A NEW PTERASPIDID OSTRACODERM FROM THE DEVONIAN SENNI BEDS FORMATION OF SOUTH WALES AND ITS STRATIGRAPHIC SIGNIFICANCE

by E. J. Loeffler and R. G. Thomas

ABSTRACT. A pteraspidid ostracoderm, Allothazis senniensis sp. nov., is described from the Senni Beds Formation of central South Wales. An associated assemblage of dispersed microspores indicates a mid Middle to lower Upper Silurian age for this fossil. A typical Breconian macroflora is also present. The Downtonian aspect of the ostracoderm supports the suggestion that there is overlap between the Downtonian and Breconian Stages of the Lower Old Red Sandstone.

The pteraspidid ostracoderm described herein was found by Dr. D. Goujet (Paris), in a fallen block of blue-grey mudstone on the floor of the disused Heol Senni Quarry, Powys, South Wales. This quarry was visited during the course of one of the post-symposium field excursions (Excursion B2) which formed part of the programme of the Palaeontological Association's Devonian Symposium (PADS), held in Bristol in September 1978. The quarry, which is situated on the north-eastern face of Fan Bwlch Chwyth (SN 9145 2210), 7 km south of Sennybridge, exposes a near flat-lying, sandstone-dominated sequence within the upper Middle part of the Senni Beds Formation; the succession is described by Edwards et al. (1978) in the field guide to the excursion.

The block containing the pteraspidid is of unlayered, blue-grey mudstone and was found amongst other fallen debris at the base of the main quarry face; its original position in the sequence is uncertain. The pteraspidid plates, including a ventral disc, rostral plate, branchial plate, and some scales, were disarticulated but found in close proximity to one another on the same surface, within an area of 400 cm². Careful splitting of the block yielded a single, unidentifiable plant fragment, but no additional fish material.

Palaeontology of Heol Senni Quarry

Flora. Plant fragments are common within the Senni Beds Formation at Heol Senni Quarry. Vegetative vascular macroplant axes several centimetres long are preserved as carbonaceous compressions in some blue-grey to grey-green coloured, very fine grained siltstone units. Examples of cf. Psilophyton princeps (Croft and Lang 1942) and Hostinella have been found in loose blocks of blue-grey, fine-grained sandstone and siltstone on the quarry floor. Additional fertile material collected during the PADS excursion has been identified by D. Edwards (pers. comm. 1979) as Glossingia breconensis Heard and Zosterophyllum sp. She drew attention to the similarity between the Heol Senni flora and that of the Brecon Beacons Quarries, where all of these taxa are found, and of Llanover, where Glossingia and cf. P. princeps occur.


D. sp. nov.; Emphasisporites cf. E. micromanus Richardson and Lister, 1969; E. neglectus (Vigran) sensu McGregor, 1973; E. obscura McGregor, 1961; E. rotatus (McGregor) McGregor, 1973; Aneurospora minuta McGregor, 1973; Aneurospora comb. nov. et. var. nov.; Camptozonotriletes cf. C. caperatus McGregor, 1973; Clinospora torquata McGregor, 1973 var. nov.; ?Lyxospora sp. nov.; and Archaeozonotriletes chulus var. chulus and nanus. Other genera represented within these assemblages include: Punctatisporites; Acanthotriletes; Anapiculatisporites; Apiculatisporites; Verrucoisporites; Convolutispora; Dicyotriletes; ?Iberespora; Stenozonotriletes; and Ambitusporites. Several Heol Senni miospore samples contain derived Tremadocian and Wenlockian acritarchs.

On the basis of palynology and lithofacies, Thomas (1978a) considered the Senni Beds Formation to be the facies equivalent of the lower and middle portions of his Mill Bay Formation of the Cosheston Group, and its age to be mid Middle to lower Upper Siegenian.

**Fauna.** The ostracoderm fish which is described here is the best preserved and most complete yet recovered from the Senni Beds, and the first to have been found at Heol Senni Quarry. Vertebrates are extremely rare in the Senni Beds, having been recorded from only two other sites. The enigmatic *Pteraspis discon* White, considered by White (1938, 1950) to be a very primitive pteraspid, occurs together with *Cephalaspis* sp. indet. low down in the Senni Beds near Ferryaid in Carmarthen on: *Rhinopteraspis cornubica* (McCoy) has been found high in the Senni Beds of Primrose Hill Quarry, near Crickhowell, Powys (White 1938).

**SYSTEMATIC PALAEONTOLOGY**

**Family PTERASPIDIDAE White, 1935**

**Subfamily PTERASPIDINAE Denison, 1970**

**Genus ALTHASPIS Zych, 1931**

**Diagnosis.** See Dineley and Loeffler (1976, p. 129).

**Type species.** *Pteraspis elongata* Zych (non Alth) = *Althaspis samsonowici* Tarlo.


**ALTHASPIS SEMIENSIS** sp. nov.

**Plates 35 and 36**

**Derivation of name.** From Heol Senni.

**Diagnosis.** Rostrum long and tapered (median length of rostral plate = 56 mm), with antero-lateral margins converging at approx. 35°. Subrostral surface covered in dentine ridges which are largely, but variably, deflected forward in the longitudinal mid-line.

**Holotype.** A rostral plate, BMNH P.59744a, plate 35, figs. 2 and 3.

**Other material.** A ventral disc, BMNH P.59744b, pl. II, fig. 5. An incomplete branchial plate, BMNH P.59744c, pl. 35, fig. 1. Nine disarticulated scales, BMNH P.59744d-I, pl. 36, figs. 1-4.

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**EXPLANATION OF PLATE 35**

Figs. 1-3. **ALTHASPIS SEMIENSIS** sp. nov. 1, Incomplete branchial plate (BMNH P.59744c), ×2.5 approx.

2, Rostral plate in ventral view, showing subrostral surface (BMNH P.59744a, holotype), ×2.3 approx.

3, Rostral plate in dorsal view (BMNH P.59744a, holotype), ×2.3 approx.
LOEFLER and THOMAS, Pteraspoid ostracoderm
Description

Rostral plate (Pl. 35, figs. 2, 3). The rostral plate has a median length of 56 mm and a maximum width of 28 mm. The free, antero-lateral margins converge at an angle of approximately 35°; the postero-lateral margins, which would presumably have been in contact with the orbital and pinal plates, converge at an angle of about 105°. On the dorsal surface of the rostrum, the dentine ridges have a density of approximately 7.5 mm; the surface of the plate is subdivided into three distinct areas by two deep grooves, which are interpreted as growth lines. Within the more posterior of these three divisions, ridges are concave forward (i.e. deflected backwards in the longitudinal mid-line), arranged parallel to the postero-lateral margins. Within the central division, the backward deflection of the ridges is increased, but reduced again at the rear of the anterior division. The curvature of the ridges increases toward the extremity of the rostrum, to become almost concentric around the tip.

On the underside of the rostrum the ventral preoral surface extends back some 30 mm (over half the total length of the rostral plate). This surface is covered with dentine ridges which are continuous with the dorsal ornament. The growth lines can also be traced ventrally, producing three slightly less distinct subdivisions. Posteriorly, the ridges are transverse to weakly convex forwards (i.e. deflected forwards medially), becoming more strongly convex in the central area. Anteriorly, the ridges change from being convex, to become transverse or slightly concave right at the tip of the rostrum.

There is no indication of an ascending lamella but, as the posterior margin of the preoral surface is discordant to the ridge pattern, it is possible that this is a broken edge. This is difficult to confirm, as the bone is crushed. The whole preoral part of the rostrum is rather thin, suggesting that the cancellous layer has been completely crushed.

Branchial plate (Pl. 35, fig. 1). The anterior 46 mm of the branchial plate is preserved; its maximum width is 7.5 mm. Dentine ridges, with a density of 6–8 mm converge on the longitudinal mid-line, toward the anterior end of the plate.

Ventral disc (Pl. 36, fig. 3). The ventral disc is approximately 87 mm long, with a maximum width of 50 mm being achieved about 25 mm behind the anterior margin, and a minimum width of 38 mm about 18 mm in front of the posterior margin. The plate is vaulted both longitudinally and transversely, from a narrowest part. The anterior margin is broadly rounded, the posterior margin is incomplete. Ornamentation is of rather flat-topped dentine ridges with weakly developed lateral crenulations; ridge density varies from 4.5 to 7.5 mm per cent, coarsest ornament being developed anteriorly and medially. The pores of the lateral line system are barely visible, but several growth lines are distinguishable.

Scales. Three distinct types of scale are recognized:
1. Lateral scales (Pl. 36, figs. 1, 2). Represented by seven specimens, these are flat, rhomb-shaped scales which are in the order of 4.5 mm long and 4–5 mm wide, and which have a narrow overlap in front of the mid-line.
2. Fulcral scales (Pl. 36, fig. 3). Represented by a single specimen which is long (12 mm) and narrow (3 mm) and strongly arched about the mid-line.
3. Ridge scales (Pl. 36, fig. 4). Again strongly arched about the mid-line, this unique scale is of similar length to the fulcral scale, but almost twice as wide.

Discussion. The mode of preservation of this material suggests that all of the plates and scales belonged to a single individual, which had not been transported a great distance after death. The fact that the rostral plate is disarticulated suggests that it was weakly, or incompletely attached to the rest of the dorsal shield; these could be the remains of an immature, or recently mature individual.

Pteraspis classification relies heavily on the morphology of the subrostral surface (Tarlo 1961; Denison 1970; but see Novitskaya 1975, for an alternative view). The presence of an extensive subrostral surface covered in dentine ridges which are continuous with those of the dorsal surface is the basis for referring the Heol Semni specimen to the genus *Althusapis*.

EXPLANATION OF PLATE 36

Figs. 1–5. *Althusapis semniensis* sp. nov. 1, Lateral scale (BMNH P.59744d), ×3 approx. 2, Lateral scale (BMNH P.59744c), ×3 approx. 3, Fulcral scale (BMNH P.59744k), ×2.7 approx. 4, Ridge scale (BMNH P.59744l), ×2.7 approx. 5, Ventral disc (BMNH P.59744b), ×2 approx.
Only one species of *Althaspis* has previously been recorded from Britain, and that is the late Dittonian zonal form, *A. leachi* (White), now known from south-west Dyfed (White 1938), the Clee Hills (Ball and Dineley 1952), and the Forest of Dean (Allen et al. 1968). Rice (1967), describing them as *Rhinogieraspis cornubica*, recognized two forms of rostral plate amongst the specimens from Mitcheldean in the Forest of Dean: a long, narrow form and a squat form, in which the breadth to length ratios are 0.29–0.34 and 0.38–0.40 respectively (calculated from Rice's published data). Referring to additional material, but without publishing detailed palaeontological descriptions, Allen et al. (1968) re-identified the Mitcheldean pteraspids as *A. leachi*; they agreed that two types of rostrum were present, figuring BMNH P.49119 (p. 146, fig. 2d) as an example of the squat form. Although it is approximately 1-3 times longer, this particular specimen is close in shape to the rostral plate from Heol Senni. Examination of material in the collections of the British Museum (Natural History), however, revealed the specimen to be somewhat atypical of the squat rostra from Mitcheldean; typical examples (e.g. P.49183; P.49186) are about 100 mm long and 40 mm wide (width ratio 0.40), while the specimen figured by Allen et al. (1968, fig. 2d) is about 75 mm long and 35 mm wide (width ratio 0.46). Ventral discs of *A. leachi* show little variation in shape and proportion (Rice 1967). At 136 mm, the median length of the ventral disc figured by Rice (1967, fig. 11) is approx. 1.6 times greater than that of the ventral disc from Heol Senni; the width ratios of the Mitcheldean and Heol Senni ventral discs are also quite different, being 0.42 and 0.57 respectively.

Other species of *Althaspis* are known from Belgium, Spitsbergen, and Podolia (Ukraine). On the basis of rostral shape alone, the Heol Senni material is readily distinguishable from *A. anatasirostra* (Bleek 1975) and *A. spatulirostra* (Stensio 1964). The remaining species, all of which have rather long, tapered rostra, are more difficult to separate, largely because the Podolian species have not been adequately defined or described. In size, the rostrum from Heol Senni resembles a small, possibly juvenile, rostrum which White (1960) referred to *A. viniensis*; in that species, however, the rostrum is more robust and has a more bluntly rounded tip.

A striking feature of the Heol Senni rostrum, and one in which it apparently differs from all of the other species except *A. leachi*, is the irregularity and curvature of the subrostral ridges; in other species, the ridges seem to be regular and more transverse.

As the pteraspisid from Heol Senni cannot readily be accommodated elsewhere, a new species, *A. senniensis*, has been established to receive it.

**DEPOSITIONAL ENVIRONMENT OF THE SENNI BEDS FORMATION**

The Senni Beds Formation crops out from the head of Carmarthen Bay in the west to the Black Mountains in the east. It comprises a 150-450-m-thick (Allen 1974) sand-dominated sequence of fluvial and fluvo-lacustrine origin, which is distinguished from the sediments of the underlying Red Marlts and overlying Brownstones by its primarily grey-green coloration, diagnostic macroflora and dispersed-miospore assemblages, and distinctive lithofacies associations.

Whilst the important Senni Beds Formation macroflora has been, and is still being, intensively studied, comparatively little is known about the sedimentology and provenance of the Formation. The most recent general account of the litostratigraphy and sedimentology of the Senni Beds is contained in Allen's (1974) review of the Devonian rocks of Wales and the Welsh Borderland. To date, no detailed interpretations of the depositional environment(s) represented by the Senni Beds Formation have been published.

In central south Wales, where it attains a thickness of 300-380 m (Dineley and Williams 1978, fig. 31), the Senni Beds Formation consists of intraformational conglomerates (many of which are calcified) plus subordinate extraformational conglomerates, coarse to very fine grained sandstones, coarse to fine grained siltstones, some claystones, and occasional poorly developed calcrites. Whilst these lithologies are often rhythmically arranged (as, for example, in fining-upward cycloths of variable complexity and completeness) there are many Senni Beds Formation sections, including that at Heol Senni Quarry, in which no over-all 'cyclic' organization of the constituent lithofacies units is discernible.
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We interpret the Senni Beds Formation sequence of the Brecon Beacons area as having been deposited by a comparatively high discharge, mixed-load (but sand dominated), braided stream complex. Relatively high sedimentation rates and water-table levels during accumulation of the Senni Beds are indicated by the combination of the vertical succession of lithofacies units and the prevalence of grey-green colours within the Formation, plus the suites of stratification types and other sedimentary structures it contains.

In-channel and extra-channel sequences have been identified. In-channel facies recognized include: channel lags; channel-fill deposits; units formed by the migration of linguoid, transverse, lateral and ?turbidite mid-channel bars, and low amplitude sand waves; bar delta wedges; and bar top sequences. Thick, multistorey sand bodies containing interbeds and/or lenses of intraformational conglomerate that overlie basal erosion surfaces imply repeated channel superimposition, filling and re-excavation. Many channel sand units are draped by thin mudstones deposited from suspension during lowering flood stages. Local, comparatively rapid, channel shifting and consequent complete or partial channel abandonment, was common. Ponding of floodwaters occurred in channel cut-offs and (between flood stages) in parts of the secondary and tertiary distributaries of the active channel network. This local ponding, combined with decomposition of plant material (with the subsequent lowering of redox potentials), plus the presence of reworked calcite glauconites and calcified plant fragments (high pH and bicarbonate ion concentrations) resulted in the calcification of many channel-lag intraformational conglomerates.

Extra-channel and floodplain deposits of the Senni Beds Formation comprise proximal and distal crevasse-splay sediments, some possible levee sediments, and thin, fine-grained, fluvialacustrine units laid down in temporary floodplain lakes. Sandstones interbedded with these mudstone-dominated fluvialacustrine units are thought to represent incursions of crevasse-splay sands deposited during major avulsion episodes. The Heol Senni pteraspid may well have been carried from its habitat within the main channel system and deposited within a floodplain lake or channel-fill mud unit during one such flood event. Strongly reducing post-depositional conditions are indicated for the majority of these fluvialacustrine sediments by their typically blue-grey to grey-green coloration, and the preservation within them of pyrite nodules, macroplant cuticles, and miopores.

Vascular plants flourished along the shores of the temporary floodplain lakes, and colonized abandoned-channel fills and near-channel overbank deposits. High sedimentation rates and water-table levels, plus post-burial reducing conditions meant that the potential for preservation of these plants was comparatively good.

In the Brecon Beacons the Senni Beds Formation: Brownstones boundary has been drawn at the junction between the predominantly grey-green coloured sequence and the overlying red-brown succession, even though there are no major sedimentological differences between the lithofacies immediately below and above the contact. However, the Brownstones higher in the succession were laid down by sandy braided streams of a more shallow and ephemeral nature than those which deposited the Senni Beds.

The Senni Beds Formation is the lateral litho- and chronostratigraphic equivalent of the lower and middle portions of the 540–600-m-thick Mill Bay Formation (Cosheston Group) of south-west Dyfed, which Thomas (1978a, b) interpreted as the deposits of a braided-meandering river system (cf. Shelton and Noble 1974).

STRATIGRAPHY

The Senni Beds, together with the Brownstones of central south Wales, constitute the Breconian, one of four Stages into which the Old Red Sandstone of the Anglo-Welsh area has been subdivided. The stages, in ascending order, are the Downingian, Dittonian, and Breconian of the Lower Old Red Sandstone, which are unconformably overlain by the Farlovian of the Upper Old Red Sandstone. The foundations of this classification were laid by King (1925, 1934) who, using a combination of faunal (mainly ostracods) and lithostratigraphic evidence, recognized four discrete 'series' or 'divisions' in the Old Red Sandstone of Shropshire. These were, (I) Downingian (or Anaspida Marls),
(II) Dittonian (or *Pteraspis cornubica*) followed by a group of 'false-bedded brown sandstones' which King (equating them with the Black Mountains sequence) termed (III) the 'Brownstones'. Together these comprised the Lower Old Red Sandstone, and were succeeded unconformably by (IV) the Farelo Sandstones (Farnlovan Stage of King 1934) of Upper Old Red Sandstone age. Although retained at formation level, the term 'Brownstones' is now no longer used sensu King (1925). Instead, the stage-name Breconian was proposed by Croft (1953) to circumscribe the highest Lower Old Red Sandstone of the Anglo-Welsh Basin, namely that part 'lying between the Dittonian and Farnlovan Stages' of King (1934).

Attention has already been drawn to the difficulties of interpreting the Breconian Stage division, and to the possibility of its overlap with the preceding Dittonian Stage (Allen et al. 1968; Allen 1974). These difficulties arise essentially because the Downonian and Dittonian Stages are defined on a largely biostratigraphical basis in the vertebrate-rich succession of the Clee Hills, whilst the Breconian Stage is defined on a largely lithostratigraphical basis in the Brecon Beacons where vertebrates are extremely rare. As a consequence, the Dittonian-Breconian boundary has never been satisfactorily fixed.

In the Clee Hills, refinement of King's (1925, 1934) original vertebrate stratigraphy by White (1950, 1961) and Ball and Dineley (1952, 1961) has resulted in the recognition of a number of ostracoderm zones which have proved to be of some value in correlation (White 1950, 1956). The Dittonian is characterized by its pteraspid faunas, the highest zone being that of *A. leachi* which is some 183 m (600 feet) thick (Ball and Dineley 1961), but which terminates well below the top of beds which are assigned on lithological grounds to the Dittonian Series (Ball and Dineley 1961). Biostratigraphically, the Dittonian Stage is regarded as being terminated by the appearance of *Rhinopteraspis cornubica* (Allen et al. 1968). However, although *R. cornubica* (McCoy) (syn. *R. diemensis* (Roemer)) has come to be accepted as the 'Breconian zonal fossil' (Allen 1974), it has not yet been recorded from the Clee Hills and, in the whole of the south Wales Breconian, appears to be restricted to a single locality. This lack of evidence makes it impossible to determine the precise position of a faunal boundary between the *A. leachi* and *R. cornubica* zones. While it was long assumed that such a boundary would correspond to lithostratigraphical divisions, the discovery that the pteraspids from the Brownstones of Mitcheldean was *A. leachi* and not *R. cornubica* (Allen et al. 1968) demonstrated that this was not so.

In the Brecon Beacons, the Breconian Stage, as envisaged by Croft (1953), is characterized by its abundant and distinctive macroflora which includes *Drepanopanax* and *Glossinia*, and by the presence of *R. cornubica*. Its junction with the Dittonian is drawn at a colour change (Allen 1974) in an area where ostracoderms are very rare. The flora occurs at many localities within the Senni Beds but the Brownstones appear to be unfossiliferous. The one locality at which *R. cornubica* has been found is a quarry high up in the Senni Beds, which are there in the region of 300 m (1000 feet) thick. This level would seem to be substantially above the highest appearance of *A. leachi* in the Clee Hills (Allen 1974). The macroflora of the Senni Beds, although probably the most extensive and representative Lower Old Red Sandstone flora in Britain, is of little stratigraphical value. The Breconian plants are relatively scarce and their distribution is facies controlled. Furthermore, owing to the lack of faunal control, it must be considered as a distinct possibility that they are Dittonian in age in terms of the ostracoderm zones.

**THE STRATIGRAPHIC SIGNIFICANCE OF THE HEOL SENNI PTERASPIDID**

The discovery of pteraspid material in association with a typical Breconian macroflora, and datable on the basis of a dispersed spore assemblage, is a significant contribution toward resolving the dubious status of the Breconian Stage division. Unfortunately, the pteraspid from Heol Senni cannot be referred either to *R. cornubica* or to *A. leachi*; it is a distinct species of *Alithaspis*, showing similarities to forms from Podolin and France, as well as to the British species. It does, however, provide some support for the view that there is overlap between the Dittonian and Breconian Stages.
The fact that *A. sehnensis* is smaller, and has a less attenuated rostrum than *A. leachi*, does suggest that it is more primitive. While this alone is insufficient evidence to suggest that it occurs at a lower stratigraphic level, it is relevant to note the stratigraphic distribution of other species of *Althaspis*. The rather similar *A. vaniensis* White, from Belgium (White 1960; Bieck 1977), occurs only 17 metres above *Belgicaspis crouchii*; the latter is the characteristic pteraspidid of the zone immediately preceding that of *A. leachi* in Britain. The stratigraphic distribution of the species described by Stensio (1958, 1964) was not given, but the range of *A. samsonowiczii* Tarlo (syn. *A. elongata* (Zych) overlaps with that of *B. crouchii* in the Old Red Group of Podolia (Obruchev and Talman, 1967). In Spitsbergen, *A. anatostroza* Bieck is found at a level correlated with the base of the *B. crouchii* or top of the Protopteraspidis leathiensis zone of the Dittonian (Goujet and Bieck 1977). Thus *A. sehnensis* can be considered to be a pteraspidid of Dittonian aspect. Its presence in the Senni Beds indicates overlap between the Dittonian and Breconian Stages, as currently defined, but the extent of this overlap remains uncertain. In view of the scarcity of ostracoderms at this level in the Lower Old Red Sandstone, it seems unlikely that they, alone, will ever be of use in resolving the problem of the Dittonian-Breconian boundary; the eventual solution must involve choosing other organisms for zonal purposes. Work by Mortimer (1967), Chaloner and Street (1968) and Richardson and Lister (1969) has drawn attention to the great potential of dispersed miospore assemblages for use in relative age determinations and stratigraphic correlations within the Anglo-Welsh Lower Old Red Sandstone. Thomas (1978a) has already used such assemblages to correlate between the Breconian of Pembrokeshire and Breconshire; it seems probable that they could eventually be used to define the Dittonian-Breconian junction.

In view of this, the discovery of a diverse, well-preserved and distinctive miospore assemblage, in association with an ostracoderm, is of great stratigraphic significance. It is noteworthy that the mid Middle to lower Upper Siegenian age of the Senni Beds Formation, as deduced from the miospore assemblage (Thomas 1978a), agrees well with the Middle to Upper Siegenian age suggested by White (1956) on the basis of *R. corrobica*, and is supported by Richardson and Rassul's (1979) comparison with the Apley Barn Borehole.

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