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A new dinichthyid fish (Placodermi: Arthrodira) from the Upper Devonian of Western Australia, with a discussion of dinichthyid interrelationships

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Abstract

A new dinichthyid arthrodire, *Westralichthys uwagedensis* gen. *et* sp. nov. is described from the Upper Devonian carbonates of the Canning Basin, Western Australia. Although the exact location of the specimen is unknown an associated conodont fauna indicates a mid-Famennian (toIIB) age, and suggests that the specimen may have come from the Virgin Hills Formation. *Westralichthys*, known from one incomplete skull roof, is characterised by having a skull roof pattern with a broad trapezoidal nuchal plate, weakly trilobate centrals and very elongated marginal and postorbital plates, whilst lacking dermal ornamentation. The visceral surface has massive nuchal and lateral thickenings, deep mesial pits on the paranuchals, and well developed ventral postocular processes. The braincase had a well developed supraorbital process. *Westralichthys* is regarded as more derived than *Eastmanosteus* and *Golshanichthys* in possessing elongated postorbitals, a broad nuchal plate, lacking dermal ornamentation and in having well developed inframarginal laminae, and is placed as the sister taxon to *Dunkleosteus* plus higher dinichthyids. Paedomorphosis may have played a role in the evolution of the dinichthyids from the Middle Devonian coccosteomorphs.

Introduction

Although fish fossils from the Upper Devonian reef complexes of the Kimberleys are well known from the Frasnian Gogo Formation (Gardiner and Miles 1975) reports of Famennian vertebrates are scarce. Radke and Druce (1979) refer to fish remains from the Late Famennian Gumhole Formation, including mention of large brachythoracid arthrodires. These remains, which are currently under study by Dr Gavin Young (Bureau of Mineral Resources, Canberra) are readily distinguished from the large dinichthyid skull described in this work by their coarse tubercular ornamentation. Aside from the Gumhole Formation fishes there have been recent discoveries of other Famennian vertebrates from the Canning and Bonaparte Basins which are under study by the author.

The large placoderm skull described herein was found inside the Geology Museum, at the University of Western Australia (henceforth UWA) in February 1986. The specimen had been allocated UWA number 32614, but no locality information was recorded. It had been collected in the late 1930s or early 1940s

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by Curt Teichert, and shortly after sent to Prof. Hills at Melbourne University for further study. Prof. Hills eventually returned the specimen to the UWA in 1973. Thus the specimen was overlooked by Mr Harry Toombs of the British Museum of Natural History who came to Western Australia in 1963 and recognised the scientific value of the Gogo fish material. Hills (1958 p. 90) cites Teichert (1949) and makes brief mention of the specimen as "a giant arthrodire of dinichthyid type from the *Cheiloceras* zone'. Teichert's paper lists assemblages of invertebrates and mentions fish remains in limestone concretions from the *Manticoceras* zone (Gogo Formation) and also from zone 2 (*Cheiloceras* zone; Teichert 1949, p. 17) but does not mention the spectacular dinichthyid skull. Gilbert-Tomlinson (1968, p. 210) mentions the dinichthyid skull from the *Cheiloceras* zone found by Teichert and states that it came from sediments then assigned to the Virgin Hills Formation. Unfortunately, despite recent correspondence, no further information could be obtained apart from "somewhere probably in the south-eastern part of the Canning Basin" (Prof. Teichert, pers. comm.). The specimen is of scientific interest in being the first record of a large dinichthyid placoderm from Australia, and with an estimated size of up to 3 metres long, possibly the largest member of the Placodermi yet known from Australia. In addition the specimen indicates that further fish material might be obtained from younger horizons of the Upper Devonian reef complex in the Kimberley. Miles and Gardiner (1975) recorded *Eastmanosteus* sp., a medium-sized arthrodire intermediate in form between the coccosteids and the large dinichthyids, from the Gogo Formation. The phylogenetic position of this species and the new dinichthyid is discussed at the end of this paper.

During acetic acid preparation of the specimen samples of the residue were sieved and a conodont fauna extracted in order to determine the precise age of the specimen and its possible stratigraphic source (see Long 1987)). The skull was found in several pieces which were individually prepared from the rock resulting in some small gaps between the adjoining pieces in the reconstructed skull. As the skull had suffered some post-mortem damage prior to fossilisation the anterior margin, and the pineal-rostral plate region is missing. Despite this the visceral surface shows good preservation of important morphological features, and radiographs of the lateral sides of the roof have provided further details of suture patterns. Red iron oxides obscured much of the dorsal surface of the specimen necessitating removal of up to 1 mm of the external surface of the bone using a strip of sandpaper mounted to a drive belt. This enabled accurate determination of the plate boundaries and details of sensory-line canals.

Abbreviations used in figures

ant. po. pr	depression for anterior postorbital process of endocranium
ant. pr	antorbital process of endocranium
att. rhc	attachment area for rhinocapsular bone
att. SO	attachment area for suborbital plate
brl, 2	mesial grooves branching from saccular groove
CE	central plate
csl	central sensory line canal
cuc. f	cucullaris fossa
d. e	opening for endolymphatic duct
f. cuc	depression on skull roof for cucullaris muscles
font?	presumed orbitotemporal fontanelle
glf	glenoid fossa
gr. sac	groove in pre-endolymphatic thickening
ifo	infraorbital sensory-line canal
in. p	infranuchal pit
lam. im	inframarginal lamina
llc	main lateral line canal
MG	marginal plate
med. dep	median depression
med. nu. th	median nuchal thickening of endocranium
mes. p	mesial pit of paranuchal plate
mes. th	mesial thickening of endocranium
NU	nuchal plate
orb	orbit
P?	presumed pineal plate
pmc	posterolateral corner of headshield
PNU	paranuchal plate
pos. th	posterior thickening of supraorbital vault
ppl	posterior pit-line groove
pr. ant	antorbital process of endocranium
pr. art	para-articular process of paranuchal plate
pr. crs	craniospinal process of endocranium
PRO	preorbital plate
pr. p. a	anterior postorbital process of endocranium
pr. so	supraorbital process of endocranium
PTO	postorbital plate
pt. th	lateral postorbital thickening of skull roof
R?	presumed rostral plate
r	ridge
rhc	rhinocapsular bone
sac. th	thickening above sacculus on endocranium
soc	supraorbital sensory-line canal
suo. v	supraorbital vault
th. nu	nuchal thickening
th. pre	pre-endolymphatic thickening
v. po. pr	ventral postocular process

Systematics

Class Placodermi
Order Arthrodira Woodward 1891
Family Dinichthyidae Newberry 1885

Diagnosis

Moderate to large-sized pachyosteomorph arthrodires having powerful gnathal plates with prominent anterior cusps on the inferognathal and anterior superognathal, and anterior superognathal which is like an open ring when seen in dorsal view.

Remarks

The above diagnosis is taken from Lelievre *et al.* (1981) who discussed the relationships of the Dinichthyidae and determined the above synapomorphies defining the family as monophyletic. Denision (1978, p. 86) gave an expanded diagnosis of the family, but did not isolate synapomorphies, although in a later paper he discussed other specialised characters of the family (Denison 1984). *Westralichthys* is only known from the skull roof, and therefore does not show any of the characters of the gnathal plates listed above. However, in possessing a specialised lateral consolidated region on the visceral surface of the skull roof, large size and absence of tubercular ornament *Westralichthys* resembles *Dunkleosteus* and is provisionally placed within the family Dinichthyidae. The Dinichthyidae are presumably derived from Coccosteoidea (Denision 1975, 1978, 1984) by acquiring a specialised dentition with highly developed anterior cusps on the gnathal plates. It should be noted, however, that the group underwent a major secondary radiation in the Famennian, and many of the later species are known only from gnathal bones (Denison 1978). Some of the other specialised larger arthrodires of this time may be derived from the Dinichthyidae, but due to changes in feeding adaptations have lost the characteristic cusps on the gnathals (e.g. *Bungartius, Titanichthys, Dinomylostoma,* Denison 1978).

Westralichthys gen. nov.

Type species

Westralichthys uwagedensis sp. nov.

Diagnosis

An arthrodire with a skull roof length attaining at least 27 cm, and having an estimated breadth/length index of 122, and a moderately emarginate posterior margin; nuchal plate approximately trapezoidal, twice as broad as long and 43% as long as the mid-line length of the skull as preserved; centrals weakly trilobate with short posterior lobe; marginal and postorbital plates very long and narrow; postorbital plate being approximately half as long as skull roof. The visceral surface of the skull roof has massive nuchal thickenings which meet the paranuchal plates to form deep mesial pits posterior to the pronounced pre-endolymphatic thickenings; lateral thickening of skull roof well developed into extensive inframarginal lamina twice as long as the supraorbital vault, and with inframarginal crista present and mesial face having an embayment for the anterior postorbital process of endocranium; ventral postocular processes well developed. Supraorbital vault is 30% as broad as the transverse line through the postorbital corners of the skull roof. Endocranium with supraorbital processes developed. Dermal bones lacking ornamentation.

Westralichthys is distinguished from the primitive dinichthyids *Golshanichthys* and *Eastmanosteus* by its broader nuchal plate, lack of tubercular ornamentation, longer postorbital and marginal plates and by the massive thickenings and pits on the visceral surface of the skull roof. It is distinguished from *Dunkleosteus* by the trilobate centrals, broader skull roof, shape and relative size of the nuchal plate, and by the mesial pits of the visceral surface. The remaining dinichthyids for which the skull is known *(Hadrosteus; Gorgonichthys, Heintzichthys)* are readily distinguished from *Westralichthys* by their distinctive skull roof patterns, all featuring small triangular nuchal plates, and larger orbits. It is also noted that a supraorbital process on the endocranium is not developed for other dinichthyids (Stensio 1963, Dunkle and Bungart 1940, Lehman 1956).

The genus is named after the state of Western Australia and the Greek "ichthys", fish.

Westralichthys uwagedensis sp. nov.

Figures 1-9, 10C

A large dinichthyid from the *Cheiloceras* zone — Hills 1958: 90.

A dinichthid from the *Cheiloceras* zone — Gilbert-Tomlinson 1968: 210.

Holotype

WAM 86.9.664 (formerly UWA 32614), only specimen. South-eastern Canning Basin, Western Australia, probably Virgin Hills Formation, Late Devonian (Middle Famennian) age.

Diagnosis

As for genus.

Description

The specimen lacks the central and anterior regions of the skull roof (Figure 2), but is otherwise well preserved and has not undergone post-mortem compaction. The three-dimensional shape of the skull roof is clear. The anteriormost part of the left side of the specimen shows the recessed notches for the rhinocapsular bone and the antorbital process of the endocranium, indicating from comparison with most other arthrodires (e.g. Stensio 1963; Miles and Dennis 1979) that

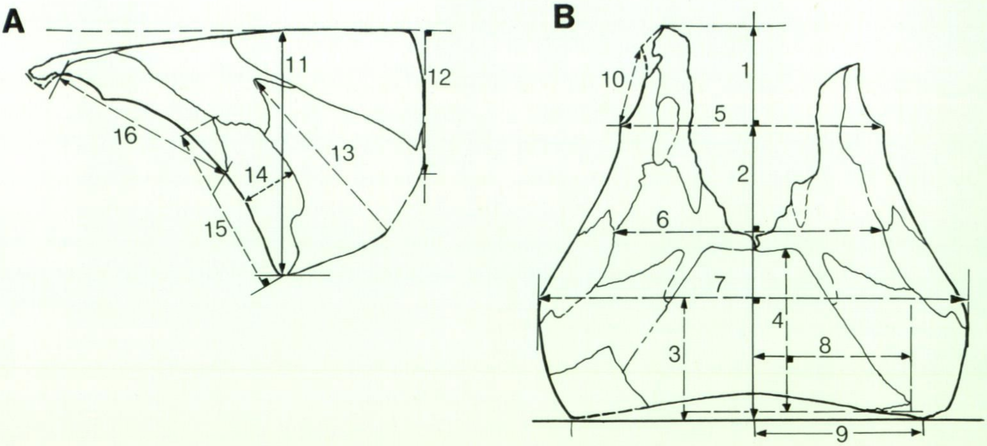

Figure 1 Measurements given in Table 1, taken on the holotype skull of *Westralichthys* gen. nov. A, lateral view. B, dorsal view.

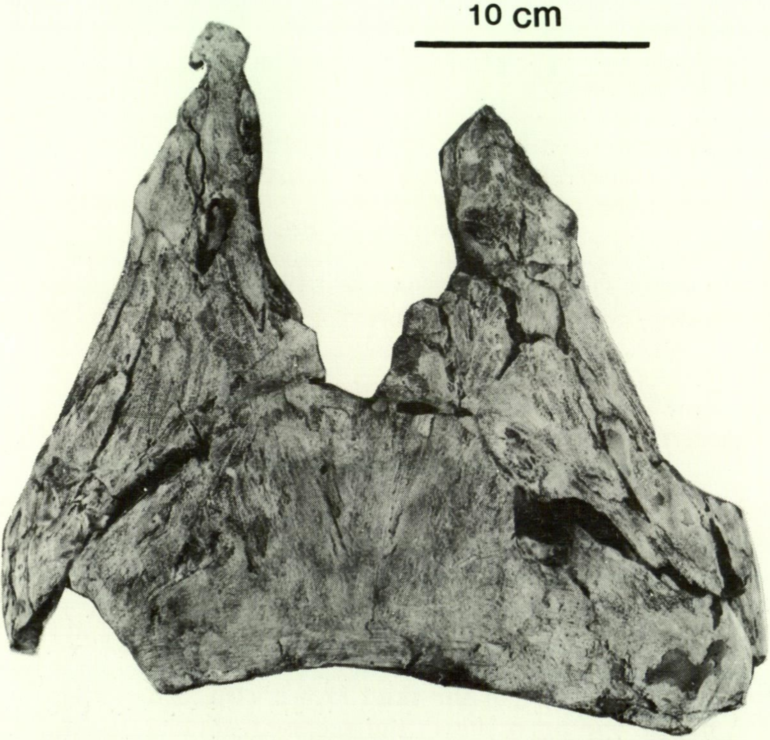

Figure 2 *Westralichthys uwagedensis* gen. *et* sp. nov., Late Devonian, Western Australia. Holotype. WAM 86-9-664, skull roof in dorsal view.

almost the entire length of the skull is preserved. The skull of *Golshanichthys asiatica* was found with a similar pattern of post-mortem damage (Lelievre *et al.* 1981). Measurements taken on the skull are shown in Figure 1 and listed with relevant proportional indices in Table 1. All proportional statements referred to in the diagnosis and description are based upon these measurements.

Table 1 Measurements and relevant proportions of *Westralichthys uwagedensis* gen. *et* sp. nov., holotype skull. All measurements (in mm) refer to points taken on Figure 1, measurements 1-10 refer to Figure 1-B, measurements 11-17 refer to Figure 1-A.

1.	midline length of skull as preserved	270
2.	midline length to postorbital corners	205
3.	length to postmarginial corners	90
4.	length of nuchal plate	115
5.	breadth across postorbital corners	173
6.	breadth across middle of central plates	177
7.	breadth of skull (postmarginial corners)	330
8.	half nuchal plate breadth	115
9.	half breadth of skull to glenoid fossa	140
10.	orbital diameter (from inside vault)	56
11.	depth of skull (postmarginial corner)	155
12.	depth to glenoid fossa	80
13.	greatest dimension of paranuchal plate	170
14.	greatest breadth of marginal plate	37
15.	maximum length of marginal plate	133
16.	maximum length of postorbital plate	152
17.	approximate length of obstantic margin	90-100

Some relevant proportions (indices multiplied by 100).

A. skull breadth/length index = 122 (as preserved).
B. nuchal breadth/length index = 200
C. orbit diameter/skull length = 21
D. skull depth/length = 57
E. length postorbital plate/skull length = 56
F. length marginal plate/skull length = 49

Overall the skull roof (Figures 2, 3, 7) is broad posteriorly and narrow anteriorly. In posterior view (Figure 4-A) it is inflected strongly downwards at the postero-lateral corners, so that the depth of the posterior region of the skull (Figure 7) is just over half of its length. The posterior margin of the skull roof (pm) is moderately emarginate, and the lateral margins are gently concave up to the well defined postorbital corner. In cross-section the posterior end of the skull is triangular as each side of the nuchal plate meets to form a mid-line angle of approximately 120°, before the skull table flattens out anteriorly. As the posterior margin of the skull was projecting out of the rock it has suffered some weathering, and there is no trace of a posterior median process on the nuchal plate. Despite

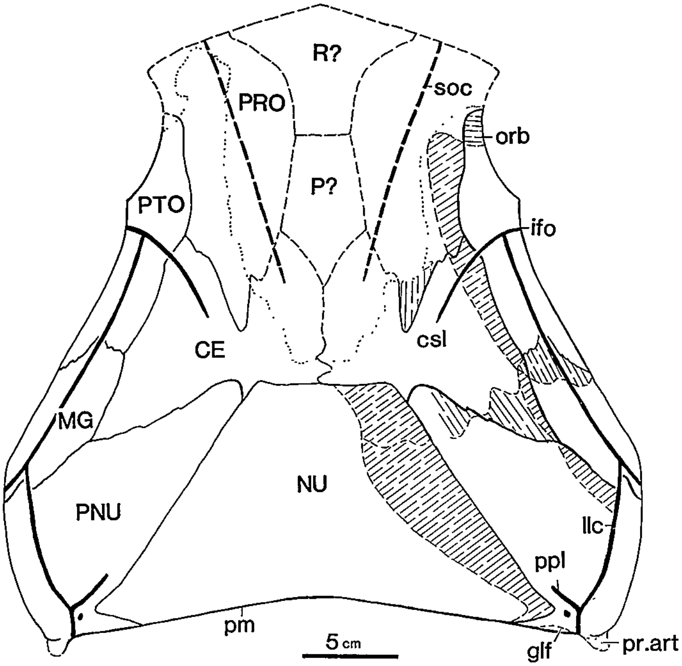

Figure 3 *Westralichthys uwagedensis* gen. *et* sp. nov., Late Devonian, Western Australia. Attempted restoration of skull roof in dorsal view, overlapping plate boundaries shown on right side. Shaded areas are restored after *Dunkleosteus* (after Heintz, 1932). Actual extent of specimen shown by a dotted line.

this the thick posterior margin of the nuchal plate is well preserved to show the shape of the posterior margin of the skull roof. Similarly the glenoid fossa (glf) is poorly preserved, although it can be seen to have been rather small and not elongated horizontally. There is a weak para-articular process (pr.art) present. The postmarginal corners (pmc) are situated one-third the length of the skull roof from its posterior margin, although as the posterior margin is moderately emarginate the postmarginal corners are only a short distance anterior of the posterior mid-line point of the skull roof.

In dorsal view the skull roof pattern (Figure 3) is characterised by the very broad nuchal plate (NU), which is 70% as broad as the roof, very large paranuchal plates (PNU), weakly trilobate centrals (CE) and elongated postorbital (PTO) and marginal (MG) plates. The nuchal is trapezoidal with a straight anterior margin one-third the plate's breadth in extent. It has broad overlap margins for the paranuchal and also overlaps part of the central plates. The paranuchal is the longest plate on the skull roof, having a maximum dimension of 63% the length of the roof. It meets the central along a slightly irregular suture and is overlapped by that plate both mesially and laterally. The lateral corner of the paranuchal features a short, rounded anterior lobe which projects into the rear of the marginal plate. The mesial division of the centrals is poorly preserved on the specimen although there are several smaller pieces of these plates which became detached during preparation. They indicate that the posteriormost contact between the central plates was along a slightly irregular suture. The posterior lobe of the centrals is very short and anteriorly there is a deep notch for the preorbital plate (PRO) which comes close to meeting the anterior margin of the paranuchal plate. The lateral margins of the centrals are quite straight where they overlap the postorbital and marginal plates. The marginal plate has a maximum breadth/length ratio of 28, and is approximately as broad as the postorbital plate, which is slightly longer than it. It has a well produced anterior point which has irregular suture with the postorbital, similar to, but not as well developed as in *Dunkleosteus marsaisi*

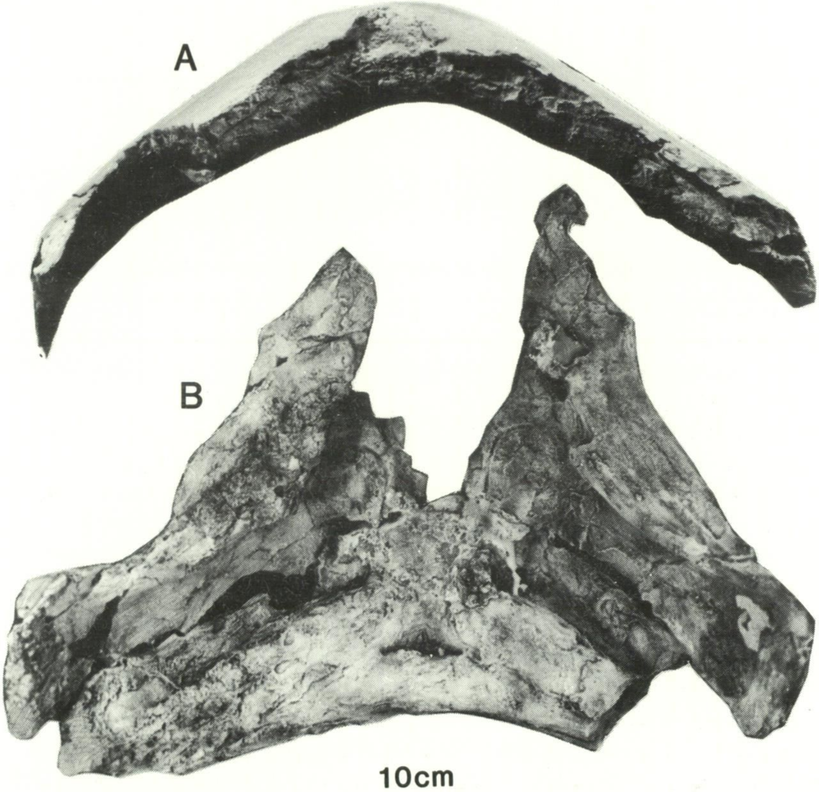

Figure 4 *Westralichthys uwagedensis* gen. *et* sp. nov., Late Devonian, Western Australia. Holotype. WAM 86-9-664, skull roof in A, posterior and B, ventral views. Whitened with ammonium chloride.

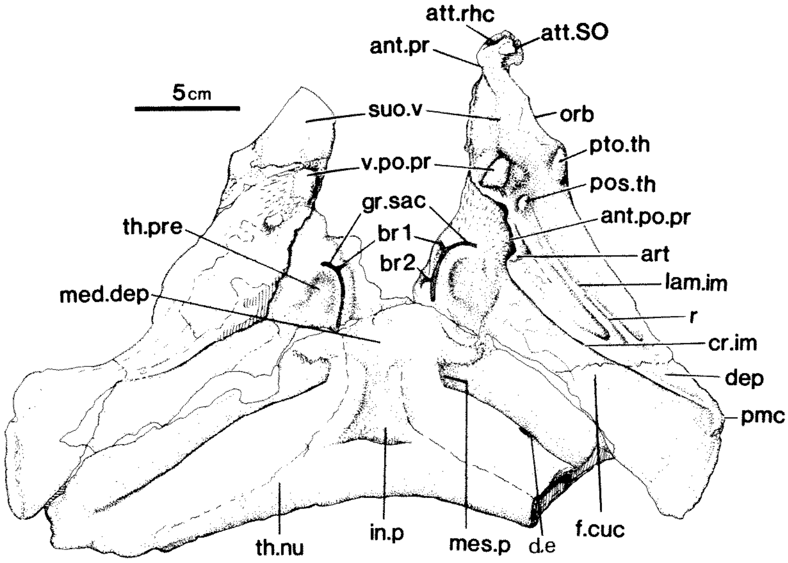

Figure 5 *Westralichthys uwagedensis* gen. *et* sp. nov., Late Devonian, Western Australia. Interpretation of visceral surface of the holotype skull roof, WAM 86-9-664.

(Lehman, 1956). The postorbital plate has a well developed postorbital corner and is broadest just posterior to the orbit, tapering anteriorly before meeting the preorbital plate. The anteriormost section of the postorbital overlaps the preorbital plate, although the latter overlaps most of the postorbital along its mesial margin. The junction of the infraorbital (ifo) and central (csl) sensory-line canal grooves can be seen on the specimen, although only faint traces of the supraorbital (soc), main lateral-line (llc) and posterior pit-line (ppl) grooves are preserved. Little is preserved of the preorbital plate, and its reconstructed shape is based on the margins of the known plates and the pattern seen in *Dunkleosteus.*

The visceral surface of the skull roof (Figures 4-B, 5, 6) shows massive thickenings along the posterior and lateral borders. The nuchal thickening (th.nu) increases in breadth mesially before ending at two deep mesial pits (mes.p) situated posterior to the pre-endolymphatic thickenings (th.pre). These pits face laterally (Figure 6-B) and are deepest close to the dorsal wall of the skull roof. The function of the pits is not clear, although as they have a roughened internal surface they were either muscle insertion areas for cucullaris muscles which normally insert on the lateral wall of the endocranium in most arthrodires (Miles 1967) or for a mesial thickening of the endocranium (mes.th, Figure 9) to strengthen the attachment area for the cucullaris muscles. There is a deep infranuchal pit (in. p), lacking a median crista (Figure 6-B), located in the centre of the nuchal thickening and this pit expands in breadth posteriorly, presumably to brace the dorsal median thickening of the braincase (not the craniospinal process of the endocranium, Schultze 1973). Anterior to the infranuchal pit there is a broad, smooth depression (med.dep) leading anteriorly to the pre-endolymphatic thickenings. The opening for the endolymphatic duct (d.e) is on the anterior face of the nuchal thickening (on the paranuchal plate) about midway along its breadth, but the dermal ridge of bone which braced the dorsal surface of the supravagal process is not seen as it is covered by iron oxide deposits. The pre-endolymphatic thickenings are very well developed and each shows a semicircular groove (gr.sac) with two small mesial branches (br1, br2) situated along its thickened mesial border. These grooves may have been for the supratemporal branch of the vagus nerve for innovation of the central and posterior pit-line organs (Young 1979, Stensio 1963). There are large nutritive foramina piercing the bone around the postocular process and behind the anteriorly-facing articulation area on the mesial margin of the inframarginal lamina.

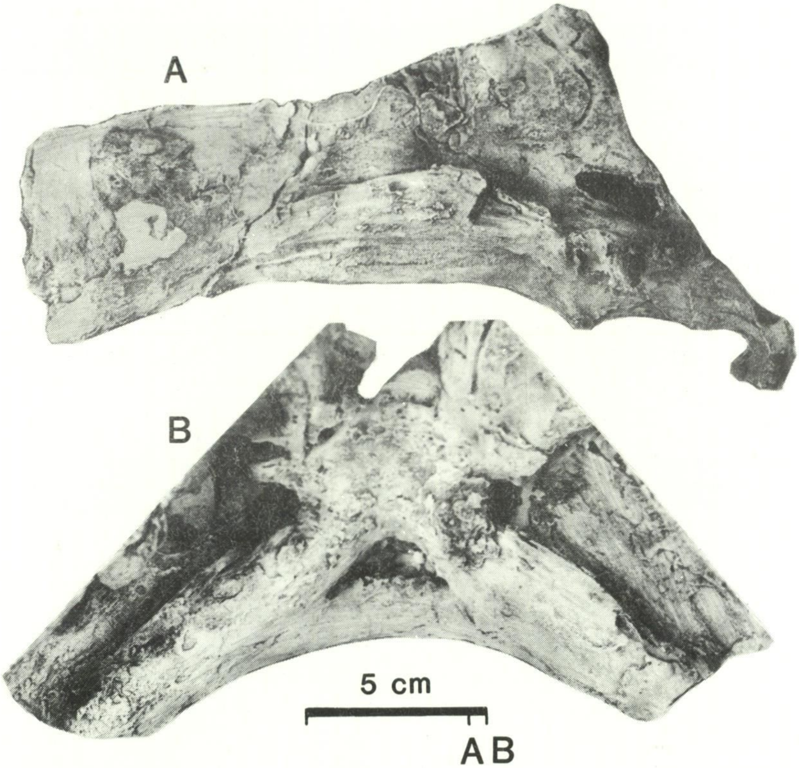

Figure 6 *Westralichthys uwagedensis* gen. *et* sp. nov., Late Devonian, Western Australia. Holotype. WAM 86-9-664. A, mesial view of left side of skull roof in visceral view, showing features of the supraorbital vault and inframarginal lamina. B, anterior view looking into the infranuchal and mesial pits on the visceral surface of the skull roof. Whitened with ammonium chloride.

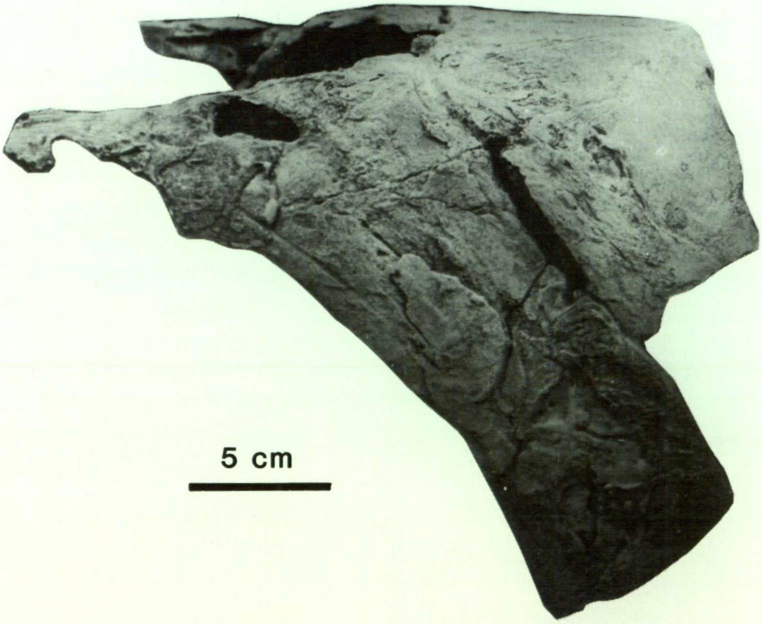

Figure 7 *Westralichthys uwagedensis* gen *et* sp. nov., holotype skull roof in oblique left lateral view, WAM 86-9-664. Whitened with ammonium chloride.

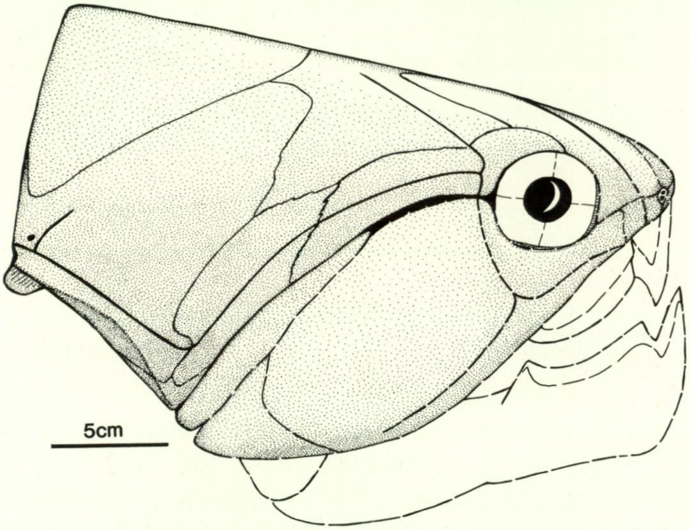

Figure 8 *Westralichthys uwagedensis* gen. *et* sp. nov., Late Devonian, Western Australia. Attempted restoration of the head in lateral view. Cheek complex inferred from similar lateral skull margin as in *Dunkleosteus* (after Stensio 1963), although gnathal plates and sclerotic ring are completely unknown and are included here to complete the restoration, based also on *Dunkleosteus.*

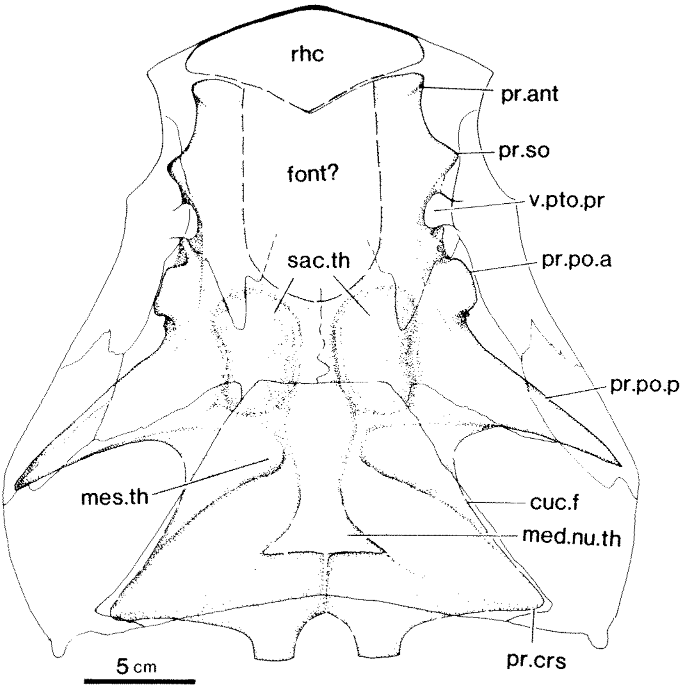

Figure 9 *Westralichthys uwagedensis* gen. *et* sp. nov., Late Devonian, Western Australia. Attempted restoration of dorsal endocranial shape in relation to skull roof pattern, based on features of the visceral surface of the skull roof and comparison with Stensio's (1963) restoration of the endocranium in *Dunkleosteus.*

The supraorbital vault (suo.v) is bounded anteriorly by a small process which bears two recessed concave notches, one facing anteromesially for abutment of the rhinocapsular cartilage (att.rhc) and one facing posteromesially for bracing the antorbital process of the endocranium (ant.pr). There is a roughened small area of bone facing ventrally on this prominence for attachment of the suborbital plate (att.SO). The roof of the supraorbital vault is smooth and relatively flat, not distinctly concave as in most arthrodires. There are three distinct processes developed at the posterior border of the supraorbital vault (Figure 10-A). One of these situated laterally at the postorbital corner, is a thickening for articulation of the suborbital plate (pto.th) The largest of the other two processes, on the posteromesial border of the supraorbital vault, is a ventral postocular process (v.po.pr) for bracing the endocranium, as also occurs in *Dunkleosteus* (Heintz 1932), *Harrytoombsia,* and some of the other Gogo arthrodires (Miles and Dennis 1979; Dennis and Miles 1980). It slopes evenly up from the posterior border of the supraorbital vault and has a broad base which extends anteriorly for a short distance. A smaller posterior thickening (pos.th) is located on the posterior side of the base of the larger process, and as it does not extend ventrally very far, it would not have supported the lateral endocranial wall. It possibly served as an attachment site for ligaments connecting the palatoquadrate to the side of the skull roof, rather than having an endocranial articulation to the subocular shelf as in *Buchanosteus* (Young 1979, p. 336) and other arthrodires which lack a pronounced lateral thickening on the skull roof. The posterior division of the extensive lateral thickening (i.e. posterior to the supraorbital vault) is here termed the inframarginal lamina (lam.in). In *Westralichthys* this structure is very similar to that of *Dunkleosteus* ("lateral consolidated part", Heintz 1932, Lehman 1956) in

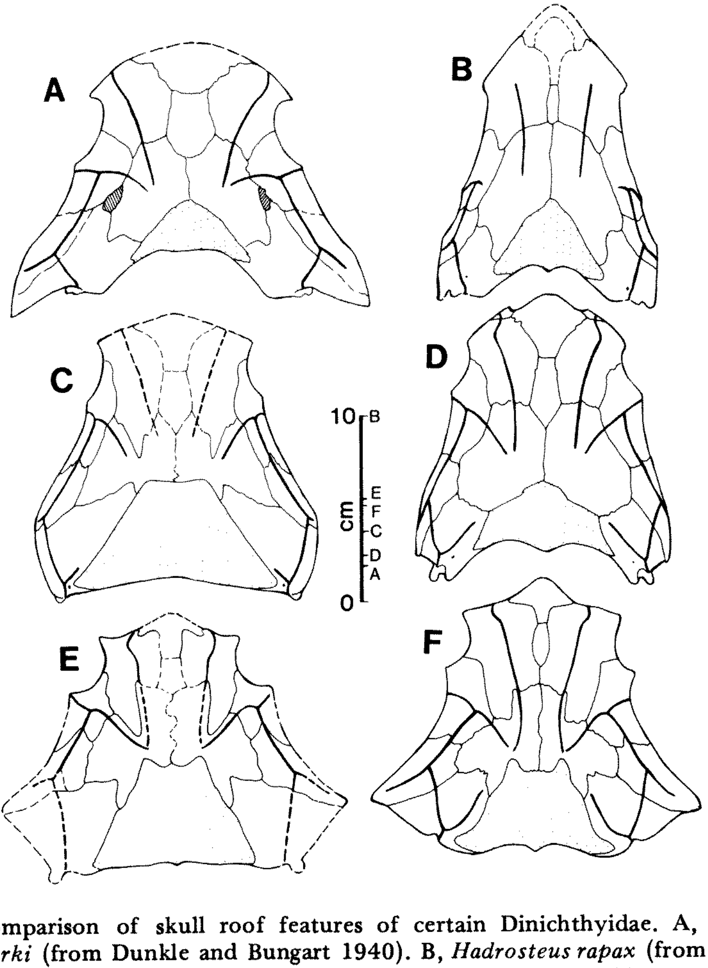

Figure 10 Comparison of skull roof features of certain Dinichthyidae. A, *Gorgonichthys clarki* (from Dunkle and Bungart 1940). B, *Hadrosteus rapax* (from Stensio 1963). C, *Westralichthys uwagedensis* gen. *et* sp. nov. D, *Dunkleosteus terrelli* (from Stensio 1963). E, *Golshanichthys asiatica* (from Lelievre *et al.* 1981). F, *Eastmanosteus pustulosus* (from Denison 1978). Nuchal plates stippled.

terms of its size relative to the lateral margin of the skull roof, breadth across the postorbital corners, and development of bony processes. It is bordered mesially by a ridge, the inframarginal crista (cr.im), which braced the posterior postorbital process of the endocranium. The inframarginal lamina has a concave medial division and thickened mesial margin which is indented lateral to the pre-endolymphatic thickenings for the anterior postorbital process of the endocranium (ant.po.pr). The posterior end of this embayment has an anteriorly-facing roughened articulation area (art, shown clearly in Figure 6-A), possibly an attachment area for arcus palatoquadratini muscles. These muscles attached from the dorsal lamina of the palatoquadrate in *Buchanosteus* (otic process) to the endocranium, although in *Holonema* they are inferred to attach onto the dorsal inner surface of the suborbital plate (Miles 1971). The extensive concave region of the inframarginal lamina may have braced the dorsal division of the palatoquadrate during jaw adduction, although the presumed presence of an opercular cartilage running from the submarginal anteromesially to its articulation on the anterior postorbital process, as occurs in other arthrodires (Young 1986), would obscure much of the area between the palatoquadrate and the inframarginal lamina unless the submarginal was particularly long and narrow as in *Dunkleosteus.* The posterior corner of the inframarginal lamina has development of weak ridges (r) and there are discrete concave surfaces (dep) possibly for insertion of the levator and dilator operculi muscles from the submarginal plate. Although the presence of these muscles in placoderms has not been discussed previously, all operculate fishes (including Holocephali) possess muscles to move the operculum, and it is assumed that they must have been present in placoderms. However, whether the submarginal was moved by dilator and adductor operculi, which attached onto the side of the skull roof (as in actinopterygians, Lauder 1980, Kesteven 1942) or whether the operculum was moved by simple modification of the dorsal constrictor muscles of the hyoidean arch (as in holocephalans, Kesteven 1942, Stahl 1967) would require further study of the cheek regions in placoderms and other fishes, beyond the scope of this work, to be resolved. A reconstruction of the head of *Westralichthys* in lateral view is shown in Figure 8, the cheek complex being restored based on similar lateral skull margins as in *Dunkleosteus.*

An attempt at reconstructing the dorsal form of the endocranium is shown in Figure 9, based on the morphology of the visceral surface of the skull roof and comparison with Stensio's restoration of the braincase of *Dunkleosteus* (Stensio, 1963, fig. 89A). The supraorbital processes (pr.so) are developed as thin triangular projections from high up on the lateral wall of the braincase, confluent with the dorsal surface abutting the skull roof. In their overall shape and size they are not unlike that process in actinolepids (Goujet 1984, fig. 107) a feature thought to characterise that group (Goujet 1984; Long 1984), although in *Westralichthys* the supraorbital processes are situated more anteriorly. Immediately posteroventral to them the braincase is buttressed by the ventral postocular processes, and the anterior postorbital processes (pr.po.a) emerge from mid-way along the lateral endocranial wall behind these dermal buttresses. The relative shape and size of the anterior postorbital processes is here taken from the incised depression along the mesial thickening of the inframarginal lamina. At the posterior end of this embayment is the roughened articulation area possibly for muscle attachment (as described above), but as most of the embayment is smooth it is presumed to be for an endocranial process. The full lateral extent of the process is not known, but it probably did not extend far, as one of its functions, to meet the head of the opercular cartilage, could only be achieved if the submarginal was particularly elongated as it is in *Dunkleosteus.* An orbitotemporal fontanelle (font?) is restored after Stensio. As most of this region was caved in on the specimen, the presence of such a fontanelle is therefore possible. The deep mesial pits on the paranuchals are here restored as thickenings of the endocranium (mes.th) above the cucullaris fossa (cuc.f). Unlike Stensio's restoration in *Dunkleosteus* the saccular thickenings (sac.th) below the pre-endolymphatic thickenings of the skull roof are not confluent with the cucullaris fossa as the endocranium must have been raised well above the depression to insert mesially into the pits, then presumably shallowed out laterally into the cucullaris fossa. The posterior division of the endocranium apparently resembled that of *Dunkleosteus* in its development of a strong median nuchal thickening (med.nu.th), although there is no evidence for postulating an occipital fontanelle (cf. Stensio 1963).

Etymology

The species is named from a composite of the first letters from the University of Western Australia, Geology Department, where the specimen was uncovered in early 1986.

Relationships of *Westralichthys*

Relationships between the major dinichthyids were briefly discussed by Lelievre *et al.* (1981), and I have here modified their cladogram to include *Westralichthys* as well as some other taxa (Figure 11). Only taxa in which the skull is well known are considered. Newly prepared specimens of *Eastmanosteus* sp. and several coccosteids from the Gogo Formation have also been studied in order to clarify some of the morphological points raised. The following character states are utilised in competing hypotheses of dinichthyid interrelationships (Figure 11). The taxonomic distribution of these characters is shown in Table 2. Outgroup comparison with the Coccosteoidea is here used to establish plesiomorphy in dinichthyid characters, as most workers agree on the Dinichthyidae being derived from coccosteid stock (Denison 1975, 1978, 1984; Miles 1969, Moy-Thomas and Miles 1971, Lelievre *et al.* 1981).

1. Powerful gnathal plates with prominent anterior cusp on inferognathal, anterior superognathal like an open ring in dorsal view.

This character was discussed by Lelievre *et al.* (1981) as defining the family Dinichthyidae. Whilst there is no doubt about the distribution or development of the first of these features in most dinichthyids *(Dunkleosteus, Gorgonichthys,*

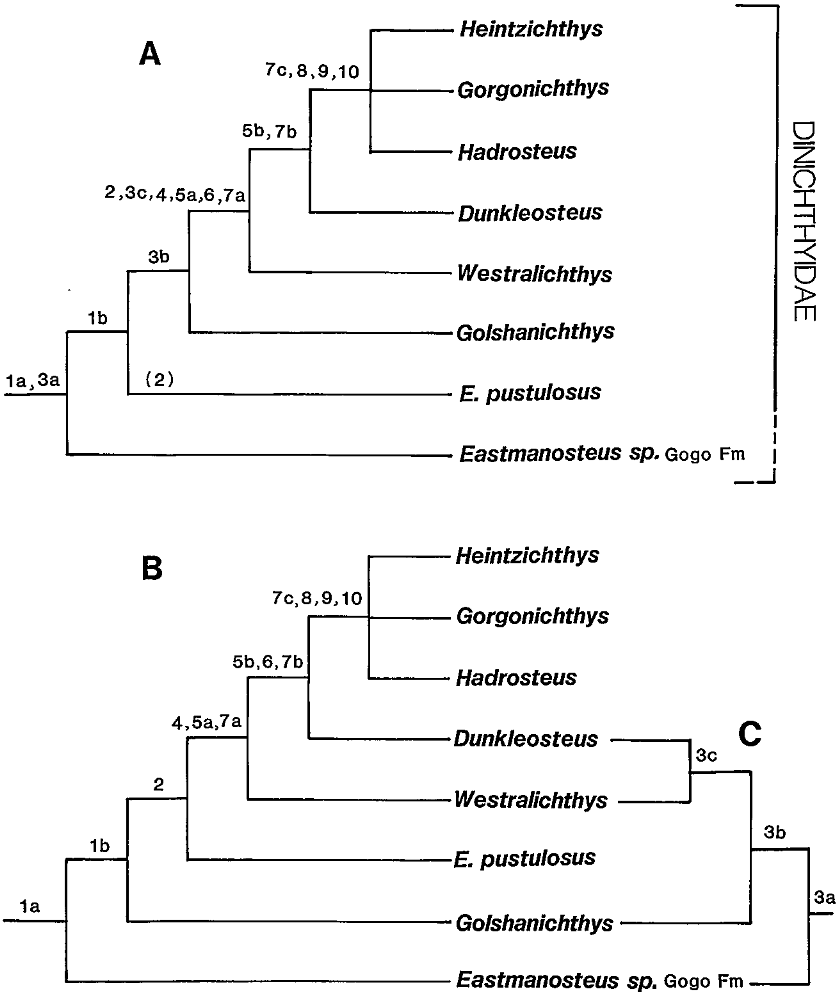

Figure 11 Hypotheses of dinichthyid interrelationships. Numbered synapomorphies are listed and discussed in the text, and taxonomic distribution of character states is summarised in Table 2. Hypothesis A assumes that the inframarginal lamina was primitively present in all higher dinichthyids (even if secondarily lost in some forms). Hypothesis B ignores the inframarginal lamina as a widespread dinichthyid character. Hypothesis C utilises only the development of the inframarginal lamina in taxa for which it is known.

Table 2 Distribution of character states in certain dinichthyids.

	Eastmanosteus sp. Gogo Fm	*E. pustulosus*	*Golshanichthys*	*Westralichthys*	*Dunkleosteus*	*Hadrosteus*	*Gorgonichthys*	*Heintzichthys*
1a. Inferognathal with well developed anterior cusp.	■							
1b. Powerful gnathal plates with prominent anterior cusp on inferognathal, anterior supragnathal with almost ring-like dorsal part.		■	■	?	■	■	■	■
2. Elongated postorbital plate.		■		■	■	■	■	■
3a. Lateral consolidated part of skull roof very thick.	■							
3b. Inframarginal lamina present.		?	■			?	■	?
3c. Inframarginal lamina extensive.				■	■			
4. Loss of ornamentation.				■	■	■	■	■
5a. Postmarginal corners more posteriorly situated than for normal arthrodires.				■				
5b. Neck-slit vertical or near vertical.					■	■	■	■
6. Central plates not trilobate.					■	■	■	■
7a. Nuchal plate twice as broad as long.				■				
7b. Nuchal plate broad, diminished in size and pentagonal.					■			
7c. Nuchal plate smaller, and triangular in form.						■	■	■
8. Spinal plates absent.			?	?		■	■	■
9. Orbits enlargened.						■	■	■
10. Suborbital plate with deep rounded postorbital blade.			?	?		■	?	■

Heintzichthys, Hadrosteus, Golshanichthys) there is some uncertainty about the gnathal plates in *Eastmanosteus. Eastmanosteus pustulosus* apparently had gnathals similar in form to those of *Dunkleosteus* (Denison 1978, Kulczycki 1957), and is therefore united with the other genera. *Eastmanosteus* sp. from Gogo, however, has only moderate development of the anterior cusps, and although they are clearly present as pointed fangs they are not very high relative to the level of the biting division of the blades (on both inferognathal and posterior superognathal).

In some respects they are comparable to the well developed cusps of some coccosteomorphs (e.g. *Plourdosteus,* Ørvig, 1980; Vezina, 1986) and certainly are not as prominent as cusps on the gnathals of some other placoderms (e.g. *Malerosteus,* Kulczycki, 1957). I therefore regard the development of this character in *Eastmanosteus* sp. from Gogo (character 1a) as being intermediate between that of coccosteids and that of other dinichthyids (character 1b). Although this character is not known for *Westralichthys,* it is assumed to be present due to overall similarities in skull features to *Dunkleosteus,* and in showing more derived cranial features than *Golshanichthys* or *E. pustulosus,* both of which possess this character. The character of the anterior superognathal having an open-ring shape in dorsal view is clearly seen in *Dunkleosteus* (Heintz, 1932, fig. 28-III) and *Eastmanosteus* sp. from Iran (Janvier 1977, fig. 2-C), and apparently present in higher dinichthyids (Lelievre *et al.* 1981). However it is not known for *Westralichthys* or *Golshanichthys,* and is not developed in *Eastmanosteus* sp. from Gogo, in which these bones are essentially like those of coccosteids. Using Lelievre *et al.*'s definition of the Dinichthyidae *Eastmanosteus* sp. from Gogo would have to be excluded from the family as it lacks both synapomorphies. It is noted that some of the most advanced dinichthyids are known only by their gnathal bones which show the distinctive cusp on the inferognathal (e.g. *Holdenius, Hussakoffia, Dinichthys*). Some forms also underwent specialisation of the dentition (e.g. *Hadrosteus*).

2. Elongated postorbital plate.

In coccosteids the postorbital is a short, broad plate, as it is also in *Eastmanosteus* sp. from Gogo, and *Golshanichthys.* By contrast the postorbital of *E. pustulosus, Westralichthys, Dunkleosteus, Heintzichthys, Gorgonichthys* and *Hadrosteus* is elongate, being of similar shape and length as the marginal plate. This is seen as a derived condition for dinichthyids. In *Selenosteus* the postorbital is also elongated but quite unlike that of dinichthyids as the anterior division of the plate (forward of the junction of the infraorbital and main lateral line sensory grooves) is extended, not the posterior division as in dinichthyids.

3. Well-developed inframarginal lamina.

The term "inframarginal lamina" is introduced to denote the smooth ventrally-facing extension of the supraorbital vault which is developed on the lateral consolidated region of the skull roof, equivalent to the "post-ocular division of supraorbital area", of Stensio (1963, fig. 112A). As such it is not found in any coccosteids (cf. Gogo coccosteids, Miles and Dennis 1979, Dennis and Miles 1979a, 1979b, 1982, 1983; *Coccosteus,* Miles and Westoll 1968, Obrucheva 1962; *Protitanichthys,* Miles, 1966) as in this group the lateral consolidated region of the cheek is present as a moderate thickening of bone along the inside edge of the skull margin. In *Westralichthys, Dunkleosteus terrelli* (Heintz, 1932) and *D. marsaisi* (Lehman, 1956) the inframarginal lamina is well developed, being approximately twice the length of the supraorbital vault. *Golshanichthys* appears to have a short inframarginal lamina present (ep. lat, Lelievre *et al.* 1981, fig. 2) which is approximately the same length as the supraorbital vault. The condition in *Eastmanosteus pustulosus* is not clear. Kulzycki (1957, p. 307) described part of the inside of the skull roof of *E. pustulosus* and this together with his illustration indicates that the inframarginal lamina was not fully developed in this species. In *Eastmanosteus* sp. from Gogo the lateral consolidated region has a middle region comprising a bulbous rounded thickening, anterior to which is a well defined depression bordered anteriorly by the supraorbital vault. Posterior to the middle thickening is another depressed area, possibly a muscle insertion area, where the lateral consolidated region merges evenly with the postmarginal corner of the skull. In the largest specimens examined the median division becomes quite flatter, but is still discontinuous with the depressions anterior and posterior to it. I therefore regard the condition in *Eastmanosteus* sp. from Gogo, and possibly in *E. pustulosus,* as being a more derived state of the lateral consolidated part of the skull (character 3a) relative to coccosteids, but not as specialised as the short inframarginal lamina in *Golshanichthys* (character 3b) or the long, broader inframarginal lamina present in *Westralichthys* and *Dunkleosteus* (character 3c). The visceral surface of the skull roof of *Gorgonichthys* has been badly distorted (Dunkle and Bungart 1940, p. 34) but shows that an inframarginal lamina might have been present (cf. "descending orbital exoskeletal bone lamina," Stensio 1963, fig. 112B). The condition in *Hadrosteus* and *Heintzichthys* is not certain, so at most this character might be useful to denote a relationship between *Westralichthys* and *Dunkleosteus* (Figure 11-C), or be inferred to be a synapomorphy of higher dinichthyids which might be diminished or lost in some forms (Figure 11-A). A similar type of inframarginal lamina occurs in the durophagous Gogo arthrodires *Kendrickichthys* and *Bullerichthys* (pers. observ.). It is assumed to have developed in parallel with that of dinichthyids due to similar adaptation of a powerful jaw adduction, one for predatory actions (dinichthyids) and one for durophagy. More detailed study of this region in arthrodires is required to determine the function of the lamina and its depressions and pits.

4. Loss of tubercular ornamentation.

A tubercular ornamentation is primitively present in all arthrodires, and typifies the coccosteids and some dinichthyids. The loss of tubercular ornament in some dinichthyids is here considered a specialised condition. *Eastmanosteus* sp. from Gogo has a well developed tubercular ornamentation, but in *E. pustulosus* the tubercles are scarce and restricted to ossification centres when at all present (Kulzcycki 1957, Schultze 1973). *Golshanichthys* has a fine ornamentation, but all the other dinichthyids dealt with here have smooth bone surfaces.

5. Vertical or near vertical neck-slit.

The obstantic margin of the skull in most arthrodires is inclined anterolaterally, thus giving the skull its characteristic broad postmarginal corners (a synapomorphy once used to define the Arthrodira, Young 1979, but also present in antiarchs, Young and Gorter 1981, Dennis and Miles 1983). In dinichthyids, brachydeiroids, trematosteids and some other forms the neck slit has a vertical orientation. The development of this condition is assumed to have arisen only once within the Dinichthyidae as it is shared by certain higher dinichthyids *(Dunkleosteus, Gorgonichthys, Heintzichthys, Hadrosteus). Eastmanosteus* sp. from Gogo, *E. pustulosus* and *Westralichthys* all possess anteriorly inclined obstantic margins, although in *Westralichthys* the postmarginal corners are more posteriorly situated than for the other two species. I regard the condition in *Westralichthys* (character 5a) as more derived than for the *Eastmanosteus* species, which show a regular coccosteid type of neck-slit, but not as derived as that of higher dinichthyids (character 5b). Correlated with this character is the enlargement of the nuchal gap in higher dinichthyids *(Gorgonichthys, Heintzichthys, Hadrosteus, Dunkleosteus).*

6. Central plates not trilobate.

Trilobate central plates typify the coccosteids (Denison 1978) and are retained in *Eastmanosteus* spp., *Golshanichthys* and *Westralichthys.* The derived condition is seen in *Dunkleosteus, Gorgonichthys, Heintzichthys* and *Hadrosteus* where the centrals are not trilobate and have fairly straight margins. They are large bones, generally equivalent in size to the preorbital plates (Denison 1978).

7. Nuchal plate diminished and of triangular shape.

A trapezoidal nuchal plate is a characteristic feature of the Brachythoraci (Young 1979) and is found in all known coccosteids. It is retained in *Eastmanosteus* sp. from Gogo, *E. pustulosus* and other species (Schultze 1973), *Golshanichthys* and *Westralichthys,* and in these forms it is long, occupying more than 40% of the skull length. In *Westralichthys* however it is considerably broader than is normal for coccosteids and this is considered more derived (character 7a) than for the afore-mentioned dinichthyids. *Dunkleosteus* and higher dinichthyids show diminution of the nuchal plate which only occupies approximately one-quarter or so of the skull length, and is very broad (character 7b). In *Gorgonichthys, Heintzichthys* and *Hadrosteus* the nuchal is smaller and has an approximately triangular outline (character 7c).

8. Spinal plates absent.

Stensio (1959, 1969) argued for a division of the Arthrodira into forms lacking a spinal plate (Aspinothoracidi) and those with a spinal plate (Spinothoracidi). A major problem with this scheme was the presence and absence of spinals in members of the Dinichthyidae. Stensio tried to resolve this by arguing that the spinal plates in some dinichthyids were "pseudospinals" not homologous to those of other arthrodires as they lacked an internal endoskeletal component. This was refuted by Heintz (1968) using *Dunkleosteus* and *Homosteus* as examples. The presence of spinal plates in dinichthyids is therefore regarded as a primitive feature shared with coccosteids, but generally differing in their relative sizes (cf. *Eastmanosteus* sp. Gogo, Gardiner and Miles 1975). The spinals are lost in advanced forms *(Hadrosteus, Gorgonichthys* and *Heintzichthys),* although it should be noted that they are not known for *Westralichthys* or *Golshanichthys,* but are assumed to be present in these species as they are present in *Dunkleosteus.*

9. Large orbits.

The diameter of the orbits in *Eastmanosteus* sp. from Gogo, *E. pustulosus, Golshanichthys, Westralichthys* and *Dunkleosteus* all fall within the common size range for coccosteids (average about one-fifth skull length). *Hadrosteus, Gorgonichthys* and *Heintzichthys* show relatively large orbits, here considered a derived condition within the family.

10. Suborbital plate having a rounded deep postorbital section.

The previous character (enlarged orbits) is also correlated with the change in shape of the postorbital region of the suborbital plate from being relatively long and rectangular to almost rounded in form. As the cheek bones are not known for some dinichthyids, the shape of the suborbital can be inferred from the lateral margin of the cheek. In *Dunkleosteus* and *Eastmanosteus* the suborbital is elongated, typical of its form in coccosteids, and this type of suborbital is inferred to be present in *Golshanichthys* and *Westralichthys* (restored in Figure 8). Similarly *Heintzichthys* is inferred to have had a deep rounded suborbital similar to that of *Gorgonichthys* due to its enlarged orbits.

The following characters may be of use when more is known of their distribution in dinichthyids: interolateral plate with smooth, non-denticulated ascending lamina (present in *Dunkleosteus,* not present in *Eastmanosteus* sp. from Gogo, uncertain for others); and parasphenoid with posterolateral processes (present in *Dunkleosteus,* Stensio, 1969, fig. 141; absent in *Eastmanosteus* sp. from Gogo, unknown in others). In addition Lelievre *at al.* (1981) have used the loss of lateral and nuchal thickenings on the visceral surface of the skull roof (to unite *Heintzichthys* and *Gorgonichthys*) although this character is discussed in detail above. The tritorial type of inferognathal is also used to unite *Dunkleosteus* with *Heintzichthys* and *Gorgonichthys* by Lelievre *et al.* (1981) although this condition is difficult to resolve from that in *Golshanichthys* and is unknown for *Westralichthys.*

The average coccosteids were small fishes no more than about half a metre or so in length, although some forms were considerably larger (Miles 1964, Obrucheva 1966). The dinichthyids include some of the largest known placoderms, a condition which is clearly specialised. The maximum sizes for headshield length in the dinichthyids are: *Eastmanosteus* sp. from Gogo — about 27 cm, *Golshanichthys* — up to 25 cm; *E. pustulosus* — up to 30 cm; *Westralichthys* — 27 to 30 cm estimated maximum length; *Dunkleosteus* – up to 65 cm; *Hadrosteus* – 16 cm; *Gorgonichthys* – to 70 cm; *Heintzichthys* – 25 cm. Size is here not correlated with number of acquired synapomorphies. Some species of an individual genus may be variable in size (e.g. *Dunkleosteus marsaisi,* skull length 35 cm; *D. terrelli* up to 65 cm), and at most, this character may be useful at this level for determining species relationships.

The most plausible hypotheses of dinichthyid interrelationships using the above character states are shown in Figure 11. The first scheme (Figure 11-A) is based on the assumption that the inframarginal lamina is well developed in *Golshanichthys* and present in higher dinichthyids, even if secondarily modified or degenerated. One problem with this scheme is the assumed independent acquisition of a long postorbital plate in *E. pustulosus* and certain higher dinichthyids. The second hypothesis (Figure 11-B) ignores the inframarginal lamina (characters 3a, 3b, 3c) as a valid synapomorphy, and thereby places *Golshanichthys* as a sister taxon to *Eastmanosteus* sp. from Gogo by virtue of their absence of a long postorbital plate. Figure 11-C shows a conservative hypothesis based on the distribution of the inframarginal lamina in dinichthyids, leaving out taxa in which the development of this character is not known. In either of the two major schemes the position of *Westralichthys* is as a sister taxon to the higher dinichthyids *Dunkleosteus, Gorgonichthys, Heintzichthys* and *Hadrosteus.*

Dinichthyid evolution and paedomorphosis

There is little known data on the ontogenetic development of advanced arthrodiran fishes (*Coccosteus,* Miles and Westoll, 1968;*Incisoscutum,* Dennis and Miles, 1981) and amongst other placoderm groups it has only been discussed for antiarchs (Stensio 1948, Werdelin and Long 1986). Some of the characters described in juveniles of *Coccosteus cuspidatus* agree with observations for juveniles of *Incisoscutum,* and within these characters are found some traits of the dinichthyids. These characters are (1) the retention of a straight median suture between the centrals, (2) neck-joint is proportionally larger, (3) sensory-line deeply incised, (4) smooth anterior face on ascending laminae of the interolateral plate. In addition the presence of well defined (i.e. unworn) cusps on juvenile gnathal bones may have preceded the development of strongly developed anterior cusps on dinichthyid gnathals by transition of wear surfaces area, thereby preventing wear on the anterior biting edge of the jaws. If the dinichthyids are derived from coccosteid stock, as is generally accepted (Denision 1978, 1984, Lelievre *et al.* 1981, Moy-Thomas and Miles 1971), then it is feasible that retention of some juvenile characters (paedomorphosis, McNamara 1986) with increased overall size may have been the evolutionary mechanism by which the dinichthyids arose. Character development is seen as most accelerated from the transition between *Eastmanosteus* and higher dinichthyids whereby the central plates retain a straight suture, the nuchal changes shape and diminishes in size, the ornamentation is lost or not developed, the neck-joint becomes vertical, the interolateral plate loses rows of tubercles on its ascending lamina, the spinal plate is lost, the sensory-line canals become deeply incised and the gnathal plates have an accentuated anterior cusp. Although examples of heterochrony for fossil invertebrates may show a clear trend between change in environmental conditions and retardation (paedomorphosis) or continued development of ontogenetic trends (peramorphosis, e.g. McNamara 1982), examples within fossil fishes (e.g. Bemis 1984) do not show a connection between speciation and gradual environmental changes. One would suspect that the major factors influencing the evolution of dinichthyids would include changes to vertebrate faunas across the Frasnian-Famennian boundary (and therefore changes in competition and food sources) and increased competition resulting from a secondary radiation of advanced dinichthyids (Famennian). Both of these factors may be causally related.

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