Further petalichthyid remains (placoderm fishes, Early Devonian) from the Taemas–Wee Jasper region, New South Wales

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New material referable to the order Petalichthyida (Placodermi) is described from the Early Devonian limestones of the Taemas–Wee Jasper area, New South Wales. *Shearsbyaspis oepiki* gen. et sp. nov. is represented by two incomplete skulls, one including parts of the endocranium. It differs from other genera in having discrete rostral and pineal plates that completely separate the preorbitals of each side. It resembles *Lunaspis* in the size of the central plates, and *Wijdeaspis* in the shape of the anterior paranuchal plate. In the endocranium, a lateral preorbital space is identified, communicating posteriorly with the orbital cavity. In the orbit, the optic nerve foramen and eyestalk attachment area are described. Two foramina behind the optic nerve

foramen, possibly for anterior and posterior branches of the oculomotor nerve, are not associated with a myodome. Isolated median dorsal, spinal, and ventral trunk-shield plates are assigned to *Lunaspis* sp. on the basis of ornament. The median dorsal plate carries a median ventral cavity near its posterior margin, a structure not previously described in petalichthyids. Three competing hypotheses of petalichthyid relationships are briefly discussed. It is suggested that the ventral cavity on the median dorsal is primitive for placoderms, and the position of the corresponding cavity in antiarchs, anterior to the transverse thickening, might be a derived condition.

Introduction

The Baltic region is a classic area for the study of early vertebrates, and, in particular, the fishes and agnathans from the Middle–Late Devonian Old Red Sandstone facies in Latvia, Estonia, and the Leningrad region of Russia have been under scientific investigation since early in the nineteenth century. Some of the earliest collections and studies of placoderm fishes were made in Estonia by S. Kutorga, H. Asmuss, and C. Gravingk on exceptionally well-preserved remains from the Aruküla caves deposits just outside Tartu, where A.A. Öpik commenced his academic career and later served as Professor of Geology and Palaeontology at the University of Tartu during 1930–1944. The description of giant arthrodire material from Aruküla by A. Heintz (1934) is now a standard work in the placoderm literature. This was one of the many research publications on palaeontology and stratigraphy emanating from the Geological Institute of the University of Tartu, of which Öpik was also director. There can be little doubt, therefore, that when A.A. Öpik arrived in Australia in 1948 he brought with him a knowledge of the Devonian vertebrates of his homeland that inevitably stimulated in a small but significant way an area of palaeontological research that was still in its infancy here. It can be difficult to assess the extent of a scientist's contribution outside that recorded in his own published works, but Öpik's influence can be seen in several BMR publications that present the results of field investigations carried out in the 1950s and 1960s, and report his identifications of new Devonian fish occurrences (e.g. Traves, 1955; Smith, 1964; Veevers & Roberts, 1968).

Closer to his new home base of Canberra, where Öpik's investigations of the Ordovician–Silurian geology of the local area are well known, it was inevitable that one of his early field excursions was to the highly fossiliferous Siluro-Devonian deposits in the Yass–Taemas area. It was, no doubt, on one such visit that he collected a remarkable specimen of the arthrodire *Buchanosteus*, which was sent by the then Chief Geologist of BMR, N.H Fisher, to E.S. Hills in Melbourne for examination, in October 1950. This specimen, after acetic acid preparation, has proved to be most significant in displaying the detailed internal morphology of the placoderm braincase (see Young, 1979, fig. 5; pl. 2A). It is not inappropriate, therefore, that the new species of placoderm fish from the Early Devonian Taemas fauna described below be named in Öpik's honour.

At the time Öpik collected the specimen of *Buchanosteus* mentioned above, the existence of a highly interesting and diverse Devonian fauna in the Devonian limestones of the Taemas–Wee Jasper area around Burrinjuck Dam was not known. Etheridge (1906) had reported the discovery of the early lungfish *Dipnorhynchus sussmilchi* from near Taemas, and Woodward (1941) described a new placoderm, *Notopetalichthys hillsi*, from near Wee Jasper. A few other specimens were at that time under study at the British Museum (Natural History) in London, and the first results of E.I. White's investigations on the Taemas–Wee Jasper vertebrate fauna were published in 1952. Since then there have been a number of contributions dealing with this fauna (e.g. Campbell, 1965; Schultze, 1968; Thomson & Campbell, 1971; White & Toombs, 1972; White, 1978; Young, 1978, 1979, 1980, 1981; Giffin, 1980; Campbell & Barwick, 1982, 1983). A new lungfish (*Speonesydrion iani* Campbell & Barwick) should now be added to the vertebrate faunal list given in Young (1981). The cosmoid scale figured by Giffin (1980) may well be dipnoan, but isolated scales and a detached entopterygoid in the BMR collections now confirm the presence of a porolepiform rhipidistian in the fauna.

Placoderms are the dominant group in the fauna, and euarthrodires are the most common and diverse placoderms (e.g. White, 1978). There are also several other placoderm groups that are less well represented. With the new material described here, the order Petalichthyida is represented by four taxa: *Notopetalichthys hillsi* Woodward 1941, *Wijdeaspis warrooensis* Young 1978, *Shearsbyaspis oepiki* gen. et sp. nov., and *Lunaspis* sp. These are represented by relatively few specimens, and it seems that the petalichthyids were not a common element in the vertebrate fauna.

The Early Devonian limestones of the Taemas–Wee Jasper area occur in two separate outcrops: an eastern area, in the valley of the Murrumbidgee River near Taemas Bridge, and along the upper reaches of Burrinjuck Dam (Browne, 1959); and a western outcrop, near Wee Jasper, in the valley of the Goodradigbee River about 18 km west of Taemas (Pedder & others, 1970). All the material described below comes from the eastern outcrop, near Taemas Bridge (Fig. 1). The age of the limestone sequence is regarded as Emsian (see Strusz, 1972; Savage, 1973). Petalichthyids are also known from the western outcrop of the Murrumbidgee Group (see Young, 1978). A different and slightly younger vertebrate assemblage is known from a thick sequence of terrigenous clastics that overlies the limestones of the Murrumbidgee Group near Wee Jasper (Young & Gorter, 1981). Elsewhere in Australia, the group has
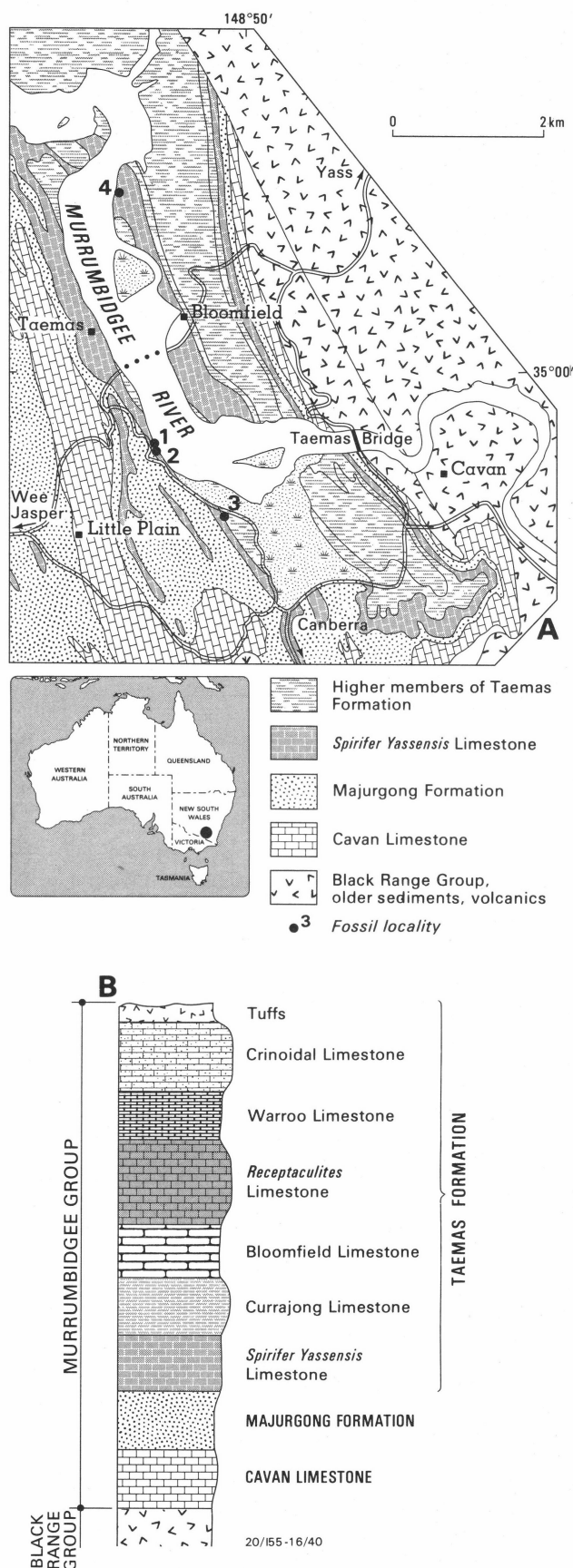
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Figure 1. Devonian geology in the vicinity of Taemas Bridge and the upper reaches of Burrinjuck Dam, showing localities (1–4) for specimens described in this paper (A), and generalised stratigraphic section for the Murrumbidgee Group in the Burrinjuck Dam area (B).

so far been recorded only from limestones of equivalent age in the Buchan area of eastern Victoria (J. Long, personal communication).

Material described below is housed in the British Museum (Natural History), London (prefix P), and the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Canberra (prefix CPC). Prepared specimens were developed by the acetic acid techniques of Toombs (1948) and Toombs & Rixon (1959). Classification of placoderms generally follows that of Miles (1969).

Systematic palaeontology

Subclass **Placodermi**
Order **Petalichthyida** Jaekel, 1911.
Genus *Shearsbyaspis* nov.

Name. After Mr. H.J. Shearsby, an early collector in the region.

Definition. Petalichthyids in which the preorbital plates are completely separated by discrete rostral and pineal bones, and dermal bones are ornamented with low concentric or radiating ridges and occasional tubercles.

Type species. *Shearsbyaspis oepiki* sp. nov.

Remarks. This new genus differs from *Macropetalichthys* Norwood & Owen and *Wijdeaspis* Obruchev in having discrete rostral and pineal plates, and from *Lunaspis* Broili, *Epipetalichthys* Stensiö and *Notopetalichthys* Woodward in lacking a median suture between the preorbital plates. The preorbitals are not known in *Ellopetalichthys* Ørvig, but this genus has a different ornamentation on the dermal bones, and larger orbits.

Shearsbyaspis gen. nov. can also be distinguished from *Notopetalichthys* (see Woodward, 1941; White, 1952) by the shape of the central plates, the absence of a flattened border around the preorbital skull margin, and the fact that the supraorbital sensory canals join some distance behind the orbits; from *Epipetalichthys* (e.g. Stensiö, 1925) in the size of the orbits, the shape of the preorbital and central plates, and the configuration of the posterior pitline; from *Lunaspis* (e.g. Gross, 1937, 1961) in the ornament, and some minor differences in the shape of the skull-roof bones; from *Wijdeaspis* (e.g. Heintz, 1937; Obruchev, 1964; Young, 1978) in the position of the pineal foramen and, possibly, the shape of the rostral margin; and from *Macropetalichthys* in overall size, size and shape of the central plates, and ornamentation of dermal bones.

Shearsbyaspis oepiki sp. nov.
(Figs. 2–6)

Definition. As for genus (only species)

Holotype. P33580, an incomplete skull-roof with endocranial ossifications attached.

Other material. CPC24622, an incomplete skull-roof preserved in visceral view.

Locality. The holotype was collected by H.A. Toombs as a loose sample below the outcrop known as 'Shearby's Wallpaper', on the western bank of the Murrumbidgee River, about 1 km upstream from the site of the old Taemas bridge (1, Fig. 1). CPC24622 was part of a small collection of vertebrate remains from the same locality made by C.G. Gatehouse in about 1964.

Horizon. The 'Shearsby's Wallpaper' outcrop occurs in the *Spirifer yassensis* Limestone, the lowest unit of the Taemas Formation in the Murrumbidgee Group (Fig. 1). The limestone matrix of CPC24622 contains the brachiopods *Spinella yassensis* and *Notochonetes culleni*, which are both very common to abundant in the *Spirifer yassensis* Limestone.

Remarks. From the information provided by these two specimens, the species cannot be placed in existing genera. The shape and arrangement of plates in the preorbital region of the skull have previously been used as generic characters within the Petalichthyida, and, on this basis, a new genus has been erected. The ornament on the holotype is readily distinguished from that of other petalichthyids in the Taemas–Wee Jasper fish fauna, and CPC24622 is tentatively referred to the species because of its similar dermal bone pattern in the preorbital region of the skull.

Description. The two specimens permit a restoration of the sensory canal and dermal bone patterns in the skull-roof, although the posterior and posterolateral margins remain unknown. Part of the anterolateral margin is, however, well preserved in the holotype (Fig. 4B). It is convex behind a notch for the infraorbital sensory canal, and, in front of the notch, is thickened and deeply embayed, but with a slight rounded angle developed within the embayment (*a.pro*).

Sutures between the skull bones are partly visible on both specimens. Bone margins are also indicated by the pattern of ornament on the holotype and striations radiating from ossification centres on CPC24622. CPC24622 is too fragile to be easily removed from its matrix, and only the visceral surface is available for study. In both specimens (Fig. 2) the suture between the rostral and pineal bones is clear, these plates completely separating the preorbitals of each side. The form of the rostral margin is uncertain, but the restoration in Figure 5 assumes that a bevelled edge at the anterior extremity of the right preorbital and along the projecting right margin of the rostral plate in CPC24622 (Figs. 2,3) indicates the free rostral margin of the skull. A projecting rostral plate is also seen in *Notopetalichthys* and *Lunaspis*. The supraorbital sensory canals (*soc*, Fig. 3) converge towards the midline in front of the preorbital ossification centre, as in several other petalichthyids. However, this is not the case in *Notopetalichthys*, nor in the holotype of *Wijdeaspis arcticus*, which has been restored with a wide rostral margin (Heintz, 1937). Another specimen referred to this species by Obruchev (1964, pl. 1, fig. 1) suggests a much narrower rostral plate and convergent canals, and this may also have been the condition in uncrushed *Lunaspis* (cf. Gross, 1961). The shape of the rostral margin in flattened specimens is clearly difficult to interpret.

The pineal opening in the holotype of *Shearsbyaspis oepiki* is a perforation in the thin dermal bone roofing the pineal region, lying just behind the level of the anterior border of the orbits, and, thus, at about the same position as in *Lunaspis* (Gross, 1961). In other genera, the foramen is either farther in front (*Macropetalichthys, Epipetalichthys, Notopetalichthys*) or farther behind, as in *Wijdeaspis* (see Ørvig, 1957, fig. 5; Denison, 1978, fig. 25). On the visceral surface of the pineal there is a deep pit (*p.pin*, Fig. 3) surrounded by a low crest of bone and generally similar to the pineal pit of *Arenipiscis* (Young, 1981), except that the foramen is situated at its posterior end, as in *Brindabellaspis* (Young, 1980). The foramen is slightly off the midline to the left, indicating a larger left part of a paired pineal organ, as has been reported in other placoderms (Edinger, 1956; Miles & Westoll, 1968). The presence of the opening in CPC24622 suggests that the pineal foramen in *Shearsbyaspis* was open in life.
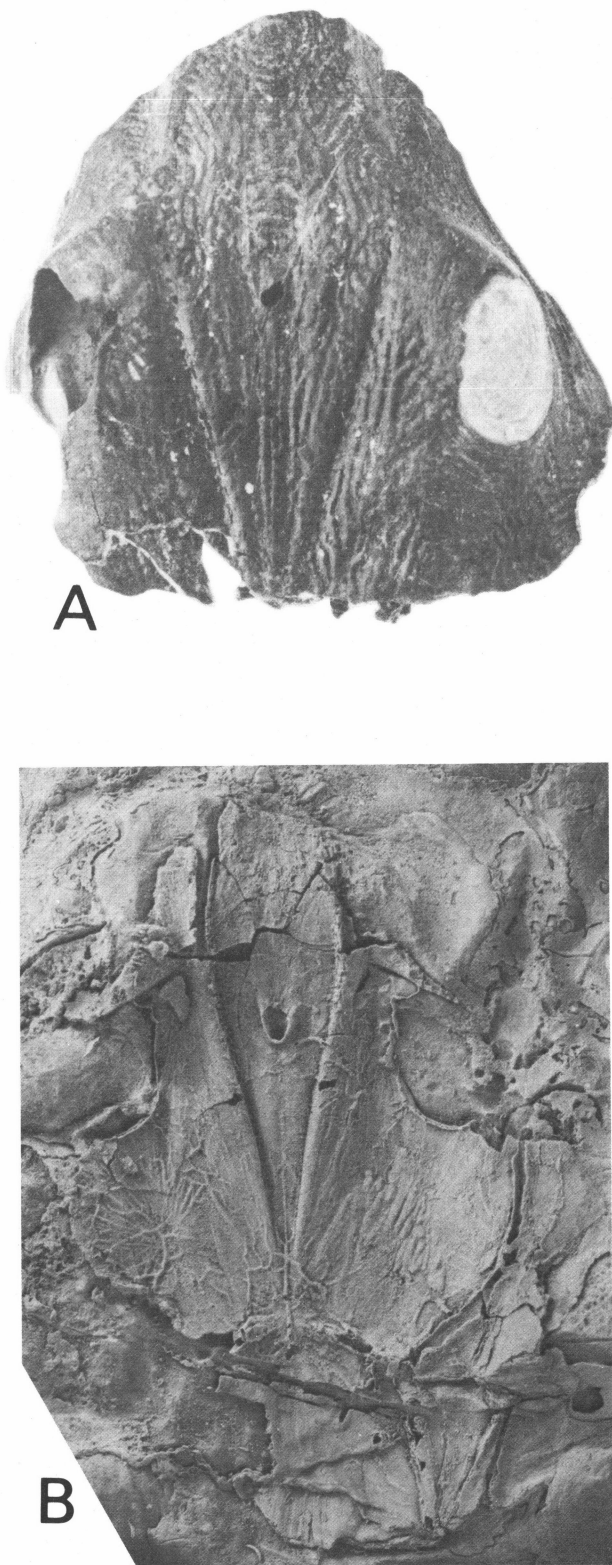
Figure 2. *Shearsbyaspis oepiki* gen. et sp. nov.
A, holotype, an incomplete skull in dorsal view, P33580 (x3); B, CPC24622, an incomplete skull-roof in visceral view (x2).

In both specimens, the pineal plate occupies a notch in the anterior end of the nuchal plate. The shape of the anterior part of the nuchal is well shown (Figs 2,3,4A), but on CPC24622 the bone margins behind the ossification centre are not clear, although radiating striations suggest that it was fairly long and narrow, as in other petalichthyids.
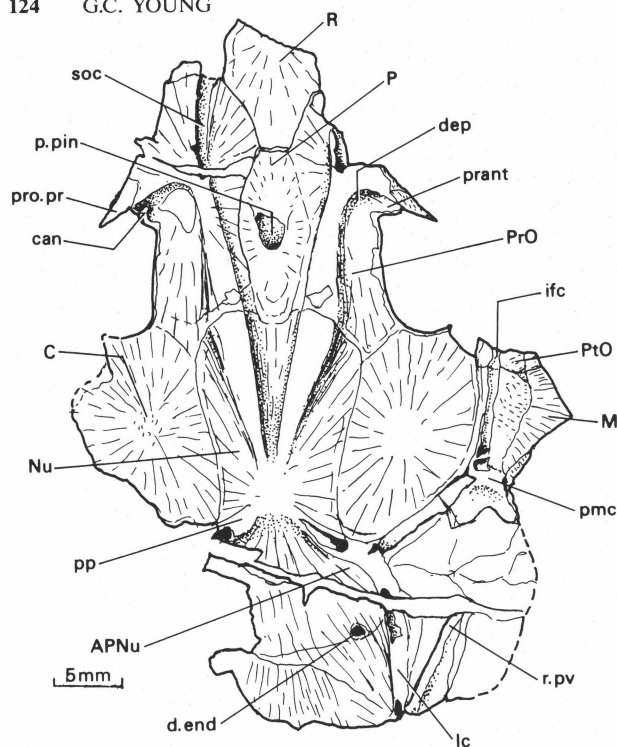
Figure 3. *Shearsbyaspis oepiki* **gen. et sp. nov.**
CPC24622, an incomplete skull-roof in visceral view (cf. Fig. 2B). *APNu,* anterior paranuchal plate; *C,* central plate; *can,* canal and foramen, possibly for the ophthalmicus superficialis and profundus branches of the trigeminal nerve; *d.end,* possible endolymphatic duct opening; *dep,* depression beneath preorbital recess; *ifc,* infraorbital sensory canal; *lc,* main lateral line sensory canal; *M,* marginal plate; *Nu,* nuchal plate; *P,* pineal plate; *pmc,* postmarginal sensory canal; *pp,* posterior pitline; *p.pin,* pineal pit; *pr.ant,* dorsal part of endocranial antorbital process; *PrO,* preorbital plate; *pro.pr,* dermal preorbital process; *R,* rostral plate; *r.pr,* postvagal ridge; *soc,* supraorbital sensory canal.

Of the paired bones in the skull, the shape of the preorbital plate is indicated on both specimens (*PrO,* Figs. 3,5). On its inner surface, a well-developed ridge runs from the ossification centre towards the suture with the postorbital plate. The latter encloses the orbit laterally, and is well preserved on the right side of the holotype (*PtO,* Fig. 4). The similar form of the dermal preorbital process on each side in CPC24622 (*pro.pr,* Fig. 3) suggests that this approximates the position of the preorbital-postorbital suture. A small posterior part of the postorbital plate is also preserved on the left side of CPC24622 (Fig. 3). The central plate in this specimen (*C,* Fig. 3) is an oval-shaped bone, elongate, and extending back almost to the posterior pitline. The central plate of *Lunaspis* is of similar proportions, but more angular, whereas in *Macropetalichthys* this plate is relatively small, and in *Notopetalichthys* it has a more complex shape, as it forms part of both the mesial and posterior margins of the orbit (White, 1952, fig. 37).

The more posterior parts of the skull are preserved only in CPC24622. The anterior paranuchal is present on the left side, but its margins are not clear. Its ossification centre must have been situated at the junction of the posterior pitline and main lateral line canal, as in other petalichthyids, and the shape of the central plate shows that its anterior margin was deeply embayed, a feature otherwise best developed in *Wijdeaspis* (Young, 1978, fig. 3; Denison, 1978, fig. 25C). An opening on the visceral surface is appropriately placed for the endolymphatic duct (*d.end,* Fig. 3). Part of the marginal plate is preserved on the left side of the specimen, where the junction of the lateral line and postmarginal sensory canals marks its ossification centre (*M,* Fig. 3). Its mesial suture with the central plate is well defined, and a somewhat sigmoid crack approximates the position of its posterior suture with the paranuchals. Part of its free lateral margin is preserved, along which a slight notch

marks the position of the postorbital-marginal suture. The smooth lateral parts of the visceral surface of the marginal and postorbital plates are clearly delineated from the more roughly textured mesial parts, to which the endocranium was attached (Fig. 2B). The posterolateral part of the marginal plate, which in other petalichthyids extends along the postmarginal canal, is assumed to have broken off. It is worth noting, however, that the assumed broken edge is straight and clean, and reminiscent of a bone suture. In some other placoderm groups, this portion of the skull is occupied by the postmarginal plate, a bone that has not been identified in petalichthyids as a separate element.

The posterior part of the skull in CPC24622 is fractured, and few details are clear. A low ridge near the posterolateral edge of the preserved part (*r.pv,* Fig. 3) corresponds to the dermal postvagal ridge identified in *Wijdeaspis warrooensis* (Young, 1978, fig. 4). It joins the tube for the lateral line canal at the posterior preserved edge of the specimen, suggesting that the skull-roof margin was a short distance farther behind, as restored in Figure 5. There is no indication of any of the structures associated with the dermal neck joint as described for *Wijdeaspis* (Young, 1978).
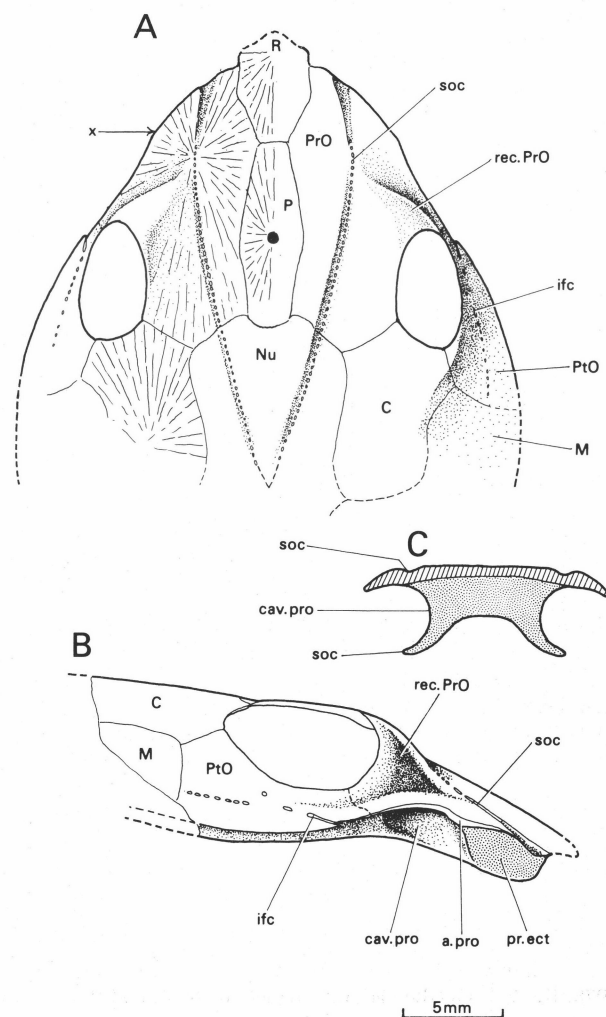

Figure 4. *Shearsbyaspis oepiki* **gen. et sp. nov.**
Preserved part of the skull-roof, restored after the holotype (P33580). A, dorsal view, ossification centres shown on the left; B, right lateral view; C, transverse section through preorbital region at level shown in A. Cartilage denoted by regular stipple, *a.pro,* preorbital angle of skull-roof; *cav.pro,* lateral preorbital space; *f.pi,* pineal foramen; *pr.ect,* ectethmoid process; *rec. PrO,* preorbital recess; *sos,* subocular shelf of endocranium. For other abbreviations see Fig. 3.
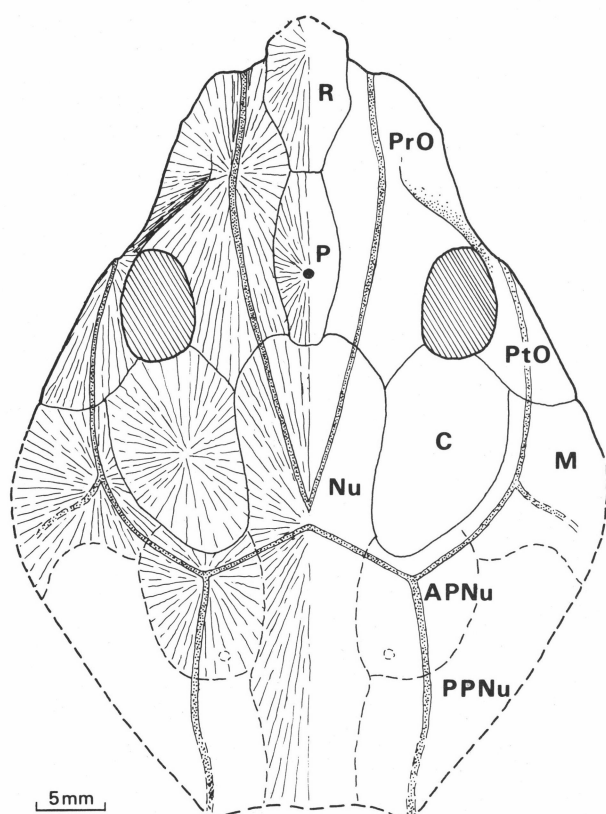
Figure 5. *Shearsbyaspis oepiki* **gen. et sp. nov.**
Restoration of the dermal bone and sensory canal pattern of the skull-roof. After P33580 and CPC24622. Ossification centres of dermal bones indicated on the left side. *PPNu,* posterior paranuchal plate. For other abbreviations see Figs. 3, 4.

Other features of the visceral surface of the skull, as displayed in CPC24622, are the network of fine canals (Fig. 2B), which clearly correspond to the subcutaneous vascular plexus described for *Ellopetalichthys* by Ørvig (1957, p. 307; pl. I, fig.1), and the strong development of the ridges containing the sensory canals (*soc, pp, lc, ifc,* Fig. 3). The ridges for the supraorbital canals are very prominent, extending across the preorbitals to the slightly elevated ossification centre of the nuchal plate, where the ridges for the posterior pitlines also come together. It is probable that, externally, these sensory canals were either confluent at this point, as in *Ellopetalichthys* and *Macropetalichthys,* or else closely associated near the ossification centre, as in *Lunaspis* (e.g. Denison, 1978, fig. 25). In several places, the ridges are broken to show the enclosed tube for the sensory canal, a typical feature of the lateral line system in petalichthyids. Externally, the sensory canals open through rows of pores, although this can only be observed in *Shearsbyaspis* on the holotype (Fig. 2A). The supraorbital sensory canals are very clearly defined (*soc,* Fig. 4). Near the anterior margin, each canal forms a broad groove, which sinks beneath the bone surface in front of the preorbital ossification centre and continues posteriorly as a row of distinct pores in a shallow groove. The infraorbital canal (*ifc*) forms a row of irregularly placed pores, and leaves a notch as it passes off the lateral margin of the postorbital plate (Fig. 4B).

CPC24622, as preserved, has been partly flattened on the bedding plane of the sample, but the holotype appears to have retained the original curvature of the skull. The external dermal bone surface shows a slight rostrocaudal curvature, but otherwise is flat to slightly concave between the orbits. As in *Macropetalichthys* (Stensiö, 1969, fig. 130A; cf. Stensiö, 1925, fig. 15) and *Notopetalichthys* (Woodward, 1941, fig. B), the

orbits are set out from the anterolateral surface of the head by the development of conspicuous expanded inflections of thickened bone on the preorbital plates in front of the orbits (*rec.PrO,* Fig. 4). Consequently, the orbits face dorsolaterally rather than anterodorsolaterally. This feature has not been described in other petalichthyid genera, but is suggested by the ornament in some specimens of *Lunaspis* (e.g. Gross, 1937, pl. 9, fig. 2) and, especially, in *Wijdeaspis* (Obruchev, 1964, pl. l, fig.1), and could be widespread in petalichthyids. There are corresponding depressions on the visceral surface of the preorbital plates (*dep,* Fig. 3).

The dermal ornament of *Shearsbyaspis oepiki,* as exhibited by the holotype (Fig. 2A), consists of low ridges with a radiating or concentric arrangement, along which rounded tubercles are irregularly developed. The ridges are closer together than in *Lunaspis* (see below), and are lower and broader than in *Wijdeaspis* (Young, 1978).

Remains of the endocranium associated with these two specimens are of special interest, and the holotype, in particular, provides new information on the structure of the braincase in petalichthyids. Although the endocranium in the holotype is well ossified, the fragile perichondral laminae are partly obscured by a silty matrix, which does not readily dissolve in acid. Nevertheless, some significant details of the structure of the anterolateral margins and the orbital cavity can be determined. In the region anteroventral to the right orbit, where the lateral border of the dermal skull-roof is entire, the concave lateral endocranial wall can be seen to be set in from the skull margin. The space thus formed (*cav.pro,* Fig. 4B,C) probably corresponds to the lateral preorbital space in *Macropetalichthys* and *Brindabellaspis* (Stensiö, 1969, fig. 22B; Young, 1980, fig. 14). Posteriorly, this space opens into the orbital cavity. Anteriorly, the perichondral lamina turns outward to the skull-roof margin beneath or just in front of the preorbital angle (*a.pro,* Fig. 4B). The lateral face of this expanded portion is not preserved, but it is presumed to correspond to the ectethmoid process of *Macropetalichthys* (Stensiö, 1969, fig. 22). Behind the orbit, the ventral endocranial face extends right to the edge of the postorbital plate, but the structures on the adjacent face of the anterior postorbital process are not exposed (cf. Stensiö, 1969, fig. 22B). Slightly farther back, the visceral surface of the left marginal plate exhibited by CPC24622 shows that, at the posterior end of the postorbital plate and behind the postorbital-marginal suture, the endocranium was again set in from the skull-roof margin. This aspect of the cranial morphology of *Macropetalichthys,* as described by Stensiö (1925, 1963, 1969), is very poorly known (see Young, 1980, p. 28). Beneath the orbit in the holotype the subocular shelf is partly preserved, but it is not clear whether the orbit was completely enclosed ventrally or whether there was an embayment in front of the anterior post-orbital process, as in *Macropetalichthys.*

Limited areas of the ventral face of the endocranium are visible on the holotype anteriorly and posterolaterally. They show the endocranium to be a broad low structure of little depth. Posteriorly, the ventral face is gently concave, and, anteriorly, it becomes deeply concave between the subocular shelves (*sos,* Fig. 4C). Stensiö reconstructed this region in *Macropetalichthys* quite differently, but Gross (1961, p.41, and fig. 10) noted a similar depression in *Lunaspis,* in a position corresponding to the 'cavum precerebrale' of Stensiö's first account of *Macropetalichthys* (1925). A much deeper depression exists in the corresponding part of the endocranium in *Brindabellaspis* (Young, 1980, fig. 4). In front of the ectethmoid processes, the median part of the endocranium becomes increasingly shallow, but its anterior border is not preserved.
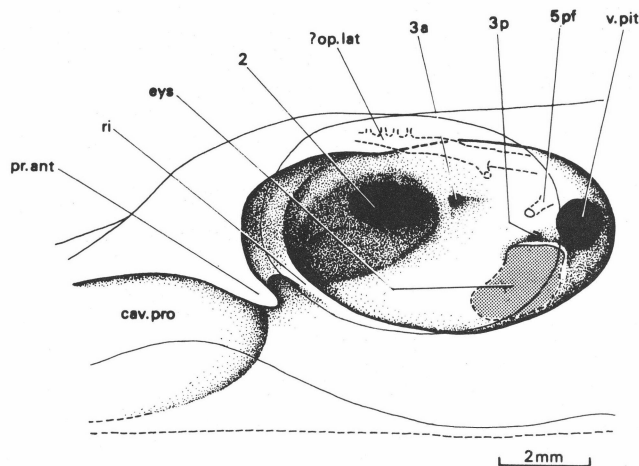
Figure 6. *Shearsbyaspis oepiki* **gen. et sp. nov.**
Left orbital region of endocranium in lateral view. Orbital and lateral skull-roof margins shown in outline. (After P33580.) *2*, optic nerve foramen, *3a, 3p,* foramina for anterior and posterior branches of third (oculomotor) cranial nerve; *5pf,* incompletely preserved canal, possibly for the profundus nerve; *cav. pro,* lateral preorbital space; *eys,* eyestalk attachment area; *op.lat,* canal for the ramus ophthalmicus superficialis lateralis; *pr.ant,* antorbital process; *ri,* ridge separating lateral preorbital space from orbital cavity; *v.pit,* foramen, probably for pituitary vein.

The right orbit of the holotype is filled with matrix, but the left is clear, and parts of the inner orbital wall are visible (Fig. 6). The mesial face of the orbital cavity is deeply recessed into the endocranial wall, with the result that the cavity has extensive, transversely oriented anterior and posterior walls, and is roofed over by a well-developed supraorbital shelf. As noted above, the degree to which the orbit was closed in ventrally by the subocular shelf is not known, but anteroventrally it is in communication with the lateral preorbital space (*cav.pro*), through a passage bounded dorsally and dorsolaterally by an endocranial process (*pr. ant*) fused to the inner surface of the preorbital plate. This condition is similar to that developed in *Macropetalichthys* or *Brindabellaspis* (Stensiö, 1969, fig. 60; Young, 1980, fig. 8). A dorsal part of the antorbital process is also preserved in CPC24622 (Fig. 3).

On the mesial side of the passage just described, a vertical ridge slopes back from the anterior wall to the floor of the orbit (*ri*, Fig. 6). Although not clearly shown in the holotype, the ridge probably marks the anterolateral edge of the subocular shelf. Mesial to the ridge, a rounded depression forms the anteroventromesial corner of the orbital cavity, posterodorsal to which on the mesial wall is a large oval-shaped foramen (*2*). This may be readily compared with the optic nerve foramen in *Radotina*, as interpreted by Gross (1958, fig. 5; also Stensiö, 1969, fig. 51). This foramen, and the depression anteroventral to it, form together the most deeply recessed part of the mesial orbital wall, and the whole region would seem to correspond to the large opening in *Macropetalichthys* interpreted by Stensiö (1963, figs 30,31; 1969, figs. 60,74) as an optic nerve canal enlarged for the insertion of the oblique eye muscles. The anterodorsal corner of the orbit is not clearly exposed, but remains of the dorsalmost part of the perichondral lining are preserved in CPC24622 (Fig. 2B). On the right side of this specimen, a short section of canal opens through a slightly expanded foramen into the anterodorsal corner of the orbit, just behind the base of the antorbital process (*can*, Fig. 3). In *Macropetalichthys*, a canal in much the same position is interpreted by Stensiö (1963, fig. 30) as having carried the ophthalmicus superficialis and profundus branches of the trigeminal nerve out of the orbit.

Behind the optic foramen in *Shearsbyaspis*, a second smaller foramen (*3*a, Fig. 6) opens through the more prominent

posterior part of the mesial orbital wall. This foramen in *Radotina* and *Macropetalichthys* was interpreted by Stensiö (1969) as having transmitted the oculomotor nerve. The conspicuous myodome associated with this foramen in *Brindabellaspis* (Young, 1980, fig. 3) was apparently not developed in *Shearsbyaspis*. Another slightly larger foramen, positioned posterodorsally with respect to the oculomotor foramen in *Radotina* and posteriorly in *Macropetalichthys*, was interpreted as the profundus opening by Stensiö. Unfortunately, this part of the mesial face and much of the adjoining parts of the posterior face of the orbital cavity are not preserved. However, a perichondrally ossified canal (*op.lat*) is visible through the broken orbital wall, running just beneath the dermal bone, and giving off a series of short dorsal branches to the supraorbital sensory canal. This evidently represents the ramus ophthalmicus superficialis lateralis of *Macropetalichthys* (Stensiö, 1963, fig. 30). A second canal (*5pf*) passes anterolaterally towards the non-preserved part of the orbital wall. Its point of origin is unknown, but it may be the profundus canal. The region is too poorly preserved to permit a more definite interpretation.

Ventrally, two further structures can be inferred. Both are badly preserved as extremely thin perichondral laminae, around which are scattered fragments of the mesial orbital face. A large round foramen (*v.pit*) is developed in a corresponding position to that interpreted by Gross (1958) as the opening for the trigeminal and facial nerves in *Radotina*, but considered here to be the foramen for the pituitary vein. The pituitary canal in *Macropetalichthys*, as depicted by Stensiö (1963, fig. 32), is much smaller and joins the trigeminal canal in the orbital wall, but in both *Buchanosteus* and *Brindabellaspis* (Young, 1979, fig. 4; 1980, fig. 8) it has a similar size and position to that described here. Anteroventral to this foramen, the dorsal margin of a second large opening is preserved (*eys*). This opening is here interpreted as an eyestalk attachment area on the basis of what appears to be an everted perichondral rim around its dorsal margin. Such a position is more posterior than in *Radotina* and *Macropetalichthys*, and this interpretation is provisional, since the region immediately in front, and posteroventral to the optic nerve foramen, is not preserved. Another small canal (*3p*) opens just above the rim of the eyestalk attachment area, in much the same position as the posterior foramen for the oculomotor nerve in *Brindabellaspis* (e.g. Young, 1980, fig. 8).

The posterior wall of the orbital cavity is poorly preserved, and openings for the jugular vein and facial nerve have not been identified.

Genus *Lunaspis* Broili

Definition. Petalichthyids of small to medium size, with an ornament of small tubercles normally completely fused into fine widely spaced ridges. Ridges are generally continuous and concentrically arranged. Preorbital plates meet in the midline to separate rostral and pineal plates. Sensory canals with uniserial rows of pores.

Type species. *Lunaspis heroldi* Broili, 1929

Occurrence. Siegenian-Emsian (Hunsrückschiefer) of the Rhineland.

Remarks. The relationship of the preorbital, pineal, and rostral plates exhibited by *Lunaspis* is seen only in *Notopetalichthys* amongst other petalichthyid genera. However, *Notopetalichthys* differs in many other features, such as the large orbits, the flattened border around the preorbital skull-roof margin, and the shape of the central and nuchal plates (White, 1952). The dermal ornament in *Lunaspis* the feature by which it is

mainly in the development of median processes (*amp,pmp*) on the anterior and posterior margins. On this point, it is noted that several specimens of *Lunaspis* figured by Gross (e.g. 1937, pl.9, fig 1; 1961, fig. 4A) suggest a less concave anterior margin than indicated by his reconstruction (Gross, 1961, fig. 2A). In P33632, there are at least nine concentric ridges developed, a number reached in some specimens of *Lunaspis broilii* (Gross, 1961, fig. 4), and exceeded by another specimen (Gross, 1937, pl. 8, fig. 3) with very closely spaced ridges. According to Gross (1961, p.32), the ridges are more widely spaced in *L. heroldi*, but this difference is not evident in figured examples of the median dorsal plate.

As in *Lunaspis* (Gross, 1937, fig. 27A, B), this new specimen has a distinct median dorsal ridge, formed by a row of coalesced tubercles (*mdr*, Fig. 7A). The ridge reaches maximum height posteriorly, but terminates in front of the posterior margin. Behind the ridge, the bone surface is slightly depressed (*dep*).

A reconstruction of the ventral surface is given in Figure 7C. There are no signs of contact faces for the dorsolateral plates of the trunk-shield, but these are often indistinct in placoderms. However, the posterior part of the plate shows some interesting new features. A broad transverse thickening (*tr.th*) is developed posteriorly, from which a median ventral ridge (*mvr*) runs anteriorly for a short distance beneath the posteriorly placed ossification centre of the bone. The thickening may be compared with the dorsal part of the crista transversalis interna posterior in antiarchs (e.g. Stensiö, 1948, fig. 47), and possibly with the various anterolaterally directed ridges extending from the base of the carinal process on the median dorsal plate of various brachythoracid euarthrodires (e.g. Heintz, 1932, fig. 44; Miles & Westoll, 1968 p.423). Gross (1961, p.43) described a similar thickening in *Lunaspis*, and also commented on its resemblance to the thickening on the posterior median dorsal plate of antiarchs.

In the midline, just inside the posterior margin, a deep pit is developed (*vc*, Fig. 7B,C). It opens into an internal cavity that extends upwards and forwards to reach inside the high posterior part of the median dorsal ridge. The latter appears to be roofed over only by a thin external bone layer. The ventral opening of the cavity is surrounded by an everted rim, which continues forward across the transverse thickening as the short median ventral ridge. The opening faces posteroventrally, as shown in Figure 7B. This structure has not previously been described in petalichthyids, and in Obruchev (1964) it is stated that the petalichthyid median dorsal plate has a high inner carina, although the evidence on which this is based is not known. The pit described here may be compared with the large opening leading to the cavity of the dorsal spine in *Palaeacanthaspis* (Stensiö, 1944, fig. 5C), and also the posterior ventral pit of the posterior median dorsal plate in antiarchs. Acid-prepared specimens of *Bothriolepis* from the Gogo fauna of Western Australia indicate that both anterior and posterior ventral pits in this form are rimmed by a free-standing lamina similar to that described here. Finally, a cavity has been described within the ventral keel of the median dorsal plate in ptyctodontids (Ørvig, 1960; Miles & Young, 1977, p.86). Behind the keel in *Ctenurella gardineri* is a pit-like depression, opening posteriorly and roofed over by the median dorsal ridge of the median dorsal plate, in a similar fashion to that just described. These resemblances suggest that this feature was primitive for placoderms generally, or at least for a subgroup including antiarchs, ptyctodontids, and petalichthyids.

The probable ventral plate of the trunk-shield is too incomplete to be positively identified. It is a thin slightly tumescent bone, with well-developed concentric ridges around a presumed laterally placed ossification centre. This is a feature of both anterior and posterior ventrolateral plates in *Lunaspis* (Gross,

1961, p.15), but the shape of the specimen as preserved is not closely comparable to either. No overlap areas or contact faces are visible around the margins of the plate.

The ornament differs in some respects from that of the median dorsal plate just described. The ridges are more even and closely spaced, and the tubercles, where developed, are dense and regular, giving the ridges a finely serrated appearance. However, along the straighter margin of the specimen, the tubercles are larger and irregularly placed along the ridges, giving an ornament that closely resembles that on P33632, suggesting that P33602 may be regarded as conspecific for the present.

Finally, the left spinal plate included here (P50216; Fig. 8) has an extensive dorsal lamina, numerous (over 50) pointed tubercles along the lateral margin, and about 10 curved spines along the distal part of the inner margin. It is complete at both ends, and, except for some differences in the shape of the dorsal lamina, is similarly developed to the spinal plates of *Lunaspis* previously figured by Gross (1961). It differs from the *Wijdeaspis* spinal plate described from the same fauna (Young, 1978) in having an ornament of fewer, more widely spaced ridges, resembling, in this respect, other *Lunaspis* species rather than *Wijdeaspis*. As in the undetermined ventral plate just described, the ridges have a serrated appearance caused by the fine evenly spaced tubercles. The tubercles along the lateral margin are mostly arranged in pairs, one above the other. Distally, near the tip, only a single row is developed, but, proximally, the margin becomes broader and more rounded, with crowded tubercles several rows deep.

Discussion

The order Petalichthyida is a reasonably well-defined group within the Placodermi. With the new genus described above, there are seven genera in the order (*Ellopetalichthys* Ørvig, *Epipetalichthys* Stensiö, *Lunaspis* Broili, *Macropetalichthys* Norwood & Owen, *Notopetalichthys* Woodward, *Wijdeaspis* Obruchev, and *Shearsbyaspis* nov.). I exclude the Chinese form *Quasipetalichthys*, which Denison (1978) included as an aberrant petalichthyid, but which lacks two clearly defined pairs of paranuchal plates in the skull-roof and laterally enclosed orbits, both characteristic features of the other genera. Other characters of the group are the elongate occipital region, long nuchal plate, absence of postmarginal and suborbital plates in the skull, the special construction (when present) of the dermal articulation between the skull-roof and trunk-shield, the enclosed sensory canals, and the relatively short trunk-shield, with prominent spinals, but lacking a posterior lateral plate and pectoral fenestra.

The phylogenetic position of the Petalichthyida within the Placodermi has been the subject of some debate, and there are currently three competing hypotheses. Miles & Young (1977) interpreted petalichthyids as the most primitive members of one of two major groupings within the Placodermi (the Petalichthyomorpha). The second major grouping (the Dolichothoracomorpha) included phyllolepids, antiarchs, and euarthrodires; ptyctodontids were placed as the sister-group to the common accestor of all petalichthyomorphs and dolichothoracomorphs (Fig. 9A). The main assumptions on which this scheme was based were that two pairs of paranuchal plates in the skull-roof are a derived condition, that the pectoral fin, enclosed posteriorly by large dermal bones of the trunk armour, is a synapomorphy of euarthrodires and antiarchs, and that the absence of pelvic and prepelvic claspers in all placoderms except ptyctodontids is a secondary and specialised condition. A second viewpoint was proposed and elaborated

most readily distinguished from other petalichthyids. The ornament of *Wijdeaspis* is most similar, but, as previously noted (Young, 1978, p. 104), *Lunaspis* can be distinguished on the continuity and wider spacing of the ridges. *Wijdeaspis* also differs in having a biserial row of pores on the posterior pitline, but several other differences exhibited by the type species (Heintz, 1937) are of uncertain taxonomic value (e.g. the short posterior paranuchal and the shape of the nuchal plate), since another specimen assigned by Obruchev (1964) to *Wijdeaspis* is similar to *Lunaspis* in these respects. These features can be properly assessed only after new material has been described.

Lunaspis sp.
(Figs 7,8)

Material. P33602, an incomplete ventral plate of the trunk-shield; P33632, an incomplete median dorsal plate; and P50216, a left spinal plate.
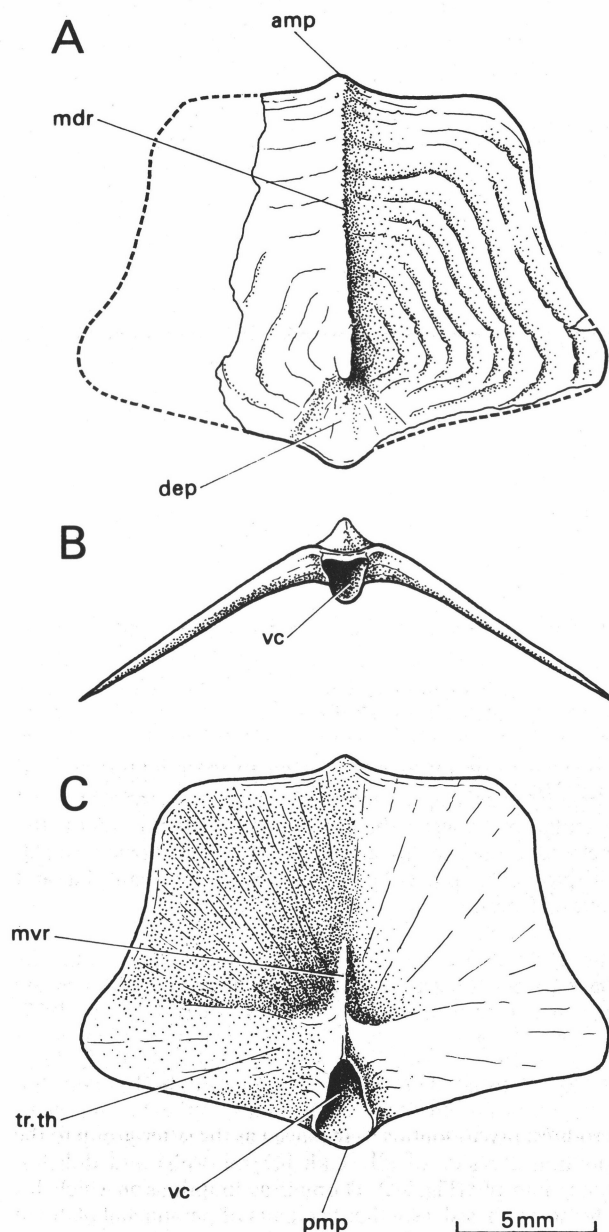
Figure 7. *Lunaspis* sp.
Median dorsal plate, P33632. A, Dorsal view; B, posterior view; C, visceral view. *amp,* anterior median process; *dep,* median depression; *mdr,* median dorsal ridge; *mvr,* median ventral ridge; *pmp,* posterior median process; *tr.th,* transverse thickening; *vc,* ventral cavity.
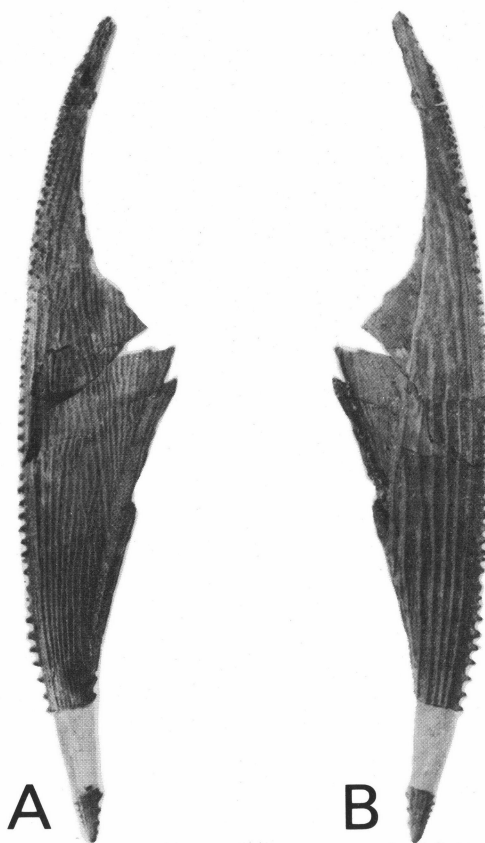
Figure 8. *Lunaspis* sp.
Left spinal plate, P50216 (x2). A, dorsal view; B, ventral view.

Localities. The three specimens are from the same area, near the Murrumbidgee River up to about 6 km downstream from Taemas Bridge (Fig. 1). Details are:

P33602: loose sample on the left bank of the Murrumbidgee River, about 140 m upstream from the scree below 'Shearsby's Wallpaper' (2,Fig.1);

P33632: loose sample on the hillside, about 2 km southwest of Taemas Bridge (3, Fig. 1);

P50216: loose sample on the right shore of the Murrumbidgee River, about 2.3 km east of Majurgong trig station (4, Fig. 1).

Horizon. Collection records of H.A. Toombs (BM(NH)) indicate that the three samples were approximately in situ, and derived from the lower part of the *Spirifer yassensis* Limestone, the lowest unit of the Taemas Formation in the Murrumbidgee Group.

Remarks. The three specimens are readily distinguished on ornament from other petalichthyids in the fauna. The ornament ridges are widely spaced and continuous, both features, as noted above, being apparently characteristic of the genus *Lunaspis*. The spacing of ridges has also been used as a specific character, the ridges being more densely arranged in *L. broilii* (Gross, 1961, p.19). However, these comparisons are based on a small number of specimens, and are unlikely to apply to other species. For the present, the three specimens described below are placed in an unnamed species of *Lunaspis*.

Description. The median dorsal plate (Fig. 7) includes most of the right and part of the left side of a small bone, with a preserved length of about 14 mm. It is ornamented with widely spaced concentric ridges, along which small pointed tubercles are developed at irregular intervals. In overall shape and ornament the specimen closely resembles the median dorsal plate of *Lunaspis* described by Gross (1937, 1961), from which it differs
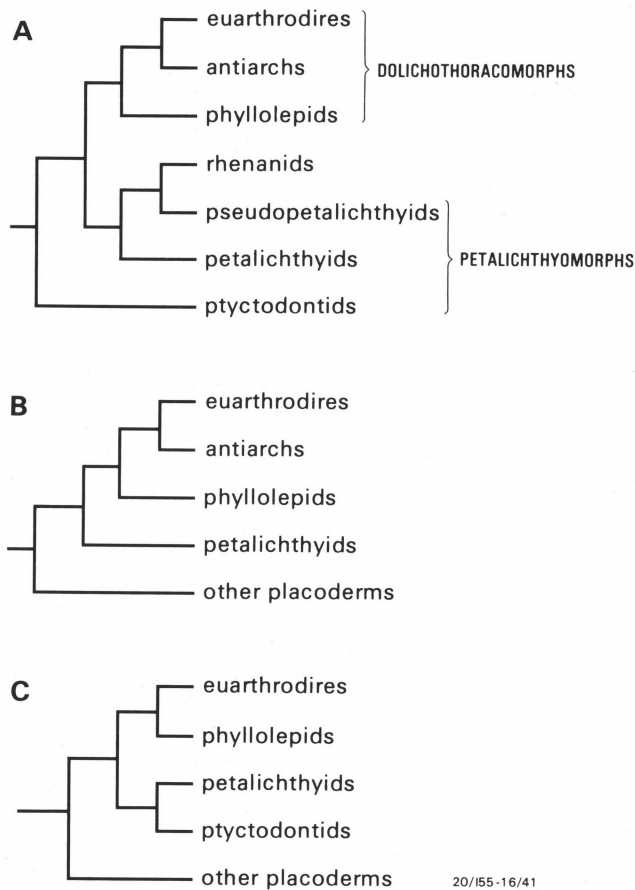
Figure 9. **Three competing hypotheses of petalichthyid relationships.** A, after Miles & Young (1977); B, after Denison (1978); C, after Goujet (in press). For discussion see text.

by Denison (1975; 1978, fig. 10). Under this scheme, petalichthyids are a sister group to dolichothoracomorphs (Fig. 9B), with which they share the presence of an anterior median ventral plate in the trunk-shield as a derived feature. A third viewpoint, proposed by Goujet (in press), unites petalichthyids and ptyctodontids as sister groups on the basis of sensory canal morphology, which is specially developed in both groups. Rather than being in open grooves on the dermal bones, the usual condition in placoderms, the sensory canals in petalichthyids and ptyctodontids are enclosed within the dermal bone, in tubes that open to the exterior through a series of pores. Other synapomorphies proposed by Goujet to support this relationship are the absence of the central sensory groove, the cruciform pattern of sensory canals on the median bone of the skull, the fragmentation of suborbital and postsuborbital plates, and the similar structure of the dermal neck joint in the two groups. Under this scheme (Fig. 9C), it is assumed that the enclosed pectoral fin in antiarchs and euarthrodires is independently acquired.

Each of these schemes has certain unparsimonious consequences, in that similar structures require independent evolution within the Placodermi: just which structures depends on the assumed primitive placoderm condition and on how certain poorly known structures are interpreted.

In the petalichthyids, one such aspect is the composition of the ventral wall of the trunk-shield. As previously discussed (Young, 1980, p.63), the trunk-shield of *Lunaspis*, the only form represented by preserved articulated specimens, has been variously interpreted. Denison (1978, p.20) followed the inter-

pretation of Gross (1961), that paired posterior ventrolateral and posterior ventral plates were present in *Lunaspis*, and suggested that the former might be homologous to the posterior ventrolaterals of euarthrodires, antiarchs, and phyllolepids, although the possibility that they were only analogues was not excluded. However, it is also possible (Young, 1980, p.63) that the suture assumed by Gross to separate the posterior ventrolateral and posterior ventral plates is only a transverse lineation in the ornament, resulting from the persistence from early ontogeny of a reversal in the overlap relations between the posterior ventrolaterals of each side. It is significant that a similar complex overlap between posterior ventrolaterals is also seen in euarthrodires, making it less likely that these plates in petalichthyids were independently acquired. As previously pointed out (Young, 1980, p. 63), the evidence of the petalichthyid trunk-shield is critical to a decision between the placoderm phylogenies of Denison (1975, 1978) and Miles & Young (1977). My current view is that, within the context of these alternative hypotheses, the evidence from *Lunaspis* indicates that the petalichthyomorph grouping proposed by Miles & Young (1977) was based on a symplesiomorphy (two pairs of paranuchals in the skull). I previously stated (Young, 1980) that if the existence of a petalichthyid posterior ventrolateral could be definitely established, there were two phylogenetic implications – either that any grouping based on two pairs of paranuchals as a shared derived feature would be paraphyletic, or that a ventral trunk-shield incorporating enlarged posterior ventrolaterals with extensive median contact was the primitive placoderm condition. But, both implications can, of course, be expressed alternatively in terms of independent development of these features in several placoderm groups. With respect to Goujet's scheme, however, (Fig. 9C), this argument does not apply, as, on other grounds, he regards the closely similar ventral trunk-shield of antiarchs and euarthrodires as being separately evolved. Goujet (in press) agrees that the posterior ventrolateral in petalichthyids is homologous to the corresponding plate in arthrodires and phyllolepids, but he suggests that the 'posterior ventral' is a separate dermal element covering the pelvic girdle, as in *Sigaspis* (Goujet, 1973). This leads to the conclusions that not only is the absence of a lateral lamina on the posterior ventrolateral in phyllolepids and petalichthyids a symplesiomorphy (Goujet, in press), but also that the independent development of this lamina in antiarchs and euarthrodires is an unparsimonious consequence of Goujet's scheme.

Regarding other plates in the petalichthyid trunk-shield, Goujet points out that the presence of an interolateral plate is doubtful, but there is good evidence for the existence of a posterior median ventral. Together with the anterior median ventral, the posterior median ventral may be regarded as synapomorphy uniting petalichthyids with arthrodires and phyllolepids (Goujet, in press, fig. 12), as also proposed by Denison. Thus, the main differences between Goujet's and Denison's proposals do not directly concern the petalichthyids, but rather the placement of other groups (antiarchs, ptyctodontids) as additions to a basic phylogeny involving three taxa (arthrodires, phyllolepids, petalichthyids), with phyllolepids and arthrodires as the more closely related pair.

There are, however, aspects of petalichthyid morphology that may be relevant in providing information on the primitive state for certain features of the placoderm skeleton. One such point, arising from the descriptions presented above, is the ventral pit on the median dorsal plate of *Lunaspis*, a structure not previously known in petalichthyids. As previously noted, the occurrence of such a pit in several placoderm groups (petalichthyids, palaeacanthaspids, ptyctodontids, antiarchs) suggests that this is a primitive placoderm feature. In most antiarchs, the pit lies in front of the transverse thickening on the

posterior median dorsal plate, whereas, in the specimen described above, it is situated behind the thickening. It is of some interest, therefore, that in an antiarch of uncertain affinity from south China (*Xichonolepis*; see Zhang, 1980), the pit is also situated behind the thickening. Except for the new evidence presented above, this condition would readily be interpreted as derived within the Antiarcha.

Finally, comment should be made on the wide distribution of *Lunaspis*, which is only the second reasonably well-known placoderm in the Taemas – Wee Jasper fauna that can be referred to a European genus, the other being the closely related petalichthyid *Wijdeaspis*. All other placoderms so far described from this fauna have been assigned to endemic genera. The petalichthyids were exclusively marine, as far as is known (Denison, 1978, p.17), and this may be the reason for the wide distribution of *Lunaspis*, which has recently also been described from China (Liu, 1981).

Acknowledgements

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