NEW EVIDENCE ON *JAMOYTIUS KERWOODI* WHITE, AN IMPORTANT OSTRACODERM FROM THE SILURIAN OF LANARKSHIRE, SCOTLAND

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ABSTRACT. *Jamoytius kerwoodi* White, based on two specimens from the Silurian of Lanarkshire, Scotland is reviewed in the light of many new specimens from the original locality. The associated fauna and probable habitat are discussed. *Jamoytius* is shown to be a cephalaspidomorph agnathan closely related to the anaspids and to the living cyclostomes. The presence is established of an annular cartilage, of sclerotic cartilages and of a cyclostome-like branchial basket. Lateral trunk scales of unusual structure and composition are present. Some further evidence is presented concerning the interpretation of continuous dorsal and lateral finfolds and the caudal fin is shown to be heterocercal (probably hypocercal). *Jamoytius* is thus a marine anaspid-like ostracoderm unspecialized enough to be on or near the line leading to the living cyclostomes, and could not, as was previously suggested, have represented the ancestral condition from which either the Cephalochordata or the Gnathostomata have arisen.

THE original material of *Jamoytius kerwoodi* White consisted of two specimens (BM P11284–5) discovered amongst some ostracoderm material purchased in 1914 by the British Museum (Natural History) from a local collector, William McPherson. The material came from the Silurian inlier near Lesmahagow, Lanarkshire, Scotland and the locality was given as 'the Logan Water, 1 mile below the watershed with Dippal'. The specimens were tentatively labelled 'allied to *Lasanius*', an anaspid which is common in a much younger horizon in the same inlier—the 'Downtonian' fish bed of Peach and Horne (1899), now thought to be of U. Wenlock–L. Ludlow age (Rolfe and Fritz 1966). Although mentioned by Smith Woodward (1921, p. 26) in his first Linnaean address, they lay undescribed for more than twenty years until White (1946) published the first account of the material. In his interesting and detailed interpretation he pictured *Jamoytius* as a primitive, naked, fish-like chordate which, although geologically late was 'probably a conservative element of the main stock from which the various groups of craniate chordates arose'.

The order Euphanerida and family Jamoytiidae were erected on the following diagnosis (White 1946, p. 96): 'Fossil Agnatha without armour or endoskeletal calcification; notochord persistent; simple lateral finfolds present; median fin-folds represented by elongated dorsal and anal fins. Eyes probably simple, very large and anteriorly placed. Muscle-segments simple and numerous with single flexure and undivided by horizontal septum. Mouth ? terminal; intestine short and straight.'

This interpretation placed *Jamoytius* in a very important position in relation to the early evolution of the vertebrates and White (1946, p. 93) said that in his opinion, *Jamoytius* was 'undoubtedly the most primitive of the 'vertebrate' series of which we have knowledge' and that it may perhaps be considered 'a more likely ancestor for Amphioxus than any of the other, specialized Agnatha . . .'. *Jamoytius* in many ways appeared to fit closely the role of an 'ancestral agnathan' postulated by White (1935) in a suggested phylogeny of the Agnatha.

White's interpretation has not, however, been accepted by all vertebrate palaeontologists and alternative suggestions have been put forward which may be summarized as follows. Gregory (1951) accepted White's interpretation, adding that 'taken altogether this very ancient type tends to connect Amphioxus with the anaspid ostracoderms', and 'quite conceivably, however, the boneless *Jamoytius* may well have been on the way toward Amphioxus while the bony *Cephalaspis* may have been on or near the line leading to the lampreys'. Wängsjö (1952, p. 566) suggested that *Jamoytius* was a naked or larval thelodont and Robertson (1953, p. 734) that it was a euphaneropsid anaspid. Berrill (1955), in a general review of the form with especial emphasis on the nature of the eyes, remarked on the absence of branchial structures and suggested the presence of a pharynx and atrium comparable with that in Amphioxus. Denison (1956) and Robertson (1957) in comprehensive reviews on the habitats of the early vertebrates, discussed the Scottish Silurian inliers and their faunas. Robertson accepted White's interpretation but Denison considered *Jamoytius* to be 'for its time, an advanced though not necessarily highly specialized vertebrate. The absence of dermal armour, the fusiform body, the presence of long lateral and dorsal fin-folds (if they really do exist), the highly developed metamerism and large eyes are all characters of a very active, fast-swimming vertebrate, functionally more progressive than most of his contemporaries'. Denison and Robertson both concluded, from the associated fauna, that *Jamoytius* lived in a marine environment.

White (1958, p. 229) summarized several of the above views and reiterated that *Jamoytius* was, as had been originally suggested, 'the conservative derivative of the ancestors of them all'. In the same volume Westoll (1958, p. 196) reinterpreted the 'lateral fin-folds' as remains of the dorsal and anal fins. Stensiö (1958) suggested for the first time that the 'carbonized remains of the body muscles' of *Jamoytius* were, in fact, exoskeletal structures; he compared them with the scales of the Anaspida and included the family Jamoytiidae in the Anaspida. Smith (1957) agreed with Stensiö and further suggested that the 'myocommata' of White were actually the thickened, basal, dorsoventral ridges of the scales. Tarlo (1960, fig. 5) re-examined the holotype, confirmed Stensiö's interpretation and suggested that dorsal ridge scales were also present near the midline of the body in the holotype.

The writer (Ritchie, 1960) published a preliminary account of *Jamoytius* based on new material and the light it threw on the type specimens. It was shown that *Jamoytius* possessed a terminal, subcircular mouth, lateral eyes and a heterocercal (probably hypocercal) caudal fin. The presence of scales was confirmed and evidence of a branchial apparatus resembling that of the Anaspida and the living petromyzontids was observed in the holotype. One specimen (P.U. 12865 in counterpart) which was referred to as a small *Jamoytius* (1960, p. 648) has since been borrowed for examination and found to be wrongly identified. It is a new and rather problematical organism which, with a second similar specimen found during the present research, will be described elsewhere.

Jamoytius has also been described as a possible ammocoete of an ostracoderm (Newth, in Young 1962, p. 128) and, more recently Dechaseaux (1963) and Lehman (1964) have again reviewed its relationships with *Amphioxus* and the fossil and living agnathans. The conflicting interpretations underline the importance of new and well-preserved material of this important agnathan.

STRATIGRAPHY

The Lesmahagow Silurian inlier and the smaller Hagshaw Hills inlier to the south were first described in detail by Peach and Horne (1899) and the stratigraphy has recently been revised by Jennings (1961) and Rolfe (1961)—accounts which have been summarized by Walton (1965, pp. 194–9, figs. 5.15, 5.16).

Peach and Horne (1899, pp. 572–5) described the *Ceratiocaris* beds (Bed 3) in detail, mentioning that they included the so-called Ludlow fish-band. From their description of the various localities where *Ceratiocaris* and the coelolepid *Thelodus scoticus* Traquair occurred it is apparent that Peach and Horne considered the horizon exposed below Logan Water Dam (Shanks Castle) as the equivalent of another horizon exposed along Logan Water some 700 yd. SSW. of Logan House. The latter bed, which during the present research has yielded abundant ceratiocarids and numerous specimens of *Thelodus scoticus* Traquair, *Jamoytius kerwoodi* White and the problematical *Ainiktozoon loganense* Scourfield (1937), will be referred to below as the '*Jamoytius* horizon'. It became apparent to both Jennings and the writer that the *Jamoytius* horizon and the *Ceratiocaris* beds of Shanks Castle differed significantly in lithology and fauna. Jennings located *Ceratiocaris* beds of the Shanks Castle type in tributaries to the west of Logan Water, some distance upstream from the exposures of the *Jamoytius* horizon and at a stratigraphic level estimated to be about 700 ft. above the latter horizon.

In Jennings's Lesmahagow succession (Walton, 1965, fig. 5.16) the *Jamoytius* horizon is within the Patrick Burn Formation and the *Ceratiocaris* beds are near the base of the Kip Burn Formation.

Remains of thelodonts have been discovered at many different levels within the Patrick Burn Formation but the majority consist of pockets of disarticulated denticles, probably of coprolitic origin, enclosed in small calcareous nodules. A similar thelodont-bearing nodule has been recorded from the Hagshaw Hills in the Ree Burn Formation which may be roughly equivalent in age (Rolfe, 1961, p. 254). In only one horizon of the Patrick Burn Formation have articulated thelodonts been discovered and here—in the *Jamoytius* horizon—they are associated with a rich and varied fauna.

The *Jamoytius* horizon is exposed along both banks of the Logan Water some 700 yd. SSW. of Logan House (NGR 737346—738347). The beds dip 12–15°/290° and as the result of two small NNW.–SSE. faults which downthrow to the west the full thickness of the horizon is accessible in three separate outcrops within 60–80 yd. The central exposure is a cliff face some 30–40 ft. high with massive greywackes forming the top. At least one of the famous 'Camp Siluria' sites was at this locality (Macnair, 1905, Pl. VI, figs. 1, 2) and it seems probable that the bulk of the original material discovered by Macnair and the various amateur collectors came from this cliff face, but during the present research the face was worked back until it became difficult to obtain further material due to the steepness and danger of falling rock. The exposure to the east of the cliff consists of rock which is either very weathered and fragmentary or extremely fresh and difficult to work.

A third outcrop of the fish-bearing horizon was located and exposed by the writer immediately upstream from the main cliff on the opposite (south) bank of the stream. Originally covered by scree, it proved possible without great difficulty to uncover the fossiliferous section diagonally across the slope to expose an almost complete section

from which suitably weathered material could be obtained with relative ease. The present investigations have, therefore, been largely concentrated on this outcrop.

The *Jamoytius* horizon, 30–35 ft. in thickness, consists of alternating grey-black, carbonaceous siltstones which are finely laminated (40–60 laminae per inch) and of non-laminated, olive to greyish-green mudstones. The siltstone:mudstone ratio changes very rapidly vertically through the bed but so far as could be observed the units maintained remarkably constant thickness areally. The individual siltstone/mudstone units vary considerably in thickness ($\frac{1}{4}$–4 in.) with the siltstones more frequently the thicker members. The siltstone laminae in thin section are seen to be rich in organic debris; the carbonaceous content of the mudstones appears to be low and macroscopic remains are almost entirely confined to the laminated siltstones. These remains occur throughout the *Jamoytius* horizon but are noticeably more abundant and best-preserved in the middle 20 ft. or so.

Calcareous nodules occur throughout but are especially common in certain horizons when they may be spaced less than 2 ft. apart. Generally the concretions lie within the siltstone units but several instances were noted where a nodule layer occurred either partly or wholly within the mudstone layer, in which case organic remains were extremely rare in the concretions. In the siltstone units the concretions almost always enclose, and appear to have formed around, organic remains. The siltstone laminae continue undisturbed through the nodules but the degree of compaction within the nodules is considerably less than in the surrounding sediment. Jennings (1961, p. 122) has shown that 'manganese is often enriched and both potassium and phosphorus deficient in the concretions when compared to the shales in which they occur'.

The majority of the nodules are small (90–95% < 2 in. in diameter) and enclose the carapace or the abdomen and telson of *Ceratiocaris papilio* Salter. A considerable number contain thelodont remains, either articulated individuals, patches of skin or more commonly thick layers of disarticulated denticles, probably of coprolitic origin. Approximately half of the articulated thelodonts discovered here were in normal siltstone and the rest were partly or almost completely enclosed in nodules which reached 7–8 in. in length and were of an elongate, oval shape tapering from the anterior to the posterior end of the fish. The lateral and caudal fins almost always lay outside the margins of the nodule. A small number of nodules (< 1%) partly enclosed *Ainiktozoon* individuals; four of these were discovered *in situ* and four in museum collections from the same locality. No specimen of *Jamoytius* has, as yet, been discovered in a nodule.

The fauna of the *Jamoytius* horizon and relative abundance of the various members is as follows:

Chordata
 Thelodus scoticus Traquair   moderately common
 Jamoytius kerwoodi White   rare

Protochordata?
 Ainiktozoon loganense Scourfield   moderately common

Arthropoda
 Ceratiocaris papilio Salter (small form) very common
 Ceratiocaris papilio Salter (giant form) very rare

Beyrichia sp.	very rare
Cyamocephalus loganensis Currie	very rare
Slimonia acuminata Salter	rare
Pterygotus (*Erettopterus*) *bilobus* Woodward	very rare
Hughmilleria sp.	very rare

Mollusca
Pteronitella? sp.	rare
Platyschisma cf. *helicites* Sowerby	rare
small orthocone cephalopods	rare

Problematica
Dictyocaris ramsayi Salter	common
Taitia catena Crookall	very rare
'stem' and 'disc-shaped' structures	common
Gen. et sp. nov.	very rare

The last named is a striated hook-like object of uncertain affinities which will be described elsewhere with a similar specimen from the Lower Palaeozoic of Norway. Traquair recorded a second species of *Thelodus, T. planus* Traquair, from this horizon, but the writer has been unable, despite the large number of *Thelodus* individuals now available from the same locality, to assign any, with certainty, to *T. planus.* Pending a full review of the thelodonts, which is under preparation, *T. planus* is regarded as a species of doubtful validity.

Apart from one nodule layer which yielded several well-preserved *Thelodus* individuals there was little evidence that either *Ainiktozoon* or the fish were more common in certain layers. The ceratiocarids occasionally appeared to be more abundant in some siltstone units than in others but the extremes of weathering and varying degrees of fissility encountered at different levels throughout the *Jamoytius* horizon had the effect of making sparsely fossiliferous units appear quite prolific and vice versa.

A noticeable feature of the weathered zones is the abundance of black carbonized remains around 1–2 in. across, many of which appear to show organized structures composed of fibrous material; no regular shape could, however, be discerned. These organic remains, possibly of an algal nature, on occasion almost cover the bedding planes but when they are traced laterally into the unweathered zone they become indistinguishable against the grey-black siltstone.

PRESERVATION

The state of preservation in the *Jamoytius* horizon varies greatly in different layers of apparently identical lithology; *Jamoytius* and *Ceratiocaris* (cf. Rolfe, 1962) are the two forms which are most affected. The exoskeleton of *Jamoytius* may be preserved in considerable detail along with the softer tissues of the scale-free cephalo-branchial region (Pl. 3, 4, 6) but the preservation may also be such (Pl. 5, fig. 3) that there is little trace of the scales and the outline of the body remains only as a faint carbon stain.

The ceratiocarids show similar variation ranging from specimens with considerable detail preserved to those where even the thickened margins of the carapace are barely

visible. These diagenetic effects are possibly related to the varying lengths of time the organisms lay exposed before being covered with sediment. *Thelodus* is not affected to the same extent.

There would appear to have been a complete absence of burrowing organisms and no evidence of tracks or trails was detected on bedding plane surfaces. The relative rarity of molluscan remains is probably an original feature and not the result of selective diagenesis—the few lamellibranchs, gastropods, and cephalopods which did turn up were quite well-preserved. The association of small colonies of lamellibranchs (*Pteronitella?*) with patches of carbonized material suggests that the former may have floated into the area attached to pieces of seaweed. Pockets of thelodont denticles, most often enclosed in small calcareous nodules, are probably of coprolitic origin; only two specimens showed these denticles strung out in something resembling a worm casting.

AGE

Although many horizons of the Lesmahagow and Hagshaw Hills successions have yielded a wealth of ostracoderm and arthropod remains few of the forms encountered are of any stratigraphic value and most are peculiar to the inliers. The other invertebrates present suggest an U. Valentian–L. Wenlock age for the Patrick Burn Formation (containing *Jamoytius*, *Thelodus scoticus*, *Ainiktozoon*, etc.), and various ages between U. Wenlock and M. Ludlow (Rolfe and Fritz 1966) have been proposed in recent years for the later fish beds which yield *Birkenia*, *Lasanius*, *Thelodus taiti*, *Lanarkia* (3 spp.), *Ateleaspis* and eurypterids (Downtonian fish bed of Peach and Horne, 1899). Unless, or until, better material for dating becomes available these dates must be regarded as provisional. There can be little doubt, however, that *Jamoytius kerwoodi* White and *Thelodus scoticus* Traquair are the oldest complete vertebrates known to date in Europe.

Preparation and Photography. Since very few specimens of *Jamoytius* were completely exposed during discovery, mechanical preparation often proved necessary. This was carried out by means of a Burgess Vibrotool adapted to take steel gramophone needles and small chisels. With only a thin carbon stain present even the better preserved specimens proved difficult to expose satisfactorily and the much fainter specimens were virtually impossible. During experiments on isolated fragments with acid preparation it was discovered that exposure to 15% HF for several minutes (with subsequent neutralization and extensive washing) had the effect of whitening the rock surface without noticeably affecting the carbonized body stain. The increased contrast which resulted made it possible to obtain good photographic results from even the faintest individuals. The specimens were photographed under alcohol and none of the prints have been retouched.

SYSTEMATIC DESCRIPTION

Family JAMOYTIIDAE White 1946
Genus JAMOYTIUS White 1946

Jamoytius kerwoodi White 1946

Plates 3–6

Material. Holotype, in counterpart, BM P.11284 a, b (White 1946, text-fig. 1) and BM P. 11285 (1946, text-fig. 2). Scottish Geological Survey, in counterpart, GSE 1182, 1183 (Ritchie 1960, p. 647). Professor F. H. Stewart, Grant Institute of Geology, University of Edinburgh possesses several specimens

of which the best preserved are F.R. 1393 a,b (Ritchie 1960, p. 647) and F.R. 1601 (Pl. 4, fig. 2, Pl. 6, fig. 1). Other specimens collected by the writer and figured herein have been presented to the British Museum (Natural History) and to the Royal Scottish Museum. The Royal Scottish Museum has recently purchased another specimen, RSM 1965. 59.1 a and b, collected by E. Stollery. The writer still possesses several rather poor specimens. The total number available to date, including incomplete specimens (but not counterparts) is around twenty.

MORPHOLOGY

Jamoytius kerwoodi is a moderately large agnathan reaching 180–200 mm. in length. The head is bluntly rounded and slightly narrower than the long, tubular trunk. The scale covering which is the major feature of the trunk is absent over the anterior 4 cm. of the head.
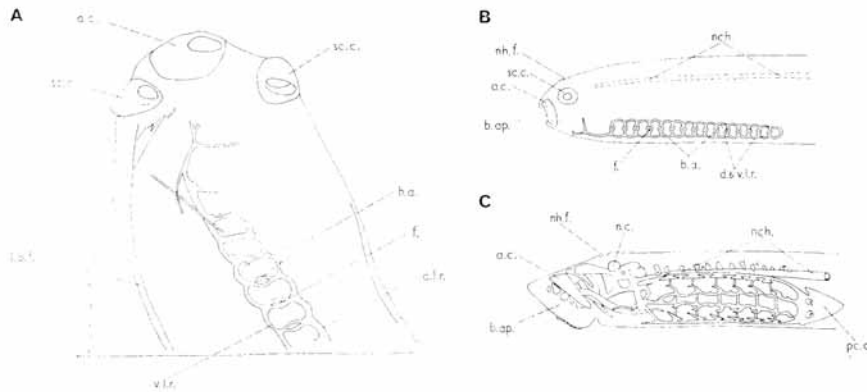
TEXT-FIG. 1. *Jamoytius kerwoodi* White. *a*, interpretation of isolated head showing well-preserved branchial remains, BM P47787 (cf. Pl. 5, fig. 1). *b*, attempted reconstruction in lateral view of the cartilaginous structures in the head and branchial region of *Jamoytius*. *c*, Cartilaginous skeleton of *Lampetra fluviatilis* for comparison. a.c. = annular cartilage; b.a. = branchial arch; b.ap. = buccal aperture; d.l.r. = dorsal (epitrematic) longitudinal rod; f. = foramen in the branchial arch; l.b.f. = crushed remains of the left branchial framework; nch. = notochord; nh.f. = naso-hypophysial foramen; pc.c. = pericardial cartilage; sc.c. = sclerotic cartilage; v.l.r. = ventral (hypotrematic) longitudinal rod.

Head and branchial region. The head region is somewhat narrower than the trunk and most specimens show clear evidence of three distinct stains near the anterior end of the bluntly rounded head, one in a subterminal position and two in an extreme antero-lateral position. These strongly carbonized structures are interpreted as the remains of the mouth and eyes (Pl. 3, figs. 1, 2, Pl. 4, fig. 1, Pl .5, figs. 1–3).

Near the anterior end of most individuals in which the head is preserved is a round, oval, or irregular structure, 6–7 mm. across, with fairly distinct margins. In the holotype (White 1946, text-fig. 1, Ritchie 1960, fig. 1*a*) and in other specimens (Ritchie 1960, fig. 1*b*; this paper, Pl. 3, fig. 2, Pl. 4, figs. 1–3) the stain is ring-shaped with a well-defined rim and less deeply carbonized central area. From its position and shape

therefore it appears to be the carbonized remains of an annular structure, presumably cartilaginous in original composition, which might have encircled the buccal aperture (text-fig. 1 *a, b*). Such an annular cartilage is present in the living cyclostomes (text-fig. 1*c*) although not in a terminal position as a result of the anterior extension of the buccal margins into a broad sucker. If this interpretation is correct the circular shape in *Jamoytius* would seem to indicate that it is equivalent to the adult and not the ammocoete stage of the living cyclostomes since the latter has a vertical, oval slit-like aperture. The fuller implications of the nature of the mouth in *Jamoytius* are covered in the discussion.

In most of the specimens with the annular cartilage preserved two other distinct stains, 4–5 mm. across, are present near the antero-lateral margins of the head (Pl. 3, fig. 2, Pl. 4, fig. 1, Pl. 5, figs. 1–3). These structures, lying about 1 cm. posterior to the terminal or subterminal mouth are almost certainly remains of the eyes. The extreme antero-lateral position rules out any possibility that they could represent other paired cranial structures such as otic capsules. In shape they vary from circular to irregular with margins which may be sharply or poorly defined. That they are not structureless, as White suggested (1946, p. 94), can be readily observed in the new material (Pl. 5, fig. 1). The eye-stain near the right margin gives the impression of a crushed hollow ball with apertures on the upper and lower (or external and internal) surfaces which are super-imposed but slightly offset (text-fig. 1*a*).

Dark stains representing the remains of eyes are not uncommon in fossil fish, and many specimens of anaspids (*Birkenia* and *Lasanius*) and coelolepids (*Thelodus* and *Lanarkia*) from a much younger horizon in the same inlier show distinct traces of the eyes. It is not even necessary to suggest that the soft tissues of the eye have left the carbon stain. The answer is probably provided by the cephalaspids where the eyeball was almost completely enclosed in a subspherical, sclerotic ossification with a laterally directed slit (cf. *Aceraspis*, Heintz, 1939). The eye-stains of *Jamoytius*—and the other anaspids and coelolepids—may therefore be reasonably interpreted as the remains of unossified, pre-sumably cartilaginous, sclerotic structures surrounding the actual eyeball (text-fig. 1*a, b*).

Nothing which can be interpreted as the remains of a lens has yet been observed in the *Jamoytius* eyestains, but since *Jamoytius* would appear to have been a fairly large, active swimmer it seems unlikely that it would have possessed simple, light-sensitive, lensless cups as suggested by Berrill (1955, p. 206). Although there is no direct evidence there seems little reason to doubt that a lens of some sort was present. The position of the eyes in relation to the annular cartilage and, as will be shown later, to the branchial framework, is not markedly different from that in *Petromyzon*. The petromyzontid eye has come to occupy a lateral position, not by posterior migration of the eye itself, but through the enlargement of the sucker anterior to the annular cartilage.

The branchial apparatus. As mentioned in an earlier paper (Ritchie 1960) very faint markings which appeared to be remains of branchial structures were observed in the

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EXPLANATION OF PLATE 3

Figs. 1, 2. *Jamoytius kerwoodi* White. 1, complete specimen seen from the dorsal surface, BM. P47784 (figured Ritchie 1960, text-fig. 1*b*), ×1. 2, Anterior end of same specimen, ×1·8. a.c. = annular cartilage; a.f. = anal fin: b.b. = branchial basket; e.c. = epichordal lobe (of caudal fin): l.ff. = lateral fin-fold; n.s. = nasal structure (?); sb.s. = suprabranchial scales; s.c. = sclerotic cartilage. Specimen photographed under alcohol.

head region of the holotype (1960, fig. 1*a*) but it was impossible at that time to determine whether these were remains of the actual branchial pouches, of the external apertures or of some related structures. The remains in question extended backwards from just behind the right eye (parallel to the margin of the head) to a position opposite the anterior scales.

The new material includes several specimens with similar branchial remains preserved in even greater detail (Pl. 4, fig. 1, Pl. 5, figs. 1, 3) and a much fuller understanding is now possible. These branchial structures are most clearly preserved in an isolated specimen of a *Jamoytius* head, some 45 mm. in length (Pl. 5, fig. 1, text-fig. 1*a*). The annular and sclerotic cartilages are well preserved and, in addition, running along the midline of the head from about 1 cm. posterior to the mouth to the edge of the specimen is a well-defined ladder-like framework with seven or eight crossbars at regularly spaced intervals. The most likely interpretation is that we have, preserved here for the first time in the fossil record, a simple 'branchial basket' the original material of which was almost certainly cartilage. Only one side of the branchial framework is clearly visible but if the specimen is viewed from the dorsal aspect with the right side of the 'basket' the better preserved, then the left-hand framework is probably represented by a strongly carbonized line which converges to meet the margin behind the left eye. This is the situation also in the holotype (Ritchie 1960, fig. 1*a*) and other specimens (Pl. 4, fig. 1); this peculiarity of preservation, with one half of the branchial basket seen in detail and the other side crushed vertically, is typical of most specimens and suggests the head was rounded in cross-section. That the basket framework was indeed paired is confirmed by the latest faint specimen to be discovered in which both right and left sides are clearly visible.

The branchial basket (Pl. 5, fig. 1, text-fig. 1*a*) appears to have been of a relatively simple construction with two sinuous longitudinal rods linked at regular intervals by vertical crossbars, the branchial arches. In this specimen some seven, possibly eight arches are visible, 5 mm. in length and 3·5 mm. apart. The last three arches are widest in the middle and give the appearance of bifurcating around an oval perforation; the more anterior arches, which are less distinctly preserved, do not show this feature although one has a projecting spur on the posterior margin. The ventral (? hypotrematic) longitudinal rod continues anteriorly, curving in the direction of the mouth and terminating some 5 mm. short of it. Near the anterior end another transverse rod meets the longitudinal rod at right angles, parallel to the branchial arches but separated from the anterior arch by 1·5–2 times the average inter-arch distance. Since this specimen is incomplete posteriorly we have to look elsewhere for evidence concerning the full extent of the branchial framework. In a more complete specimen, (Pl. 5, fig. 3) the branchial remains extend from just behind the left eye for a considerable distance parallel to the margin, becoming narrower posteriorly. Some ten or eleven arches are visible up to a break in the specimen but there is evidence that they continue at least 10–12 mm. beyond the fracture. From this and other specimens it would appear that the total number of branchial arches may reach or even exceed fifteen, which is not unlikely when one recalls that the anaspid *Pharyngolepis oblongus* Kiaer had fifteen branchial apertures and that a similar number of pouches is still present in some of the living myxinoids (e.g. *Bdellostoma*).

The difficulties (and pitfalls) in interpreting such nebulous structures as those in the

head and branchial region of *Jamoytius* are obvious but text-fig. 1*a–c* shows a possible interpretation of the best preserved head, an attempted reconstruction of the cartilaginous structures in *Jamoytius* and a sketch of the corresponding features in *Petromyzon*. There is no evidence in *Jamoytius* that the branchial arches continued past the dorsal (epitrematic?) longitudinal rod to connect with the notochord or that they extended ventrally to meet in the midline such as we find in *Petromyzon* and *Lampetra*. In these respects the *Jamoytius* branchial basket is of a basically simpler pattern than the complex framework of the adult lampreys and is closer to that found in the ammocoete. The general similarity of the *Jamoytius* and petromyzontid branchial baskets would seem to indicate that the gill pouches in the former were of normal cyclostome type—oval or sub-spherical chambers with a lining of folded respiratory epithelium. The comparatively large size of *Jamoytius*, the well-developed lateral eyes, and the small, circular buccal aperture must surely imply that the gills were of the adult cyclostome type and not that found in the ammocoete. Watson (1954) reached the same conclusion about the nature of the gills in the Osteostraci, Stensiö (1927) having earlier considered them to be of the ammocoete type. Since it seems unlikely that any ciliary mechanism could have produced sufficient respiratory or feeding current for an active animal the size of *Jamoytius*, it must be assumed that a muscle-pump system had been developed.

The structures described above are all fairly distinct and any attempt to label other features in the head region verges on guesswork; it should be noted, however, that an extremely faint subcircular stain has been observed just behind the annular cartilage in two specimens (Pl. 3, fig. 2, Pl. 5, fig. 3). This is tentatively interpreted here as a nasal structure, perhaps the nasal foramen. There are no signs of the otic capsules, of semicircular canals nor of a cartilaginous piston which might indicate the presence of a rasping tongue.

The trunk. The trunk of *Jamoytius* appears to have been long, straight, and tubular, perhaps slightly flattened on the ventral surface and tapering only towards the base of the caudal fin. The well-preserved segmental structures present in the trunk of the holotype were interpreted by White (1946, text-fig. 1, p. 91) as the remains of the myomeres (with longitudinal fibres occasionally preserved) 'separated by the clear infillings of the spaces left by the decayed septa, giving the effect of a series of hollow rods or bones'. The myomeres were apparently of a simple type with single forward flexure and no horizontal septum—a feature found only in vertebrates above the cyclostome level. The suggestion that the soft parts of the animal had been preserved in the holotype was apparently supported by the almost complete absence of segmental structures in the second specimen (1956, text-fig. 2), a type of preservation which White, with some justification, considered to be more normal. As described above Smith (1957) and Stensiö (1958, 1964) suggested that the segmental remains in question were, in fact, scales, a view supported by Tarlo (1960) and the writer (Ritchie 1960) after examination of the original and new material respectively.

EXPLANATION OF PLATE 4

Figs. 1, 2. *Jamoytius kerwoodi* White. 1, complete specimen seen from the dorsal surface, RSM 1966. 3.1 (cf. also Pl. 6, fig. 2). 2, specimen seen in lateral view, F.R. 1601 (cf. also Pl. 6, fig. 1). a.c. = annular cartilage; a.f. = anal fin; b.b. = branchial basket; d.ff. = dorsal fin-fold (?); e.l. = epichordal lobe (of caudal fin); l.ff. = lateral fin-fold; sb.s. = suprabranchial scales; sc.c. = sclerotic cartilage. Specimens photographed under alcohol. Both natural size.

Although the new interpretation is not so dramatic as the original the trunk scales of *Jamoytius* are nevertheless remarkable structures. The head region lacks any scale covering for some 4 cm. posterior to the mouth; from this point to the caudal pedicel (where they become so faint as to be indistinguishable) the trunk is covered by some 60–65 scales on either side. Each scale, slightly less than 2 mm. in width, is separated from the next by an extremely regular, uncarbonized strip about 0·4 mm. wide (Pl. 3, fig. 1, Pl. 4, fig. 1, Pl. 6, figs. 1, 2). Since most of the available specimens are flattened dorso-ventrally the scales are frequently folded and distorted making it rather difficult to visualize their exact shape during life. Only one individual, F.R. 1601, discovered and prepared by Professor F. H. Stewart, shows the animal in lateral view (Pl. 4, fig. 2, Pl. 6, fig. 1). In this instance the scales over the mid-trunk region are well preserved but anteriorly and posteriorly they were covered with a thin film of matrix which proved extremely difficult to remove. The scales of the right side are almost completely preserved but those of the left side are partly visible along a narrow strip with strongly carbonized margins which follows approximately the line of flexure (Pl. 6, fig. 1). The complete scales, best displayed anteriorly and posteriorly to this strip, show a single forward flexure with an angle of 100–5° which is probably close to the condition in life. The point of flexure is smoothly rounded, not angular as in most of the anaspids, and the scales appear to be continuous from the mid-dorsal line to the ventral terminations, with the portion ventral to the flexure at least one and a half times as long as the shallower dorso-lateral part. Anteriorly, where the scales and branchial structures are both present, the ventral portions of the scales are poorly developed; this corresponds to the supra-branchial region in the anaspids (Stensiö 1958, fig. 127) and the lampreys where the segmental musculature continues forwards over the branchial region.

The continuous nature of the trunk scales suggests (*a*) that they coincided very closely with the external surface of the myomeres and (*b*) that the material of which the *Jamoytius* scales were composed was not heavily mineralized and rigid but possessed considerable flexibility. If this were not the case each scale row would be subdivided into several articulating elements such as we find in *Pharyngolepis*, *Birkenia*, etc. (Kiaer 1924, p. 65, fig. 29). The only transverse fissures observed in the trunk scales of *Jamoytius* lie in the posterior suprabranchial region (Pl. 6, fig. 1).

The individual scales do not appear to have overlapped, as earlier workers suggested, and the uncarbonized, inter-scale strip does not represent either the myocommata (White 1946) or the dorso-ventral ridge present on the inner surface of more typical anaspid scales (cf. Gross 1938, 1958). Certain aspects in the preservation of *Jamoytius* scales suggest a rather unusual composition, quite different from that in *Birkenia* and the Norwegian anaspids. Only occasionally do they display a slight relief; in several instances the scales have been folded almost double without fracturing (Pl. 3, fig. 1, Pl. 6, fig. 2) or the ventral and dorsal portions may be dragged almost into line. These features suggest not only considerable flexibility but firmness and extremely strong connective tissue between the scales since few of the specimens known to date show much evidence of disarticulation. There would appear to have been an almost complete absence of mineralization and there is nothing to indicate the presence of bone or dentine, so the earlier reference (Ritchie 1960) to 'exoskeletal ossification (scales)' in *Jamoytius* is incorrect. The original scale material, now preserved only as a carbonized

stain, may have been a horny, epidermal substance, perhaps akin to keratin which is present in the teeth of lampreys and in small quantities in the scales of living fish and amphibians.

In most *Jamoytius* specimens the scale surface is evenly carbonized with more deeply carbonized margins but occasionally the surface is traversed by an intricate network of minute, branching fissures (Pl. 6, figs. 1, 2). There are several possible explanations; the fissures may represent an original canal system within and between the scales, they may indicate post-mortem fungal invasion or they may simply be the result of posthumous cracking during the processes of burial. This effect may explain the structures taken by White (1946) to be the remains of longitudinal muscle fibres, and by Stensiö (1958) to be a scale ornamentation comparable with that of the Norwegian anaspids. Such an ornamentation is certainly not visible in most of the better preserved specimens of *Jamoytius*. The only features of significance, other than those described above, are to be seen in the interscale strips of a few individuals (Pl. 6, fig. 3); the junction between the scales is marked by a line of minute, regularly spaced, circular 'pores' which in places become elongate and confluent. The may represent the bases of hollow tubercles whose tops have been removed with the counterpart or they may indeed have been pores connecting with the surface. Their position—between the scales—and the fact that they are not visible in many of the better-preserved individuals make interpretation difficult.

In about two-thirds of the *Jamoytius* specimens known to date the scales are extremely faint or almost completely lacking (Pl. 5, fig. 3; White 1946, text-fig. 2), although the same individuals frequently have well-preserved remains of the mouth, eyes, and branchial structures. This absence of scales is almost certainly the result of diagenesis and the individuals in question are usually more shapeless and broader in the head and trunk than are individuals with the scale covering well preserved.

Other structures in the trunk region, similar to those which White interpreted as remains of the notochord and intestine (1946, text-fig. 1), are to be seen in several of the new specimens (Pl. 3, fig. 1, Pl. 4, fig. 2, Pl. 6, fig. 1). In the holotype (White 1946, text-fig. 1) the structure interpreted by White as the notochord is probably one margin of the wide, straight intestine, the other side being correctly labelled (cf. Tarlo 1960, fig. 5). Anteriorly, where the notochord was interpreted as forking, the branch running towards the left margin is more likely to be the remains of the left side of the branchial basket. RSM 1966.3.1 (Pl. 4, fig. 1) which shows a remarkable resemblance to the holotype (Ritchie 1960, fig. 1*a*), displays an almost identical preservation of the branchial remains. In the laterally compressed individual, F.R. 1601 (Pl. 4, fig. 2, Pl. 6, fig. 1), a similar strip with deeply carbonized margins extends for a considerable distance along the trunk approximately parallel to the body axis, appearing to turn downwards at its posterior end. This must represent either the notochord or the intestine, but is rather wide for the remains of a simple, unconstricted notochord and more dorsally placed than one might

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EXPLANATION OF PLATE 5

Figs. 1–3. *Jamoytius kerwoodi* White. 1, head with well-preserved mouth, eyes, and branchial structures, BM P47787, ×2 (for interpretation see text-fig. 1a). 2, head with extremely fine annular cartilage, RSM 1966.3.3, ×1·5. 3, anterior end of specimen in which trunk scales are barely visible, RSM 1966.3.2, ×1. a.c. = annular cartilage; b.b. = branchial basket; n.s. = nasal structure (?); sc.c. = sclerotic cartilage. Specimens photographed under alcohol.

expect to find the intestine preserved (cf. *Endeiolepis*, Stensiö 1939, Pl. 1, figs. 1, 2, text-fig. 7). It is interpreted here as more probably the intestine slightly displaced in the processes of decomposition, but the alternative explanation is by no means impossible.

The attitude and nature of preservation of the *Jamoytius* individuals would appear to indicate that the fish was not, unlike most of the anaspids, markedly laterally compressed. The frequency of dorsally compressed individuals (Pl. 3, Pl. 4, fig. 1, Pl. 5, fig. 3) need not, however, imply that the actual animals, in life, were similarly flattened. If, as seems probable, the head and trunk were long, straight, and subcircular in cross-section, post-mortem muscular contraction would twist the animal, in the horizontal plane, to one side or the other; consequently, it would tend to come to rest either on the dorsal or on the ventral surface and to be preserved in this attitude. Laterally flattened remains of *Jamoytius* would thus be relatively rare, as appears to be the case in the material available to date.

Fins. In the original interpretation of *Jamoytius* (White 1946) certain structures were taken to be the remains of long fin-folds, a long dorsal fin, a shorter anal fin and undivided ventro-lateral fin-folds (cf. text-fig. 2*a*) which were envisaged as extending 'along the length of the body to the caudal pedicel without interruption'. Ever since the work of Goodrich (1906) provided good morphological evidence for the 'Lateral Fin-fold Theory' of earlier workers, it had been hoped that the fossil record would yield evidence of such fin-folds in geologically early chordates. *Endeiolepis aneri* Stensiö (1939) from the U. Devonian of Canada and *Jamoytius kerwoodi* White from the Silurian of Scotland were the two forms which appeared to provide the best evidence, but several dissenting views have been expressed, especially on the interpretation of *Jamoytius*.

Denison (1956) questioned the existence of fin-folds in *Jamoytius*, and Westoll (1958) reinterpreted White's lateral fin-folds (1946, text-fig. 1) as the remains of the dorsal and anal fins. Ritchie (1960) presented evidence that neither the interpretations of Westoll nor White were correct, and that the structures in question could be better explained as the ventral termination of the body scales with an intervening scale-free strip running the length of the ventral surface. It was suggested that the remains lying outside the main body stain in the holotype—interpreted by White as 'displaced skin' (1946, text-fig. 1)—were in fact those of the lateral fins and that faint but definite lines running postero-laterally were probably the fin rays of these lateral fin-folds (Ritchie 1960, fig. 1*a*).

The way is thus clear for a reappraisal of the fin-fold interpretation. While the new material of *Jamoytius* does provide additional evidence on this important aspect it is much less definite and conclusive than had been hoped, for several reasons. The lateral fins of *Jamoytius* must have been rather flimsy structures lacking a covering of scales; against a background of well-preserved scales they would be indistinguishable. Even if they lie outside the main body stain (as in the holotype) they are extremely difficult to observe against the grey-black matrix, especially in specimens prepared by Vibrotool or dental mallet. The best hope, not yet realized, is for a completely exposed specimen on a naturally splitting bedding plane.

Meanwhile the best evidence is provided by the one specimen in lateral view, F.R. 1601 (Pl. 4, fig. 2). The head and caudal parts are not preserved but in the posterior trunk region a distinct ventral margin can be distinguished some 10 mm. below the ventral ends of the well-preserved, lateral scales. The remains of the intestine (?), described above, appear to slope down in the direction of a deep, rounded notch

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situated at the posterior end of the ventral margin. This probably indicates the position of the anal opening, in which case the ventral margin anterior to the anus may represent the lower edge of a lateral fin-fold while that posterior to the anal notch may be interpreted as the remains of a low, rounded, anal fin.

In the dorsally compressed individuals remains of the fins are even more difficult to recognize. Longitudinal carbon stains are often visible along the trunk (Pl. 4, fig. 1), especially in faint specimens, where they may be the remains of fins or perhaps only the result of folded skin material. A lateral fin is possibly present in BM P47784 (Pl. 3, fig. 1).

Evidence for the dorsal fin is equally inconclusive. Although 'dorsal fin rays' were identified by White (1946, text-fig. 1) and reinterpreted as 'ridge scales' by Tarlo (1960, fig. 5) little trace of similar structures has been seen in other specimens. The dorsal fin-fold is possibly present along the dorsal margin in F.R. 1601 (Pl. 4, fig. 2) as a long, low stain extending over most of the trunk.

The caudal fin is preserved, although rather poorly, in two specimens (Pl. 3, fig. 1, Pl. 4, fig. 1); in both the body axis, or caudal pedicel, is turned to one side while a triangular stain on the other side reveals the presence of a well-developed fin lobe. The caudal fin is thus heterocercal but the nature of preservation makes it impossible to distinguish from the material whether it is normal heterocercal or reversed (hypocercal). From the general similarity of *Jamoytius* to the anaspids and to the living cylostomes it is assumed that the triangular fin represents the dorsal, or epichordal, lobe and that the caudal axis turns downwards to form a hypocercal fin. Several fin rays can be distinguished in the epichordal lobe of RSM 1966.3.1 (Pl. 4, fig. 1). The full extent of the fin is not visible but there can be little doubt that it resembled the general anaspid type (e.g. *Birkenia*).

The fins of *Jamoytius* thus appear to have been developed as follows: the median fin-fold is represented by a long, low, continuous dorsal fin, a hypocercal caudal fin with sub-triangular epichordal lobe and a low, rounded anal fin. The lateral fin-folds probably extended from the posterior end of the branchial row to the anus with a more or less straight outer margin (text-fig. 2b). As Westoll pointed out (1958, p. 196) White's original interpretation implied 'that the paired fin-folds extended on either side of the anal fin, which would be unique' (cf. text-fig. 2a).

The discovery of well-developed lateral fins in *Endeiolepis aneri* Stensiö (1939), *Pharyngolepis oblongus* Kiaer, *Pharyngolepis heintzi* Ritchie, and an undescribed form from the Downtonian of Stonehaven (Ritchie 1964) indicates that such fin-folds were the rule rather than the exception in the active fusiform anaspids. This provides some support, therefore, for the still rather inconclusive evidence concerning the lateral fin-folds of *Jamoytius*.

DISCUSSION

The new evidence concerning *Jamoytius kerwoodi* White confirms that in most respects it is a cephalaspidomorph agnathan which most closely resembles the known

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EXPLANATION OF PLATE 6

Figs. 1–3. *Jamoytius kerwoodi* White. 1, detail of F.R. 1601 (Pl. 4, fig. 2) × 2·4. 2, detail of RSM 1966.3.1 (Pl. 4, fig. 1) × 2·5. 3, detail of fragment displaying pores (or truncated tubercles) between the scales, BM P47785, × 6. int.? = intestine (or possibly notochord); ir.f. = irregular fractures; t.f. = transverse fissures. Specimens photographed under alcohol.

anaspids and the living cyclostomes (especially the petromyzontids). The writer agrees with Denison (1956, pp. 374–5, 424) and Robertson (1957, pp. 166–7) that the associated fauna of abundant phyllocarid crustaceans, occasional lamellibranchs, gastropods, cephalopods, and ostracods suggests that *Jamoytius* lived in a marine environment. The very thin, regular laminations in the enclosing siltstones and the undisturbed
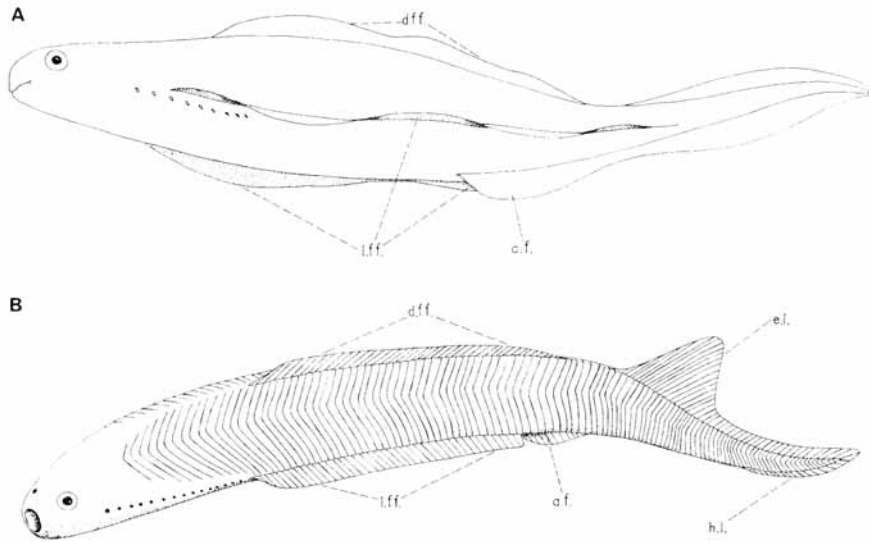
TEXT-FIG. 2. *Jamoytius kerwoodi* White. *a*, reconstruction after Wilson (in Swinton 1961) to show original interpretation of fin-folds (for an earlier reconstruction, without branchial openings, see Lehman, 1964, fig. 4). *b*, new reconstruction of *Jamoytius* based on all available material. a.f. = anal fin; d.ff. = dorsal fin-fold; e.l. = epichordal lobe; h.l. = hypochordal lobe; l.ff. = lateral fin-folds.

nature of many of the remains indicate very quiet conditions of deposition with no evidence of a burrowing fauna and an apparent absence of scavengers. As Robertson pointed out, there is little to indicate that the chordates were swept on death into the sea from rivers or estuaries. The elongate, tubular shape of *Jamoytius* contrasts strongly with the dorso-ventrally flattened thelodonts from the same deposits and it seems unlikely that the former, at least, was a bottom-dwelling animal.

The nature of the buccal opening in anaspids provides a limited amount of evidence on the probable nature of their feeding mechanisms. Heintz (1958, fig. 4) and the writer (Ritchie 1964, fig. 1a–c) have both interpreted the buccal aperture, at least in certain anaspids, as a vertically elongate, oval slit and find no evidence to support Stensiö's

interpretations (1964, p. 155, fig. 25 A, B) in which a considerable area of soft tissue is depicted projecting beyond the rostral scales; his *Birkenia* restoration (fig. 25 B), modified after Heintz (1958), seems especially unrealistic. The buccal aperture in *Jamoytius*, as indicated by the size and shape of the annular cartilage, was surprisingly small for the size of the animal and was certainly not appropriate for a plankton feeder such as *Pharyngolepis* and *Birkenia* may have been. The feeding mechanism of agnathans has been discussed by Denison (1961, pp. 178–9) who pointed out that 'if the anaspids did not have mechanisms for biting or nibbling, if they were too large and active to be adequately nourished by ciliary currents and mucus entanglement of small particles, and if they were not adapted for plankton or bottom feeding, about the only possibility left is suctorial feeding of some sort. It is not impossible that their feeding was similar to that of some living cyclostomes, though it is unlikely that they were as highly specialized for parasitism as are lampreys.'

This certainly sums up the position in *Jamoytius*, if not in all other anaspids, and one is led to consider which of his contemporaries *Jamoytius* may have relied on for nourishment by suctorial means. The exoskeletons of the numerous ceratiocarids and less frequent eurypterids show no evidence of such attacks, nor do the well-preserved remains of thelodonts from the same deposits. The only organic remains in the *Jamoytius* horizon which display possible evidence of suctorial attack are the large carbonaceous sheets of *Dictyocaris*, a problematical organism interpreted as a phyllocarid crustacean by Størmer (1935). These sheets, which may be up to 1 ft. across and are often irregular in shape, are frequently found to be perforated by numerous circular or subcircular holes, 3–5 mm. in diameter, apparently randomly distributed over the surface (Størmer 1935, fig. 1*f*, pp. 275–6). Similar holes are found in specimens of *Dictyocaris* from other localities in Scotland and Norway. The size of the holes compares closely with the internal diameter of the *Jamoytius* annular cartilage. Since sections of perforated *Dictyocaris* show no disturbance of the laminae either above or below by burrowing organisms, and since no other member of the fauna shows similar features the circumstantial evidence supports the identification of *Jamoytius* (and possibly *Thelodus*) as a causal factor. The writer is not convinced by the evidence for interpreting *Dictyocaris* as a phyllocarid crustacean, or even, perhaps, as an animal. If *Jamoytius* did create the holes in *Dictyocaris* this might imply the presence of a rasping device such as Stensiö reconstructed in the Norwegian anaspids (Stensiö 1958, figs. 126–7; cf. also Ritchie 1964, p. 17). Although no trace is visible in the head of *Jamoytius* of a rasping tongue it need not have been a very substantial structure. It seems probable that the petromyzontids initially fed on plant material and scraped algae from rocks and from the skin of other fish and that, almost by accident, they later developed a taste for blood; or as Hendrickson (in Strahan 1963, p. 98) has suggested, 'the ectoparasitic habit may have arisen in ostracoderms that had developed a suctorial mouth in connexion with a benthic microphagous (or perhaps grazing) habit and were able with this device to feed on the epizootic or epiphytic organisms of other bottom-living animals. Transition from this to an ectoparasitic habit would follow an evolutionary pattern which has been demonstrated in many groups of animals.'

However it fed, the anterior position of the first branchial arches in *Jamoytius* and the apparently horizontal position of the branchial basket must mean that the buccal cavity was quite small, that the external openings were opposite the holobranchs and that the

'conduits branchiaux externes' were not posteriorly directed as they must have been in *Pterygolepis* (Stensiö 1964, fig. 28c). With such indefinite branchial remains and no knowledge of the position of the otic capsules it would be foolhardy to label the individual gill arches but it seems probable that *Jamoytius* and the other anaspids, like the petromyzontids, retained one or more prevagal innervated gills. In its horizontally aligned, uncompressed branchial apparatus, which begins immediately behind the orbit, *Jamoytius* differs from the other known anaspids. It also differs in possessing flexible, unossified scales which run unbroken from the mid-dorsal to ventro-lateral surface, and in the apparent persistence of a long, low, dorsal fin-fold which in most anaspids is represented by a row of median, dorsal, ridge scales; in this respect, probably a primitive feature, *Jamoytius* resembles *Endeiolepis* (Stensiö 1939, text-fig. 7) and there could conceivably be a close relationship between them.

Jamoytius differs from the living cyclostomes in the presence of scales and lateral fin-folds. The scales may easily have been lost but the absence of lateral fins in the petromyzontids and myxinoids is more difficult to explain away. There is still considerable disagreement over the relationships of the various ostracoderms with the cyclostomes. Stensiö's views that the petromyzontids are derived from cephalaspidomorph ancestors and the myxinoids from heterostracans have been strongly criticized by many workers on the grounds that the Heterostraci were probably diplorhinal while the Osteostraci, Anaspida, and Cyclostomata are monorhinal (Tarlo 1961, Heintz 1963). If this latter interpretation is correct then the Heterostraci 'cannot be regarded as more closely related to the Myxinids than to other agnathous groups' (Wängsjö 1952, p. 564).

The living cyclostomes may therefore be reasonably regarded as an offshoot of the basic cephalaspidomorph stock which has split into the petromyzontid and myxinoid groups since Silurian times.

The cephalaspids, despite all their anatomical similarities to the petromyzontids, are surely too specialized even from their first appearance to be possible ancestors. It seems more likely that the anaspid stock, and in particular *Jamoytius* as an unspecialized anaspid, is on or near the line leading to the petromyzontids, and, less certainly, to the myxinoids. Strahan (1958, p. 93) in an interesting study of living and fossil agnathans using D'Arcy Thompson's method of coordinate deformations, comes to similar conclusions regarding the origin of lampreys but expresses strong reservations about deriving myxinoids from the same stock. Robertson (1954, 1957) from his studies on osmotic regulation and the salt content of plasma has demonstrated that the myxinoids may be derived directly from marine chordate ancestors and not secondarily from unknown freshwater ancestors. 'The related lampreys, on the other hand, have acquired osmotic regulation, essential for anadromous habits and permanent life in fresh water, and the persisting anadromous members maintain this regulation even in sea water' (Robertson 1957, pp. 174–5).

Jamoytius kerwoodi White, as a Middle Silurian cyclostome inhabiting a marine environment is well placed to give rise to either, or both, of the surviving lines of agnathans, and the absence of lateral fins in the specialized, and probably degenerate, living forms may be a secondary, and not a primary, feature. The presence, in *Jamoytius*, of a lamprey-like branchial apparatus must remove any lingering suspicion that it might represent the stock which gave rise either to the Cephalochordata (Amphioxus) or to the Gnathostomata.

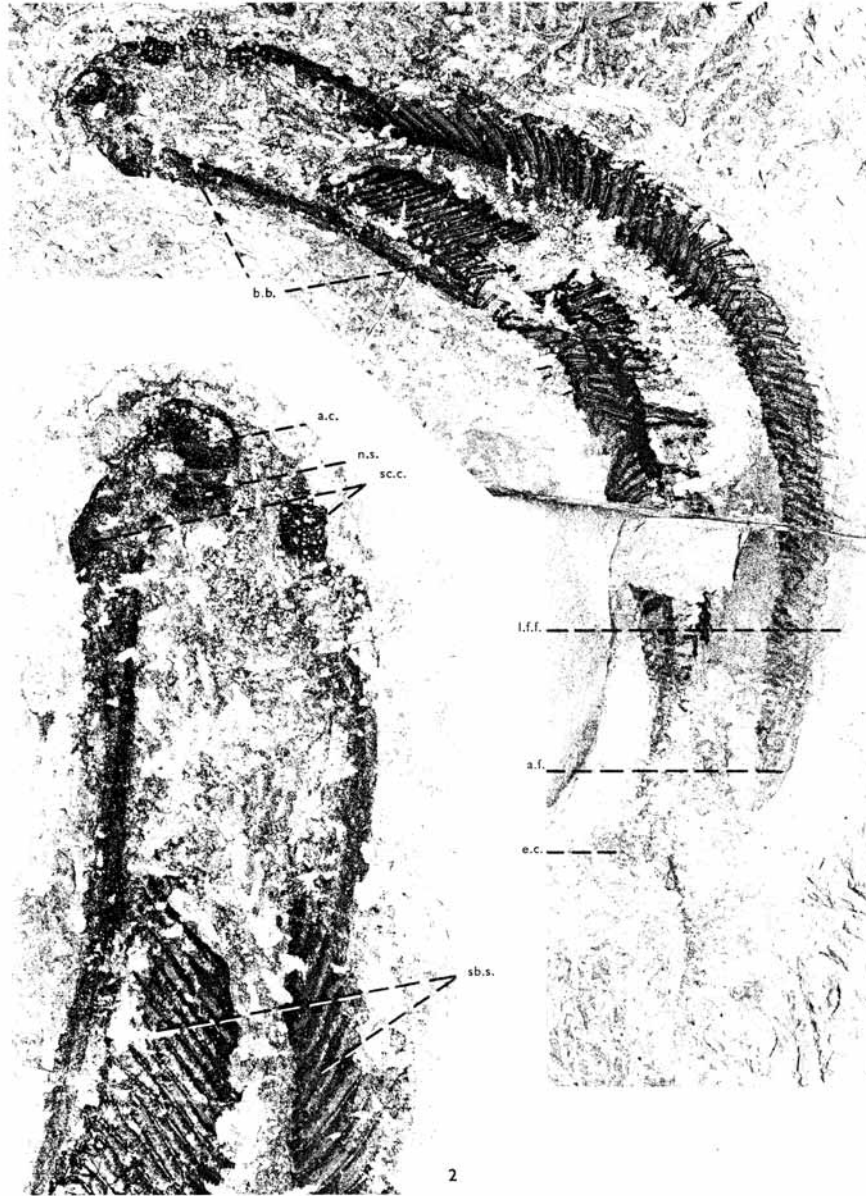# REFERENCES

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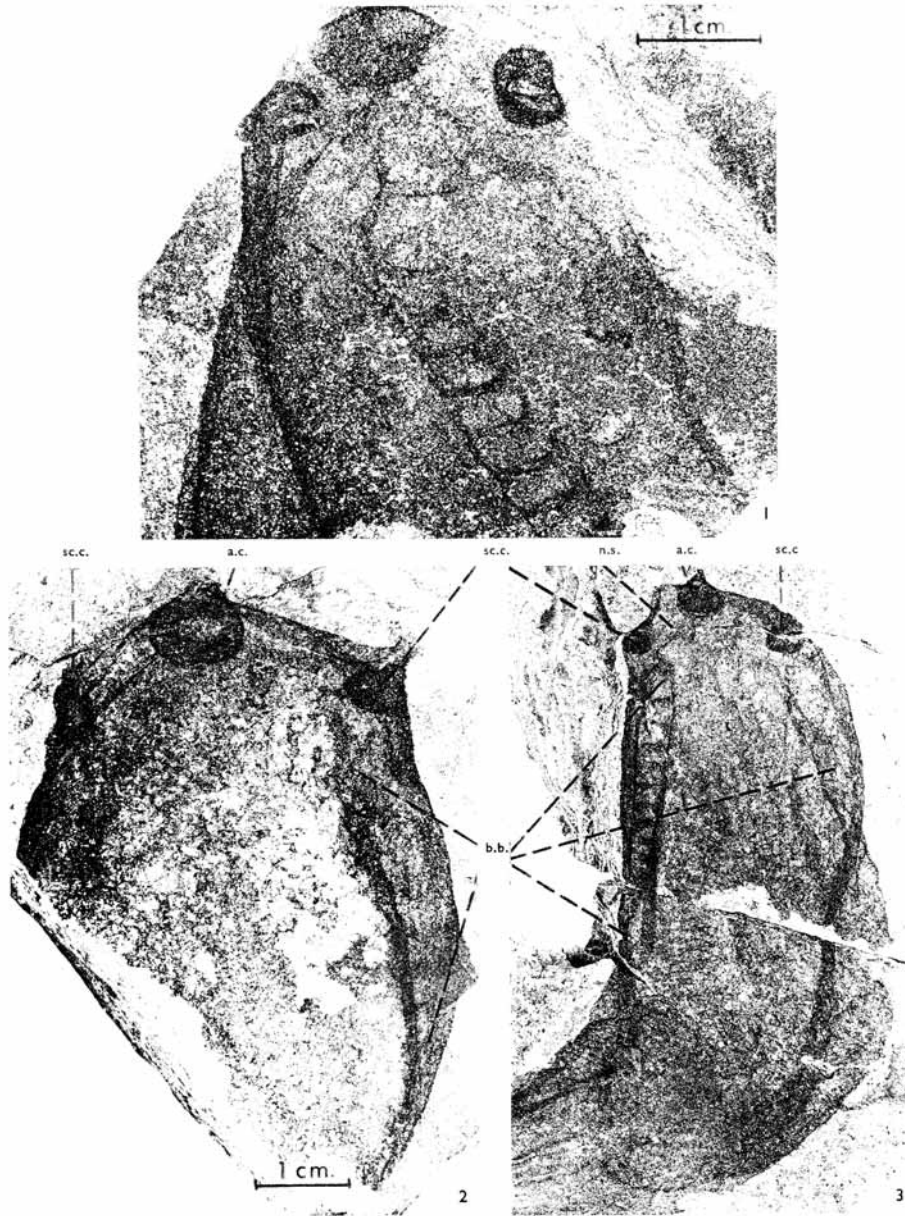Department of Geology,
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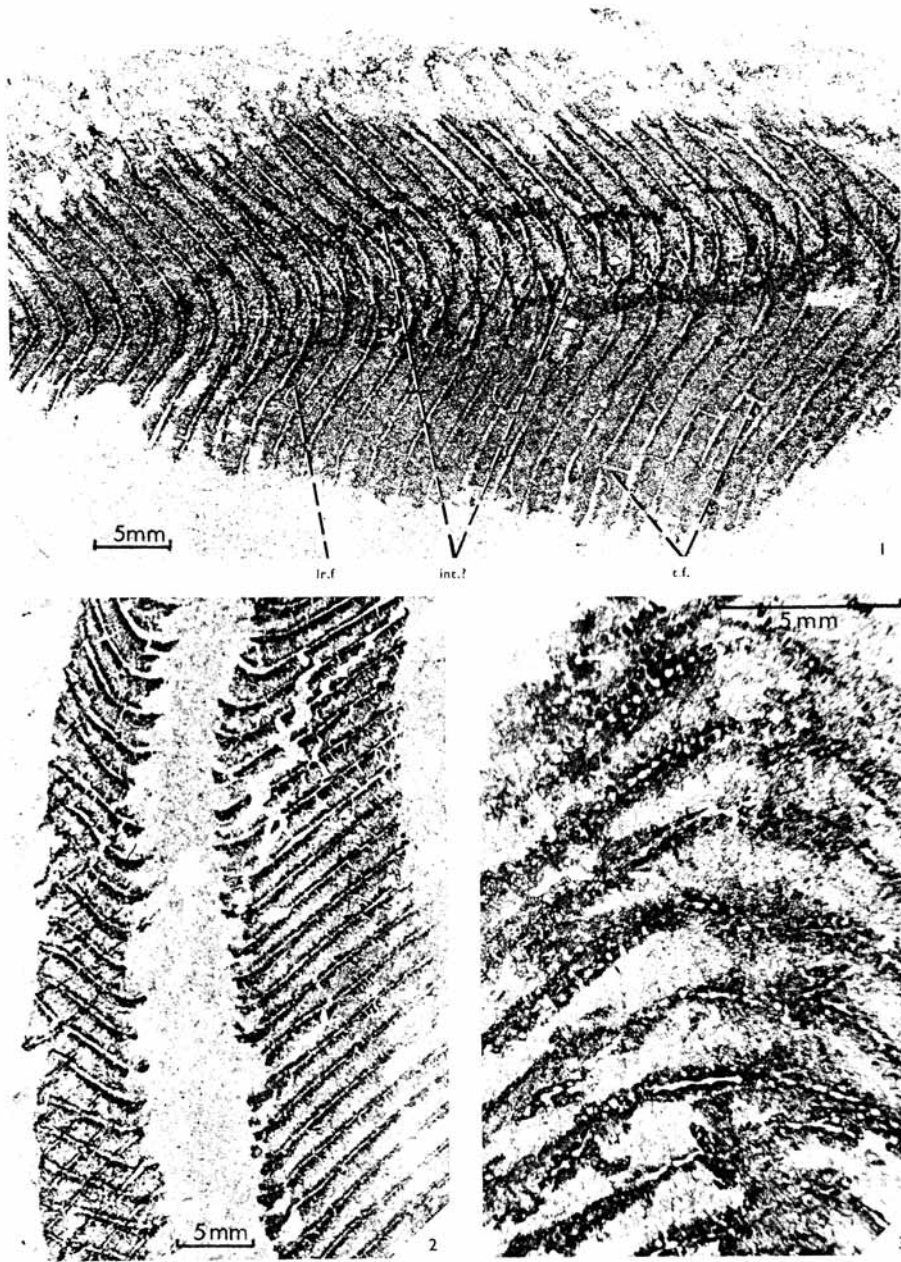Sydney, N.S.W.,
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