid book lungs (e.g. Reisinger *et al.* 1990), so that the lamellae would probably have collapsed in air. However, it is worth noting that certain extant terrestrial crabs, e.g. *Cardisoma* and *Geograspus* (Mill 1972; Farelly and Greenaway 1992), have reduced lamellate gills with thickened and stiffened lamellae which help support the structure in air and allow effective ventilation and draining of the gills when the crab comes onto land. The total number of lamellae comprising any particular eurypterid gill found in this study, and the shape and variation in shape of the entire lamellae, cannot be determined for this fragmentary material. The *Rhenopterus?* specimen (Text-fig. 1) and comparisons with *Limulus* suggests that the lamellae were quite large, occupying most of the space in the branchial chamber.

The dorsal surface of the eurypterid Blatfüsse has not been described satisfactorily (Selden 1985). We speculate that, as in *Limulus*, where the gills attach to the gill operculum, the dorsal surface of the homologous eurypterid Blatfüsse is the attachment site of their lamellae. The large fragments of cuticle attached to some specimens (Pl. 2, fig. 1) may represent part of this dorsal surface. The Blatfüsse appear to have served the dual purpose of attachment area and protection for the lamellate gill. If the animal did come onto land, the lamellate gills would probably have collapsed onto the dorsal surface of the Blatfüsse without the support of water. A collapsed gill would probably have been ineffective for aerial respiration and this could explain the need to evolve an accessory aerial respiratory organ in a partially terrestrial animal.

Reconstruction of the eurypterid respiratory system

While Kiemenplatten and lamellate gills have not been recorded from a single specimen to date, we have no evidence that the two structures belong to two different taxa. On this basis the eurypterid respiratory system is reconstructed as possibly comprising two elements (Text-fig. 2), as suggested by Selden (1985): lamellate book-gills and the accessory Kiemenplatten. The multiple lamellae of the book-gills were probably attached to the dorsal surface of the Blatfüsse and were presumably the principal means of aquatic respiration. By analogy with *Limulus*, the Blatfüsse and their gills would have connected to a blood sinus towards the midline of the animal and there would have been a tidal flow of haemolymph in and out of the lamellae. The Kiemenplatten hung above the gills within the branchial chamber and was probably also backed by a blood sinus, gas exchange occurring with the haemolymph in this sinus.

The 'branchial lung' model of Kiemenplatten function

The eurypterid Kiemenplatten has no counterpart in any other chelicerate group and thus represents a previously unknown respiratory system in arthropods. The pseudotracheal model for the Kiemenplatten proposed by Størmer (1976) appears inappropriate. Isopod pseudotracheae are invaginated cutaneous tubules lying within the blood sinus of an appendage (Snodgrass 1952), whereas the eurypterid Kiemenplatten is interpreted as a vascularized region of evaginations of the body wall (Pl. 1, figs 1–2). The plastron model of Kiemenplatten function (Rolfe 1980) was rejected by Selden (1985) because the cuticular projections were claimed to be too widely spaced to hold a meniscus. This study suggests that cuticular projections on the Kiemenplatten (Pl. 1, figs 3–5) are over twice as long and wide as typical hydrofuge plastron hairs. There is no evidence that the Kiemenplatten projections were water repellent or that they had linkages between the tops of the projections (Pl. 1, figs 4–5) to provide an incompressible air space as in a plastron (Mill 1972). More significantly, a plastron is a secondarily aquatic-adapted respiratory mechanism originally of terrestrial arthropod lineages, whereas eurypterids are suggested as having been primarily aquatic animals attempting terrestrialization (Selden 1985).

The closest arthropod analogues to eurypterid Kiemenplatten are the cutaneous brachial lungs of certain terrestrial crabs, e.g. *Ocypode* and *Pseudothelphusa* (Mill 1972; Little 1990), formed from

highly vascularized regions of the branchial chamber wall (i.e. not the gills, as in *Cardisoma*) and which act as osmoregulatory and aerial respiratory organs. However, it is worth comparing the apparent strengthening structures both on eurypterid and crab gill lamellae, which may suggest that the eurypterid lamellae had some terrestrial adaptations. Terrestrial crabs must still keep their gills or branchial lungs moist (Mill 1972), presumably to avoid desiccation. The cuticular projections on the eurypterid Kiemenplatten may have served principally to trap a fine meniscus of water, in order to keep the area moist, a requirement of all respiratory surfaces (Hill and Wyse 1989), and functioning longer on land. This is similar to a plastron, except that, rather than trapping air as the animal enters water, and then holding a meniscus of water away from a tract as in the hydrofuge hairs of a plastron, these projections may have held a meniscus of water next to the Kiemenplatten. It is worth noting that, when removed from water and dried on SEM stubs, the fragments of Kiemenplatten took longer to dry than comparable cuticular fragments.

It is interesting to observe that recent crabs attempt terrestrialization in two ways: adapting their gills directly into lamellate 'lungs' (Mill 1972; Little 1990; Farrelly and Greenaway 1992), as has occurred with the arachnid book-lungs (Selden and Jeram 1989); and, alternatively by vascularization of the branchial chamber wall (Mill 1972; Little 1990), which is apparently analogous to the eurypterid Kiemenplatten. Different eurypterid taxa may similarly have used different strategies for aerial respiration, i.e. Kiemenplatten or strengthened book-gills, but we have no evidence for this dual adaptation at present, and we favour the model proposed in Text-figure 2. Eurypterids, however, appear ultimately to have failed to colonize land and this may be the result, in part, of their reliance on the Kiemenplatten, whereas the successful terrestrial chelicerates transformed their lamellate book-gills directly into lamellate book-lungs.

Acknowledgements. We thank Dr P. A. Selden for his encouragement and advice, Drs W. A. Shear, A. J. Jeram and S. Braddy for helpful discussions, Dr W. D. I. Rolfe for the loan of the *Rhenopterus?* specimen, Mr R. Hartley for drawing Text-figure 2 and Mr D. F. A. Nicholson and English Nature for permission to collect from Ludford Corner. JAD acknowledges a NERC studentship to conduct research into early terrestrial ecosystems.

REFERENCES

- ANTIA, D. D. J. 1979. Bone-beds: a review of their classification, occurrence, genesis, diagenesis, geochemistry, palaeoecology, weathering, and microbios. *Mercian Geologist*, **7**, 93–174.
- BASSETT, M. G., LAWSON, J. D. and WHITE, D. E. 1982. The Downton Series as the fourth Series of the Silurian System. *Lethaia*, **15**, 1–24.
- CLARKE, J. M. and RUEDEMANN, R. 1912. The Eurypterida of New York. *Memoir of the New York State Museum*, **14**, (2 vols), 1–439, pls 1–88.
- FARRELLY, C. A. and GREENAWAY, P. 1992. Morphology and ultrastructure of the gills of the terrestrial crabs, Crustacea, Gecarcinidae and Grapsidae: adaptations for air-breathing. *Zoomorphology*, **112**, 39–49.
- HILL, R. W. and WYSE, G. A. 1989. *Animal physiology*. 2nd Edition. Harper and Row, New York, 656 pp.
- HOLM, G. 1898. Über die Organisation des *Eurypterus fischeri* Eichw. *Memoirs of the Academy of Science, St. Petersburg*, **8**, 1–57.
- JERAM, A. J., SELDEN, P. A. and EDWARDS, D. 1990. Land animals in the Silurian: arachnids and myriapods from Shropshire, England. *Science*, **250**, 658–661.
- KJELLESVIG-WAERING, E. N. 1986. A restudy of the Fossil Scorpionida of the world. *Palaeontographica Americana*, **55**, 1–287.
- LAURIE, M. 1893. The anatomy and relations of the Eurypteridae. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **37**, 509–528.
- LITTLE, C. 1990. *The terrestrial invasion: an ecophysiological approach to the origins of land animals*. Cambridge Studies in Ecology, Cambridge University Press, Cambridge, 304 pp.
- MANNING, P. L. 1993. Palaeoecology of the eurypterids of the Upper Silurian of the Welsh Borderland. Unpublished M.Sc. thesis, University of Manchester.
- MAQUAKER, J. H. S. 1994. Palaeoenvironmental significance of bone-beds in organic-rich mudstone successions: an example from the Upper Triassic of South West Britain. *Zoological Journal of the Linnean Society, London*. **112**, 285–308.

- MILL, P. J. 1972. *Respiration in the invertebrates*. Macmillan Press, London, 212 pp.
- MOORE, P. F. 1941. On gill like structures in the Eurypteridae. *Geological Magazine*, **78**, 62–70.
- REISINGER, P. W. M., FOCKE, P. and LINZEN, B. 1990. Lung morphology of the tarantula, *Eurypelma californicum* Ausserer, 1871 (Aranae: Theraphosidae). *Bulletin of the British Arachnological Society*, **8**, 165–170.
- ROLFE, W. D. I. 1980. Early invertebrate faunas. 117–157. In PANCHEN, A. L. (ed.). *The terrestrial environment and the origin of land vertebrates*. Academic Press, London and New York, 633 pp.
- SELDEN, P. A. 1985. Eurypterid respiration. 209–226. In CHALLONER, W. G. and LAWSON, J. D. (eds). *Evolution and environment in the Late Silurian and Early Devonian*. *Philosophical Transactions of the Royal Society of London, Series B*, **309**, 342 pp.
- and JERAM, A. J. 1989. Palaeophysiology of terrestrialisation in the Chelicerata. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **80**, 303–310.
- SHEAR, W. A., SELDEN, P. A., ROLFE, W. D. I., BONAMO, P. M. and GRIERSON, J. D. 1987. New terrestrial arachnids from the Devonian of Gilboa, New York (Arachnida, Trigonotarbida). *American Museum Novitates*, **2901**, 1–74.
- SCHMITZ, B. 1992. An iridium anomaly in the Ludlow Bone Bed from the Upper Silurian, England. *Geological Magazine*, **129**, 359–362.
- SMITH, R. D. A. and AINSWORTH, R. B. 1989. Hummocky cross-stratification in the Downton of the Welsh Borderland. *Journal of the Geological Society, London*, **146**, 897–900.
- SNODGRASS, R. E. 1952. *Textbook of arthropod anatomy*. Cornell University Press, New York, 363 pp.
- STØRMER, L. 1976. Arthropods from the Lower Devonian (Lower Emsian) of Alken-an-der-Mosel, Germany. Part 5: Myriapoda and additional forms, with general remarks and problems regarding invasion of land by arthropods. *Senckenbergiana Lethaea*, **57**, 87–183.
- and WATERSTON, C. D. 1968. *Cyrtoctenus* gen. nov., a large Palaeozoic arthropod with pectinate appendages. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **68**, 63–104.
- TAUGOURDEAU, P. 1967. Débris microscopiques d'euryptéridés du Paléozoïque saharien. *Revue de Micropaléontologie*, **10**, 119–127.
- TOLLERTON, V. P. 1989. Morphology, taxonomy and classification of the Order Eurypterida, Burmeister 1843. *Journal of Paleontology*, **63**, 642–657.
- WATERSTON, C. D. 1975. Gill structure in the Lower Devonian eurypterid *Tarsopterygia scotica*. *Fossils and Strata*, **4**, 241–254.
- 1979. Problems of functional morphology and classification in stylonurid eurypterids, Chelicerata, Merostomata, with observations on the Scottish Silurian Stylonuroidea. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **70**, 251–322.
- OELOFSEN, B. W. and OOSTHUIZEN, R. D. F. 1985. *Cyrtoctenus witterbergensis* sp. nov. Chelicerata: Eurypterida, a large sweep feeder from the Carboniferous of South Africa. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**, 339–358.
- WILLS, L. J. 1965. A supplement to Gerhard Holm's 'Über die Organisation des *Eurypterus fischeri* Eichw.' with special reference to the organs of sight, respiration and reproduction. *Archiv für Zoologi*, **18**, 93–145.

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Typescript received 28 September 1993
Revised typescript received 27 May 1994