A Devonian Brachythoracid Arthrodire Skull (Placoderm Fish) from the Broken River Area, Queensland

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An incomplete brachythoracid arthrodire skull acid-prepared from the Devonian limestones of the Broken River area of Queensland is described as *Doseyosteus* gen. et sp. nov. It supposedly comes from strata dated by conodonts as late Early Devonian in age (Emsian stage), but shows several derived features of the skull, typical of Middle-Late Devonian brachythoracids, and not seen in any arthrodire from the Emsian limestones of the Burrinjuck area of NSW. The alignment with conodont zones of stratigraphic subdivisions of the Burrinjuck sequence is revised. Published information on the provenance and age of all previously described placoderm taxa from Broken River is reviewed and amended. The new taxon may be most closely related to Late Devonian (Frasnian) brachythoracids from Iran and the Gogo Formation of Western Australia.

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INTRODUCTION

Devonian sedimentary rocks, including many marine limestones, are well exposed in the Broken River area of Queensland (Fig. 1). Conodonts form the basis for dating the sedimentary sequence (Mawson and Talent 1989; Sloan et al. 1995). Vertebrate remains reported from this sequence include microfossils from many horizons (De Pomeroy 1996; Turner, Basden and Burrow 2000), and less well known vertebrate macro REMAINS. The latter include two genera of antarctic placoderms described by Young (1990), a ptyctodont toothplate ascribed to *?Ptyctodus* sp. by Turner and Cook (1997), a new species of the brachythoracid arthrodire *Atlantidosteus* Lelièvre 1984 described by Young (2003a), an isolated subbital plate of another arthrodire illustrated by Turner et al. (2000, fig. 8.7), and jaw remains of an onychodontid (Turner et al. 2000, fig. 5). Undescribed vertebrate macro REMAINS include various placoderm bones, most of which belong to brachythoracid arthrodires. The Arthrodira is the most diverse order within the class Placodermi, and its major subgroup, the Brachythoraci, comprises nearly 60% of about 170 genera within the Arthrodira (Carr 1995). The brachythoracid arthrodires were one of the most successful groups of early gnathostome fishes (e.g. Young 1986; Janvier 1996). In marine environments of the Late Devonian they included probably the largest predators of their time. The major radiation of brachythoracid subgroups had apparently already occurred by the Middle Devonian, and primitive representatives were already widespread in shallow marine environments of the Early Devonian (e.g. Young et al. 2001; Mark-Kurik and Young 2003), and are important in considering the origins and interrelationships of major brachythoracid subgroups (e.g. Lelièvre 1995).

The stratigraphic occurrence of various placoderm remains in the Broken River sequence were reviewed by Young (1993, 1995, 1996), De Pomeroy (1995, 1996), and Turner et al. (2000), and they have been mentioned in relation to conodont studies by Sloan et al. (1995). There has been conflicting information published about the provenance of some of the described placoderm taxa. These were collected from the Broken River area many years ago by Professor John Jell, University of Queensland, and sent to Canberra for acid preparation and study. In this paper I describe a new arthrodire skull from this collection, and review the locality information and age determinations for previously described placoderm taxa.
Figure 1. (A) location of the Broken River area in Queensland, Australia; (B) geological map of the collecting area (modified from Turner, Basden and Burrow 2000, fig. 2), showing localities for previously described placoderm taxa, and the specimen described in this paper (ANU V1026).

LOCALITY AND AGE OF DESCRIBED PLACODERM TAXA FROM THE BROKEN RIVER AREA

Wurungulepis denisoni Young 1990

According to information provided with this specimen, it came from University of Queensland locality L4399 (not L4339, given in error by Young 1990: 45), on the north bank of the Broken River, Grid Reference 640 460 on the Burges 1:100 000 sheet, and was assigned a Middle Devonian (?Eifelian) age within the Broken River Formation (J.S. Jell, letter of 17 April 1980). Judging by the map of the area
published by Sloan et al. (1995: fig. 2), the locality lies within outcrop referred to as 'undifferentiated Broken River Group'.

A 'Wurungulepis-Atlantidosteus fauna', of assumed Eifelian age, was listed in the macrovertebrate zonation of Young (1993, 1995, 1996). However De Pomeroy (1995: 480) assigned Wurungulepis to the late Emsian serotinus Conodont Zone (CZ), citing a personal communication of J.A. Talent. This information was repeated by Turner et al. (2000: 498). Later (pers. comm. 28/8/95) J.A. Talent had advised A. Basden that this specimen was collected from the grid reference cited above, situated on a bend of the Broken River in an anticline, in strata which were pre-Dooney Limestone in the sequence, and equivalent to the Bracteata Formation and Lomandra Limestone (spanning the Emsian-Eifelian boundary; Sloan et al. 1995: fig. 3).

No conodont data were obtained from the specimen, so its precise position relative to the standard conodont zonation is uncertain. Wurungulepis is an early representative of the asterolepidoid antiarchs, with a high short trunk armur (Young 1990), and was placed within the asterolepidoid cladet adjacent to Sherbonaspis, and as sister group to Stegolepis, Asterolepis, Remigolepis and Pambulaspis, by Zhu (1996: fig. 29). As earlier discussed (Young 1990: 48) the initially suggested Eifelian age was consistent with the oldest asterolepid (pterichthyoid) occurrence in Europe, cited as Gerdalepis from the Eifelian of Germany by Denison (1978), although this occurrence is slightly younger (early Givetian) according to Otto (1998: 118). However Gardiner (1994) cited Young (1974) for an older record (Emsian) of the asterolepid antiarchs, but the 'cf. Pterichthyes' mentioned by Young (1974) was based on an erroneous attribution by Hills (1958: 88) to the Early Devonian limestone sequence of an 'Antiarchan from Taemas'. In fact, the specimen in question came from the overlying Hatchery Creek Formation, of presumed Eifelian age (Fig. 2). This specimen was assigned to the new genus Sherbonaspis by Young and Gorter (1981). Previously, the suggested Emsian age of a pterichthyoid antiarch from the Georgina Basin (Young 1984a) was noted as possibly the oldest occurrence of this group anywhere recorded.

New evidence now indicates that two assemblages may have been mixed in this region (Burrow and Young, in press), with the limestone occurrence yielding the antiarch probably younger than the diverse

Figure 2. Proposed alignment with conodont zones of subdivisions of the Early Devonian limestone sequence (Murrumbidgee Group) around Burrinjuck Dam, N.S.W., revised from Basden et al. (2000: fig. 2). Abbreviations for stratigraphic subdivisions are: B - Bloomfield Limestone Member; CB - Cavan Formation; CR - Crinoidal Limestone Member; CU - Currajong Limestone Member; HC - Hatchery Creek Formation; M - Majurgong Formation; R - Receptaculites Limestone Member; SY - Spirifer yassensis Limestone Member; W - Warroo Limestone Member; 1-6 - units of Upper Reef Formation. V1370 - horizon for highest known arthrodire in the sequence.
**Devonian Arthrodirre Skull from Queensland**

Wuttagoonaspis fauna from underlying sandstones (Young and Goujet 2003).

The antiarchs are a major subgroup of the class Placodermi, ranging in age from Early Silurian to latest Devonian. In recent years there has been a significant expansion in our knowledge of the group. A cladistic analysis of their distribution in relation to phylogeny by Young (1984b) involved 22 taxa and 40 characters. In a recent review of antiarch phylogeny, Zhu (1996) noted some 45 genera and 154 species, and his data matrix used 66 characters for 40 genera. The original age assessment of Eifelian for Wurrengalepis from Broken River is most consistent with our current knowledge of this large and diverse group.

**Navagiaspis wadeae Young 1990**

This specimen is recorded from locality BRJ68D (University of Queensland locality L4428; 'small limestone outcrop on eastern side of gully 1 km upstream from Six Mile yard'), Grid Reference 596 442 on the Burges 1:100 000 sheet, which was assigned a Middle Devonian ('Givetian') age within the Broken River Formation (J.S. Jell, letter of 17 April 1980). Apparently this specimen was found by Dr Mary Wade.

Again, De Pomeroy (1995: 480) referred this taxon to the significantly older (late Emsian) *serotinus* CZ, based on its assigned position within the Bracteata Formation in section Br4 of Sloan et al. (1995, fig. 6). This information was repeated by Turner et al. (2000: 498, 506). However Prof. J.A. Talent’s previous advice to the author (pers. comm. 5/8/92), was that this specimen was considerably younger (ensensis – varcus Zones; late Eifelian – Givetian). Clearly, there was some confusion about which fish specimen was being referred to. Subsequent advice given to A. Basden (pers. comm. 28/8/95), was that *N. wadeae* came from the bank of Dosey Creek (Grid Reference 616 437), the location of section Br2 within outcrop of the Bracteata Formation (Sloan et al. 1995: fig. 2). The different, and presumably correct, locality information provided with the specimen, as cited above, corresponds to the vicinity of the boundary between the Papilio and Mytton Formations on the map of Sloan et al. (1995: fig. 2). This is consistent with the Givetian age first suggested by J.S. Jell.

**Navagiaspis wadeae** is another antiarch, originally interpreted as possibly a primitive bothriolepidoid (Young 1990), although in Zhu’s (1996) phylogeny it comes out as a basal asterolepidoid. Apart from primitive Chinese antiarchs, and the erroneous Emsian pterichthyoid occurrence discussed above, the stratigraphic record of this group is Middle-Late Devonian (Gardiner 1994, fig. 32.1). The bothriolepidoid clade had an earlier history in Asia, and apparently expanded its range to most regions of the world in the Givetian (Young 2003b).

The confusion about the provenance of this specimen may have resulted from the misconception that it was a recognisable ‘skull’ when collected. Turner et al. (2000) used this term to refer to the type, but the specimen as collected was a largely complete trunk armour, and the incomplete skull, missing its central portion, formed a minor part of the specimen. The whole specimen may have appeared to a non-vertebrate worker to represent a ‘skull’. Such fish remains, when collected in the field, are generally not determinable until after acid preparation (e.g. the type specimen of *Atlantidosteus pacifica* Young 2003a, before preparation, was assumed to be a ventral plate of the trunk armour, rather than a large suborbital bone from the cheek).

A summary list of prepared fish remains from the original J.S. Jell collection was provided to J.A. Talent in 1995 to check on age and locality data. This list mentioned only one skull, the brachythoracic specimen described below, of which locality data provided by J.S. Jell are almost the same as stated by Sloan et al. (1995) for *N. wadeae*. Thus it seems that the specimen described below, previously listed as a ‘skull’, has been confused with the type of *N. wadeae*, leading to erroneous locality and age information being given in De Pomeroy (1995), Sloan et al. (1995), and Turner et al. (2000). In the context of the global distribution in time and space of this major placoderm subgroup (see above), it is almost certain that *Navagiaspis* is Middle Devonian in age, and a Givetian age, as first suggested by J.S. Jell, is most consistent with other information about the stratigraphic distribution of the more derived antiarchs.

**Atlantidosteus pacifica Young 2003a**

This specimen came from locality BRJ 67B (University of Queensland locality L 4472), Grid Reference 675 485 on the Burges 1:100 000 sheet, described as 'Top of ridge to three-quarters way down western slope, west of road between Six Mile Dam and Diggers Creek' (J.S. Jell, letter of 17 April 1980). This is the locality (with a slightly different grid reference) referred to as 'Fish Hill' by Turner et al. (2000: 507). They assigned it a middle Eifelian age (*costatus - australis* conodont zone), but noted that Sloan et al. (1995) gave a slightly longer *partitus - early kockelianus* zonal range for the Fish Hill section. This is consistent with the original assignment of a Middle Devonian ('Eifelian') age within the Broken River Formation by Prof. J.S. Jell. This occurrence is

Doseosteus talenti gen. et sp. nov.

This specimen, described below, was the only one in the J.S. Jell collection lacking a sample number at the time of preparation. It is highly probable that it was a sample collected the year before the other material, and was taken to Canberra separately by Dr P. Jell (J.S. Jell, letter of 17 April 1980). The following locality details, provided by Prof. J.S. Jell (letter of 17 April 1980), indicate that it is the specimen collected from the alternative erroneous locality for Nawagiaspis just discussed: 'BR334 = L 4054. Grid Reference 616 438 Burges 1:100,000 sheet. Western bank of Dosey Creek, 750 m upstream from its junction with Broken River. Base of thick limestone lens in Broken River Formation, Middle Devonian. ? Eifelian'.

In a published listing of University of Queensland locality numbers (Turner et al. 2000: 506), UQL4054 is assigned to 'basal part of limestone, Lomandra/Dosey Limestone, Broken River Group', with a slightly different grid reference (615 438), but the same locality description as above. However, it is assigned to the Emsian serotinus CZ, citing Sloan et al. (1995).

Again, no conodonts were obtained from the sample, and section Br4 through the Bractatea Formation at this locality did not produce identifiable conodonts (Sloan et al. 1995: caption to fig. 6). Nevertheless, these authors (p.5) considered the entire formation to belong to the serotinus CZ, making it equivalent to the upper part of the Burринjuck (NSW) limestone sequence, which extends from the top of the pirenae CZ (latest Pragian) into the serotinus CZ (the second youngest zone of the late Emsian). It is therefore relevant to make comparisons with the stratigraphic distribution of the diverse arthrodire assemblage described from the Burринjuck limestone sequence.

The described arthrodire fauna from the Burринjuck sequence (White 1952, 1978; White and Toombs 1972; Young 1979, 1981, in press a, b; Young et al. 2001; Mark-Kurik and Young 2003) includes 10 genera of brachythoracid, amongst which the most derived taxa (Cathlesichthys and Dhammadra) come from the upper part of the Wee Jasper limestone sequence. Basden et al. (2000, fig. 2) showed the youngest arthrodire skull from the Wee Jasper section (ANU V1370; the holotype of Dhammadra) to come from the uppermost unit 6 of the 'Upper Reef Formation' of Young (1969). This specimen is more advanced than other arthrodires known from the Burринjuck sequence in possessing several derived characters of the skull, a feature of more derived eubrachythoracics (character 5 of Carr 1991; character 4 of Lelièvre 1995). Eubrachythoracics were the most diverse fish group of the Middle and Late Devonian, and the new Broken River brachythoracid described below clearly belongs to this group, with a skull which is more advanced in several respects than any of the known Burринjuck arthrodires (see below). Gardiner (1994) lists the first occurrence of this grouping (his family Coccosteidae) as Coccosteus Miller 1841 from the Middle Devonian (Eifelian) of Scotland, for which a late Eifelian age is indicated by spores of the devonicus-naumoveae zone (V.T. Young 1995). The same species (Coccosteus cuspidatus) is recorded from the Kernave Member of the Narva Formation in the Baltic sequence, although a related brachythoracid 'Protitanichthys' occurs a little earlier, and in equivalent strata (costatus CZ) in the Rhenish sequence (Mark-Kurik 2000). However Otto (1997: 115) suggested that remains of early eubrachythoracics (coccosteids) first occur in the early Eifelian of Scotland, Germany, and the Baltic sequence.

Dhammadra johnstoni Young (in press a) comes from a horizon about 420 m stratigraphically above the boundary equivalent of the Bloomfield and Receptaculites Members of the Taemas Limestone. A similar horizon high in the limestone sequence has produced the large lungfish Dipnorhynchus cathlesae Campbell and Barwick 1999. The lungfish locality is close to localities L537 and L538 of Pedder et al. (1970) which yielded tetracorals Vepresiphymum dumosum, Sulcorphymum pavimentum, Chalicophyllum vesper and C. gigas. This represents the uppermost 'tetracoral teilezone' of the Murrumbidgee Group (Pedder et al. 1970: fig. 4), and is Coral Fauna F in the scheme of Garratt and Wright (1989). These authors considered the succeeding G and H Coral Faunas to overlap, and belong to the late Emsian, rather than Eifelian as previously assessed. Garratt and Wright (1989) also aligned Coral Fauna F from Wee Jasper (and the Sulcor Limestone of northern NSW) with the mid-Emsian inversus CZ (see column 13 of Young 1995, 1996). However Basden et al. (2000: fig. 2) showed the uppermost beds of the limestone sequence at Wee Jasper (containing Coral Fauna F) extending well into the next youngest serotinus CZ. Evidence supporting this (summarised by Basden 2001, table 2.1) derives from reassignment of some of the conodonts from the highest productive sample (C62) in Pedder et al.’s (1970) section 2, referred to them by Polygnathus linguiformis

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linguiformis, but reassigned to Polygonatus inversus by Klapper and Johnson (1975), and to Polygonatus serotinus (delta morphotype) by Mawson (1987). On the other hand, the age in terms of conodont zone alignment of several constituent members of the Taemas Limestone, as indicated by Basden et al. (2000, fig. 2), seem to be too young, and should be revised downwards on the following evidence. Lindley (2002a: 275) noted that the occurrence of the index species of Coral Fauna D (Chalcidophyllum recessum) in the Currajong Limestone Member indicates that it should be aligned with the dehiscens rather than the perbonus CZ. The overlying Bloomfield Limestone Member may also have lower beds of dehiscens rather than the perbonus CZ age (Basden 2001: table 2.1). The Warroo Limestone Member contains perbonus CZ elements (Nicoll, in Lindley 2002b), and the uppermost Crinoidal Limestone Member in the Taemas sequence may align with both the inversus and the serotinus CZ (Basden 2001: table 2.1).

These revised alignments are summarised in Fig. 2. Correlation with the upper part of the Wei Jasper sequence is unclear, because the constituent members of the Taemas Limestone are difficult to recognise in the thicker upper part of the sequence, represented by units 1-6 of Young (1969). If the new arthrodire skull described below from Broken River is of serotinus CZ age, as proposed by Sloan et al. (1995), it is still considerably more derived (see below) than any arthrodire from the Burrinjuck sequence. If correctly dated, this would indicate that derived features characterising the Middle-Late Devonian eubrachythoracid arthrodires had originated at least by late Emsian time.

To summarise, it is emphasised that there is no overlap in the arthrodire skull characters just discussed between the Burrinjuck and Broken River limestone sequences, even though the youngest occurrences in the former sequence are also the most derived taxa within the better-documented Burrinjuck arthrodire fauna. For the new taxon described below, this evidence would support either a latest Emsian age (but younger than the Burrinjuck sequence), or an Eifelian age as originally suggested by Prof. J.S. Jell.

**ABBREVIATIONS**

The specimen described below (prefix ANU V) is housed in the Earth and Marine Sciences Department, Australian National University, Canberra (GCY Vertebrate Collection). Standard abbreviations for placoderm dermal bones are used in the text and figures, and together with other morphological abbreviations are listed as follows:

**SYSTEMATIC PALAEONTOLOGY**

Class PLACODERMI McCoy, 1848
Order ARTHRODIRA Woodward, 1891
Suborder BRACHYTHORACI Gross, 1932

*Doseyosteus talenti* gen. et sp. nov.

**Name**

From Dosey Creek, the type locality, and the Greek *osteus* (bone). The species name recognises
Professor John A. Talent, Macquarrie University, who has had a long and distinguished career in Devonian research, including extensive work in the Broken River area of Queensland.

**Diagnosis**

A eubrachythoracid arthrodir in which the skull shows an embayed anterior margin of the nuchal plate resulting from overlap from the central plates, the central plates have strong posterolateral lobes separating the nuchal and paranuchal, and a mesial process of the marginal plate extends to the anterior angle of the paranuchal. Subobstantic area of skull extending onto marginal plate. Dermal bones smooth, or ornamented with fine tubercles.

**Remarks**

Since only the skull is known, and it is incomplete, several features characterising the derived subgroup ‘Eubrachythoraci’ are for the present inferred for this new taxon. Definition of the eubrachythoracid arthrodirises is discussed by Carr (1991: 379-381) and Long (1995: 55). Thus *Doseyosteus talenti* gen. et sp. nov. is assumed to have had a T-shaped rostral plate, a posteriorly placed pineal plate separating the preorbitals, a dermal process of the preorbital plate forming the anterodorsal margin of the orbit, and trilobate central plates. The holotype shows a strongly developed posteriorm thickening of the skull roof, which in the midline is represented by the anterior nuchal thickening. This is much more prominent than the transverse ridge on the posterior margin of the nuchal plate, and is a derived feature seen in coccosteomorph and pachyosteomorph brachythoracids, but generally lacking in Early Devonian taxa, for example the genus *Cathlesichthys* from Burriunjuck, NSW (Young, in press a). The embayed anterior margin and inferred proportions of the nuchal plate, and the strong posterolateral lobe of the Ce plate, are resemblances to the Late Devonian taxa *Eastmanosteus* and *Golshanichthys*, but the former differs in having the posterior pitline well developed on the posterolateral lobe of the central plate, and both forms lack the mesial process of the marginal plate inferred for this new taxon.

**Material**

ANU V1026 (holotype), an incomplete skull preserved as two unconnected portions.

**Locality and Horizon**

Locality BRJ34 (University of Queensland locality L4054), Grid Reference 616 438, Burges 1:100 000 sheet; western bank of Dosey Creek, 750 m upstream from its junction with Broken River (J.S. Jell, letter of 17 April 1980; see discussion above). Horizon was described as the ‘base of thick limestone lens in Broken River Formation’, assigned to the Bracteata Formation (Sloan et al. 1995) or the ‘Lomandra/Dosey Limestone, Broken River Group (Turner et al. 2000).

**Age:** late Emsian - Eifelian (see discussion above).

**Description**

ANU V1026 represents a large part of the posterolateral region of a brachythoracid skull roof, preserved as two separate portions. The larger portion (Fig. 3A, D) includes parts of the Nu, PNu and Ce plates (Fig. 4A, B), and the right postmarginal corner of the skull is preserved as a separate portion (Figs. 3B, C, 4C, D). The specimen was extracted from the rock in six pieces, but they are well preserved, suggesting that it was broken up before incorporation in the sediment. The nuchal (Nu) plate is represented by most of its right half, including the midline, so its overall shape can be estimated. Midline length of the Nu is about 70 mm. It has an embayed posterior margin, with a prominent posterior median process (mppr, Fig. 4). Except for the posterior lateral corner the right lateral margin of the Nu plate is fairly well displayed on the external surface. The bone is fractured in its middle region, and shows anteriorly that it was both overlapped and underlapped by the central (Ce) plate, a condition also reported in *Holomema* (Miles 1971). Along the anterior margin of the plate a thin overlapping lamina of the Ce plate has broken away to reveal an extensive overlap area (oa.Ce, Fig. 4B). In unbroken condition the anterior margin of the Nu plate would have been deeply embayed (Fig. 5). On its visceral surface extensive contact faces for the central plates are developed in the normal manner (cf.Ce, Fig. 4A). Other features shown are the prominent infranuchal pits (if.p) and ridge (if.r) and the transverse nuchal thickening or ridge (nth).

Noteworthy is the strong development of the anterior nuchal thickening (anth), which is relevant to the question of the age of this specimen (see discussion above). This is a derived feature of brachythoracids, and in ANU V1026 is more pronounced than in any Emsian brachythoracid from the Burriunjuck fauna. These have Nu plates which are fairly flat in front of the infranuchal pits. This is the case even in a form like *Cathlesichthys*, which is derived in having a very strong transverse nuchal ridge (Young in press a). In posterior view ANU V1026 shows that the anterior nuchal thickening is more pronounced than the transverse nuchal ridge, the reverse of the condition in *Cathlesichthys*. This advanced character is also seen in most Middle-Late Devonian brachythoracids, such
as *Golshanichthys*, *Tafilalicthys*, and various Gogo forms (e.g. Lelièvre et al. 1981; Lelièvre 1991; Miles and Dennis 1979; Long 1988, 1995; Dennis-Bryan 1987). These taxa all resemble the giant Famennian form *Dunkleosteus*, where the ‘posterior consolidated arch’ of the skull roof (‘PCA’ of Heintz 1932: fig.13) is a broad thickening running in front of the infranuchal pits, as the main transverse thickening of the skull. In contrast, in the Early Devonian form *Cathlesichthys* from Burrinjuck, the transverse nuchal ridge located behind the infranuchal pits forms the main thickening supporting the posterior skull margin.

The right paranuchal (PNu) plate of *Doseyosteus* gen. nov. is represented externally by an elongate portion including the mesial margin forming sutures with the Nu and Ce plates (PNU, Fig.4B). There is also a small broken part of the postmunchal process (pnp). The PNu and Ce plates were also connected by a complex interlocking suture; a broken part around the anterior end of the PNu exposes an overlap area (oa.Ce, Fig. 4B), and the edge of a more extensive contact face is shown on the visceral surface (cf.Ce, Fig. 4A). The endolympathic thickening forms a broad thickened area mesially (th.end), combining with the thickened portion of the Nu plate (anth). This thickened part of the skull is much more prominent than in primitive brachythoracids like *Buchanosteus* or *Taemasosteus* (White 1978; Young 1979). Along the broken edge of the specimen, maximum bone thickness (in the part enclosing the endolympathic duct) is almost 15 mm, which is three times the bone thickness at the anterior preserved extremity of the Nu. The exoskeletal division of the right endolympathic duct opens on the visceral skull roof surface at the anterior edge of the area of thickened bone (th.end), and is also visible on the broken margin of the specimen (d.end, Fig.4A). This is also an advanced character of the brachythoracid skull – in large Emsian brachythoracids.
from Burrinjuck the endolymphatic duct is not within the bone, but anteriorly forms a bony tube attached to or projecting from the inner surface of a much thinner PNu plate (Young in press a: figs. 3, 4, 7A, 9B). A similar condition occurs in Holonema from Gogo (J.A. Long, pers. comm.; Miles 1971: fig. 53).

The preserved part of the right Ce plate is crossed by a prominent sensory groove (csc), which must be the central sensory canal rather than the supraorbital sensory canal, because of its oblique orientation to the midline. Middle and posterior pitlines are represented by faint markings in the region of the ossification centre (mp, pp). Anterolateral and posterolateral margins of the preserved part of the Ce plate are somewhat fractured, but appear to approximate natural margins. The former is bevelled

Figure 4. *Doseyosteus talenti* gen. et sp. nov. Holotype (ANU V1026). A,B. Larger portion of skull in internal (A) and external (B) views. C,D. Smaller skull portion in internal (C) and external (D) views.
externally, and internally shows a contact face for the postorbital plate (cf. PtO), showing that it overlapped the PtO extensively, as in most other brachythoracids (e.g. Miles and Westoll 1968: fig. 2; Young 1979: fig. 1; 1981: fig. 5). Holonema is an exception in this respect (Miles 1971: fig. 12). Subdivisions of the posterior part of this contact face suggest that it also overlapped the marginal (M) plate (cf. M, Fig. 4A).

The posterolateral margin of the Ce plate is somewhat thicker, and carries a deep groove (gr.M) for an interlocking suture, the Ce plate providing external and internal laminae to enclose the margin of the contiguous bone. The nature of the preserved margins suggests that they approximate the suture position. Since the anterior end of the PNu is well shown on the specimen, and is most unlikely to have extended to this margin of the Ce plate, it seems that the intervening space must have been occupied by a mesial projection of the M plate (M, Fig. 5). This arrangement has not previously been recorded in brachythoracids. A similar but smaller process of the M intrudes the Ce plate of Buchanosteus, but this is some distance in front of the PNu (Young 1979: fig. 1).

There is a long posterolateral projection of the Ce plate partly separating the Nu and PNu plates (plpr, Fig. 4B), a feature seen in various other brachythoracids. An early example with this
morphology is *Ulrichosteus* Lelièvre, 1982a from the Givetian of Germany, but this form has the Nu plate extending anteriorly in front of the PNu, whereas in *Doseyosteus* the PNu is slightly longer. *Ardeonosteus* Lelièvre, 1982b also has a strong posterolateral lobe of the Ce, but this Famennian form differs in its sinuous interlocking sutures, broader transverse nuchal thickening, and coarse tubercular ornament. Development of a posterolateral lobe of the Ce is one of three features representing the ‘trilobate’ condition of the Ce plates (characters 13, 14, 21 of Carr 1991), a widespread condition amongst Middle-Late Devonian eubrachythoracids which has proved difficult to define. Internally this part of the Ce is more extensive, the overlapped portion extending back to the endolympathic thickening, again as in other brachythoracids. The visceral surface of the Ce is gently concave laterally, with several shallow grooves (vg) resembling the vascular grooves described in *Holonema* by Miles (1971: fig.12). This depressed region is flanked mesially by the pre-endolympathic thickening (th,pre), which forms a low broad ridge with a curved anteromesial orientation. The preserved anteromesial edge of the Ce plate is thickened and abraded (Fig. 3D).

Associated with this skull portion was a smaller part of the left preobstant corner of the skull roof (Fig. 3B,C), assumed to have belonged to the same individual. The specimen includes part of the PNu and M plates (Fig. 4C,D), and is crossed by a section of the main lateral line (llc), and the infraorbital (ifc.ot) and postmarginal (pmc) sensory canals. Unlike forms such as *Coccosteus*, *Holonema* and *Buchanosteus* (Miles and Westoll 1968; Miles 1971; Young 1979), the M plate carries part of the subobstantial area (soa, Fig. 4D). A subobstantial area of similar extent is seen in the Gogo brachytharicid *Harryoombsia* Miles and Dennis (1979: fig. 4), and in all plurordosteid sensu Long (1995). The PM plate is missing, but on the visceral surface there is a clear contact face for this bone (cf.PM, Fig. 4C). The visceral surface also shows the inframarginal crista to be strongly developed, dorsally as a very prominent irregular knob of bone (kb) separated posteriorly by a deep groove from the ventrally directed crista (cr.im), which itself carries a groove. The free ventral margin of the plate is thickened (lcp), representing the ‘lateral consolidated part’ of the skull, and a depression between the thickening and the inframarginal crista (dep) may correspond to similar structures in *Coccosteus* and *Buchanosteus* Young (1979: 314).

The external ornament on both specimens comprises fine tubercles in some areas, sometimes only faintly discernible on a generally smooth surface (Fig. 3B,D). The fine ornament is similar to that on the SO plate of *Atlantidosteus pacifica*, but that form displays affinity with the homostidi arthrodirae in a range of features (Young 2003a), whereas the skull of *Doseyosteus talenti* gen. et sp. nov. lacks various specialised characters of *Homostius* and related forms (e.g. elongate Nu and PNu plates, small dorsal orbits, etc.). The reduced ornament also distinguishes this new form from various ‘coccosteomorph’ arthrodirae remains known from the early Middle Devonian of northern Germany and the Baltic sequence (Otto 1997, 1999).

An attempted reconstruction of the skull roof of the new taxon based on available information is presented in Fig. 5. The skull could have been broader across the preobstant corners than shown, since the gap between the two preserved portions is based only on a general alignment of sutures and sensory grooves. The anterior part of the skull is unknown, and restored shape of bones is generally based on various coccosteomorph arthrodirae (e.g. Denison 1978: fig. 57). Advanced features depicted (T-shaped R plate, Pi plate separating PrO plates, trilobate Ce plates) are based on their co-occurrence with preserved skull characters in all other known taxa. They need to be confirmed with additional material. On the larger preserved portion, the breadth and anterior embayment of the Nu plate, and the marked posterior lobe of the Ce plate separating the Nu and PNu plates, are general resemblances to *Eastmanosteus* and *Golshanichthys*, as noted above. The M and Ce plates retain extensive contact to separate the PNu from the PtO, the assumed primitive condition for brachythoracids. In contrast, the plurordosteid arthrodirae, which were widespread in the Late Devonian, and apparently replaced the largely Middle Devonian coccosteids (Long 1995), have a much enlarged PtO reaching back to contact both the Ce and PNu plates. In consequence the M plate is reduced in size, whereas in *Doseyosteus* gen. nov., although not completely preserved, the M plate was clearly a more extensive bone, which apparently shows a unique feature in the large mesial process embaying the Ce plate in front of the PNu.

In summary, this new but poorly known brachythoracid shows a range of advanced characters otherwise only seen in Middle or Late Devonian taxa, and it resembles the Frasnian taxa *Eastmanosteus* and *Golshanichthys* in several features which might indicate a close relationship. *Eastmanosteus yunnanensis* Wang, 1991 from the Givetian of China would otherwise be the earliest known member of this group (family Dinichthyidae). *Kiangyosteus* Liu, 1955, also from China (Givetian of Szechuan), may be another primitive dinichthyid (Denison 1978). Both
taxa differ from the new form described here in their well-developed coarse tubercular ornament, presumably a primitive feature. *Doseyosteus talenti* gen. et sp. nov. displays an unusual shape of the M plate which is apparently unique to this new genus and species. More material, including the unknown trunk armour, which in brachythoracids comprises 17 separate bones, will clarify the affinities of this new taxon.

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REFERENCES


Lelièvre, H. (1982a). Ulrichostees miles n. g. n. sp. A new brachythoracid arthrodire (Placodermi) from the Givetian of the Rhineland. *Neues Jahrbuch fur Geologie und Paläontologie Monatshefte 1982*


Miles, R. S. (1971). The Holonematidae (placoderm fishes), a review based on new specimens of *Holonema* from the Upper Devonian of Western Australia. *Philosophical Transactions of the Royal Society of London. B. Biological Sciences* 263, 101-234.


DEVONIAN ARTHRODIRE SKULL FROM QUEENSLAND


