

# ASTRASPIS THE ANATOMY AND HISTOLOGY OF AN ORDOVICIAN FISH

by IVAN J. SANSOM, M. PAUL SMITH, MOYA M. SMITH  
and PETER TURNER

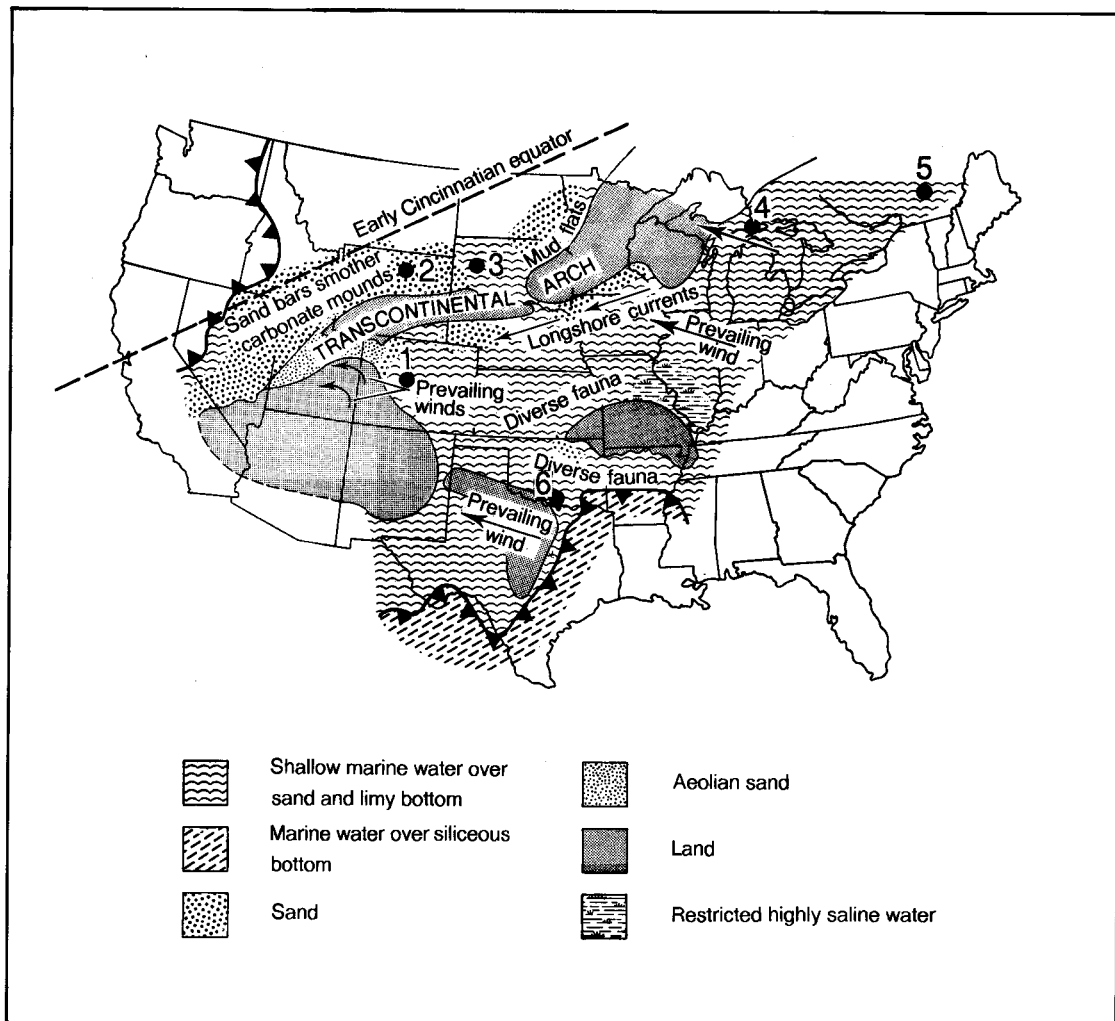
**ABSTRACT.** A newly discovered specimen of *Astraspis desiderata* Walcott from the mid Ordovician Harding Sandstone Formation of Colorado, USA, is described and represents the third, and most complete, articulated specimen of the taxon recorded to date. *Astraspis* is a pteraspidomorph agnathan with a dorsal headshield formed from polygonal tesserae, and a ventral shield composed of more irregular tesserae. The tesserae are surmounted by star-shaped or smooth, round or ovate tubercles. Well-developed orbits lie directly anterior to a series of eight uncovered, branchial openings which are arranged in a postero-ventrally slanting line. Sensory grooves flank a pineal region on the dorsal headshield. The tail is made up of large rhomboid scales, but the structure of the tail termination remains unknown. Histologically, the hard tissues of *A. desiderata* comprise a basal component of spongy aspidin with large trabeculae and large, irregular soft tissue spaces. Individual tubercles overlie the aspidin and are composed of dentine with an enameloid cap separated by a junctional zone. The dentine is characteristic of *Astraspis* and contains a high density of parallel, fine calibre tapering tubules. *Pycnaspis splendens* Ørvig is considered to be a junior synonym of *Astraspis desiderata* and the genus is monotypic. *Astraspis* has few derived characters in common with other agnathan taxa and is here placed within the monotypic Astraspida, as the sister group of Arandaspida + Heterostraci.

ARTICULATED agnathan specimens from pre-Silurian rocks are extremely rare, with only three localities and five genera recorded world-wide: *Astraspis desiderata* Walcott and *Eriptychius americanus* Walcott from the Harding Sandstone Formation of Colorado, USA (Denison 1967; Lehtola 1983; Elliott 1987); *Arandaspis prionotolepis* Ritchie and Gilbert-Tomlinson and *Porophoraspis crenulata* Ritchie and Gilbert-Tomlinson from the Stairway Sandstone (lower Llanvirn *sensu* Fortey *et al.* 1995) of Northern Territories, Australia (Ritchie and Gilbert-Tomlinson 1977); and *Sacabambaspis janvieri* Gagnier, Blicek and Rodrigo from the Anzaldo Formation (upper Llanvirn *sensu* Fortey *et al.* 1995; Albanesi *et al.* 1995) of Bolivia (Gagnier *et al.* 1986; Gagnier 1993a, 1993b). Given this scarcity, and the consequent paucity of data concerning the morphological characters of these Ordovician fish, any new data are critical for phylogenetic analyses (Janvier 1996a). Most descriptions of *Astraspis* have been based on disarticulated fragments and only two articulated specimens have been recorded hitherto: a headshield, mentioned by Walcott (1892), was figured by Bryant (1936); and a more complete specimen described by Elliott (1987). We describe here an additional articulated specimen of *Astraspis desiderata*, again from the type locality of the species, which constitutes the most complete specimen recovered to date.

The type locality for *A. desiderata* is the Harding Quarry, west of Cañon City, Fremont County, Colorado, USA, but the genus has also been recorded from a number of additional localities along the Ordovician Transcontinental Arch (Text-fig. 1; Ross 1976) in the Harding Sandstone Formation and its lateral equivalents. Accepted records of the genus in addition to the main Harding outcrop are as follows.

1. Bighorn Mountains, west of Buffalo, north-central Wyoming. Although yet to be formally named (Ross *et al.* 1982 denoted the unit as 'Harding Sandstone equivalent'), a microvertebrate fauna comprising *Astraspis* and *Eriptychius* has been recovered (Darton 1907; see comments in Elliott *et al.* 1991).

2. Darton (1909) described specimens of *Astraspis* and *Eriptychius* from the Icebox Shale Member,



TEXT-FIG. 1. Palaeogeographical map of the USA during the mid Ordovician, showing the distribution of known Ordovician vertebrate localities (after Ross 1976, text-fig. 9). 1, Harding Sandstone of Cañon City, Colorado; 2, Bighorn Mountains, north-central Wyoming; 3, Black Hills, South Dakota; 4, St Joseph Island, Ontario; 5, Ouareau River, Quebec; 6, Arbuckle Mountains, Oklahoma.

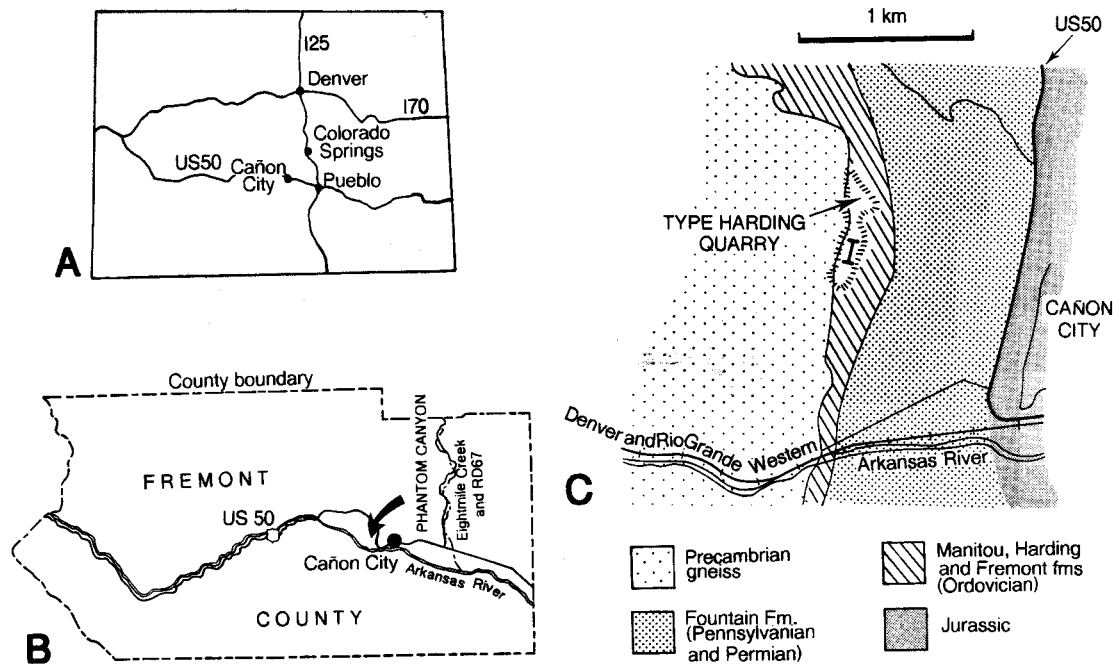
Whitewood Formation of the Black Hills, South Dakota. Boucot and Janis (1983) also mentioned that the Harding Sandstone fauna, consisting primarily of *Astraspis* and *Eriptychius*, has been recorded from Montana and the South Dakota subsurface.

3. Black River Group, St Joseph Island, Ontario, Canada. Darby (1982) recorded a microvertebrate fauna which includes *Astraspis*.

4. Eliuk (1973) has described specimens attributable to *Astraspis* from the Pamela beds, Black River Group, exposed along the Ouareau River, Quebec, Canada.

5. Ossian and Halseth (1976) reported specimens of *Eriptychius* from the Arbuckle Mountains of Oklahoma. Further collecting may yield specimens of *Astraspis*, since the genus is known from all North American localities from which *Eriptychius* has been recovered.

*Astraspis* has not yet been recorded outside of North America.



TEXT-FIG. 2. A, map of Colorado; B, map of Fremont County showing the location of the Harding Quarry (arrow); C, geological sketch map of the area around the type locality of the Harding Sandstone (adapted from Taylor *et al.* 1975).

*Institutional abbreviations.* BU, Lapworth Museum, University of Birmingham, UK; PF, Field Museum of Natural History, Chicago, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

#### LOCALITY AND STRATIGRAPHY

The Harding Sandstone Formation was first described by Walcott (1892) based on exposures in the Harding Quarry, Cañon City, Colorado (Text-fig. 2). Most subsequent work has concentrated on this area, although some studies (Sweet 1954, 1955; Fischer 1978; Graffin 1992) have encompassed localities elsewhere in the Fremont and Pueblo counties of south-central Colorado. Spjeldnaes (1979) provided a description of the lithologies encountered at the type locality, and a revised sedimentological interpretation of the Harding Sandstone is being prepared by us; preliminary results suggest that the unit in its type area consists of up to six parasequences showing inner shelf to shoreface transitions (Turner *et al.* 1994). The new specimen was recovered from a bedding plane which we interpret as a strandline.

Stratigraphically, the age of the Harding Sandstone is constrained by the locally abundant conodont fauna, which includes *Oulodus serratus* (Stauffer), *Chirognathus duodactylus* Branson and Mehl, *Erismodus quadridactylus* (Stauffer) and *Stereoconus gracilis* Branson and Mehl, suggesting an early Franklinian age (*Phragmodus undatus* Chronozone of Sweet 1984) within the middle Mohawkian—equivalent to the lower middle Caradoc in British terms. The Canadian localities appear to be slightly older than the main Harding outcrop.

The three articulated specimens, two of *Astraspis* and one of *Eriptychius*, previously recorded from the Harding Sandstone came from the type Harding Quarry (Bryant 1936; Lehtola 1983) and the Sturbaum quarries slightly to the north (Denison 1967). The new articulated specimen of *Astraspis desiderata* was found in a small quarry some 150 m due north of the type Harding Quarry

on a well-exposed bedding plane which is thought to be the same surface which forms the westerly face of the type quarry.

#### SYSTEMATIC PALAEOLOGY

Class PTERASPIDOMORPHI Goodrich, 1909

Subclass ASTRASPIDA Berg, 1940

Order ASTRASPIDIFORMES Berg, 1940

Family ASTRASPIDIDAE Eastman, 1917

*Remarks.* Halstead (1993) included both *Astraspis* and *Tesakoviaspis concentrica* Karatajüte-Talimaa, 1978 within the family Astraspididae. Blicek and Janvier (1993) also referred to the latter taxon, quoting the same source, but examination of Karatajüte-Talimaa (1978) reveals that the species was figured but not described in that publication. *Tesakoviaspis concentrica* is a *nomen nudum* and the species figured by Karatajüte-Talimaa (1978, pl. 32, figs 3–7) belongs to a new group of Ordovician fishes with cyclomorial growth, and not to the Astraspida (Karatajüte-Talimaa and Predtechenskyj 1995, p. 55). As currently understood, Astraspida is monotypic and confined to the middle and upper Ordovician of North America.

#### Genus ASTRASPIS Walcott, 1892

*Type species.* *Astraspis desiderata* Walcott, 1892.

*Diagnosis.* As for the type species.

*Remarks.* Ørvig (1958) erected *Pycnaspis splendens* for material described from the Bighorn Mountains, Wyoming. He considered the species to be closely related to *Astraspis* but distinguished by supposed histological differences, which included the presence in *Pycnaspis* of the layer later described as pallial mesodentine (Ørvig 1989). Denison (1967) considered the two forms to be representatives of the same genus, but differentiated at species level by both the size and shape of the tubercles and the ornament: *Astraspis splendens* was characterized by larger mushroom-shaped tubercles and *Astraspis desiderata* restricted to plates bearing small, stellate ornament. In our extensive collections of several thousand isolated specimens from localities in Colorado and Wyoming, there are no histological or morphological grounds for considering *Pycnaspis* to be a distinct genus. Furthermore, the collections from the Harding Sandstone and the Bighorn Mountains reveal that the variations in tubercle morphology and size form a continuum. Given the absence of morphological or histological differences, we therefore consider *Pycnaspis splendens* Ørvig to be a junior synonym of *Astraspis desiderata* Walcott.

#### *Astraspis desiderata* Walcott, 1892

Plates 1–4; Text-figures 3–8

- \*v1892 *Astraspis desiderata* Walcott, p. 166, pl. 3, figs 6–14; pl. 4, figs 1–4; pl. 5, fig. 3.
- v1917 *Astraspis desiderata* Walcott; Eastman, p. 238, pl. 12, figs 5–6.
- v1936 *Astraspis desiderata* Walcott; Bryant, p. 416, pls 1–7.
- 1951 *Astraspis desiderata* Walcott; Ørvig, fig. 22.
- 1958 *Pycnaspis splendens* Ørvig, p. 7, pl. 1, figs 1–2.

#### EXPLANATION OF PLATE 1

*Astraspis desiderata* Walcott, 1892; BU 2472; 150 m north of the Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc; articulated specimen; × 1.5.



FIGURE 1. For caption see opposite.

SANSOM *et al.*, *Astraspis*



TEXT-FIG. 3. For caption see opposite.

- v1964 *Astraspis desiderata* Walcott; Stensiö, p. 177, fig. 32.  
v1967 *Astraspis desiderata* Walcott; Denison, p. 164, figs 14–15, 20c, e.  
v1967 *Astraspis splendens* (Ørvig); Denison, p. 168, figs 16–19, 20A–B, D, F, 21–25.  
1969 *Astraspis desiderata* Walcott; Halstead, fig. 9.  
1973 *Astraspis desiderata* Walcott; Lehtola, p. 27, pls 1–2.  
1973 ostracoderm tubercles, Eliuk, fig. 2.  
non1975 *Astraspis?*; Nitecki *et al.*, fig. 7.  
1976 ostracoderm tubercles, Winder, pl. 2, fig. 10.  
1978 *Astraspis desiderata* Walcott; Fischer, pl. 9, figs b–c.  
v non1981 ?*Astraspis* sp.; Ethington and Clark, p. 120, pl. 14, fig. 6.  
1982 *Astraspis*; Darby, figs 1–3.  
v1983 *Astraspis desiderata* Walcott; Lehtola, p. 606, fig. 1.  
v1987 *Astraspis desiderata*; Elliott, figs 1–2.  
v1987 *Astraspis desiderata*; Halstead, p. 348, fig. 4.  
v1987 *Astraspis*; Carroll, fig. 3–4.  
v1987 *Astraspis*; Carroll, fig. 3–5.  
1989 *Pycnaspis splendens*; Ørvig, p. 438, figs 11–18.  
1990 *Astrapididae* [sic]; Smith and Hall, p. 298, figs D–E.  
v1991 *Astraspis desiderata*; Elliott, Blicek and Gagnier, fig. 2A.  
1991 *Astraspis*; Elliott *et al.*, fig. 3A.  
v1992 *Astraspis desiderata*; Blicek, fig. 2A–B.  
v1992 *Pycnaspis splendens*; Blicek, fig. 2C.

*Type material.* Thirteen specimens from the Harding Quarry, Cañon City, Colorado, were illustrated in support of the original description of the species (Walcott 1892, pl. 3, figs 6–14; pl. 4, figs 1–4). All were fragmentary and no types were designated. A description of a newly discovered articulated dorsal headshield was made in a postscript footnote (Walcott 1892, p. 167) but it was not figured. This latter specimen was subsequently illustrated by Eastman (1917, pl. 12, figs 5–6) and Bryant (1936, pl. 1). Eastman (1917) noted that the fragmentary material was catalogued under USNM 2351 and that the articulated shield was USNM 8121. Although the dorsal headshield was not figured by Walcott (1892) it is clear that it is a member of the type series, in accordance with ICZN Article 72b, and USNM 8121 is here designated as the lectotype of *Astraspis desiderata*. The fragmentary tesserae and tubercles figured by Walcott (1892, pls 3–4) are designated as paralectotypes.

*Locality and horizon.* All articulated material comes from the vicinity of the Harding Quarry, Cañon City, Fremont County, Colorado, USA, the type locality for *A. desiderata*. Isolated tesserae have also been recovered from the Bighorn Mountains, Wyoming. Stratigraphically, the Harding Sandstone is of *Phragmodus undatus* Chronozone (middle Mohawkian) age, equivalent to the lower middle Caradoc in British terms.

*Diagnosis.* Pteraspidomorph agnathan with multiple branchial openings; dorsal and ventral shields composed of fused tesserae, polygonal in outline on dorsal shield and more irregular on ventral shield. Tail composed of large rhomboid scales. Star-shaped and smooth, circular to ovate tubercular ornament on dermal armour, which is formed from enameloid, fine calibre dentine and aspidin.

*Description.* The anterior region of BU 2472 has undergone dorso-ventral collapse, but the compression of the tail has a lateral component (Pl. 1; Text-fig. 3). The headshield has a preserved length of 73 mm and is around 50 mm wide at its posterior margin, tapering anteriorly with markedly straight sides to 35 mm. The preserved tail is 45 mm long and shows a degree of lateral torsion, perhaps resulting from *post mortem* desiccation of the notochord. The specimen has lost an unknown amount of material from the snout region (we

TEXT-FIG. 3. *Astraspis desiderata* Walcott, 1892; BU 2472; 150 m to the north of the Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc; camera lucida drawing; specimen is 118 mm in total preserved length. Stippled areas on the unornamented inner surface of the ventral shield represent possible branchial pouches. Abbreviations: co, circumorbital tesserae; lr, lateral ridge plates; mlr, medio-lateral ridge; mr, median ridge.

estimate this to be of minor extent, but it does include the oral area) and the posterior of the tail. The total preserved length is 118 mm. The anterior of the specimen largely comprises the interior of the ventral surface, although the exterior of the dorsal shield is seen along the flanks and posterior of the head (Pl. 2, fig. 1). The external surface of the tail is displayed (Pl. 2, fig. 2).

The dimensions of the headshield are extremely close to those of USNM 8121 (Text-fig. 4; Bryant 1936) which has a preserved length of 69 mm and a width along the posterior margin of 51 mm. Five sharp, prominent ridges are present on USNM 8121, with longer median and lateral ridges running anteriorly from the posterior margin for approximately 40 mm. Between the lateral ridges and the median ridge are two shorter structures, 25 mm long, which converge on the anterior end of the median ridge, but do not meet it. BU 2472 possesses only the prominent median ridge flanked by the shorter ridges: only portions of the lateral ridges seen in USNM 8121 are preserved (Pl. 1; Text-fig. 3). Sutured polygonal plates with prominent central tubercles constitute the dorsal headshield of USNM 8121, and, where present, the dorsal tesseræ of BU 2472 have the same appearance.

USNM 8121 shows two pairs of tesseræ which have a groove running between two rows of tubercles. These linear features lie to the anterior of, and converge on, the median ridge of the dorsal headshield but do not intersect it (Text-fig. 4). They probably represent the grooves for sensory canals. We see no evidence for the additional sensory canals labelled by Stensiö (1964, fig. 32). A prominent sub-circular cluster of tesseræ lies on the mid-line of USNM 8121 to the anterior of the median ridge and is suggestive of the presence of a pineal region (Stensiö 1964). One feature of the sensory systems, and indeed the dorsal headshield as a whole, is the lack of precise symmetry developed in the ornament and tessellation (Text-fig. 4).

The ventral headshield, seen in internal aspect in BU 2472, is formed of more irregular tesseræ than the polygonal plates of the dorsal headshield. It also seems that PF 5733 is part of a ventral headshield preserved in internal aspect (*contra* Elliott 1987), since the irregular pattern of tesseræ is similar to the ventral shield of BU 2472 (Elliott, pers. comm.).

A small arcuate plate, probably a circumorbital tesseræ, is preserved in cross section towards the anterior of the headshield in BU 2472 (Pl. 1; Pl. 2, fig. 1; Text-fig. 3). Elliott (1987) also interpreted the presence of an orbital region in PF 5733 (Text-fig. 5).

Elliott (1987) identified eight branchial openings on PF 5733, extending from just posterior of the interpreted orbit down the flank of the headshield (here interpreted as the ventral shield) to the postero-lateral edge. The openings are uncovered and delineated by branchial plates attached to elongate rectangular plates on their longest, ventral, margins. Each plate is attached laterally by the shortest margins and the dorsal edge forms a point, producing a sub-triangular opening between each pair of the plates (Elliott, 1987; Text-fig. 5). Plates forming the dorsal margins of the branchial openings are not seen on PF 5733 but are preserved end-on, down the left side of BU 2472 (Pl. 2, fig. 1; Text-fig. 3). These extend posteriorly from the circumorbital plate, and delineate a series of roughly circular structures approximately 5 mm in diameter, representing the upper parts of the branchial openings. In this way, a single plate forms the dorsal margin of each opening whereas the ventral margin comprises two plates.

Elliott (1987), Elliott *et al.* (1991), Gagnier (1995) and Janvier (1996a, 1996b) all reconstructed *Astraspis* with horizontally arranged branchial openings. However, PF 5733 shows a clear sigmoidal curvature to the branchial plates (Elliott 1987; Text-fig. 5), and the branchial openings in BU 2472 have a slight angular relationship to the lateral margin of the dorsal headshield. In addition, plates of the ventral headshield are seen lateral to those of the branchial area, demonstrating that the branchial plates were not attached to the lateral ridges of the dorsal headshield. Instead they were arranged to form a postero-ventrally slanting line along the side of the animal.

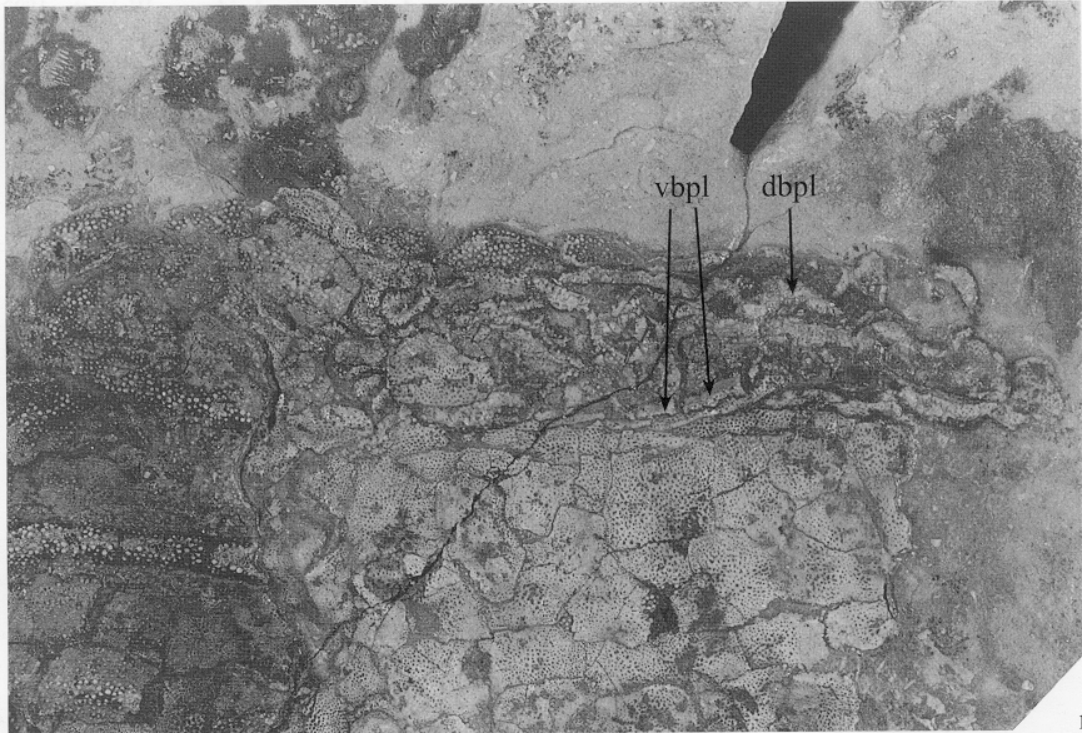
The inner surfaces of the ventral shield tesseræ are smooth with pores opening into the basal aspidin. Weakly defined elliptical depressions occur to the right of the midline (Text-fig. 6) and their location, shape and size are suggestive of branchial pouches. To the left of the midline, but slightly offset from the putative

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#### EXPLANATION OF PLATE 2

Figs 1–2. *Astraspis desiderata* Walcott, 1892; BU 2472; 150 m north of the Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc. 1, detail of left branchial region, showing the orbit and branchial plates. To the left the median ridge of the dorsal headshield is clearly seen; the paler area to the right represents the internal surface of the ventral headshield (see Text-figs 3, 6, for labelling). 2, detail of tail. Abbreviations: dbpl, dorsal branchial plate; vbpl, ventral branchial plate. Both  $\times 2$ .



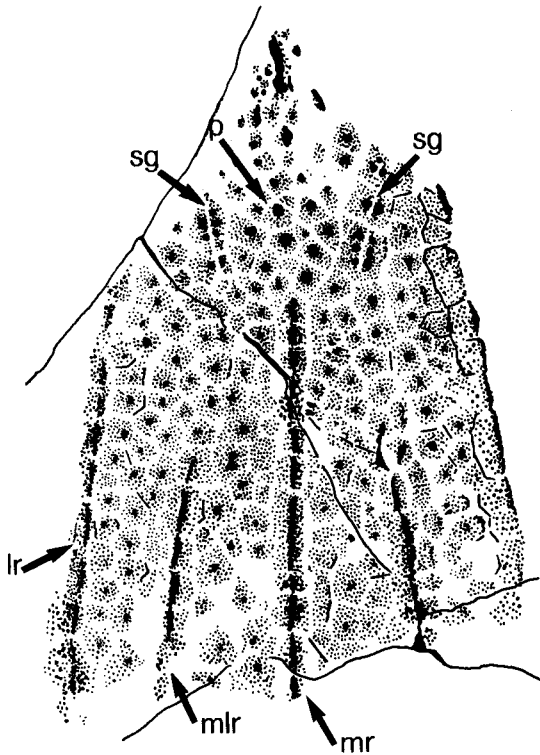


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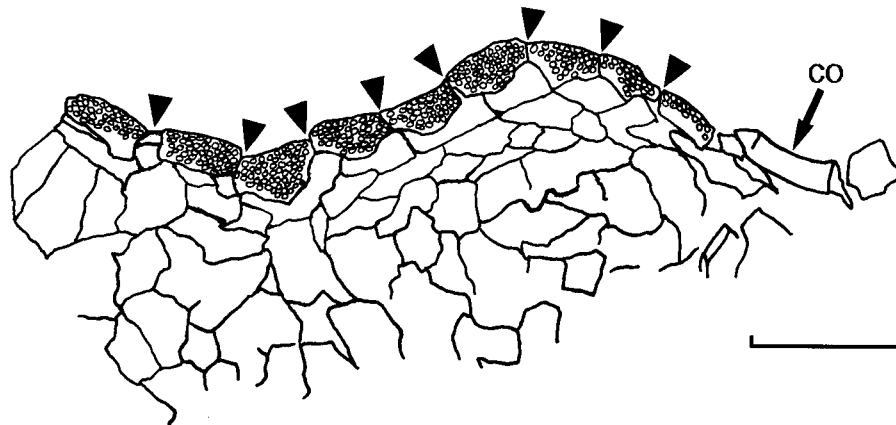


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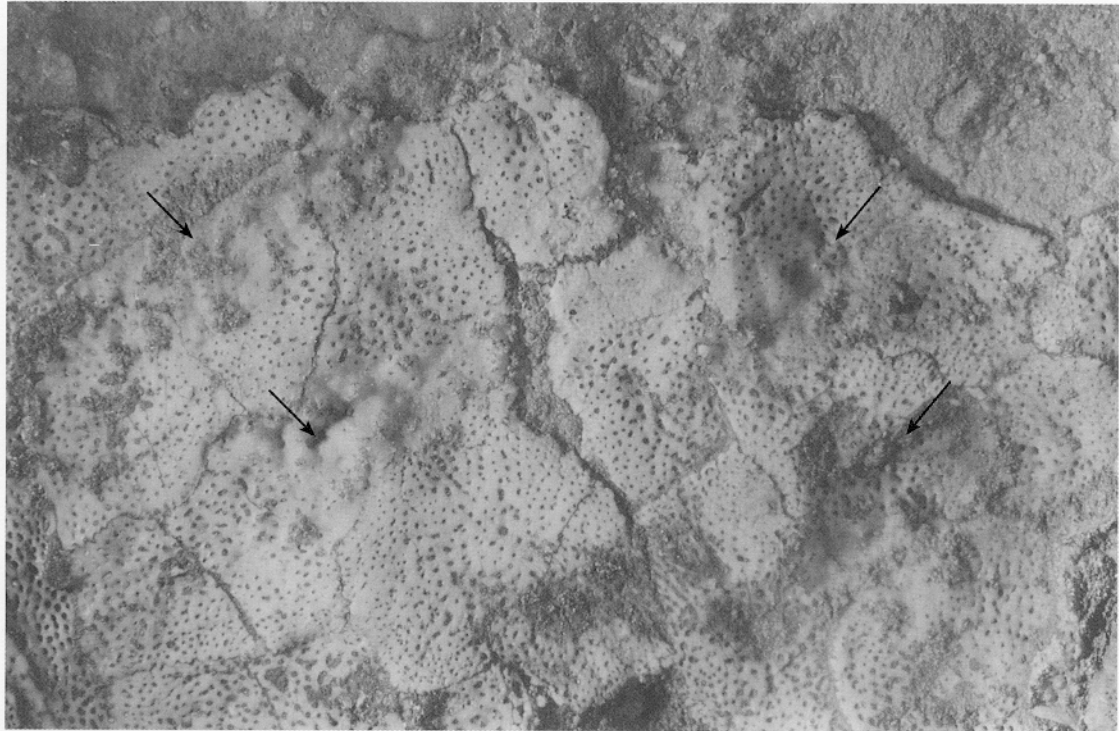
TEXT-FIG. 4. *Astraspis desiderata* Walcott, 1892; USNM 8121; Harding Sandstone Formation; Caradoc. Specimen is 69 mm in total preserved length. Abbreviations in addition to those used on Text-figure 3: p, pineal region; sg, sensory groove.



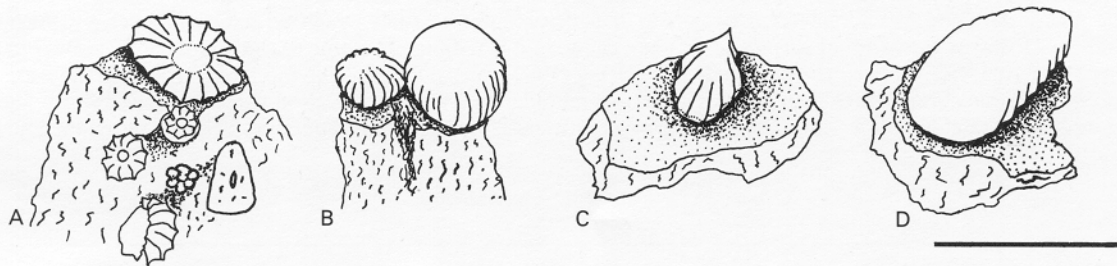
TEXT-FIG. 5. *Astraspis desiderata* Walcott, 1892; PF 5733; Harding Sandstone Formation; Caradoc. Ventral headshield seen in predominantly internal aspect, showing the position of the orbit and eight branchial openings (arrowheads) identified by Elliott (1987, fig. 2). Ornamented areas are the external surfaces of the ventral branchial plates. Scale bar represents 1 mm.

branchial pouches are textured, pitted areas which lack pores through the basal aspidin. They may represent either the sinistral branchial pouches, in different preservational aspect to those on the opposite side, or impressions of a vascularized network associated with the pouches.

The tail of BU 2472 is incomplete, but the preserved portion suggests that *Astraspis* possessed a broad tail, at least 95 mm long. Elliott (1987), basing his observations on PF 5733, reconstructed *Astraspis* with a stubby caudal fin and suggested that the termination was symmetrical in form, in contrast to the reverse heterocercal



TEXT-FIG. 6. *Astraspis desiderata* Walcott, 1892; BU 2472; Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc. Detail of anterior part of ventral shield showing shallow depressions, on the right (arrowed), interpreted as branchial pouches. The textured areas on the left (arrowed) lack pores and may represent either branchial pouches or impressions of a vascular network;  $\times 6$ .



TEXT-FIG. 7. *Astraspis desiderata* Walcott, 1892; Harding Quarry, Cañon City, Colorado, USA; Harding Sandstone Formation; Caradoc. *Camera lucida* drawings illustrating variations of scale morphology found in sieved samples; only morphologies A and B have been identified on the articulated specimen BU 2472. A, BU 2566; B, BU 2567; C, BU 2568; D, BU 2569. Scale bar represents 1 mm.

type interpreted by Lehtola (1983). It is apparent from a latex peel of PF 5733 that the tail on this specimen is also incomplete, and that the distal tail structure of *Astraspis* remains to be elucidated. The individual scales of the tail are variable in shape, with lateral scales elongated in a dorso-ventral sense and the dorsal scales more polygonal in form (Pl. 2, fig. 2). The dorso-median scales are slightly arched on BU 2472, forming a weakly developed continuation of the median ridge of the dorsal headshield.

A number of different ornaments has been recognized in discrete collections of *Astraspis* dermal plates (Text-fig. 7). However, only two tubercle morphologies are evident on the dorsal surface of BU 2472. Both are

circular in outline; one has prominent ridges radiating from a central point, whereas the other has a smooth rounded surface. The latter form appears to be dominant on the tail.

The absence of other scale morphologies observed within collections of isolated material can be explained either by intraspecific variation within the *Astraspis* population or by the presence of additional morphologies on the ventral surface of the animal, the exterior of which is not seen in any of the articulated specimens. Elliott *et al.* (1991; fig. 3A) illustrated a small rhombic scale of *Astraspis* bearing four tubercles from the Swift Current Formation, Ontario, Canada (see Darby 1982 for locality details), but we have yet to recover any specimens with such a regular shape from our extensive isolated collections from the Harding Sandstone.

*Histology.* The hard tissues of *Astraspis* have been described by numerous authors and a plethora of terms has been applied (cf. Walcott 1892; Bryant 1936; Ørvig 1958, 1967, 1989; Denison 1967; Halstead 1969, 1987; Smith and Hall 1990; Smith *et al.* 1996). Given recent developments in techniques for studying vertebrate hard tissues and a better understanding of the developmental framework, it is appropriate to present a revised description of the tissues.

The dermal armour of *Astraspis* comprises three distinct tissue types. The basal component of the tesserae is typified by a spongy appearance with large trabeculae of aspidin (acellular bone) and open, irregular, soft tissue spaces. In compact areas within this region, the spaces become constricted by the deposition of additional concentric layers of aspidin, forming aspidones. The undersurfaces of tesserae are generally penetrated by pores of up to 0.25 mm diameter (Text-fig. 6).

The tubercles, overlying the spongy or compact basal plate of aspidin, are characterized by two tissues, enameloid and dentine, with a junctional zone between them (Pl. 3, figs 2, 4; Pl. 4, figs 1–2, 5). A substantial part of the tubercle is composed of regular, tubular dentine. This contains extremely fine calibre tapering tubules, each with a maximum diameter of 0.5  $\mu\text{m}$  at their pulpal end (Pl. 3, fig. 4), and generally orientated parallel to each other with occasional cross branches (Pl. 4, figs 3–4). The pulp cavities, large in the new tubercles (Pl. 3, fig. 1), were gradually infilled by dentine during incremental growth, the pattern of which is evident from incremental lines in the dentine (Pl. 4, figs 1–2), some of which are markedly calcospheritic (Pl. 3, fig. 3). The narrow diameter and relatively high density of tubules in the dentine is characteristic of *Astraspis*.

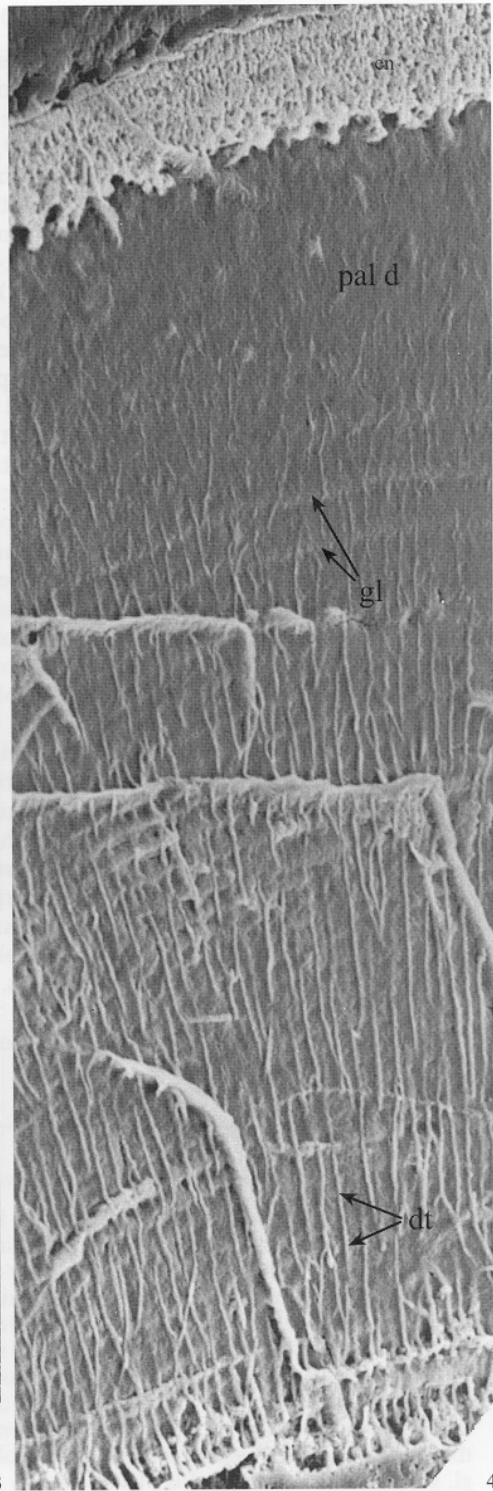
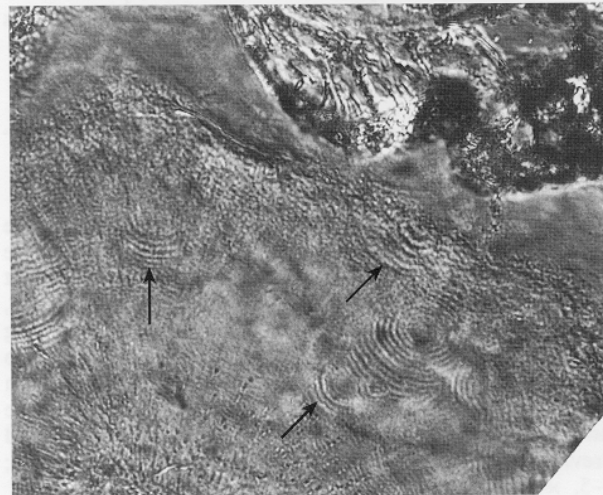
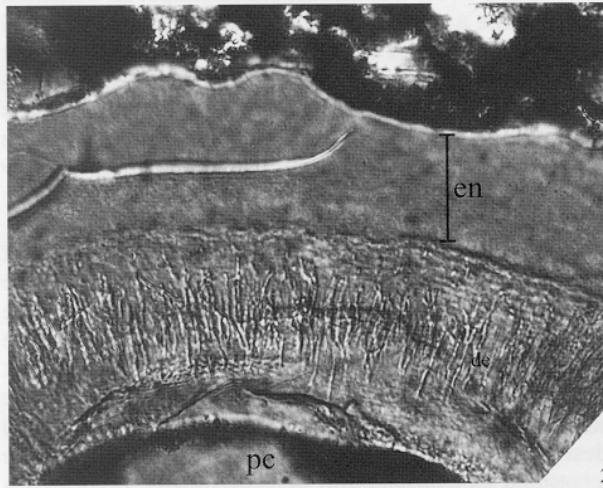
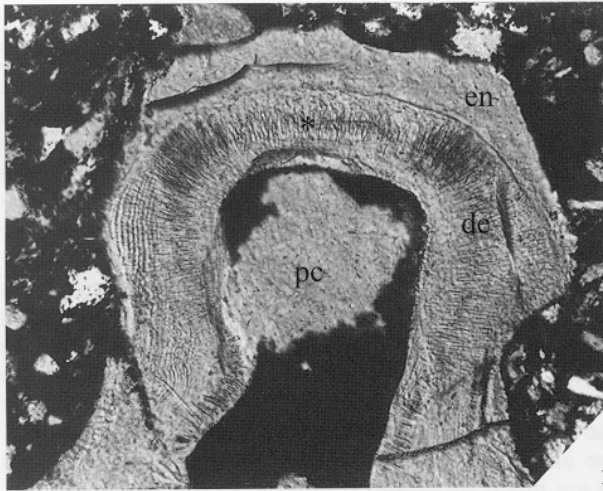
The predominant tissue of the tubercles has been variously described as orthodentine (Denison 1967), acellular bone with fibre bundles (aspidin, Ørvig 1989), or as a unique tissue, astraspidin, sharing characters of both bone and dentine (Halstead 1987). However, the identification of distinct, occasionally interconnected, tubules and a calcospheritic pattern of biomineralization supports the interpretation of this tissue as dentine (Smith and Hall 1990).

A glassy, often sculpted, cap of enameloid surmounts the dentine of the tubercles, sharply truncating incremental lines in the underlying dentine (Pl. 3, figs 1–3; Pl. 4, figs 1–2). The basal region of the cap tissue, the junctional zone, is characterized by a row of wide ascending canals which terminate in finer and finer branches towards the external surface of this cap enameloid (Pl. 4, fig. 2). Some of the finer tubules appear to be continuous with those in the dentine below. Ørvig (1989) referred to this junctional layer, where the wide ascending canals branch into finer tubules, as pallial mesodentine, an interpretation with which we disagree as there is no distinct junction within the capping tissue; instead, there is a sharp boundary between the enameloid and the dentine.

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#### EXPLANATION OF PLATE 3

Figs 1–4. *Astraspis desiderata* Walcott, 1892. 1–3, Harding Quarry, Canon City, Colorado, USA; Harding Sandstone Formation; Caradoc. 1–2, BU 2570. 1, vertical section through growing stellate tubercles with a large pulp cavity and shallow depth of dentine with a high density of parallel tubules;  $\times 189$ . 2, higher magnification of asterisked area in fig. 1;  $\times 480$ . 3, BU 2571; pallial dentine has closely spaced incremental lines of Von Ebner which are scalloped in many places where the calcification front has the characteristic calcospheritic pattern (arrows);  $\times 480$ . 4, BU2269; Bighorn Mountains, Wyoming, USA; 'Harding Sandstone equivalent'; Caradoc; SEM of an etched (1N HCl for 2 mins), polished tubercle; the dentine tubules are relative wide where they open at the pulp surface and narrow to an extremely fine diameter in the pallial dentine; the enameloid is more etch-resistant than the dentine, indicating a more highly mineralized tissue;  $\times 1080$ . Abbreviations: de, dentine; dt, dentine tubules; en, enamel; pal d, pallial dentine; pc, pulp cavity.



SANSOM *et al.*, *Astraspis*

## CLASSIFICATION OF ORDOVICIAN FISH

Morphological data on Ordovician fish are scarce. Of the five taxa known from articulated remains, only three are sufficiently well preserved to permit reliable reconstructions: *Arandaspis* from the Stairway Sandstone of Australia (Ritchie and Gilbert-Tomlinson 1977), *Sacabambaspis* from Bolivia (Gagnier *et al.* 1986; Gagnier 1989, 1993a, 1993b) and *Astraspis* (Text-fig. 8). A partially articulated fragment of *Eriptychius* from the Harding Sandstone (PF 1795) represents the rostral part of a headshield with subaponevrotic vessels (Denison 1967; Janvier 1996b), but the morphology of the remainder of the body remains unknown. Articulated fragments of *Porophorapsis* were also described by Ritchie and Gilbert-Tomlinson (1977).

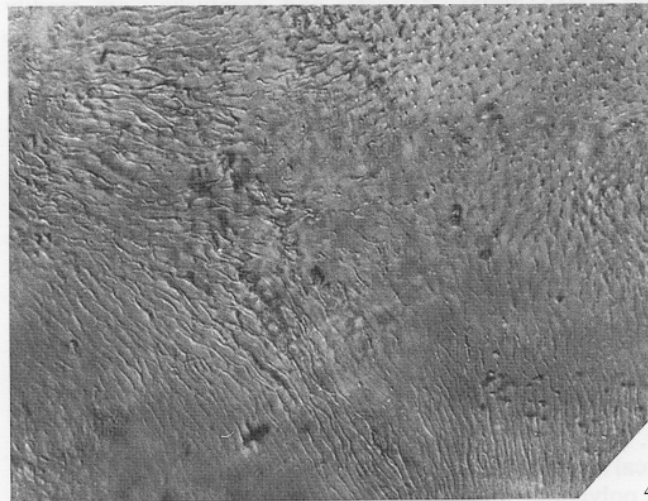
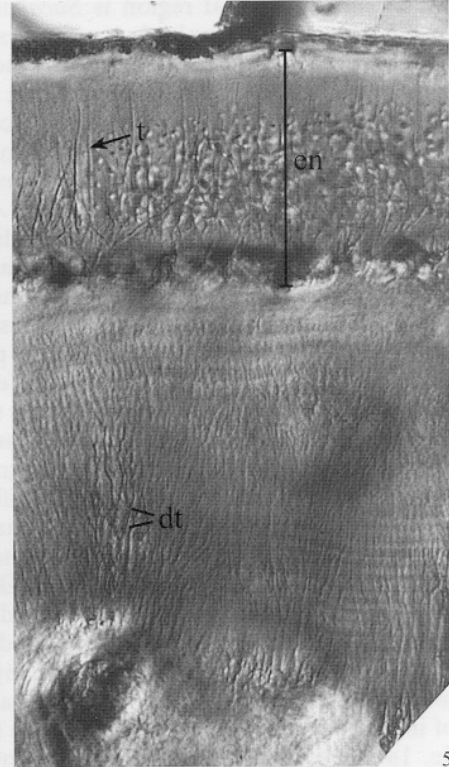
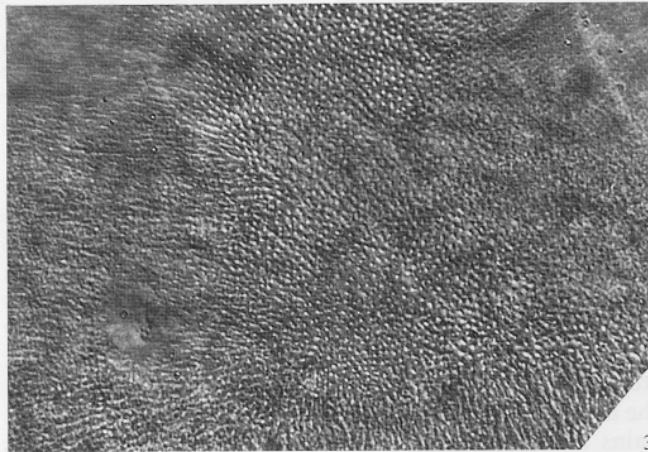
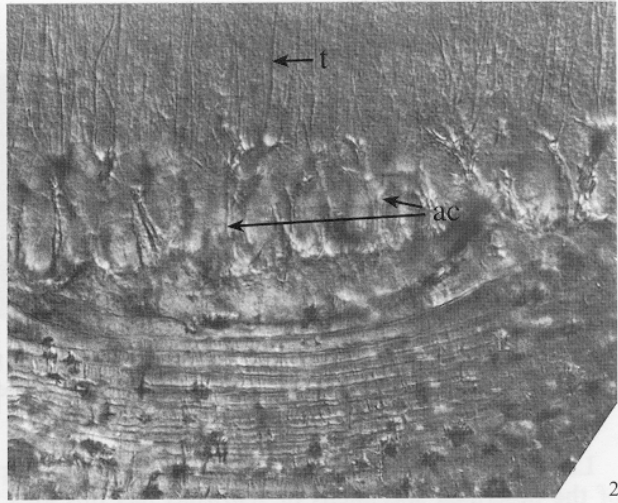
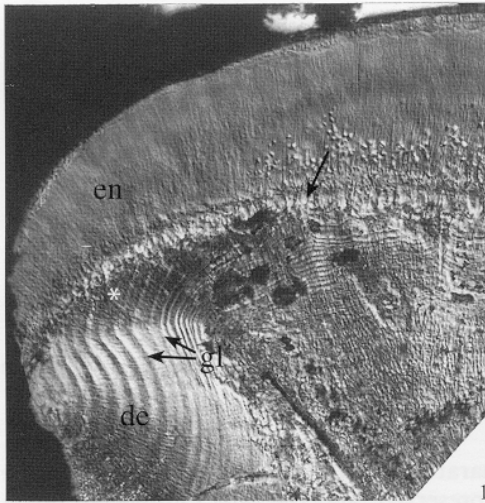
Blieck *et al.* (1991), Elliott *et al.* (1991) and Gagnier (1995) discussed possible relationships between described Ordovician fish and proposed that *Sacabambaspis* and *Arandaspis* are sister taxa within the family Arandaspididae of Ritchie and Gilbert-Tomlinson (1977). They are united by the presence of slanted and closed branchial plates, fused plates forming a headshield with double pineal-parapineal openings, multiple paired grooves for sensory canals on the headshield, and very narrow, elongate, serrated scales covering the trunk and tail.

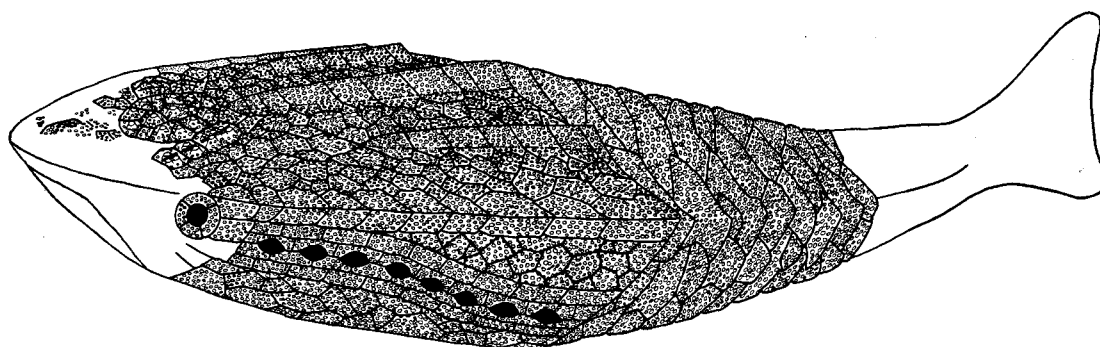
*Astraspis* is readily distinguished from the arandaspidids by its possession of eight large gill openings with no cover, and tail scales which are much wider and rhomboid in shape. In addition, *Astraspis* possessed a single pineal region located to the anterior of the median ridge of the dorsal headshield, rather than the paired pineal-parapineal openings of the arandaspidids. There is evidence for only a single pair of sensory canals on the dorsal surface of the headshield on USNM 8121 (Text-fig. 4), in contrast to the statement by Blieck *et al.* (1991, p. 14) that '... the canal system is borne in surface grooves it consists of *two pairs* of longitudinal canals together with lateral commissures in a pattern that is very heterostracan in outline' [our italics]. Although a single pair of sensory canals does appear on the reconstruction of Blieck *et al.*, they are not in a position that could be derived from USNM 8121.

The structure of the *Astraspis* tail has yet to be determined with any degree of certainty. Elliott (1987) reconstructed *Astraspis* with a stubby caudal fin, which we consider to be speculative (see *Description* above), and BU 2472 offers no additional information on this point. *Sacabambaspis*, the only Ordovician fish with a preserved tail, has a diphyccercal caudal fin (Gagnier 1993a, 1995). The elongate caudal spine featured on previous reconstructions of *Sacabambaspis* (Gagnier 1989; Blieck *et al.* 1991; Elliott *et al.* 1991) is now interpreted as the lateral margin of an underlying cephalic shield (Gagnier 1993a). *Athenaegis* Soehn and Wilson, 1990, from the Delorme Group (Wenlock) Northwest Territories, Canada, is the next oldest pteraspidomorph fish for which there is conclusive evidence of tail structure. These specimens, classified as cyathaspidid heterostracans, possessed a flexible, symmetrical tail with numerous fin 'rays' that predate similar features in the osteichthyans by some 20 million years (Soehn and Wilson 1990).

## EXPLANATION OF PLATE 4

Figs 1–5. *Astraspis desiderata* Walcott, 1892; Bighorn Mountains, Wyoming, USA; 'Harding Sandstone equivalent'; Caradoc; Nomarski differential interference contrast photomicrographs. 1–2, BU 2268; large mushroom-shaped tubercle with a thick layer of enameloid with numerous very fine tubules and a distinct junction (arrow) with the underlying dentine. This junction interrupts the pattern of the prominent, alternating incremental bands in the dentine. Fig. 2 shows the junctional tissue with wide ascending canals and arboriform branches leading to the very fine tubules ending at the cap surface. 3–4, BU 2572; two fields of dentine in a large tubercle where tubules can be seen to branch and when cut across show the high density of tubules per unit area. 5, BU 2573; comparison between enameloid and dentine showing the fine dimensions of both sets of tubules, and the contrasting disrupted and irregular course in the enameloid and the regular branched pattern in the dentine. Abbreviations in addition to those on Pl. 3: ac, ascending canals; gl, growth lines; t, tubule. Fig. 1,  $\times 189$ ; figs 2–5,  $\times 480$ .





TEXT-FIG. 8. Reconstruction of *Astraspis desiderata* Walcott, 1892. The tail and rostral areas are schematic since they are not preserved in any of the articulated specimens.

Little is known about the structure of the feeding apparatus in any of the Ordovician taxa. None of the described specimens of *Astraspis* has this area preserved, and the only Ordovician taxon which shows the oral region is *Sacabambaspis*. Gagnier (1993a) illustrated the ventral snout of *Sacabambaspis* with multiple rows of oral platelets which appear to have had a scoop-like function, comparable to that postulated for those of later heterostracans such as *Athenaegis* and the pteraspids (see Soehn and Wilson 1990; Janvier 1981, 1996b). However, the apparatus does appear to differ between these two groups since the oral plates of the heterostracans are single elongate scales; *Sacabambaspis* possessed composite plates formed from many platelets.

Both Elliott *et al.* (1991) and Blicek *et al.* (1991) claimed that aspidin can be considered to be a character shared by the arandaspidids, *Astraspis* and *Eriptychius*. The absence of histological data from *Arandaspis* and the complex and divergent histologies preserved in *Astraspis*, *Eriptychius* and *Sacabambaspis* suggest that this view is an oversimplification. The only histological character which can be confirmed as common to all forms is a highly vascularized honeycomb tissue which supports the dermal armour. It has been widely assumed that this is an acellular tissue, aspidin, based largely upon hypothetical considerations of the primitive condition in vertebrate hard tissues (Janvier 1981; Blicek *et al.* 1991; Elliott *et al.* 1991; Forey and Janvier 1993), but the available data do not lend firm support to this proposal. Although the honeycombed tissue is clearly acellular in *Astraspis* and *Eriptychius*, that of *Sacabambaspis* contains numerous small cavities, which may represent cell lacunae, and also lacks dentine (Gagnier 1993a, 1995). *Astraspis* and *Eriptychius* are readily distinguished in thin section, with significant differences in the nature of the cap material and the types of dentine which form the individual tubercles (Smith and Hall 1990; Smith *et al.* 1996). This suggests that they are not as closely related as has been proposed by Blicek *et al.* (1991). *Eriptychius* may be a primitive true heterostracan (Ørvig 1989; Blicek 1992), although more information about the body plan of this animal is required to confirm this.

Gagnier (1995) stated that dorsal-median scale/skin ridges are present as a uniting feature in all Ordovician taxa, heterostracans and myxinoids. Whilst *Astraspis* has a clearly developed dorsal median ridge on the headshield, this character is not developed prominently on the tail by a series of individual scales, as suggested by the reconstructions of Elliott (1987, fig. 3), Elliott *et al.* (1991, fig. 1B), Blicek (1992, fig. 1C) and Gagnier (1995, fig. 2B).

The development of the lateral line system is a potentially important character which may well provide insight into the relationship of these Ordovician vertebrates to more advanced Siluro-Devonian forms. *Astraspis*, with the lateral line system apparently developed only in the head region, differs from *Sacabambaspis* and the heterostracans, which show evidence for the lateral line system on head and body (Janvier 1996a, 1996b).

In summary, the significant morphological and histological characters of *Astraspis desiderata* are: dorso-ventrally compressed head; fused polygonal tesserae on the dorsal headshield, irregular



tesserae forming the ventral headshield; orbits surrounded by circumorbital tesserae; eight branchial openings arranged in a postero-ventral sloping line; branchial pouches; two dorsal sensory grooves; closed pineal region; articulated, thickened, large, rhomboid tail scales; and enameloid, fine tubular dentine and aspidin.

### CONCLUSIONS

Although some of the characters possessed by *Astraspis* may suggest a relationship with true heterostracans, the histology, and the presence of multiple branchial openings indicate a more complex picture. In addition, it is clear from available histological and morphological data that any formal grouping of the Ordovician heterostracan-like agnathans at ordinal level is artificial. Janvier's (1996a, 1996b) examination of early vertebrates demonstrates that Gagnier's (1993b, 1995) redefinition of the class Pteraspidomorphi, to include *Astraspis*, *Eriptychius*, arandaspidids and the heterostracans, does constitute a monophyletic group but one that is united only by the presence of the dorsal and ventral headshields. *Astraspis* has no clearly defined relationship with other groups and, although the heterostracans provide the nearest relatives, Astraspida probably represented an evolutionary *cul-de-sac* within Pteraspidomorphi.

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IVAN J. SANSOM

M. PAUL SMITH

PETER TURNER

School of Earth Sciences  
University of Birmingham  
Edgbaston  
Birmingham B15 2TT, UK

MOYA M. SMITH

Division of Anatomy and Cell Biology  
UMDS Guy's Hospital  
London Bridge  
London SE1 9RT, UK

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