

Gill structures in the Lower Devonian eurypterid

Tarsopteryella scotica

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The lectotype, from the Gedinnian of Angus, Scotland, has been prepared to show the ventral structures of the abdomen. Surface features of the gill tracts, the ventral body wall, the skin forming the roof of the gill chambers anterior and posterior to the gill tracts and that forming the anterior and posterior surfaces of the hinge of the plate-like abdominal appendages are described and illustrated and a tentative reconstruction of the gill chambers is given. The significance of these findings is discussed in the light of recent literature on eurypterid gill anatomy and they are found to support the general interpretation suggested by P.F. Moore and substantiated by L.J. Wills that eurypterid gill tracts are specialisations of the ventral body wall. A revised description of the general anatomy of this species will appear elsewhere.

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The respiratory organs of eurypterids were first recognised by H. Woodward in *Erettopterus* (1868: 294; 1869: 66–8) and later in *Slimonia* (1871: 115–6). Hall (1859) having established the true position of the eurypterid operculum, and the homology with the operculum in *Xiphosurus* having been recognised (Woodward 1869: 61; 1871: 114), Woodward looked for evidence of eurypterid gills in an analagous position to those of the King Crab, dorsal to the operculum. His evidence from *Erettopterus* left him in little doubt "that the normal place of attachment (of the gills) would be under the thoracic plate or operculum" (1869: 66). The "branchiae" were attached, he thought, in single or double rows to the ventral surface of the body by their anterior margins, the rounded leaf-like lateral and posterior borders being freely bathed with water. In *Slimonia* he recognised the existence of abdominal appendages with which gills were also associated on segments posterior to the operculum, but he believed them to be of similar form to the operculum, bearing genitalia, and more or less covered on the ventral side by the operculum.

M. Laurie (1893: 514–5) made a further study of *Slimonia* and rejected Woodward's idea of several plates similar to the genital operculum lying one on top of another and recognised for the first time that paired plate-like ventral appendages were borne on the mesosomatic segments. He concluded that at least one, and probably more "branchial lamellae" were carried on the inner or dorsal side of each of these abdominal appendages. Laurie seemed to make an exception of the first gill, however, for not having found any trace of gills on detached genital plates, he considered that the gill structures sometimes seen through the operculum must be attached to the soft skin of the body on the second mesosomatic somite.

A milestone was reached in the understanding of the eurypterid gill when G. Holm's classic monograph on "*Eurypterus fischeri*" (= *Eurypterus tetragonophthalmus* (Fischer)) was published in 1898. He demonstrated that the two sides of the gill tract were different and that what he termed the "*Kiemenplatten*", which he correlated with Woodward's "branchiae" and Laurie's "branchial lamellae", were therefore part of the skin and not free lamellae as previously supposed. He pointed to the inconsistency of Laurie's conclusions but in part agreed with him in supposing that the gill structures were borne on the mesosomal appendages believing that the *Kiemenplatten* were spongy thickenings of the dorsal skin of these appendages. While he did not think that the *Kiemenplatten* were themselves free lamellae he believed that they would form the attachments for such lamellae. Holm extended his study of the gills of *Eurypterus* and *Erettopterus* and had made many important discoveries but his death occurred before publication of his work. It is fortunate that some of the illustrations which he had prepared have since been

published by Professor Wills (Wills, 1965, posthumous Plate 1–5). Holm's interpretation has been adopted by many authors who have described gills in other genera (e.g. Clarke and Ruedemann 1912 in *Paracarcinosoma scorpionis* and *Onychopterella kokomoensis*, Størmer 1934, 1944 and 1955 in *Hughmilleria norvegica* and *Mixopterus kiaeri*).

P.F. Moore (1941) re-examined one of the *Slimonia* specimens studied by Laurie and concluded that the gills are not borne on the genital operculum or abdominal plates, but occur dorsal to them as highly vascular areas of the body wall. He further argued that analogies with living animals (Xiphosurans, Scorpions and Pedipalps) suggest that on a segment specialised for reproduction, as is the eurypterid operculum, the respiratory apparatus would be atrophied and he concluded that the first gill in eurypterids, which is covered by the operculum, is therefore likely to be in the body wall of the second mesosomatic segment.

The last major work on eurypterid gills was the detailed description of "*Eurypterus fischeri*" by L.J. Wills (1965) for which he used Holm's unpublished plates and preparations and new acid preparations in embedding resin made by himself. Wills supplemented Holm's findings but added a great deal of new information and, in particular, established the form of the gill chamber describing the different appearances of the cuticle in its various parts. He produced convincing evidence for the gill tract being a specialisation of the ventral body wall. He followed Moore in the opinion that the genital segment of no present day chelicerate carries a gill or lungbook, but believed that the operculum in the eurypterid included the ventral elements of the first two mesosomal segments. He concluded, therefore, that the smaller-than-usual gill pouches which he found associated with the operculum were developed on the second, or postgenital segment, of the mesosoma. (Wills 1965: 129). This interpretation was not accepted by Størmer & Kjellesvig-Waering (1969: 203) who claimed that lungs do occur in the genital segment of the recent arachnids *Uropygi*, *Amblypygi* and *Aranaea* and inferred that the first gill of eurypterids is developed on the first mesosomal segment. Were this the case it would show that the operculum in eurypterids was in a more primitive condition than had been supposed by Moore and Wills since it had retained its respiratory function as well as being specialised for reproduction.

It is clear that no settled conclusions have yet been reached as to the nature and position of the gills in eurypterids and any additional evidence will be of value in bringing us nearer to a true understanding of this aspect of eurypterid anatomy. The writer was interested, therefore, when in the course of re-describing the Scottish Devonian eurypterids, new evidence became available to him on the gill anatomy of the large and rare form, *Tarsopterella scotica*.

THE MATERIAL

Stylonurus scoticus was described by Woodward (1865, p. 484; 1872, p. 126), *Stylonurus armatus* Page (1867: 230) being a junior synonym. Clarke and Ruedemann (1912: 287) erected a new subgenus *Tarsopterus* to accommodate Woodward's species but this name was preoccupied by an amphibian and Størmer (1951: 421) made *S. scoticus* the type species of a new genus *Tarsopterella* which was referred "with considerable misgivings" to the Dolichopteridae by Kjellesvig-Waering (1966: 176).

The species was described from two specimens found in 1863 by James Powrie in an Old Red Sandstone quarry "in Montroman Muir, near the Forfar and Montrose Pike". It is likely that this locality is Balgavies Quarry (Grid No. 537519), Angus, which falls within the Arbuthnott Group of the Lower Old Red Sandstone (Gedinnian) Region of the Midland Valley of Scotland in the sense of Armstrong and Paterson (1970). One of the syntypes was an almost complete individual, lacking much of the prosomal appendages (Woodward 1872, Pl. XXIII), which is now in the Royal Scottish Museum numbered 1891.92.103. The other was a dorsal shield of the prosoma (Woodward 1872, Pl. XXII) of which the part was in Lady Kinnaid's cabinet and is now in the Royal Scottish Museum (Kinnaid 70), while the counterpart is in the British Museum (Nat. Hist.). Of these the more complete specimen R.S.M. 1891.92.103 is here designated lectotype.

The lectotype existed in three parts, the dorsal surface of the prosoma and abdomen being displayed on one slab, while the post-abdomen and telson were preserved on an adjacent block from which the natural cast of the last five body segments could be detached. Because of the importance of the specimen it was most desirable to reveal such ventral structures as could be exposed in a way consistent with the conservation of the type. Taking advantage of a natural parting in the matrix, the block containing the anterior part of the body was split in such a way that the dorsal shield of the prosoma and the anterior tergites could be preserved separately. On the remaining block many of the ventral structures were revealed in dorsal aspect including the remarkably preserved gill structures which are here described.

DESCRIPTION OF THE GILL STRUCTURES

Removal of the dorsal shield of the lectotype revealed, in addition to parts of the **prosomal appendages**, some of the ventral structures of the first three mesosomal segments and in particular the gills, gill pouches, ventral body wall and parts of the plate-like mesosomal appendages (*Blattfüsse*) of the animal, the details of which have been admirably preserved in the fine sediment. The view of the gill chambers is comparable to that of *Eurypterus tetragonophthalmus* illustrated by Holm (1898, Pl. 10: 9). The structures are complex and difficult to interpret because many types of surface are exposed. Most are natural moulds of the ventral surface of the ventral cuticle of the body wall. Others have been formed by the *Blattfüsse* and their doublures while, here and there, the cuticle itself has been preserved. These surfaces have been distorted due to compression of markedly three-dimensional structures and the segments have been telescoped, probably during ecdysis, resulting often in one surface having been superimposed upon another. For simplicity of presentation each type of surface is described with an indication of the interpretation put upon it in the light of Wills (1965) but the main discussion of how these surfaces are related to one another, together with the consequent interpretation of the anatomy of the gills and gill pouches of which they form parts, follows the descriptive section.

Seven types of surface have been recognised and their distribution is illustrated in Fig. 1. They are described as follows: (1) Gill tract, (2) Median skin of ventral body wall, (3) Microfolds, (4) Macrofolds, (5) Posterior granular skin, (6) Anterior granular skin, (7) The variously ornamented ventral surfaces of the ventral plates – operculum, *Blattfusse* etc.

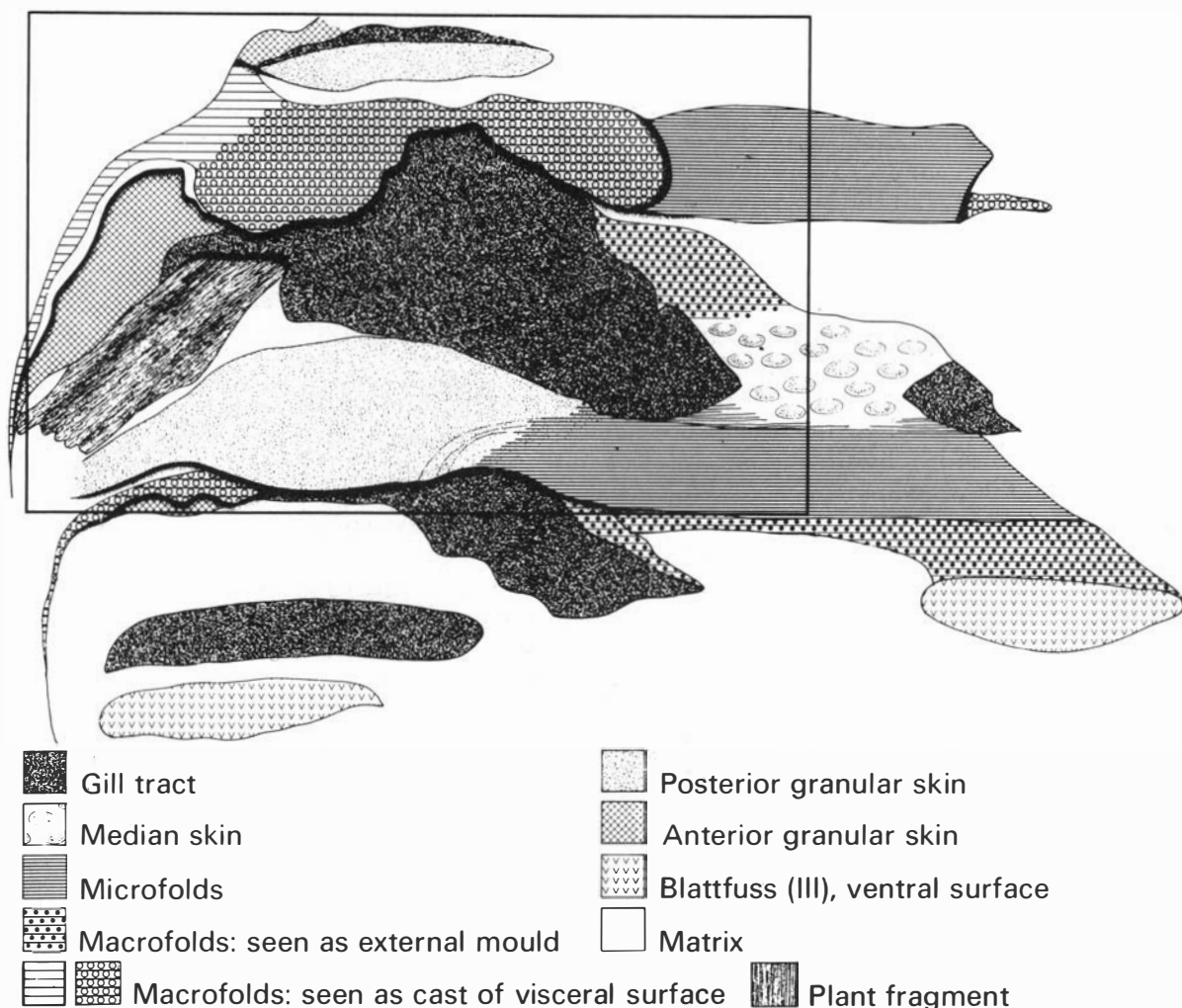


Fig. 1. Diagram to illustrate the distribution of the various types of cuticular surfaces as exhibited on the ventral surface of the mesosomal segments of the lectotype of *Tarsoptierella scotica* (Woodward) R.S.M. 1891. 92. 103. See also Pl. 1: 1, the area of which is indicated by the rectangle on the diagram.

The characteristic surfaces of the gill tracts (Pl. 1: 1, Pl. 2: 4,5) are seen on the left and right sides of the second, and left side of the first, third and fourth mesosomal segments. The most complete is that of the left side of the second mesosomal segment of which the anterior and medial parts are complete but the post-lateral portion has been broken away. This tract is 90 mm wide and, when complete, must have been some 35 mm in maximum length. The segment measures 137 mm from the mid-line to the left lateral margin so that the gill tracts must have occupied about two thirds of its total width. The tracts are therefore much broader than long, the greatest length being in the lateral part of the tract. The inner margins are extended towards the median line of the animal in a well-defined and broadly hastate prolongation so that the overall shape of the tracts is sub-triangular. This differs from the oval or elliptical form more usual in eurypterids but is reminiscent of *Mixopterus* (Størmer 1934, Fig. 38, Pls. 5 and 7) in which the gill tracts are wedge shaped having the thin end of the wedge pointing towards the mid-line of the animal. The tract of the first mesosomal segment is incomplete anteriorly but appears to have been much smaller than that of the succeeding tract described above, and is likely to have been less than half the width of the tract of the second segment. That of the third mesosomal segment is very incomplete, only that portion nearest the mid-line being present, the left tract of the fourth segment appears to be fairly complete and is lath-shaped measuring 72 mm in width but only 17 mm in maximum length.

The most conspicuous feature of the gill tracts is the branching plexus of grooves which is quite sharply defined from the spongy tissue making up the bulk of the tract. From a large trunk groove, situated within the anterior margin of the gill tract, a series of five or six major branches passes postero-medially and divides into small ramifying members to every part of the tract. The walls of the major grooves are pitted but the chitinous spinules which cover the ventral surface of the spongy tissue are sparse or lacking (Pl. 2: 4,5). The dendritic pattern of grooves has been noted by all previous workers (e.g. Holm 1898: 40, Pl. 11: 5) and is clearly equivalent to the "valleys" of Wills who noted (1965: 119–20, Pl. 6: 1, 2, Pl. 7) that on the "inner" or dorsal surface of the tract the "valleys" are represented by strips of dimpled, but otherwise featureless skin. From his reconstruction of Holm's section across a gill tract (Wills 1965, Pl. 6: 3 and 4) it is clear that the "valleys" appear as such from the ventral side of the tract. On the dorsal side, however, they also appear as depressions between the masses of spongy tissue which overlie the "ridges" of the ventral surface. What is seen in *Tarsoptereella* appears to be a natural cast of the dorsal surface of the gill tract and a mould of the exposed surface made in rubber latex (Pl. 2:5) shows the probable appearance of the blood vessels lying in the dorsal grooves of the valley system. These were papillate, the largest papillae being on the ventral crests of the vessels.

While the dendritic grooves are seen as a natural cast of the dorsal surface of the gill tract, the intricacies of the spongy surface between the grooves are such that a clean cast has not been formed, but the spongy mass has been broken apart to reveal it at different depths through the thickness of the tract. That the spongy appearance is due to small outgrowths and invaginations of the cuticle is shown by the presence of broken sections of cuticle intimately associated with and distributed throughout the mass. When examined microscopically under alcohol (Pl. 2: 4) the black cuticle is seen to be disposed in a network of polygons and circles having a diameter in the order of 0.02 mm, the walls of which have a beaded appearance. This reticulate pattern is almost certainly formed by transverse sections of spinules (Wills 1965: 119) which, by analogy with Wills' material would be expected to be borne in large numbers on the ventral side of the ridges between the "valleys". The beaded appearance of the chitin wall is probably due to sectioning through the minute polygonal patterning with which the gill tract and the basal parts of the spinules were covered in the Oesal material (Wills 1965: 119, Pl. 6: 8: noted also by Holm in *Eurypterus* in posthumous Plate 3: 5 and 6, and in *Erettopterus* posthumous Plate 1: 7–11). That the reticulate patterns seen in the spongy mass of the *T. scotica* gills is not itself this minute polygonal patterning is evident from the fact that in areas where the tract has been sectioned to a more ventral level, the continuation of the reticulate chitin ventrally into the solid apices of the spinules can be seen. The order of size of the patterning in *T. scotica* is similar to that of the diameter of the spinules of *Eurypterus* and of a larger size than the minute polygonal patterning of the gill tract and spinules in *Eurypterus*. If Wills (1965: 122) was correct in believing that the spinules performed a physiological function in the oxygenation of the blood, their size would probably be dictated by this function and it would not be expected that in larger gill tracts, such as that of *T. scotica*, they would necessarily be larger but rather that they would be more numerous. Towards the margins of the gill tracts the spinules appear to become orientated laterally, so that in the marginal areas the structures have been sectioned longitudinally instead of transversely as elsewhere.

The ventral body wall of the median region

The surface of the ventral body wall (Pl. 1: 2, 3) is displayed in its simplest form in the median region between the gill tracts and is well seen on the second mesosomal segment, where the features are preserved as a natural mould of the ventral surface. The change in character of the cuticle from the thin cuticle of the median region to the specialised spongy cuticle of the gill tracts on either side is very sharp, giving clear margins to the tracts (Pl. 1: 2). A cast of the median skin reveals the true ventral appearance of the cuticle at this point and macroscopically it appears to be smooth with small scattered squamae. Under the microscope, however, the squamate areas are seen to be formed of groups of sharply defined small pustules of differing size. The granulation in regions between the squamae is subdued. As the surface is traced posteriorly the squamate appearance is lost, the granulation becomes finer and intense lattice folds or microfolds are developed.

Microfolds

Such folds (Pl. 1. Figs. 1, 4; Pl. 2. Fig. 7) are developed in the median region and are well seen in the lectotype associated with the joints between the first and second mesosomal segments, and the second and third segments (Pl. 1: 1). They are formed of tightly folded thin cuticle, the crests of the folds being about 1 mm apart. These folds occupy belts up to 20 mm from anterior to posterior in the median region and extend laterally to a maximum width of some 120 mm. The axes of the folds run transversely across the animal and as they pass laterally they curve slightly towards the posterior. The belts taper off laterally and the anterior folds which persist into the gill chambers are seen to pass behind the gill tracts and grade into, and die out in, the posterior granular skin (see below). To the naked eye the cuticle of the microfolds appears to be smooth but under the microscope it is seen to be ornamented with a very regular pattern of fine striae which run parallel to the axes of the folds (Pl. 1: 4), an ornament which distinguishes them from every other surface in the lectotype. There are about 15 striae within 1 mm of cuticle. Similar striae have been described from a nepeonic type B median abdominal appendage of *Slimonia* (Waterston 1960: 255, Pl. 43: 1) and may prove to be a more common surface feature of thin and otherwise smooth eurypterid cuticles than has been realised up to the present. Striations of a similar kind are found on thin and otherwise unornamented cuticles in other arthropod groups. The microsculpture of insect and arachnid cuticles is of this order of size (J. Millot 1949: 283, Fig. 63) and varies from sub-parallel sinuous striae, as in the Araneae, to complex patterns found in many insects. Such microsculpture is found to have taxonomic significance among modern insects and arachnids and it would be of interest to discover whether advanced eurypterid groups developed more complex patterns than the simple striae observed in *Slimonia* and *Tarsopterella*.

As the striate cuticle is traced anteriorly it is gradually replaced by the fine granular ornament described above. On the right side of the second abdominal segment of the lectotype the microfolds may be traced posteriorly and are seen to pass into coarse lattice folds or macrofolds.

Macrofolds

Folds of this type (Pl. 1: 1; Pl. 2: 1, 2) are interposed between the microfolds and the outer, or ventral, cuticle of the *Blattfuss*. They grade into microfolds anteriorly and medially and are attached posteriorly to the forward margin of the *Blattfuss*. The attachment to the *Blattfuss* is well seen on the right side of the lectotype where macrofolds forming the most posterior surface of the second abdominal segment join the anterior margin of the *Blattfuss* of the third segment. Here the macrofolds are in the same plane as the succeeding *Blattfuss* and are seen as a natural mould of the ventral or outer surface. The true position of the macrofolds, however, is better appreciated from the macrofold surface associated with the *Blattfuss* of the post-opercular segment where, in the broken right side, it is seen to pass antero-ventrally under the microfolds at the posterior of the first abdominal appendage. On the left side of the same segment they reappear in a similar posture from beneath the microfolds of the first abdominal appendages, which occupy a median position, where these folds have been broken away to expose them. The macrofolds extend to the left lateral margin of the segment passing, for the most part, in front of the gill tract of the second mesosomal segment. They obscure this gill tract in part, however, where they now occupy a position dorsal to it. Macrofolds can also be seen in a lateral

position on the left side of the specimen where they occupy a position ventral to the posterior granular skin of the second mesosomal segment and dorsal to the anterior granular skin of the third mesosomal segment. Only in the exceptional case of the third abdominal segment on the right side is the attachment of the macrofolds to the *Blattfuss* seen since in all other cases the *Blattfüsse* are obscured by structures lying dorsal to them.

Macrofolds are fairly regular and strongly developed and, like the microfolds, their axes run transversely across the specimen. The fold crests are some 2 mm apart, about twice the distance separating the crests of the microfolds. In its greatest development the macrofold surface measures 20 mm from anterior to posterior and in width it apparently coincides with that of the *Blattfuss* with which it is associated. Details of the sculpture of the outer or ventral surface are best seen in the negative, where a natural mould of this surface has been preserved (Pl. 2: 2). It has pustules of two orders of size, the smaller giving an overall granular appearance while the larger are developed along the crests of the folds. In the negative the pits formed by the larger pustules contain the cuticle of one, or sometimes two, bristles embedded in the matrix showing that they formed bristle bases. Where the surface has been folded back upon itself, as in the area lying anterior to the left gill tract of the second abdominal segment a natural cast of the visceral surface of the cuticle is exposed, covered here and there by small patches of the cuticle itself. This cast surface (Pl. 2: 1) shows the bristle bases clustered on the fold crests but their appearance is less clear-cut than in the natural mould. Macrofolds in these positions are interpreted as the anterior skin of the movable hinge of the *Blattfüsse*.

Surfaces very similar to macrofolds are developed in the median region of the second and third abdominal segments immediately anterior to the hastate prolongation of the gill tracts (Pl. 1: 2). They are seen as natural moulds of the ventral surface and are less regular in their folding than elsewhere.

Posterior granular skin

Surfaces of this type (Pl. 1: 1, Pl. 2: 7) are preserved posterior to the gill tracts on the left side in the first and second mesosomal segments. In the second segment the surface is seen to grade medially into microfolds while medially also the anterior margin of the surface abuts the gill tract. As the surface is traced laterally it assumes an antero-ventral inclination which carries it ventral to the posterior part of the gill tract. The posterior granular skin associated with the first mesosomal segment lies dorsal to the macrofolds but has been broken away posteriorly from its associated surfaces. Medially it appears to have graded into the microfolds, while anteriorly it abuts the gill tract of the first mesosomal segment. In its greatest development behind the second gill tract it measures 28 mm from anterior to posterior and over 90 mm in width.

The surfaces are preserved as natural moulds of the outer surface of the cuticle. This mould has a rather spongy appearance having an ornament of circular pits of differing radius and depth, which entirely covers the surface. In life the surface of the cuticle must have had an ornament of rounded granules of differing size but of the same order of magnitude, the size distributions being random over the whole surface. All, except perhaps the smallest granules, formed hair bases since the chitin of the hairs remains embedded in the matrix.

The posterior granular skin is interpreted as forming the roof of the gill chamber posterior to the gill tract.

Anterior granular skin

This type of surface (Pl. 2: 6) closely resembles the posterior granular skin in having an ornament of rounded granules of differing size randomly distributed over the whole surface, but it differs in having a number of very large bristle bases sparsely distributed over the surface. Like the posterior granular skin it is preserved as a natural mould of the ventral surface and the chitin of the hairs and bristles is preserved embedded in the matrix. The rather crumpled state of the granular skins might suggest that they were formed of thin cuticle. The anterior granular skin occurs anterior to the gill tracts and is seen in this position in the lectotype in the first three mesosomal segments. Evidence from the second segment would suggest that this type of surface also extended laterally from the gill tract and appears to unite with the left lateral extremity of a tergite and may be formed in part by the lateral doublure of the tergite. As mentioned above, the anterior granular skin does not extend into the medial region since the ventral body wall is skinned by folded cuticle reminiscent of the macrofold surfaces anterior to the hastate medial extension of the gill tracts. The anterior granular skin is interpreted as forming the roof of the gill chamber anterior and lateral to the gill tract.

The ventral surface of the Blattfüsse

The character of the ventral surface (Pl. 2: 3) of the plate-like abdominal appendages is seen in the natural mould of the *Blattfuss* of the third mesosomal segment on the right side and on the mould of a detached appendage, perhaps of the fourth segment, on the left side. The ornament consists of "pterygotoid scales" which are more numerous and obtuse anteriorly and become larger, sparser and more acute posteriorly. The nature of the posterior margin of the *Blattfuss* is not known.

INTERPRETATION OF THE STRUCTURES

The surfaces described above are found in association with one another on the left side of the lectotype in the first three mesosomal segments. Unfortunately the structures of the fourth mesosomal segment have become dissociated and those on the right side of all the visible segments are very incomplete. Fig. 2 shows in schematic form the relationships of the various surfaces exhibited by the specimen. While, because of distortion or loss, the relationships of all the surfaces to one another are not seen in any one mesosomal segment, the relationship of one surface to

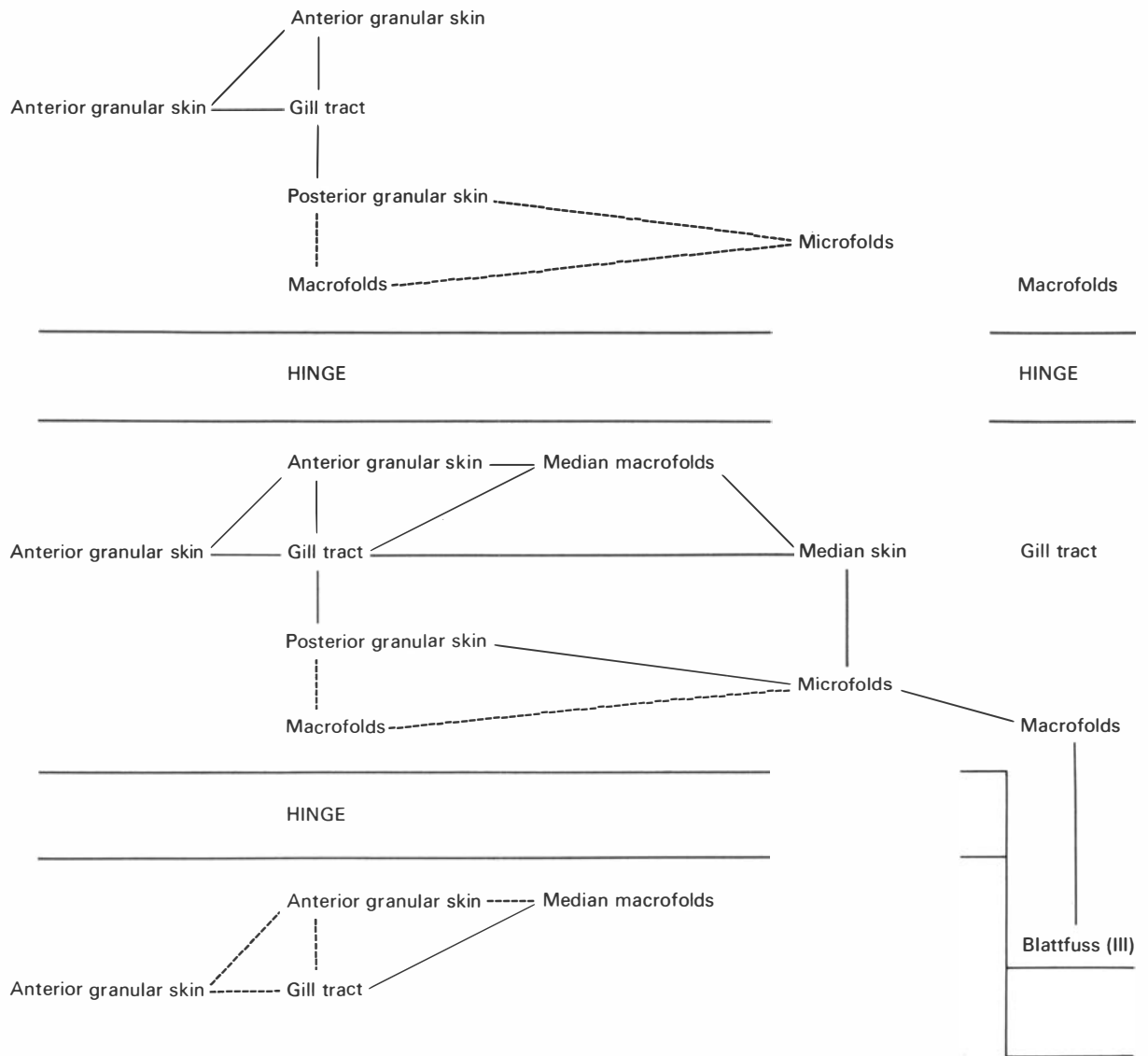


Fig. 2. Diagram illustrating the relationships of the surfaces exhibited on the ventral side of *Tarsopterella scotica* (Woodward) R.S.M. 1891.92.103. Solid lines connect surfaces which can be seen to pass into one another and broken lines indicate those which, by direct examination are thought to do so or, by analogy, with associations proved in other parts of the specimen, it is inferred must do so.

another can be established at one or more points in the specimen and thus a complete picture of the structures can be built up.

That the outer or ventral surfaces of the *Blattfusse* are attached at their anterior margins to the macrofolds is established in the right *Blattfuss* covering the third mesosomal segment where structures which would lie dorsal to the *Blattfuss* (gill tract and associated roof of the gill chamber) have been removed. In this case the *Blattfuss* has been displaced posteriorly thus pulling the attached macrofolds on the second segment into the same plane as itself and both surfaces are seen as natural moulds of the outer or ventral surface. The normal posture of the macrofolds is seen in the broken section on the right side of the first mesosomal segment and on the left side of the same segment where it is seen to pass anteroventrally for some distance before, as may be supposed, turning sharply backwards upon itself just anterior to its junction with the *Blattfuss* covering the second mesosomal segment which is not exposed. The macrofold surface must have skinned the anterior surface of the hinge bar from which the *Blattfuss* is articulated and floored the posterior portion of the gill chamber of the preceding segment (c.f. Wills 1965: 115–6).

The macrofolds associated with the *Blattfuss* of the right side covering the third mesosomal segment, which must have formed the posterior portion of the gill chamber of the second mesosomal segment, are seen to pass anteriorly into tight microfolds which cross the median region of the animal. In the preceding segment where the macrofolds assume an anteroventral posture the microfolds lie dorsal to them. The macrofold surface at this point passes backwards and upwards as the anterior skin of the hinge until it joins the ventral body wall where it folds over upon itself and passes anteriorly as microfolds on the ventral body wall.

In the median region of the second mesosomal segment microfolds pass anteriorly into smooth cuticle of the ventral body wall which in turn develops the granular squamate ornament as it is traced anteriorly. Laterally, on the left side of the second segment microfolds are clearly seen to pass into the posterior granular skin which lies posterior to the gill tract of the second segment. The hastate extension of the gill tract into the median region of the second segment is less disturbed in its relationships with neighbouring surfaces than is the main portion of the tract, and is seen to have well-defined boundaries with the squamate median ventral cuticle and that part of the posterior granular skin nearest the mid-line. In this region it is clear that the gill tract, the median squamate cuticle, and the posterior granular skin all occupy one plane and are specialisations of the ventral body wall.

From the relationships described in the second segment it is clear that the posterior granular skin forms part of the ventral body wall in a position anterior to the hinge and posterior to the gill tract. It has also been shown that macrofolds, which form the anterior skin of the hinge, pass anteriorly through microfolds into the posterior granular skin. The posterior granular skin of *Tarsopterella* thus occupies an equivalent position to the skin forming the roof of the gill pouch posterior to the tract in *Eurypterus* which Wills (1965: 115–6) showed was the anterior extension of the doublure of the *Blattfuss* which formed the anterior skin of the hinge. In *Tarsopterella*, however, this skin shows a characteristic granular ornament and probably carried a felt of fine hairs on its ventral side, unlike the equivalent in *Eurypterus* which is described as thin and devoid of ornament (Wills 1965: 114). As the granular skin is traced laterally in the left gill chamber of the second mesosomal segment it is found to extend for some distance antero-ventrally under the gill tract. Since both these surfaces represent specialisation of the ventral body wall it is clear that such a position must be abnormal and appears to have resulted from telescoping of the gill chamber to form a fold between the tract and the posterior roof of the chamber. It would be expected that such a disturbance would be greatest where the gill chamber is largest and most three-dimensional. In the first mesosomal segment, where the gill tract is greatly reduced in size, the junction of the posterior granular skin with the tract is not disturbed and the granular skin is seen to pass anteriorly into the gill tract along the whole of the exposed width. Unfortunately the posterior granular skin of this segment has become isolated from the adjacent folded cuticle by breakage but it is clear that, as in the second mesosomal segment, it must have passed medially into microfolds.

The relationships of the surfaces anterior to the gill tracts are more disturbed because of dislocation and collapse of the hinges. In the first and second mesosomal segments, however, the junction of the gill tract with the anterior granular skin can be seen and the evidence of the second segment would suggest that this surface with the large bristle bases is most strongly developed antero-laterally and laterally to the gill tract. Wills (1965: 116) showed that the skin forming the body wall anterior to the tract in *Eurypterus* also skinned the posterior wall of the hinge. He believed that in *Eurypterus* the "lattice-folds" (described Wills 1965: 113) occurred on this surface skinning the posterior of the hinge. If, as seems likely, the "lattice-folds" of Wills are equivalent to what has been termed the macrofolds in the present paper, then we must conclude

that either the present account differs from that of Wills in its interpretation of similar evidence or that the anatomy of *Eurypterus* differs from that of *Tarsopterella* since the macrofolds are here regarded as forming the anterior skin of the hinge. Only in the medial part of *Tarsopterella* anterior to the hastate prolongation of the gill tracts do surfaces similar to the macrofolds occur posterior to the hinge. As described above (p. 000), the opinion that in *Tarsopterella* the macrofolds skin the anterior surface of the hinge is based upon the evidence provided by the attachment of macrofolds to the right *Blattfuss* of the third abdominal segment, and to a consideration of the aspect and disposition of the macrofold surfaces which are consistent with the interpretation adopted. In *Tarsopterella* it would appear probable that the posterior surface of the hinge was skinned, at least in part, by bristle-bearing skin similar to that forming the roof of the gill pouch anterior to the gill tract.

Many types of bristle with many different functions occur in arthropods and of particular relevance are those described from other eurypterids as in *Eurypterus* (Holm 1898: 10, Pl. 7: 4), *Rhenopterus* (Størmer 1936: 31–2, Pl. 9: 4–5), *Erettopterus* (Tobien 1937, Pl. 20) and in a Scottish Carboniferous form (Waterston 1957, Pl. 3: 8). Others have been described from the Cyrtoctenida (Størmer & Waterston 1968, Fig. 5, Pl. 6: 14) while fossil scorpions have yielded bristles of many forms the evidence for which has been reviewed in connection with his description of *Gigantoscorpio willsi* by Størmer (1963: 25–31). Most of the bristles associated with the anterior granular skin are attached to a rounded knob-like projection of the integument and, from the works cited, it is evident that they were not movable setae but fixed spines possibly acting as water filters. It is also possible, however, that setae with a tactile function were also present.

THE STRUCTURE AND FUNCTION OF THE GILL CHAMBERS

The reconstruction (Fig. 3) is an attempt to show the probable relationship in life of the various del structures associated with the gills and gill chambers of *Tarsopterella scotica*. More reliance can be placed upon the relative positions of the surfaces than on the actual proportions of the gill chambers for which evidence is incomplete. While the relative size of the surfaces on the ventral body wall is known, the ventral extent of such structures as the hinge or the gill tract in life are not known and the depths of the gill chambers must therefore be conjectural. Enough is known, however, to permit some discussion of the structure and function of the gill chambers.

The interpretation of the structures of the gill chambers, and in particular the recognition of the gill tracts as a specialisation of the ventral body wall, have so far been based entirely on the relationships of the various body surfaces exhibited by the specimen. An important piece of confirmatory evidence lies in the fact that a portion of plant stem has been lodged within the gill pouch on the left side of the second mesosomal segment having entered the chamber post-laterally. It is seen to have passed ventrally beneath the gill tract but must lie dorsal to the associated *Blattfuss* (see Fig. 1, Pl. 1: 1).

The reconstruction may suggest the function of the bristles clustered on the crests of the macrofolds. The chitin of the macrofold surface, forming the anterior skin of the hinge, folds sharply forwards at the base of the hinge bar to continue anteriorly as the microfolds of the ventral body surface. The function of the microfolds was clearly to accommodate the extension or contraction of the abdominal segments in response to movements of the longitudinal muscles. Part of the function of the macrofold bristles must have been to prevent unwanted matter from becoming lodged within the acute fold anterior to the base of the hinge. I am grateful to Dr. J. Miller of the Grant Institute of Geology, Edinburgh, for bringing to my notice the possibility that bristles so arranged in association with an extensible surface, formed in this case by the microfolds, may also serve a sensory function in monitoring the degree of extension of the microfolds.

T. scotica was an animal approximately one metre in length and it would be reasonable to suppose that the oxygen requirements of an eurypterid of such a size, however passive its mode of life, would be greater than could be provided by simple diffusion through the gill tracts. Some mechanism would therefore be required to create a current of water over the gill tracts to increase the available dissolved oxygen. That such currents did pass through the gill chambers in a controlled fashion is suggested by the asymmetrical distribution of structures such as the occurrence of the large bristles on the anterior granular skin in front of and lateral to the gill tract but not behind or medial to it, and also by the broadly triangular plan of the gill tract itself having the broadest part laterally and the narrowest part medially. The presence of the bristles — fixed spines and possibly setae — associated with the anterior granular skin in the antero-lateral position with their probable filtering and tactile function, would strongly suggest that they guarded

the gill tract from unwanted matter, which would in turn suggest that water-currents approached the gill tracts from the antero-lateral direction and, having passed over the surface of the tract, the spent water would be expelled posteriorly.

The simple beating of the *Blattfüsse* would not produce the controlled flow through the gill chamber which the morphology indicates and which analogy with modern gill-breathers suggests must have been present. It would rather have caused turbulence which, in the sandy or muddy environment of the lakes and rivers of the Scottish Gedinnian which was the habitat of *Tarsopterella*, would have produced the harmful effect of introducing grit and dirt into the gill chambers. From the reconstruction it is apparent that there are a number of mechanisms which could have contributed to the control of water flow over the gills. Movement of the *Blattfuss* to open the gill chamber, or to close it by addressing the appendage against the succeeding one which it overlapped, could have been accomplished by muscle action in the hinge and appendage in association with the action of the macrofold integument of the hinge. Since the *Blattfüsse* are abdominal appendages modified to a plate-like form their musculature must have been analogous to that of other arthropod abdominal appendages. In *Limulus* the abdominal appendages are controlled by at least five groups of muscles, the branchio-thoracics (Milne Edwards 1873), the external branchials, the anterior and posterior entapophysio-branchials and pre-entapophysial-branchials (Benham 1885). As both Holm (1898) and Wills (1965) have noted the "lattice-folds" or macrofolds have to do with movement of the *Blattfuss* but whether the role of this robust integument was purely passive as a hinge flexing as a result of muscle action, or whether it had an elasticity which supplemented or even replaced the action of certain muscle groups in either raising or lowering the *Blattfuss*, we do not know. The volume of the gill chamber could have been controlled by lengthening or shortening of the abdomen in response to movement of the longitudinal muscles and such movements would have been accommodated in the ventral body

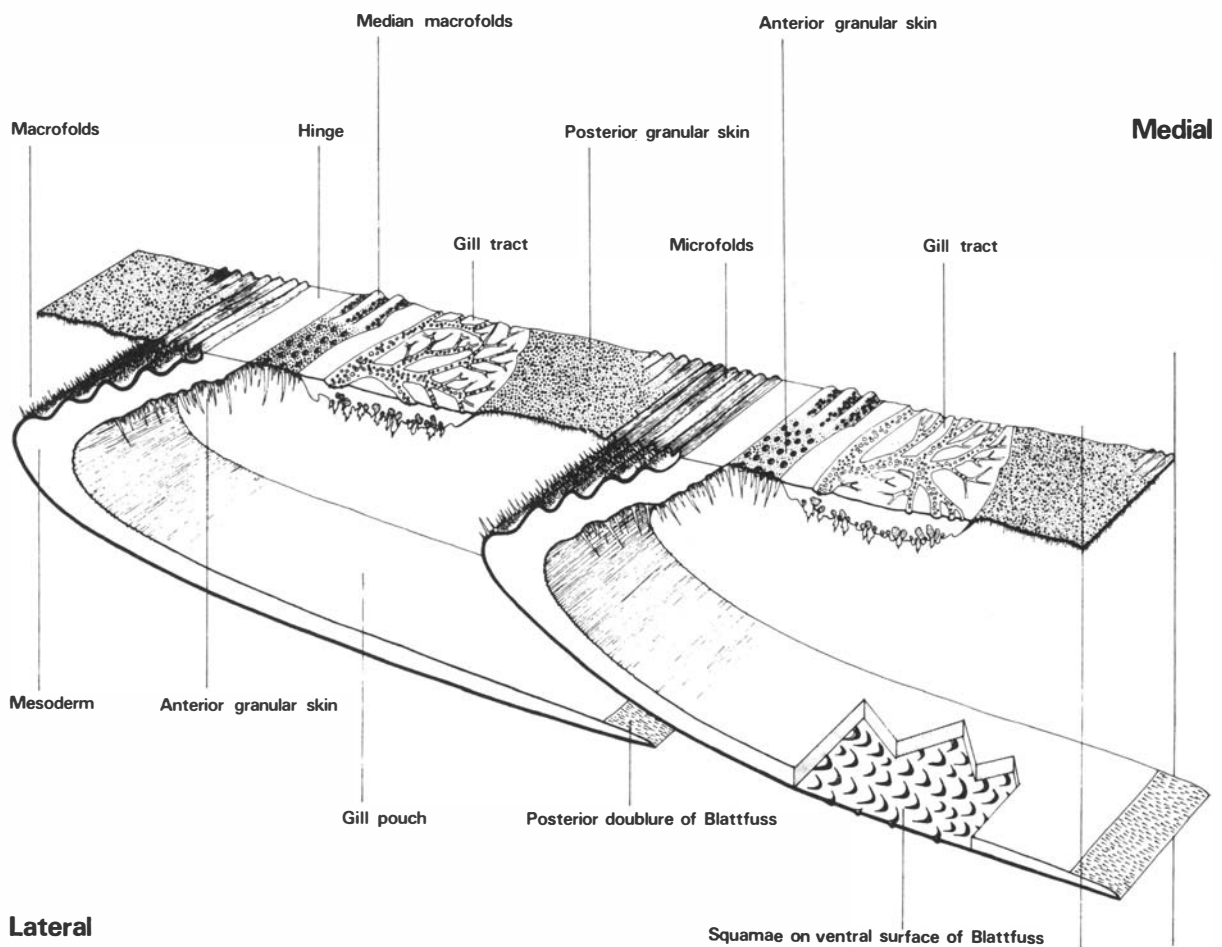


Fig. 3. Sectioned reconstruction of the post-opercular gill chambers of *Tarsopterella scotica* (Woodward). The upper surface shown in the diagram represents the dorsal view of the ventral body wall as seen in the lectotype. For the sake of clarity the lateral arching of the roof of the gill chamber has not been indicated although it is most probable that in life the roof of the chambers would be domed.

wall by expansion and contraction of the microfolds. Another way in which the volume of the gill chamber could have been altered would have been by swinging the hinge bar forward or backward and so altering the angle formed between the ventral body wall, the hinge and the *Blattfuss* and thus effectively altering the length of the anterior wall of the gill chamber. Any suggestion as to how the gill chamber functioned in life must of course be speculative but the writer believes that a current of water in the required direction could have been achieved. By closing the gill chamber posteriorly by pressing the *Blattfuss* against that of the succeeding segment, and by swinging the hinge posteriorly and so increasing the volume of the chamber, water would be inhaled laterally. By then opening the gill chamber posteriorly by a downward movement of the *Blattfuss* and by decreasing the volume of the chamber by swinging the hinge anteriorly and possibly also contracting the length of the segment, the spent water would be expelled. The forward swinging of the hinge would juxtapose the anterior part of the *Blattfuss* to the roof of the gill chamber and thus close the lateral openings and force the water backwards through the posterior gape. Such a movement of the gill chambers of each segment in turn could be achieved by the metachronal rhythm of the abdomen even when the animal was otherwise at rest.

RESPIRATORY STRUCTURES IN EURYPTERIDS, SCORPIONS AND XIPHOSURANS

The present work on *Tarsopterella* confirms the findings of Moore (1941) on *Slimonia* and Wills (1965) on *Eurypterus* that eurypterid gill tracts are specialisations of the ventral body wall (see also Wills 1964 for his deductions on the gill pouches of *Adelophthalmus*). Morphologically the eurypterid gill is thus comparable with the respiratory structures in scorpions rather than those of xiphosurans. The lung sacs of modern scorpions occur in the four abdominal segments succeeding the pectine and open by way of spiracles placed in relation to each segment in a very similar position to the eurypterid gill. Pocock (1901: 306, 1911: 15) claimed that *Palaeophonon* was an aquatic animal and that the overlapping ventral plates in lobostern scorpions probably concealed gills. (Wills (1925: 95) followed Pocock's view and later (Wills 1960: 329–30) concluded that in the Carboniferous there were two races of scorpions. One, mostly but not entirely, with lobate sternites was aquatic breathing by gills in gill pouches lying above deeply overlapping sternites, the second comprised terrestrial animals with short orthostern sternites. *Mazoniscorpio*, however, showed some characters of each race. Størmer's work on *Gigantoscrapio* (1963: 120–4) confirmed the view of Pocock and Wills and summing up the evidence he concluded that Silurian and probably Devonian scorpions and some Carboniferous scorpions led an aquatic life and that probably the aquatic forms breathed by gills like the merostomes and further that although the nature of the respiratory organs is not known in lobostern scorpions it is likely that they were gills as in eurypterids. If these assumptions are correct it is clear that the gills of eurypterids and the gills of lobostern scorpions must be homologous structures.

Many years ago Lankester (1881) demonstrated the homology between the book-gills of *Limulus* and the lung-books of scorpions. Embryological studies have confirmed his results by showing that the lung-lamellae of the scorpionids, pedipalps and areneids are formed as folds at the posterior basal surface of the embryonic limb (Kästner 1940, see also Dawydoff 1949: 365–366). Størmer (1944: 59 and 125, 1963: 99–100, 110–114) has reviewed the embryological evidence and discussed the phylogenetic significance of the structures of the ventral abdominal plates as found in trilobites, aglaspids, xiphosurans, eurypterids and scorpions and concluded that during evolution of the Chelicerata there was a gradual transition from free appendages to fixed ventral plates and that in the mesosomal appendages there was a successive simplification and reduction of the primary structures. In this morphological succession he saw the eurypterids as intermediate in structure between the Xiphosura and Scorpionida. Our present knowledge of *Eurypterus tetragonophthalmus* and *Tarsopterella scotica*, while confirming this general conclusion, would suggest that the gill structures of eurypterids are closer to the scorpions than to the xiphosurans in that, in the post-embryonic condition, the gill tracts, placed on the ventral body wall, have become entirely separated from the associated plate-like abdominal appendage. Just as the gill-books of the scorpions are known to be part of the embryonic limb, so it is likely that the embryonic limbs of eurypterids gave rise both to the gill tracts and to the *Blattfüsse* anterior to them.

The gill chambers of eurypterids appear to have been suited to protect the damp gill tracts from desiccation and thus to have permitted the animal to crawl on dry land for limited periods.

This may also have been true of the lobostern scorpions but for effective land life the invagination of the gills to form lung sacs is clearly of enormous adaptive advantage. While this was accomplished in scorpions there is no evidence that a similar adaptation was achieved in eurypterids which must have severely limited the possible adaptive response of the surviving swamp-dwelling eurypterids of the Carboniferous to the onset of the arid conditions of the Permo-Triassic.

It has been suggested in the present paper that water flowed over eurypterid gills in a controlled manner entering the gill chamber laterally and leaving it posteriorly. This control must have been achieved by the functioning of the gill pouches of each abdominal segment independently. It cannot be supposed that aeration of the gills would be very efficient even if this independent functioning was in some way co-ordinated, since five pairs of water currents must have been generated (Fig. 4A). A much more efficient way of creating the desired flow of water over the gills has been developed in the xiphosurans where the gill appendages work together to create a flow of water through what may be thought of as a single gill chamber. Firstly the jointed nature of the biramous gill appendages allows them to be moved in such a way as to beat the water in a desired direction, and by the co-ordinated beating of the five pairs of branchial appendages such a strong backwardly-directed current can be generated that the modern King Crab can use it for propulsion. Secondly, the anchylosis of the abdominal segments in the King Crab permits the formation of a beautifully streamlined deep ventral cavity in the abdominal buckler into which the gill appendages are set. In addition to providing protection to the gill appendages the shaped walls of the cavity promote water flow over the dorsally placed gill lamellae. The cavity gapes antero-laterally and water can enter it on each side by way of the laterally open joint between the prosoma and the abdomen. Posteriorly it narrows and the water is expelled near the base of the telson (Fig. 4B). The presence of the biramous gill appendage with its power to create water currents, and of the anchylosed abdominal buckler shaped to control the direction of these currents are xiphosuran characters which are in striking contrast to the gill structures of eurypterids and probably also of those of aquatic scorpions. One may speculate that the need for a more effective flow of water over the gills may have been one of the adaptive pressures which led to the anchylosis of the abdominal segments in groups of Xiphosura from the Palaeozoic onwards.

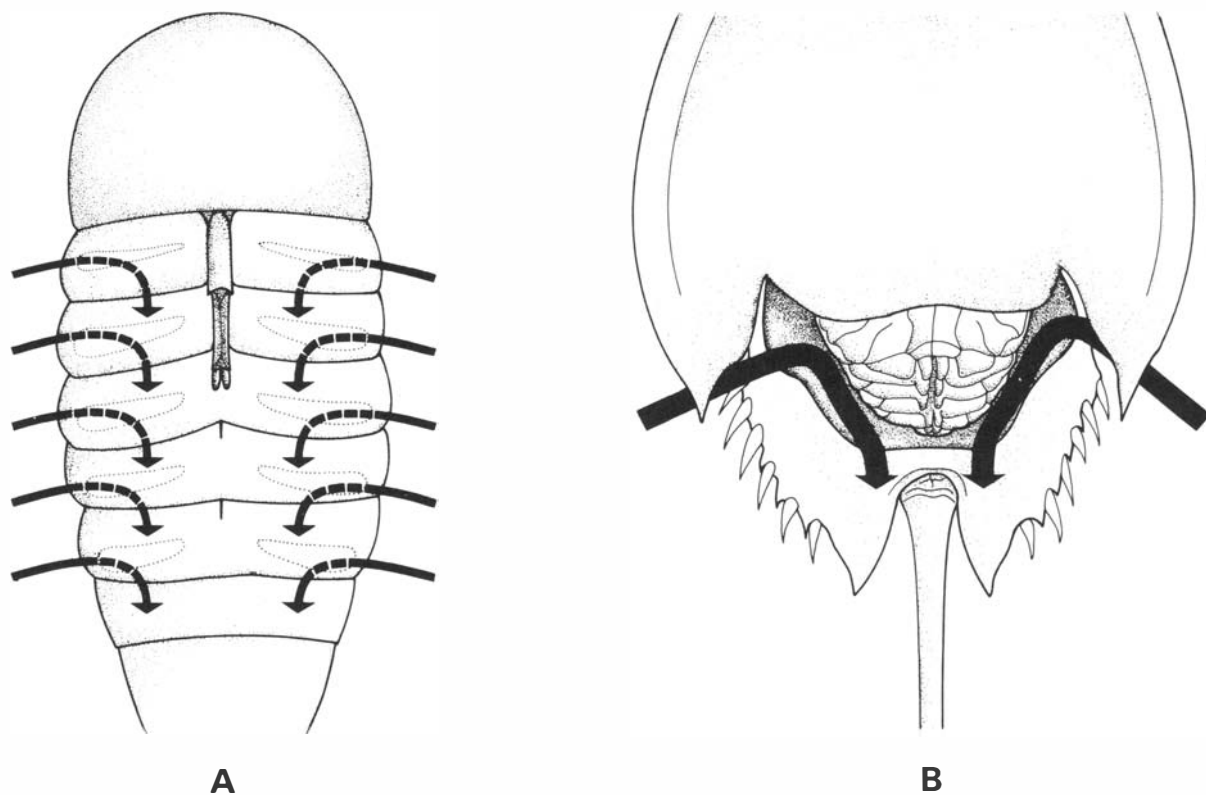


Fig. 4. A. Direction of water-currents passing through the gill chambers of an eurypterid as postulated in the present paper. B. Direction of water currents passing through the composite gill chamber formed by the anchylosed abdominal segments of *Limulus*.

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EXPLANATION OF PLATES

All illustrations are of the lectotype of *Tarsopterella scotica* (Woodward) from the Arbuthnott Group, Lower Old Red Sandstone (Gedinnian) of Angus, Scotland. Royal Scottish Museum 1891.92.103.

Plate 1

Fig. 1. Dorsal view of the gill chamber on the left side of the second mesosomal segment showing gill tract (centre), microfolds (bottom right and top right), posterior granular skin (lower left) and macrofolds (upper centre) X1.2. Compare with text Fig. 1. *Fig. 2.* Detail of dorsal view of the hastate median extension of the gill tract on the left side of the second mesosomal segment, showing the junction with the cuticle of the ventral body wall of the median region and the median macrofolds (top left) X3. *Fig. 3.* Squamae of cuticle of ventral body wall enlarged from Fig. 2. to show the concentration of larger granules at the squamae X7.5. *Fig. 4.* Detail of the cuticle of the microfolds at the postero-median region of the first mesosomal segment showing, in the upper portion of the figure, the fine parallel transverse striae X16.

Plate 2

Fig. 1. Natural mould of the "visceral" surface of the cuticle of the macrofolds anterior to the gill tract on the left side of the second mesosomal segment, showing the concentration of the larger pustules on the crests of the folds X10. *Fig. 2.* Natural mould of the exterior surface of the macrofolds anterior to the *Blattfuss* on the right side of the third mesosomal segment. The larger pustules or bristle bases are seen to be concentrated at the crests of the folds which are here seen in the negative X10. *Fig. 3.* Natural mould of the exterior surface of the *Blattfuss* on the right side of the third mesosomal segment to show the ornamentation of small crescentic squamae of varying size X10. *Fig. 4.* Dorsal view of part of the gill tract on the left side of the second mesosomal segment photographed under alcohol. The darker tone of the "spongy" tissue is due to the sectioned chitin of the spicules, while the "valley" on which the spicules are sparse or absent, shows in a lighter tone. The anterior trunk groove from which the branch is given off is situated at the top of the picture X6. *Fig. 5.* Latex cast of the gill tract on the left side of the second mesosomal segment showing pustules along the trunk groove (top) and along two major branches X6. *Fig. 6.* Natural mould of the exterior surface of the anterior granular skin on the left side of the second mesosomal segment, showing large bristle bases. The contact of the anterior granular skin with the anterior border of the gill tract is shown (bottom right) X10. *Fig. 7.* Natural mould of exterior surface of the posterior granular skin on the left side of the second mesosomal segment, succeeded posteriorly by microfolds X10.



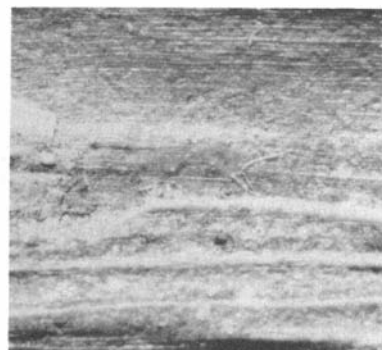
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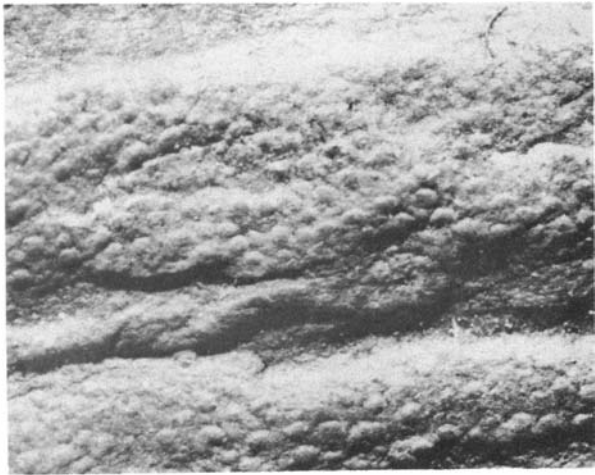
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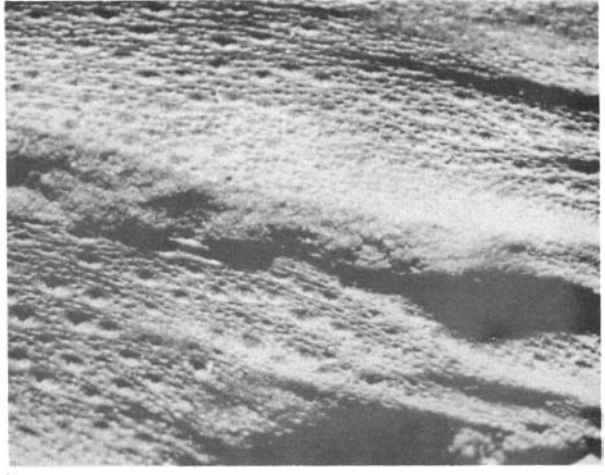
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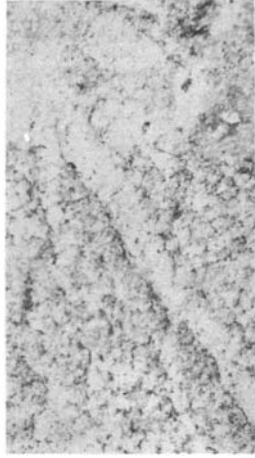
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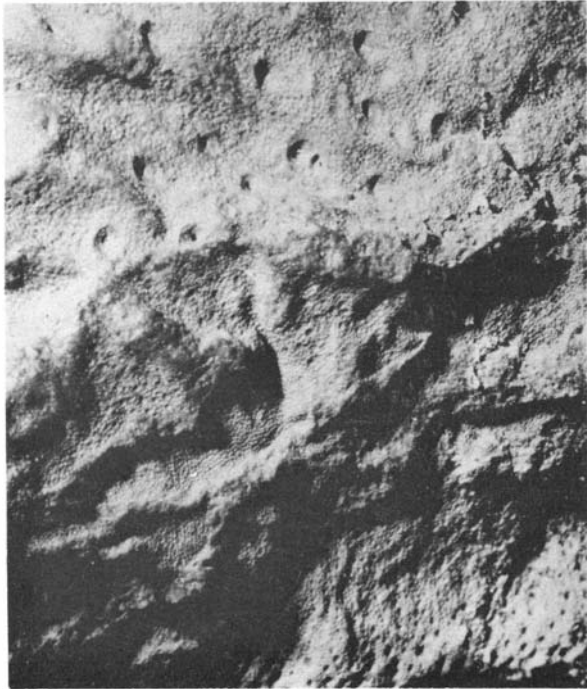
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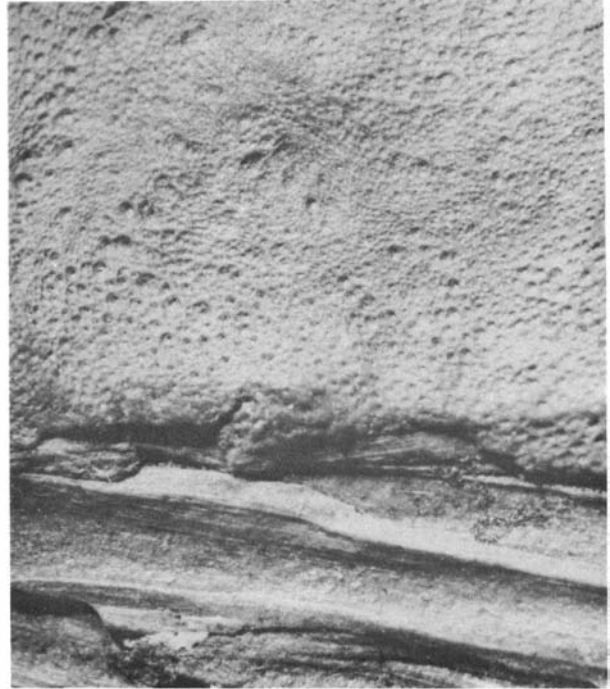
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