

A new species of *Atlantidosteus* Lelièvre, 1984 (Placodermi, Arthrodira, Brachythoraci) from the Middle Devonian of the Broken River area (Queensland, Australia)

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ABSTRACT

A new brachythoracid arthrodire, *Atlantidosteus pacifica* n. sp., is described from the Middle Devonian (Eifelian Broken River Group; *costatus-australis* conodont zone) of Queensland (Australia). This is the first record of this genus outside its type area (Early Devonian of Morocco), and adds to evidence of a similar fish fauna in shallow tropical to subtropical marine environments along the eastern and northern margins of the Gondwana supercontinent. The new species is based on a large suborbital plate of unusual shape, from possibly the largest arthrodire recorded so far from the Australian Devonian, with an estimated skull length of 50 cm. It closely resembles the suborbital of the type species (*A. hollardi* Lelièvre, 1984), with a high postorbital lamina and distinctive sensory groove pattern, but differs in the pointed anterior margin to the unornamented mesially directed suborbital lamina, and the absence of a dorsal angle on the curved dorsal margin of the postorbital lamina. *Atlantidosteus* Lelièvre, 1984 is provisionally placed as a sister group to *Homostius* Asmuss, 1856, with which it shares a suborbital plate with an elongate internal suborbital lamina.

KEY WORDS

Vertebrata,
Placodermi,
Arthrodira,
Devonian,
Morocco,
Australia,
new species.

RÉSUMÉ

Une nouvelle espèce d'Atlantidosteus Lelièvre, 1984 (Placodermi, Arthrodira, Brachythoraci) du Dévonien moyen de Broken River (Queensland, Australie).

Un nouvel arthrodire Brachythoraci, *Atlantidosteus pacifica* n. sp., est décrit. Il provient du Dévonien moyen (Eifélien du Groupe de Broken River : zone de conodontes *costatus* à *australis*) du Queensland en Australie. Cette découverte représente la première mention de ce genre en dehors de sa localité type, le Dévonien inférieur du Maroc. Par ailleurs, cette découverte souligne l'existence d'une ichthyofaune comparable appartenant à des environnements marins tropicaux ou subtropicaux le long des marges est à nord du Gondwana à cette époque. La nouvelle espèce, fondée sur une plaque sousorbitaire, partage avec l'espèce type (*A. hollardi* Lelièvre, 1984) une forme générale très particulière. C'est peut-être le plus grand arthrodire connu du Dévonien d'Australie, la longueur de son toit crânien pouvant être estimée à une cinquantaine de centimètres. Les états de caractères partagés par la plaque sousorbitaire d'Australie et l'espèce type sont la hauteur de la lame postorbitaire et le patron des sillons sensoriels. Elles diffèrent par la forme pointue du bord antérieur de la lame suborbitaire non ornementée et dirigée médialement et par l'absence d'angulation du bord dorsal de la lame postorbitaire. *Atlantidosteus* Lelièvre, 1984 est considéré provisoirement comme le taxon-frère d'*Homostius* Asmuss, 1856 avec lequel il partage une plaque sousorbitaire dont la lame suborbitaire interne est allongée.

MOTS CLÉS

Vertebrata,
Placodermi,
Arthrodira,
Dévonien,
Maroc,
Australie,
nouvelle espèce.

INTRODUCTION

The Broken River area of Queensland (Fig. 1) contains a large tract of Devonian sedimentary rocks, including many marine limestones that have yielded a range of invertebrates, including conodonts useful in dating the sedimentary sequence (Mawson & Talent 1989; Sloan *et al.* 1995). Vertebrate remains so far reported from this sequence are mainly microfossils (see Turner *et al.* 2000). These authors also noted various vertebrate macro-remains, but to date only two new genera of antiarch placoderms have been described (Young 1990). However brachythoracid arthrodire remains predominate amongst the large amount of undescribed macrovertebrate material from the Broken River limestones. The order Arthrodira is the most diverse placoderm subgroup, with almost twice the diversity of the remaining placoderm orders. Its major subgroup, the Brachythoraci, comprises nearly 60% of about 170 genera within the order (Carr 1995). Turner *et al.* (2000: fig. 8) illustrated a brachy-

thoracid suborbital plate from the Broken River sequence, and two taxa were listed by Young *et al.* (1993: 247) as belonging to a “*Wurungulepis-Atlantidosteus* fauna”, of assumed Eifelian age: *Atlantidosteus* sp. and a “eubrachythoracid”. In this paper I formally describe the specimen on which the former attribution is based, as a new species of the genus *Atlantidosteus* Lelièvre, 1984. The arthrodire material from Broken River was collected by Prof. John Jell (University of Queensland). It was sent to Prof. Ken Campbell (Geology Department, Australian National University, Canberra) who passed the placoderm remains on to me for acid preparation and study. The brachythoracid arthrodirids were one of the most successful groups of early gnathostome fishes (e.g. Young 1986; Janvier 1996), and in marine environments of the Late Devonian they included probably the largest predators of their time. They were already widespread in shallow marine environments of the Early Devonian (e.g. Young *et al.* 2001; Mark-Kurik & Young 2003), and the major radiation of brachythoracid sub-

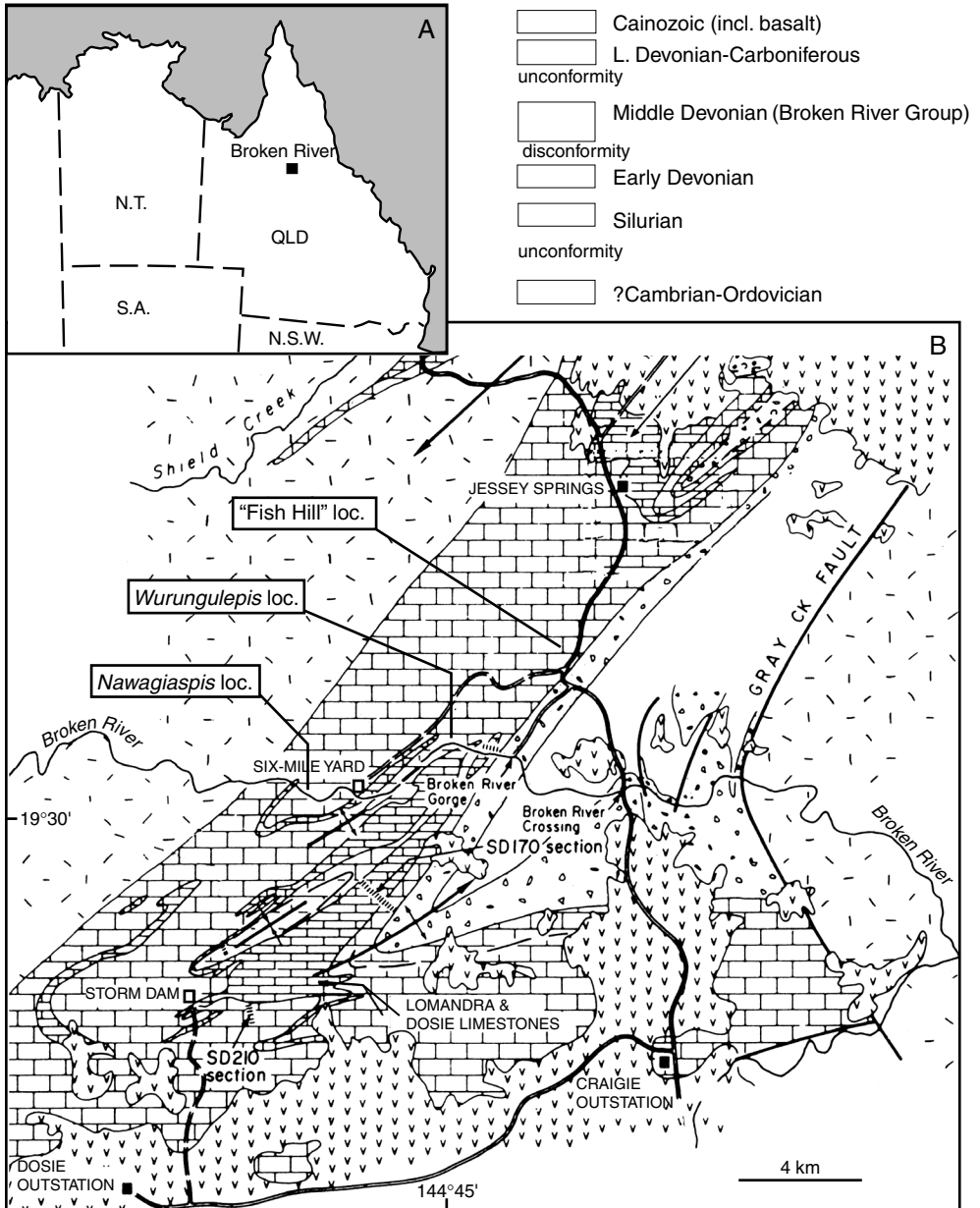


FIG. 1. — **A**, location of the Broken River area in Queensland, Australia; **B**, geological map of the collecting area (modified from Turner *et al.* 2000: fig. 2), showing the locality for the specimen described in this paper ("Fish Hill"), and the localities for antiarchs *Nawagiaspis* Young, 1990 and *Wurungulepis* Young, 1990.

groups had apparently already occurred by the Middle Devonian. The new form described here adds to evidence of a similar fish fauna extending

along the eastern and northern Gondwana margins, in shallow tropical to subtropical seas of the Early-Middle Devonian.

LOCALITY AND AGE

The specimen (collected by J. Jell) comes from University of Queensland locality UQL 4472 (BRJ 67B), Grid Reference 675 485, Burgess 1:100000 sheet. Locality description was given as: "Top of ridge to three-quarters way down western slope, west of road between Six Mile Dam and Diggers Creek" (J. Jell pers. comm. in a 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 *koekelianus* zonal range for the Fish Hill section.

ABBREVIATIONS

Standard abbreviations for placoderm dermal bones are used in the text and figures as follows:

AL	anterior lateral plate;
AVL	anterior ventrolateral plate;
C	central plate;
M	marginal plate;
MD	median dorsal plate;
Nu	nuchal plate;
PMV	posterior median ventral plate;
PN	postnasal plate;
PNu	paranuchal plate;
PrO	preorbital plate;
PtO	postorbital plate;
PVL	posterior ventrolateral plate;
SM	submarginal plate;
SO	suborbital plate.

SYSTEMATICS

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

Genus *Atlantidosteus* Lelièvre, 1984

REMARKS

Lelièvre (1984a) defined his new genus on the following features of the SO plate: suborbital lamina strongly incurved in a medial direction; high postorbital lamina; ornamentation of very small tubercles. The unusual shape of this new

example of the SO plate closely resembles that of the type species, in having a high postorbital lamina with a curved dorsal margin, an unornamented mesially directed suborbital lamina, and a distinctive sensory groove pattern.

Atlantidosteus pacifica n. sp.
(Figs 2; 3; 5B)

Atlantidosteus sp. – Young *et al.* 1993: 247.

"suborbital plate... resembling that of *Homostius*"; "*Atlantidosteus*" – Turner *et al.* 2000: 497.

HOLOTYPE. — ANU V1033 (housed in the Geology Department, Australian National University, Canberra) is the only known specimen, a right SO plate from the cheek of a large arthrodire.

ETYMOLOGY. — An allusion to proximity of the fossil locality to the Pacific margin of the Palaeozoic Gondwana supercontinent.

DIAGNOSIS. — An *Atlantidosteus* in which the suborbital lamina of the suborbital plate decreases in height towards a pointed anterior margin, the postorbital lamina has a continuously curved dorsal margin, with no dorsal angle, and the anterior end of the suborbital section of the infraorbital sensory groove has a slight upward curvature.

REMARKS

Since only two of these highly distinctive SO plates have ever been found, it is possible that new material could indicate that the differences listed above could result from intraspecific variation. However it is considered more likely that this is a closely related species, of a slightly younger age than the genotype, which is associated with mid-Emsian (*laticostatus* zone) conodonts (Lelièvre 1984a: 197).

DESCRIPTION

This almost complete right SO plate has a preserved total length of 23.6 cm, and maximum depth of the postorbital lamina of 100 mm. It is thus of similar size to the SO of the type species (estimated length 23–25 cm), but considerably smaller than the corresponding bone of *Homostius* Asmuss, 1856 (about 40 cm long; Heintz 1934: fig 22). By comparison with a cast of the specimen of

Homostius milleri Traquair, 1888 figured by Heintz (1934: pl. 14, fig. 1), in which the left SO is about 15.5 cm long on a skull roof some 33 cm in length, ANU V1033 could have come from a skull up to 50 cm long (assuming similar proportions). This would make it the largest arthrodire yet found in Australia (*Westralichthys* Long, 1987 from Western Australia is a skull roof about 27 cm long). Apart from its large size, this is a highly distinctive SO plate (Figs 2; 3), clearly very similar to the SO of the type species, *A. hollardi* Lelièvre, 1984. Various differences in shape and development suggest that it is a separate species. The dorsal margin of its postorbital lamina has an even curvature over its entire length, in contrast to the type species, in which the anterior part of the dorsal margin is relatively straight, leading up to a dorsal angle (Lelièvre 1984a: fig. 2A). Most of the posterior margin, which is missing in the type species, is broken and irregular in this new specimen, but given the thinness of the bone edge it has been assumed in the restoration that there is little missing (dashed lines, Fig. 3). The fine tubercular ornament is similar to that on the type species, and may be a generic characteristic. In both species the suborbital lamina lacks ornament, and presumably was embedded in soft tissue. A scattering of larger tubercles is developed beneath the supraoral sensory groove in the region of the ossification centre in ANU V1033, and the periphery of the dorsal and posterior margins is smooth (Fig. 2A). Posteriorly this may be partly due to abrasion, but along the anterodorsal margin it is natural, indicating either attachment of skin, or loose overlap of adjacent bones (the PtO and M plates of the skull roof). The anterior section of the dorsal margin shows a slight groove for contact with the PtO and/or M plate (gr.PtO/M, Fig. 3). The suborbital section of the infraorbital sensory canal (ioc.sb, Fig. 3A, C) has a posterior inflection enclosing an angle of no more than 70°. It terminates anteriorly in the unornamented extension of the suborbital lamina (so.la, Fig. 3A), which was presumably embedded in soft tissue. This is somewhat different to the typical brachythoracid arrangement where the suborbital lamina is in contact with the ventral

skull-roof margin in front of the orbit, for example the PN plate of *Dunkleosteus* Lehman, 1956 (e.g. Heintz 1932: fig. 34). Beneath the angular inflection is a small row of pits (sb.sp, Fig. 3A), and the supraoral sensory canal (sorc) runs obliquely downwards and backwards to pass off the ventral margin just behind a ventral unornamented flange. All of these features are similarly developed on the type species, but the groove along its anterodorsal margin is more extensive, reaching almost to the dorsal corner (b.pto, Lelièvre 1984a: fig. 2A).

Two distinct shallow grooves in the ornament of ANU V1033 have the appearance of healed wounds or lesions (le, Fig. 3A). The longer groove has intermittent enlarged tubercles around its margins, with a few scattered across it (Fig. 2A), confirming that it could not be a *post-mortem* feature. It is of interest that Lelièvre (1984a) also described an irregular depression at the start of the suborbital lamina in *A. hollardi*, which was similarly interpreted as the healed scar of a wound. From its size and depth this was evidently a more serious injury than the shallow lesions on ANU V1033. Observed differences on the external surface of ANU V1033 compared to the preserved part of the type species include the more continuous horizontal canal, which forms a short narrow posterodorsal groove (hc, Fig. 3A), and the distinct cutaneous sensory pit (cuso, Fig. 3A). This is presumably the homologue of the anterior pit on the SO of *Buchanosteus* Stensiö, 1945 (e.g. Young 1979: fig. 13) or *Coccoosteus* Miller, 1841 (Miles & Westoll 1968: fig. 14). It was not identified in the type species, but the SO is cracked right through at the appropriate position (Lelièvre 1984a: fig. 2), so it may have been present but not preserved. The lower section of the infraorbital sensory canal in ANU V1033 curves slightly upward to the front, where it expands to merge with the unornamented anterior surface of the suborbital lamina (ioc.sb, Figs 2A; 3A). The thickened exposed part of the external surface of the SO forms an irregular pointed anterior margin to the ornamented surface between the two sections of the infraorbital sensory groove. In front of this the surface is stepped in by some

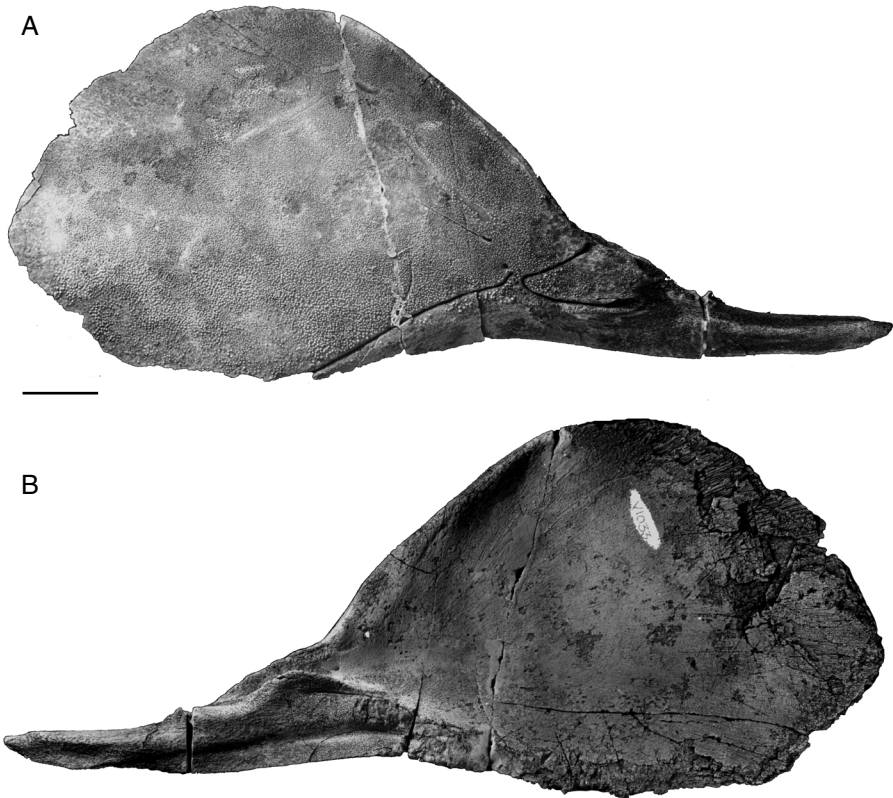


FIG. 2. — *Atlantidosteus pacifica* n. sp., holotype (ANU V1033), a right suborbital plate from the cheek in external (A) and internal (B) views (acid prepared specimen coated with ammonium chloride sublimate). Scale bar: 20 mm.

4 mm, and has a spongy open texture. In anterior view this stepped surface appears as two slightly concave facets. The clear delineation between exposed and non-exposed areas of the external surface compares closely with the SO of *Homostius*, in which Heintz (1934: fig. 22) identified several “limits” subdividing the “handle” of the SO from the “blade”, and dividing the “blade” into two portions. The important margin is that labelled a-d-c (Fig. 4A), which defines the anterior limit of the exposed part of the external surface. In *Homostius* the SO differs from that described here in having a much more extensive area covered dorsally in a loose overlap by the PtO and M plates (oaPtO+M, Fig. 4A). Since the orbit in *Homostius* is completely enclosed by the PrO and PtO, it is likely that the PrO also overlapped the SO anteriorly. In *Atlantidosteus* the

overlap for the PtO appears in lateral view as a narrow flange only at the anterior end of the blade portion (oaPtO, Fig. 3), although it is in fact a broad upwardly facing surface. The corresponding part in *A. hollardi* was identified as an “encoche orbitaire” by Lelièvre (1984a: fig. 2A), but part of this margin is not complete (Lelièvre 1984a: fig. 2C, pl. 1B), so it is possible that it was similarly developed as an overlap for the PtO (shaded area on upper margin, Fig. 5A).

The inner surface of ANU V1033 is much more complete posteriorly than in the type species (Lelièvre 1984a: pl. 1A), although the posterior part of the bone shows few features. Radiating striations on the abraded posterodorsal margin (Fig. 2B) indicate the anteriorly placed ossification centre, as in *A. hollardi*, where the striations are more prominent anteriorly in an area which is

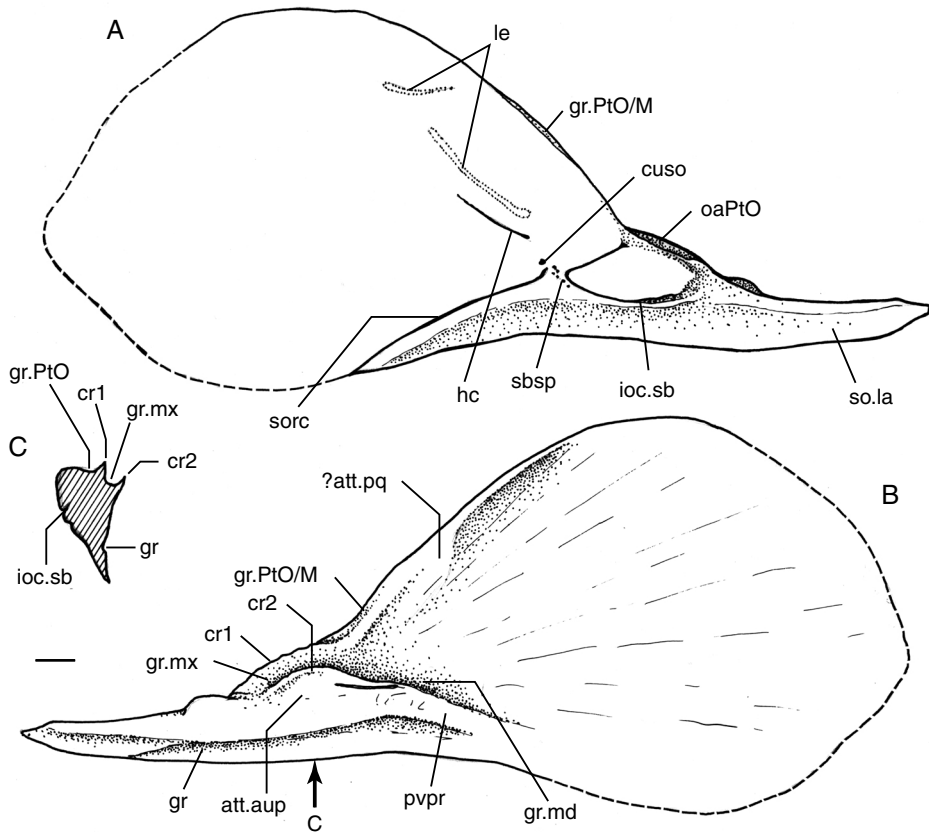


FIG. 3. — Restoration of the right suborbital (SO) plate of *Atlantidosteus pacifica* n. sp.; **A**, external surface; **B**, internal surface; **C**, section through the suborbital lamina at the level indicated (arrow in B). Abbreviations: **att.aup**, attachment surface for the autopalatine; **?att.pq**, possible attachment surface for the metapterygoid part of the palatoquadrate; **cr1, 2**, outer and inner crests on dorsal surface of suborbital process; **cuso**, cutaneous sensory organ; **gr**, groove; **gr.mx**, groove for the maxillary branch of the trigeminal nerve; **gr.md**, groove for the mandibular branch of the trigeminal nerve; **gr.PtO/M**, area abutting postorbital plate and/or marginal plate; **hc**, horizontal sensory groove; **ioc.sb**, suborbital section of infraorbital sensory groove; **le**, lesions or healed wounds on external surface; **oaPtO**, area overlapped by postorbital plate; **pvpr**, posteroventral process of SO plate; **sbsp**, suborbital sensory pits; **so.la**, suborbital lamina of SO plate; **sorc**, supraoral sensory groove. Scale bar: 10 mm.

smooth in *A. pacifica* n. sp. This difference may be due to better preservation. A depressed groove on the anterodorsal margin of the type species is interpreted by Lelièvre (1984a: fig. 2B) as an area for attachment of the palatoquadrate. In the SO of *Buchanosteus* (Young 1979: pl. 3B) the palatoquadrate attachment is similarly developed, as an area delimited by two ridges (remnants of the perichondral ossification). However in the new specimen the corresponding region is just a smooth thickened area (?att.pq, Fig. 3B), with no ridges, possibly suggesting that the palatoquadrate was not perichondrally ossified. Similarly, the

attachment for the autopalatine (att.aup, Fig. 3B) is less developed than in *A. hollardi*, with a smooth, gently concave surface in place of the irregular ridges of that species. In both species this area has a very similar convex dorsal margin forming a crest (cr2, Fig. 3B, C). This crest encloses a groove (gr.mx, Fig. 3B, C) probably for the maxillary branch of the trigeminal nerve, together with the buccalis lateralis nerve passing anteriorly, and the mandibular branch of the trigeminal nerve passing posteriorly (Lelièvre 1984a: fig. 2C). In *Buchanosteus* a groove possibly for the maxillary branch of the orbital artery was also identified

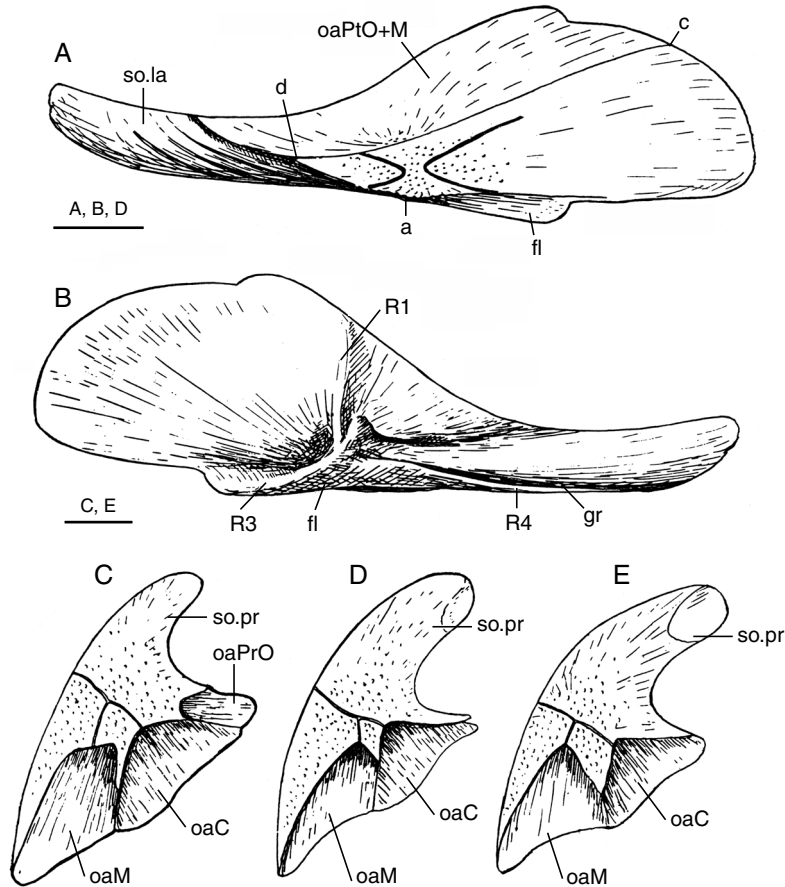


FIG. 4. — *Homostius* spp.; **A, B**, left suborbital plate (external and internal views); **C-E**, left postorbital plates, of *H. arcticus* Heintz, 1934 (**C**), *H. latus* Asmuss, 1856 (**D**) and *H. milleri* Traquair, 1888 (**E**). (Modified from Heintz 1934: figs 22, 23, 50). Abbreviations: **a, c, d**, limits to the external surface of the suborbital plate identified by Heintz (1934); **fl**, ventral unornamented flange; **gr**, groove; **oaC**, area overlapped by central plate of skull roof; **oaM**, area overlapping or overlapped by marginal plate of skull roof; **oaPrO**, area overlapped by preorbital plate of skull roof; **oaPtO+M**, area overlapped by postorbital and marginal plates; **R1, 3, 4**, internal ridges on the suborbital plate identified by Heintz (1934); **so.la**, suborbital lamina; **so.pr**, suborbital process of postorbital plate. Scale bars: A, B, D, 5 cm; C, E, 3 cm.

running anteriorly beneath the orbit (Young 1979: fig. 15). The autopalatine attachment in ANU V1033 can be assumed to extend forward to the extremity of the suborbital lamina, where its ventral limit is marked by a groove (gr, Fig. 3B, C), also as preserved in *Buchanosteus* (Young 1979: pl. 3B). The corresponding groove is evidently more pronounced in *Homostius*, with an extensive ventral lamina (R4 of Heintz 1934: fig. 23). In *A. pacifica* n. sp. the crest identified as a linguiform process in *A. hollardi* is not developed, and the shape of the suborbital lamina is different,

tapering to a point anteriorly (Fig. 5A, B). Its ventral margin is gently convex anteriorly, and concave posteriorly (Fig. 2). In contrast, in *A. hollardi* the suborbital lamina is expanded at its anterior preserved end, which is broken. Its anterior angle may have narrowed to a point, as in *A. pacifica* n. sp., in which case it seems that the suborbital lamina would have been proportionately longer in *A. hollardi* (about 35% of total length). Beneath the linguiform process there is an irregular ventral flange (Lelièvre 1984a: pl. 1A), and a similar flange may be developed in

Homostius (fl, Fig. 4B). A posterior thickening in ANU V1033 (pvpr, Fig. 3B) may correspond to that supporting the posteroventral process of the palatoquadrate in *Buchanosteus*, but its surface is somewhat abraded (Fig. 2B). This structure may be less well developed in *A. hollardi*, but is also abraded. Again, a similar but more prominent ridge is developed in the SO of *Homostius* (R3 of Heintz 1934: fig. 23), but neither species of *Atlantidosteus* shows the vertical ridge (R1 of Heintz), although the bone is thickened in this region.

In ANU V1033 the dorsal aspect of the area transitional between the suborbital and postorbital laminae is similar to that illustrated by Lelièvre (1984a: fig. 2C), but more completely preserved. Direct comparison with a resin cast of *A. hollardi* (ANU V3030) shows some minor differences. The inner crest (cr2, Fig. 3B, C) is convex mesially when viewed from above, whereas in *A. hollardi* it follows the inner bone surface, and continues farther posteriorly to define a mandibular groove of some width (g.n.md, Lelièvre 1984a: fig. 2C). In *A. pacifica* n. sp. this groove is less well defined, forming only a shallow depression. The outer crest (cr1, Fig. 3B, C) is also convex mesially (not preserved in *A. hollardi*). Lateral to this the anterior end of the groove for the PtO plate is expanded as a shallow concave depression supported by the maximum thickness of the bone (gr.PtO, Fig. 3C).

DISCUSSION

FUNCTION

The orbit of *Homostius* is unique amongst the Arthrodira in being entirely enclosed laterally by the PrO and PtO plates, with the latter plate highly modified in shape, with a form of suborbital process (so.pr, Fig. 4C-E). Nevertheless, in this taxon “the SO has preserved nearly the same form as in other *Arthrodira*” (Heintz 1934: 37), with an elongate anterior “handle” portion (the suborbital lamina), and an expanded posterior “blade” (Fig. 4A, B). Lelièvre (1984a) identified the dorsal border of the suborbital lamina in

Atlantidosteus as an “encoche orbitaire”, but whether it actually formed the lateral margin of the orbit is open to interpretation. In basal brachythoracids a distinct postorbital angle is developed to delimit the two portions of the SO plate, and it may form a moveable articulation with the PtO, as described by Young (1979: fig. 15). It is clear that such a dermal articulation was not developed in *Homostius*, where the SO was extensively overlapped by the lateral plates of the skull roof in a loose connection, as seen in some articulated examples of *Homostius milleri* from Scotland (e.g. Heintz 1934: fig. 24). In most eubrachythoracids this postorbital dermal articulation is lacking because the dermal cheek unit is less intimately attached to the lateral skull margin (e.g. Carr 1991: fig. 2). This is probably related to the fact that the cheek suspension is largely or entirely carried by the internal connection between the anterior postorbital process of the braincase, and the opercular cartilage or epihyal element attached inside the SM plate (e.g. Gardiner & Miles 1990: figs 18, 20). The length of the dorsal contact between the SO and the skull may be a useful phylogenetic character.

In *Homostius* the highly modified PtO plate has developed a similar anterior suborbital projection to the process (lamina) seen on the SO of other arthrodiras (Fig. 4C-E), which forms the lateral border of the orbit in place of the SO (ptp of Heintz 1934: fig. 16). Nevertheless, there is a good functional reason why the SO has retained its “cleaver”-like shape in *Homostius*. The suborbital lamina of the SO in all Arthrodira, and perhaps all other placoderm groups, has an additional morphological relationship and essential function in the jaw apparatus. It is always fused to the outside of the autopalatine, which in turn (in arthrodiras) supports the posterior supra-gnathal element of the upper jaw. Thus, the anterior projection in the SO of *Homostius* presumably retained its elongate shape to project anteromesially beneath the orbit, to form the connection between the autopalatine and the endocranium, with which both the upper dermal toothplates are closely associated (e.g. Young *et al.* 2001: fig. 5C).

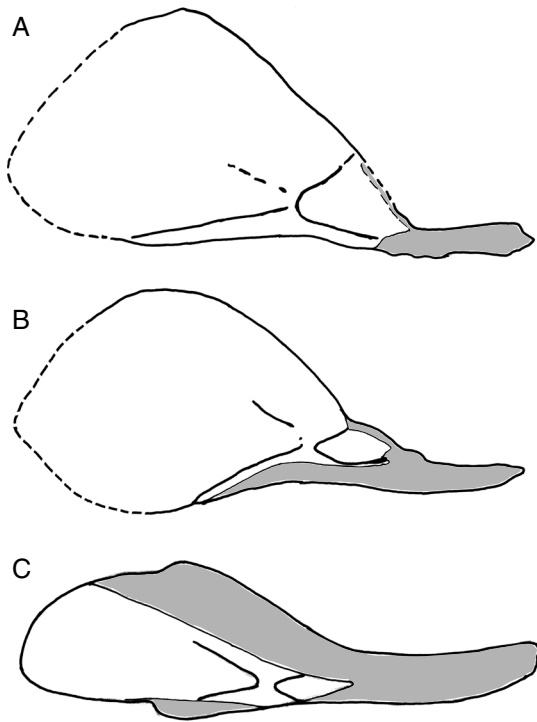


FIG. 5. — Comparison of suborbital plates of *Atlantidosteus* Lelièvre, 1984 and *Homostius* Asmuss, 1856 (not to scale; reduced to same length), showing the extent of unornamented parts of external surface (shaded); **A**, *Atlantidosteus hollardi* Lelièvre, 1984; **B**, *A. pacifica* n. sp.; **C**, *Homostius* sp. Shaded areas in *Homostius* include those overlapped by the postorbital and marginal plates of the skull (dorsal margin), and those assumed to be embedded in soft tissue (ventral margin and suborbital lamina). **A**, based on Lelièvre (1984a: fig. 2A); **C**, based on Heintz (1934: fig. 22).

PHYLOGENETIC POSITION OF *ATLANTIDOSTEUS*

Lelièvre (1984a: fig. 5) placed *Atlantidosteus* as a “primitive” brachythoracid of uncertain position, between *Buchanosteus* and homostiids on his cladogram. Its position was defined by characters of the trunk armour (high dorsal angle on AL, straight posterior border on AVL). However some additional phylogenetically informative characters can be inferred from the SO plate as described above in *Atlantidosteus pacifica* n. sp. Lelièvre (1984a: 203, 204) identified three important characters of the SO: the high postorbital lamina, the long suborbital lamina, and the narrow angle formed by the infraorbital sensory

groove and its suborbital branch. Only the last of these was used to place his new genus phylogenetically. The long suborbital lamina was assessed as a general brachythoracid character, following Miles & Dennis (1979: fig. 15), who had identified three advanced characters of brachythoracids which were absent in *Homostius*, one of which was “slender suborbital lamina on the suborbital plate”.

Young (1981: 265) interpreted the dorsal position of the orbits in *Homostius* as an autapomorphy, and concluded that the absence of a slender suborbital lamina could have been “independently acquired with dorsal migration of the orbits”. Lelièvre (1988: 293; 1995: 189) scored “development of a suborbital lamina of the suborbital plate” as character 27 in a PAUP analysis (Swofford 1991) of primitive brachythoracids. He noted that the development of the suborbital lamina may depend on the position of the orbit, with the derived state represented in several Late Devonian genera (e.g. *Tafiallichthys* Lehman, 1956, *Melanosteus* Lelièvre & Goujet, 1987, *Gymnotrachelus* Dunkle & Bungart, 1939 and *Heintzichthys* Whitley, 1933), and the disposition in *Homostius* being a special case. In the genus *Antineosteus* Lelièvre, 1984 from the Emsian of Morocco, placed by Lelièvre (1995: fig. 14) as the sister group to *Homostius*, there is no suborbital lamina (Lelièvre 1984b: fig. 13). The degree of ossification of the autopalatine may also be a factor (previously discussed by Lelièvre *et al.* 1987). The position of the homostiids was also reviewed by Carr (1991: 379), who proposed three characters supporting monophyly of homostiids-buchanosteids (his numbering retained): 29, elongation of Nu and PNu; 31, posterior position of the C/PNu/M triple point; 82, less than 90° angle between suborbital and postorbital branches of the infraorbital sensory groove. Lelièvre’s (1995) phylogenetic analysis of “primitive brachythoracids” excluded many genera (including *Atlantidosteus*), because they were too poorly known to be scored in the matrix. A strict consensus of three equally parsimonious topologies identified two main groups within the Brachythoraci, with the position of the genera

Buchanosteus and *Maideria* Lelièvre, 1995 remaining unstable (Lelièvre 1995: figs 13, 14). The Brachythoraci was diagnosed by the following three synapomorphies (his numbering retained): 1, skull roof bones with extensive overlaps; 2, posterior postorbital process with only one branch; 6, postnuchal process on PNu plate. “Primitive” brachythoracids were grouped together as “Migmatocephala”, based on two synapomorphies: 11, elongate Nu and PNu plates; and 38, MD plate shorter than broad. More advanced “eubrachythoracids” were diagnosed on the following four synapomorphies: 16, PrO plate forming an embayment of the central plate; 30, occlusal surface of anterior supragnathal smooth, rather than denticulate; 47, separated supraoral and infraorbital sensory lines on SO plate; and 48, occipital cross-commissure passing behind Nu plate onto extrascapulars.

Of these synapomorphies, only character 47 is known for *Atlantidosteus* (with separate supraoral and infraorbital sensory line grooves). However the validity of this character may be uncertain, since in *Holonema* both conditions occur (Miles 1971: figs 32A, 33A), whilst the scoring in Lelièvre (1995) may not be reliable. The sensory line arrangement on the SO in *Atlantidosteus* is essentially that of *Goodradigbeeon* White, 1978, *Buchanosteus*, *Taemasosteus* White, 1952, or *Antineosteus*, and is presumably primitive. The earlier assessment of Lelièvre (1984a: fig. 5), that two major groups of brachythoracids could be identified on the position of postsuborbital sensory groove, is invalid because one of the two conditions must be assumed primitive on the grounds of parsimony. On the other hand, the anteriorly and posteriorly facing loops of the sensory grooves on the SO of *Homostiis*, with no connection between supraoral and infraorbital grooves, may be an autapomorphy, although a similar condition in *Livosteus* Obrucheva, 1962 would be independently developed if this form is correctly placed as a coccosteid (Denison 1978: fig. 63A). However, Lelièvre (1984a: 204) discussed this point and concluded on this and other characters that *Livosteus* might be a primitive brachythoracid related to *Homostiis*. Carr (1991:

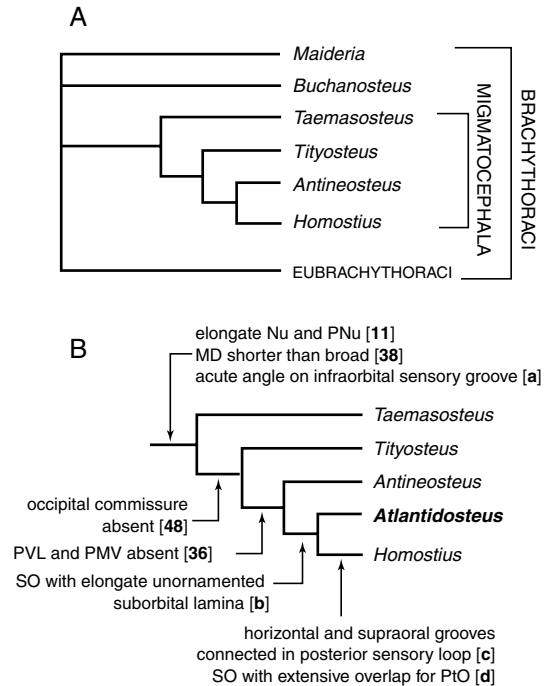


FIG. 6. — **A**, strict consensus tree on which Lelièvre’s (1995) classification of primitive brachythoracids was based; **B**, possible relationship of *Atlantidosteus* Lelièvre, 1984 within Lelièvre’s “Migmatocephala”. Characters resolved as synapomorphies in Lelièvre’s (1995) analysis are summarised [his numbers in square brackets]. Other characters (a–d), suggested by features of the suborbital plate, are discussed in the text. Abbreviations: **MD**, median dorsal plate; **Nu**, nuchal plate; **PMV**, posterior median ventral plate; **PNu**, paranuchal plate; **PTO**, postorbital plate; **PVL**, posterior ventrolateral plate; **SO**, suborbital plate.

character 83) correctly scored coccosteids as having confluent supraoral and infraorbital sensory lines, and this advanced feature is also evident in the SO plate illustrated as an “atlantidosteid gen. et sp. indet.” by Turner *et al.* (2000: fig. 8.7), which therefore can probably be referred to a eubrachythoracid. However, as earlier noted by Lelièvre (1984a: 204), the acute angle between suborbital and postorbital branches of the infraorbital sensory groove is not seen in buchanoosteids (Young 1979: pl. 3A), and may therefore be a synapomorphy of homostiids and related taxa, rather than indicating homostiid-buchanoosteid monophyly (cf. character 82 of Carr 1991). Within the Migmatocephala, Lelièvre’s (1995) analysis placed *Taemasosteus* as

sister group to *Tityosteus* Gross, 1960, *Antineosteus*, and *Homosti* (Fig. 6A), based on characters of the skull and trunk armour (occipital cross-commissure absent; PVL and PMV absent), which again are unknown for *Atlantidosteus*. However, a provisional placement for *Atlantidosteus*, based on comparisons of the SO plate (characters a-d, Fig. 6B), would require that it lacked both the occipital cross-commissure, and PVL and PMV plates in the trunk armour, and possessed elongate Nu and PNu plates in the skull, and also a shorter than broad MD plate. These all stand as predictions to be tested when more complete remains of this taxon become available.

This new occurrence establishes a distribution for the arthrodire genus *Atlantidosteus* indicating continuity of shallow tropical to subtropical marine environments along the eastern and northern margins of the Gondwana supercontinent. On most current reconstructions this margin had a palaeolatitude between 0°-30°S (e.g. Young 2003: fig. 2). The only other likely connection (constrained by palaeolatitude) would be across the proto-Pacific ocean, assuming this large ocean existed in the Early Palaeozoic (cf. Nur & Ben-Avraham 1981). If *Atlantidosteus* is correctly placed within the Homostiidae, then the wide distribution of Middle Devonian homostiids across Baltica and Laurentia would be consistent with the idea of increasing proximity between Gondwana and Laurussia (Euramerica), involving first shallow marine, and then non-marine fish dispersal during the Middle and Late Devonian (Young *et al.* 2000a, b; Young & Moody 2002; Young 2003).

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