Reanalysis of *Heintzichthys gouldii* (Newberry), an aspinothoracid arthrodire (Placodermi) from the Famennian of northern Ohio, with a review of brachythoracid systematics

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Heintzichthys gouldii is redescribed based on new material from the Interstate 71 Paleontological Salvage Project (Cleveland Museum of Natural History, 1966–67). Phylogenetic analysis of brachythoracid arthrodires clearly shows the monophyly of Camuropiscidae and the aspinothoracid arthrodires. *Heintzichthys gouldii* and *Gorgonichthys clarki* are removed from Dinichthyidae and placed within aspinothoracid arthrodires. The remaining members in the family Dinichthyidae are united solely by plesiomorphic characters. A number of putative synapomorphies for the eubrachythoracid arthrodires are questioned; however, the validity of this taxon is supported by three synapomorphies.

KEY WORDS:—Devonian – Arthrodira – brachythoracid – systematics.

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INTRODUCTION

Arthrodires are the best known subgroup of placoderms, representing over 72% of known placoderm taxa (Denison, 1978). Dating from the Gedinnian to the Famennian (395–345 my BP) arthrodires are important for understanding early gnathostome evolution (see Table 1 for range of arthrodires in current study). Within the arthrodires, Miles (1969) noted an apparent increase in generic diversification for the Dolichothoraci and Brachythoraci. A species level analysis for Arthrodira confirms the increase for the Brachythoraci in the Middle and Late Devonian. The aspinothoracid arthrodires include most of the new taxa. Study of evolutionary trends associated with changes in species diversity requires a sound phylogenetic basis. The systematics of the Brachythoraci has been uncertain, with the fossil material from Gogo Station, Australia, having added a wealth of new information. It is important to evaluate this new information and to reanalyse North American forms that have been known since the latter part of the nineteenth century. As a first step in this effort, *Heintzichthys gouldii* (Newberry) is redescribed and the systematic relationships of brachythoracid arthrodires are reviewed.

The genus *Heintzichthys* Whitley (1933) is a subgroup within the eubrachythoracid arthrodires referred by Obruchev (1964) and Denison (1978) to the family Dinichthyidae. The type species *Heintzichthys gouldii* was first named by Newberry (1885) as *Dinichthys gouldii*, based on a disarticulated, but nearly complete specimen (AMNH 160, holotype). Synonyms also include *Stenognathus gouldii* Newberry (1897), *Dinichthys corrugatus* Newberry (1889) and *Dinichthys gracilis* Claypole (1893). Later, Hussakof (1911) described another nearly

TABLE 1. Stratigraphic range for arthrodiran taxa in current study. Resolution to stage level only. Compiled from Denison (1978), with the exception of taxa from the Gogo Formation of Australia

	Ged.	Sieg.	Ems.	Eif.	Giv.	Fras.	Fam.	Tour.
Dicksonosteus		■						
Holonema			■	■	■			
Buchanosteus			■	■				
Homosteus			■	■				
Camuropiscis				■	■	■		
Rolfosteus						■		
Tubonasus						■		
Latocamurus						■		
Incisoscutum						■		
Harrytoombsia						■		
Eastmanosteus calliaspis						■		
Coccosteus				■	?	?		
Dunkleosteus						■	■	
Gorgonichthys						■		
Heintzichthys						■		
Gymnotrachelus						■		
Selenosteus					?	■		
Rhinosteus						■		
Pachyosteus						■		
	Ged.	Sieg.	Ems.	Eif.	Giv.	Fras.	Fam.	Tour.
	L. Dev.			M. Dev.		U. Dev.		Carb.

complete specimen of *Heintzichthys gouldii* (BMNH P9335) from the Natural History Museum (London); this was later restudied by Heintz (1931: figs 3, 5) who presented a reconstruction of the head and thoracic shields. *Heintzichthys gouldii* is an aspinothoracid arthrodire characterized by internal overlap of the posterior median ventral plate by the anterior median ventral plate and the presence of a posteriorly projecting posterior lateral plate that encloses, in part, the pectoral fenestra.

In 1966 and 1967, the Cleveland Museum of Natural History conducted the Interstate Highway 71 Paleontological Salvage Project. The importance of this project has been twofold: (1) it has added to the known diversity of the Cleveland Shale fauna (Table 2) and (2) it has increased significantly the number of specimens available for study, nearly doubling the Cleveland Museum's collection of Cleveland Shale fishes (Hlavin, 1976). The project provided numerous specimens of *Heintzichthys gouldii*. The *Heintzichthys* specimens collected from Interstate 71, and other material accumulated since Heintz's reconstruction, include isolated dermal plates, partially articulated dermal head and thoracic shields, and perichondrally ossified structures. In addition, the Interstate 71 material provides an ontogenetic series for *Heintzichthys gouldii*.

This material is important for analysis of the phylogenetic relationships among the eubrachythoracid arthrodires. Miles & Dennis (1979) suggested that placoderm studies had been burdened by the accumulation of data not directly related to a phylogenetic analysis. Thus, they published a series of descriptive papers on the arthrodires from the Lower Frasnian Gogo Formation, western

TABLE 2. Cleveland Shale vertebrate fauna compiled from Williams (1990) and Hlavin (1976)

Arthrodira:
"Dentognathus curvatus" (Hlavin, 1976)
Bungartius perissus Dunkle, 1947
Callognathus regularis Newberry, 1889
Coccosteus cuyahogae Claypole, 1893
Diplognathus mirabilis Newberry, 1887
Dunkleosteus terrelli (Newberry, 1874)
Glyptaspis verrucosis Newberry, 1889
Gorgonichthys clarki (Claypole, 1892)
Gymnotrachelus hydei Dunkle & Bungart, 1939
Heintzichthys gouldii (Newberry, 1885)
Holdenius holdeni Dunkle & Bungart, 1942
Hussakofia minor (Newberry, 1878)
Mylostoma eurhinus (Dunkle & Bungart, 1945)
Mylostoma newberryi Eastman, 1907
Mylostoma variabile Newberry, 1883
Paramylostoma arcualis Dunkle & Bungart, 1945
Selenosteus brevis Dean, 1901
Stenosteus glaber Dean, 1901
Titanichthys agassizi Newberry, 1885
Titanichthys attenuatus Wright, 1893
Titanichthys clarki Newberry, 1887
Titanichthys hussakofia Hay, 1929
Titanichthys rectus Claypole & Wright, 1893
Tracheosteus clarki Newberry, 1889

Chondrichthyes:
"*Prorodus variabilis*" (Hlavin, 1976)
Cladoselache acanthopterygius Dean, 1909
Cladoselache brachypterygius Dean, 1909
Cladoselache clarki Claypole, 1893
Cladoselache desmopterygius Dean, 1909
Cladoselache fyleri Newberry, 1889
Cladoselache kepleri
Cladoselache magnificus Claypole, 1894
Cladoselache newberryi Dean, 1894
Ctenacanthus clarki Newberry, 1889
Ctenacanthus compressus Newberry, 1878
Diademodus hydei Harris, 1950
Hoplonchus parvulus (Newberry, 1875)
Orodus sp.
Phoebodus politus Newberry, 1889
Stethacanthus "clevelandensis" (Hlavin, 1976)
cladodont (undescribed)

Osteichthyes:
Kentuckia hlavini Dunkle, 1964
Tegeolepis clarki Newberry, 1888

Australia, limiting their discussion to an analysis of 28 phylogenetic characters; little discussion was given to additional anatomical features. In evaluating the relationships of *Heintzichthys*, it has been found necessary to expand their data matrix. The lack of a more complete description often hinders the analysis of potentially new characters. Evaluation of the eubrachythoracid arthrodires is also hindered by the limited number of published phylogenetic analyses. The phylogenetic utility of any one character cannot be evaluated except through congruence (Patterson, 1982) and should be based on an analysis using all available data.

In the first part of this paper, the anatomy of *Heintzichthys gouldii* is redescribed in detail. This is followed by a systematic review of brachythoracid arthrodires. The relationships of *Heintzichthys gouldii* and 17 other brachythoracid arthrodires are evaluated using the computer program, Phylogenetic Analysis Using Parsimony (PAUP version 3.0—Swofford, 1989). Details concerning characters and their polarization and algorithm parameters are discussed in the systematics section. The following taxonomic groups are discussed: brachythoracid, eubrachythoracid, coccosteomorph, pachyosteomorph, aspinothoracid and selenosteid arthrodires, and the family Dinichthyidae. A discussion of eubrachythoracid synapomorphies is included to point out the need for detailed clarification in the presentation of proposed synapomorphies and to rediagnose the eubrachythoracid arthrodires.

Nomenclature and abbreviations, listed here, follow that of Dennis-Bryan (1987). Specimen number prefixes denote their respective institutions: AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; CMNH, Cleveland Museum of Natural History, Cleveland, OH; MCD, Institut de Paléontologie, Paris, MCZ, Museum of Comparative Zoology, Harvard Univ., Boston, MA. The suffix 'id' when used to form taxonomic adjectives does not refer to familial level Linnean classification and is used as a convenience for discussing informal taxonomic units.

MATERIALS

Specimens, collected before the Interstate 71 Paleontological Salvage Project, are in the collections of the American Museum of Natural History (New York), Buffalo Society of Natural Sciences (Buffalo), Natural History Museum, London, and Cleveland Museum of Natural History (Cleveland). The bulk of Interstate 71 *Heintzichthys* material was taken from a quarry located at the intersection of West 130th Street and Interstate 71, Brookpark, Ohio. A single shallow horizon, located beneath a thin unconsolidated mud containing numerous pyrite nodules, was the source for numerous fossil fishes found *in situ* within the shales (Hlavin, personal communication). Field identifications recognized *Heintzichthys*, 'type W' (a temporary field classification for similar, but unidentified specimens; CMNH 8056, 8057, 8058 and 8059), 'type X' (CMNH 8036, 8037, 8038 and 8039) and 'type Z' (CMNH 8048) material in addition to other recognizable genera. 'Type W' specimens were later re-identified in the field as belonging to *Heintzichthys*. 'Type Z, X and W' specimens represent an ontogenetic sequence for *Heintzichthys* taken from a single horizon within the Cleveland Shale.

DESCRIPTION

Heintzichthys gouldii (Newberry)
(Figs 1–18)

Head shield

General features. The head shield (Figs 1–3) is composed of 15 individual plates; three median unpaired plates (R, P, Nu) and six paired plates (PrO, PtO, C, M, PM, PNu). The marginal plates lack contact with the centrals and the preorbital plates do not meet along the midline. There is no evidence for the presence of postnasal, internasal or extrascapular plates. The orbits are large with an inconspicuous postorbital process. Sensory line canals, when present, are represented by open grooves and will be discussed with the plates on which they occur. The ventral consolidated arches are reduced in comparison with those of *Dunkleosteus*. Dermal bones typically lack ornamentation; however, ossification centres are discernible through lines of radiation. The plates of the head shield have well developed and interlocking overlaps with the exception of the rostral plate which is often missing.

Rostral (R). This plate (Figs 1, 4A) is triangular in shape with a broad, rounded anterior border. Internally, a ventral anterior thickening is evident (a.th, Fig. 4A), but it is small and continuous, as a low ridge, with the thickening of the opposite side. A similar connecting ridge is seen in *Eastmanosteus calliaspis* (Dennis-Bryan, 1987: fig. 9A) and is variable in *Dunkleosteus terrelli* (personal observation). The posterior margin is rounded and possesses a contact surface for the pineal plate (cf.P, Fig. 4A).

Pineal (P). The pineal plate (Figs 1, 3) overlaps the adjacent preorbital and central plates and lies over the orbit (this position is plesiomorphic at the eubrachythoracid level). There is an anterior overlap area for the rostral plate. The centre of this plate is tuberculated in juvenile specimens with an open pineal foramen (e.g. CMNH 8048). In adult specimens there is an internal closed pineal fossa which is bounded posteriorly by a raised ridge.
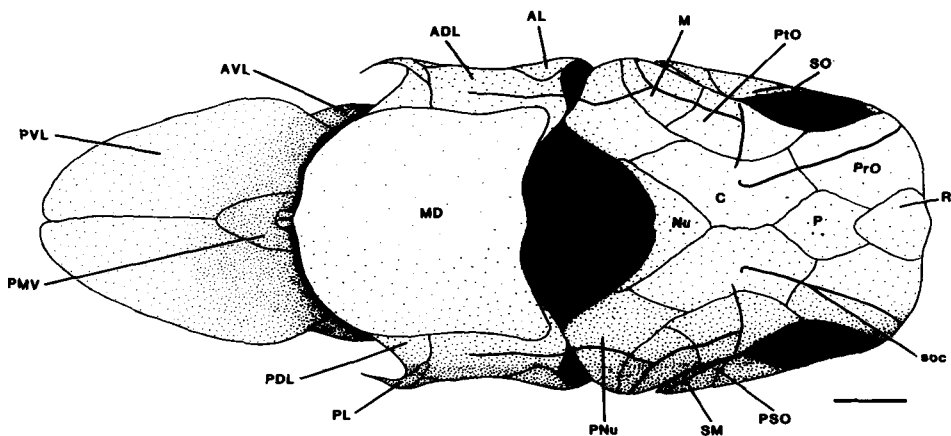

Figure 1. *Heintzichthys gouldii*. Head and thoracic shields in dorsal view. Scale bar 5 cm.
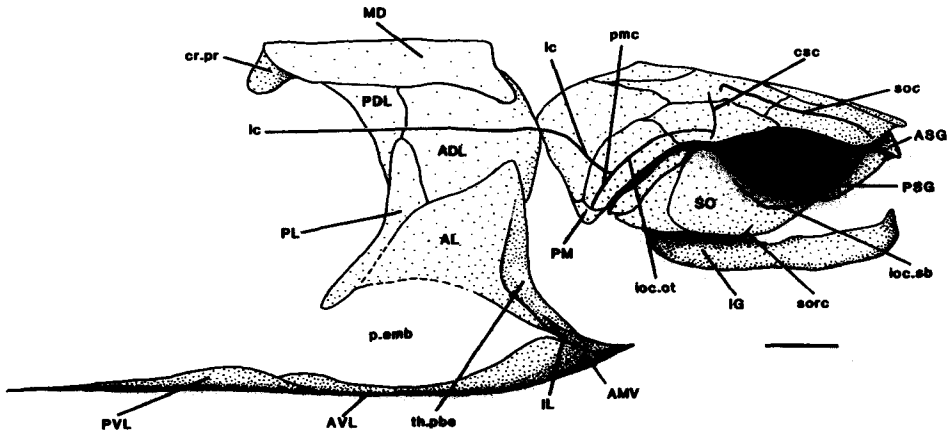
Figure 2. *Heintzichthys gouldii.* Head and thoracic shields in right lateral view. Scale bar 5 cm.

Nuchal (Nu). The nuchal plate (Figs 1, 3) is triangular in external view with a deep posterior embayment (shared among aspinothoracid arthrodires with the exception of *Gorgonichthys*). Juvenile specimens (CMNH 8048, CMNH 8037) possess a transverse anterior border (a convex anterior border in adults is shared among pachyosteomorph arthrodires with the exception of *Eastmanosteus calliaspis*). A small median posterior process (p.pr, Fig. 3B) is present. The paired pits on the visceral surface of the nuchal (pt.u, Fig 3B, housing processes of the neurocranium) are directed posteroventrally. They are bounded anteriorly by the nuchal thickening (n.th, Fig. 3B, = th.nm of Stensio, 1963: fig. 112) and are separated by a median septum (m.sept). The median septum is continuous with the median posterior process thus separating the transverse thickening into two separate halves. A second pair of pits (probable sites of muscle insertion) is located posterodorsally to the transverse thickening.

Preorbital (PrO). The preorbital plate (Figs 1–3A) possesses a well-developed dermal preorbital process (shared among eubrachythoracid arthrodires and *Homosteus*). The preorbital plate does not contact its counterpart and is separated by the pineal and rostral plates (this separation is plesiomorphic at the eubrachythoracid level). The groove for the supraorbital sensory canal (soc, Fig. 1) traverses the preorbital plate where it ends on the downturned face of the preorbital process.

The supraorbital vault (suo.v, Fig. 3A), which represents the anterior part of the lateral consolidated part of the head shield, is present on the internal surface and is continuous anterolaterally with the dermal preorbital process. The anteromedial aspect of the supraorbital vault shows a recess (ch.pro.pr, Fig. 3A) for the neurocranial preorbital process. The anterior border of this recess forms the supraethmoid crista (cr.seth, Fig. 3A) which is restricted to the preorbital plate and does not extend on to either the rostral or pineal plates as seen in some selenosteids (e.g. *Enseosteus*, Stensio, 1963: fig. 113). A deep recess is present anterior to the supraethmoid crista, representing a possible lateral expansion of the olfactory region. The rhinocapsular part of the neurocranium does not appear to be expanded laterally in this region (see discussion of neurocranium).
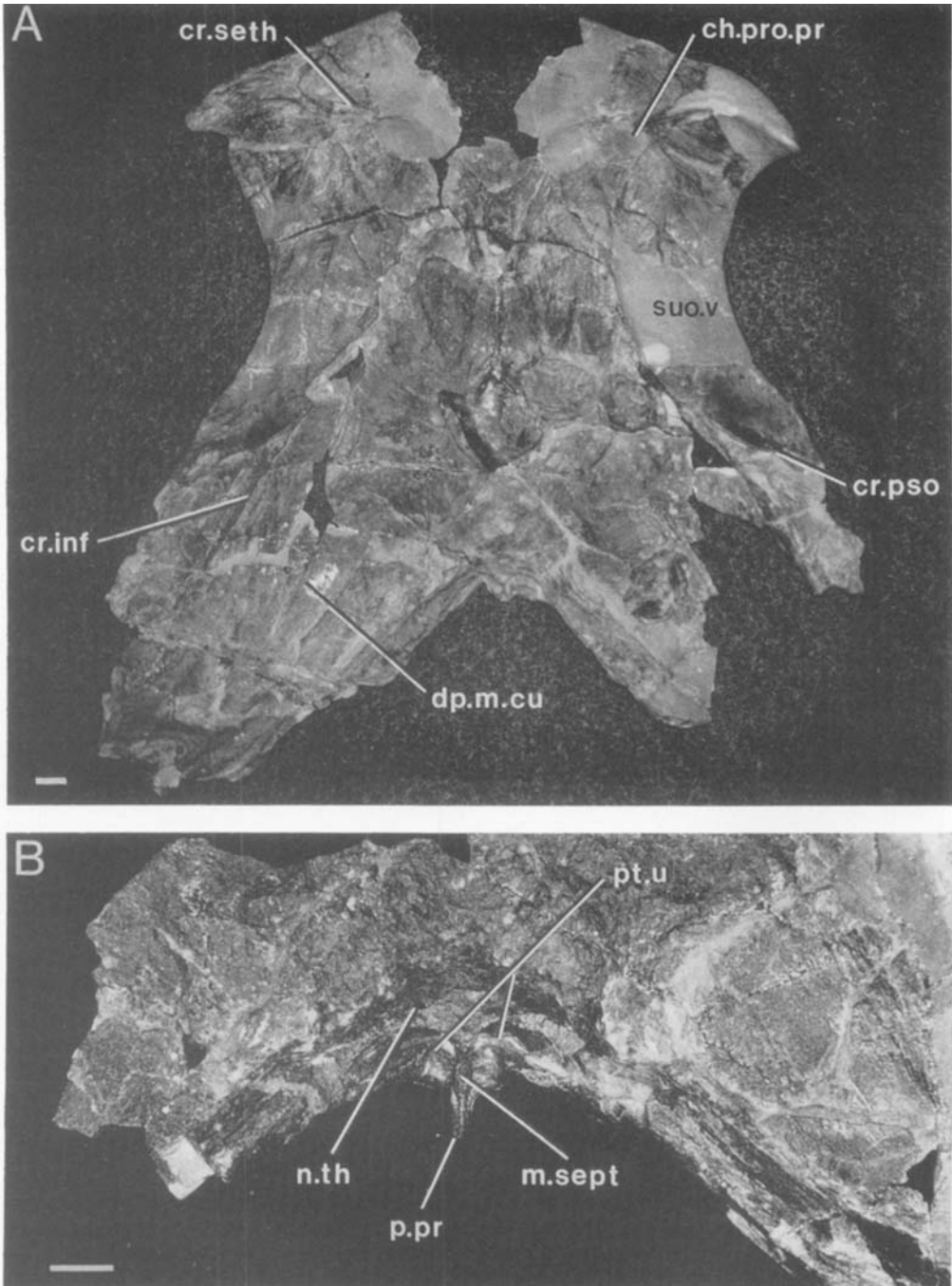
Figure 3. *Heintzichthys gouldii*. A, Skull roof (CMNH 5648) in ventral view. B, Nuchal thickening (CMNH 5130) in posteroventral view. Scale bars 1 cm.

Postorbital (PtO) (Figs 1–3A). The dermal postorbital process is poorly developed. Three sensory line grooves are present on the postorbital plate; the central sensory canal (csc, Fig. 2) and the postorbital and otic branches (ioc.ot, Fig. 2) of the infraorbital canal. The groove for the postorbital branch of the infraorbital canal is rotated posteriorly in *Heintzichthys gouldii* because of the large orbit. This sensory groove terminates prior to reaching the margin of the head shield. A closed angle between the postorbital and otic branches is diagnostic of the aspinothoracid arthrodires (as we will see, this character is independently derived in the camuropiscid arthrodires and *Incisoscutum*). The angle is further closed among derived aspinothoracids (e.g. selenosteids which have an angle of *c.* 45°).

The lateral consolidated part of the head shield continues on the internal surface (a short lateral consolidated part of the head shield is synapomorphic for the aspinothoracid arthrodires). A distinct ridge forms the medial border of the supraorbital vault. This ridge continues posterolaterally as the posterior supraorbital crista (cr.pso, Fig. 3A) to the margin of the head shield at a point just posterior to the position of the postorbital branch of the infraorbital canal. The inframarginal crista (cr.inf, Fig. 3A) originates from the supraorbital ridge and continues beneath the main lateral line canal. *Heintzichthys* lacks a ventral postocular process (= neurocranial process of Heintz, 1932; absence of this feature is plesiomorphic at the aspinothoracid level).

Central (C). The central plates (Figs 1–3A) are separated anteriorly by the pineal plate. Each plate is laterally embayed and overlapped by the postorbital plate. The longitudinal dimension of the central plate is greater than the same dimension of the preorbital plate (a shared feature of *Heintzichthys* and the remaining derived aspinothoracid arthrodires, excluding *Gorgonichthys*). Two sensory line grooves are recognized (Figs 1, 2); the continuation of the supraorbital canal from the preorbital plate and the central sensory canal. In all specimens the supraorbital canal terminates near the ossification centre in a laterally opening J-shape.

Internally, the cuccularis depression (dp.m.cu, Fig. 3A) is bounded anteriorly by a low pre-endolymphatic thickening on the central plate. The anterior margin of this thickening is not discernible.

Marginal (M). The marginal plate (Figs 1–3A) does not contact either the orbit or the central plate (lack of a marginal-central plate contact is present among the aspinothoracid arthrodires with a contact present in *Rhinosteus* and with *Selenosteus* being polymorphic; orbit-marginal contact is characteristic of selenosteid arthrodires). Three lateral line grooves occur; a continuation of the otic branch of the infraorbital canal, the postmarginal canal (pmc, Fig. 2), and the main line canal (lc, Fig. 2). The groove for the postmarginal canal branches from the infraorbital canal at an angle of *c.* 120°. It passes to the posterolateral corner of the marginal plate. The marginal plate is overlapped by the paranuchal and postorbital plates.

The inframarginal crista is continued on the internal surface to the ossification centre. A reduced thickening follows the postmarginal canal on the internal surface to the edge of the plate.

Postmarginal (PM) (Fig. 4B). The postmarginal plate forms the posterolateral corner of the head shield. Its external surface bears an overlap area for the marginal and paranuchal plates. The groove for the postmarginal canal extends
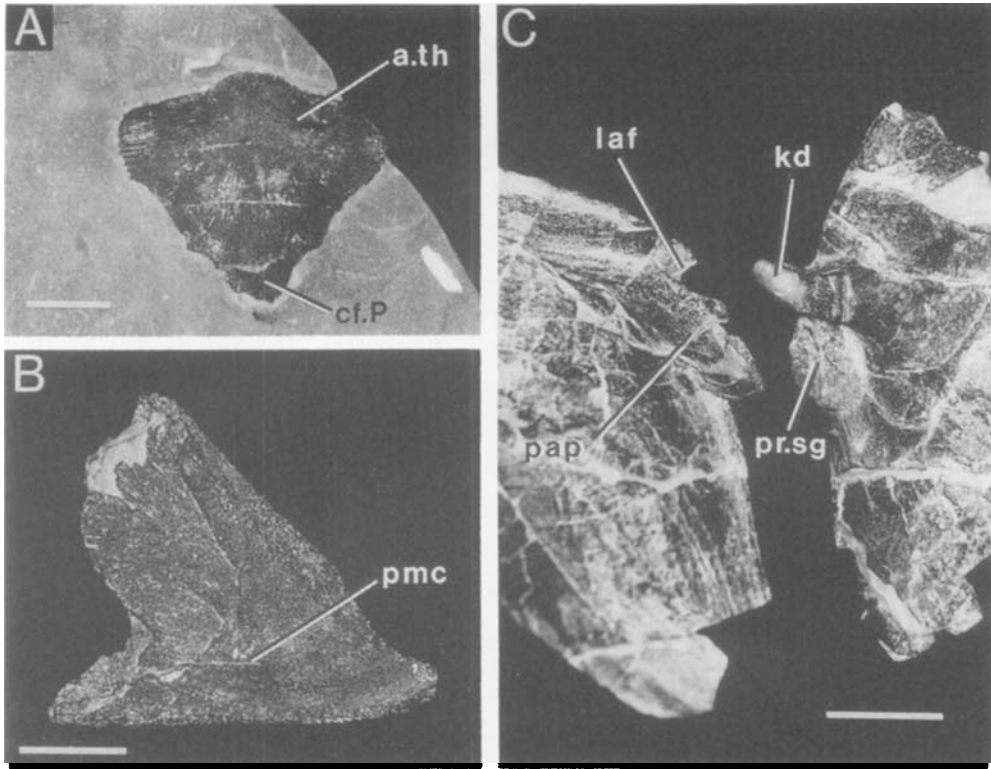
Figure 4. *Heintzichthys gouldii*. A, Rostral plate (CMNH 9425) in ventral view. B, Postmarginal plate (CMNH 9350) in external view. C, Articular joint between head and thoracic shields (CMNH 6352) in internal view. Anterior dorsolateral and paranuchal plates disarticulated. Scale bars 2 cm.

onto the postmarginal plate (pmc, Fig. 4B). The internal surface lacks any distinctive features.

Paranuchal (PNu) (Figs 1–3A, 4C). The paranuchal plate of juvenile specimens has a postnuchal process (CMNH 8048, CMNH 8037); in adults the process is either absent or very short and limited to the descending posterior face of the head shield. The plate is traversed by the main lateral line groove. A para-articular process (pap, Fig. 4C) is strongly developed lateral to the articular fossa (laf, Fig. 4C). Internally, the nuchal thickening is continued laterally along the posteromedial border of the paranuchal plate.

Cheek plates.

General features. The cheeks are composed of three paired plates (SO, PSO, SM) which do not fuse to the head shield. The submarginal plate lies between the suborbital and postsuborbital plates and the head shield.

Suborbital (SO). The suborbital (Figs 1, 2, 5A) is cleaver-shaped with an elongated handle and a short blade. The handle portion sutures with the dermal preorbital process (also seen in pachyosteomorph arthrodires and *Harrytoombsia*). The general shape is similar to that seen in selenosteids. A short groove for the supraoral sensory canal (sorc, Fig. 2) has been seen clearly only in CMNH 8056.
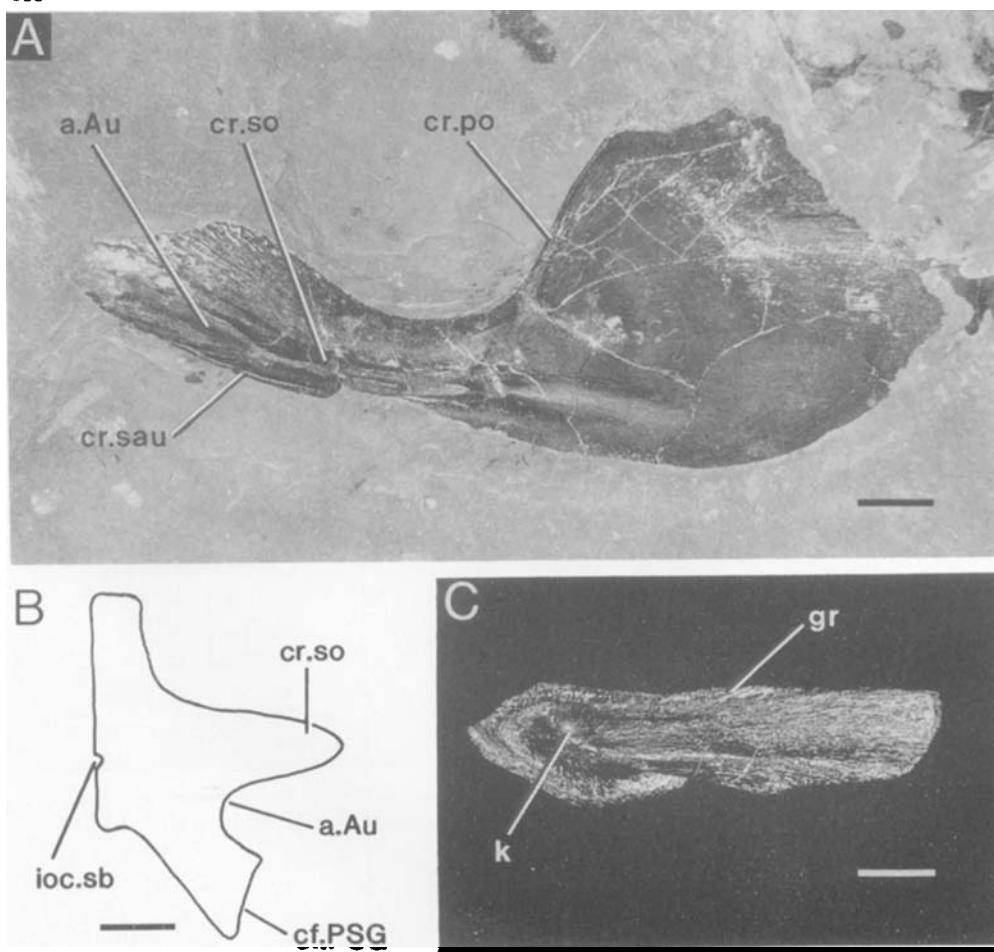
Figure 5. *Heintzichthys gouldii.* A, C. A, Suborbital plate (CMNH 9332) in internal view. B, *Eastmanosteus calliaspis*, cross-section of suborbital dermal lamina (BMNH P50894). C, Submarginal plate (CMNH 9407) in internal view. Scale bars 2 cm.

This groove remains close to the posteroventral edge of the suborbital plate and does not connect with the groove for the infraorbital canal. The postorbital groove for the infraorbital canal does not continue to the dorsal edge of the plate (Fig. 2). A suborbital groove is present (ioc.sb, Figs 2, 5B).

The internal surface of the linguiform process (Fig. 5A) is characterized by a well-developed subautopalatine crista (cr.sau, Fig. 5A; = R4 of Heintz, 1932: figs 21, 22) that lacks a contact surface for the posterior superognathal (cf.PSG, Fig. 5B). The subautopalatine crista continues posteriorly as a low ventral ridge (= R3 of Heintz, 1932: fig. 22) and dorsal to it lies a depression for the autopalatine (a.Au, Figs 5A, B). The subocular crista (cr.so, Figs 5A, B; = R2 of Heintz, 1932: figs 21,22), which is continuous with the postocular crista (cr.po, Fig. 5A; = R1 of Heintz, 1932: fig. 22), dorsally encloses the autopalatine depression. The pattern of these ridges and the autopalatine depression is variable among the eubrachythoracids. In *Dunkleosteus*, the subautopalatine crista of the sublinguiform process is ventrally enlarged and forms a support

surface for the posterior superognathal. A similar condition is found in *Eastmanosteus calliaspis* (Fig. 5B; seen in adult specimens only; see Dennis-Bryan, 1987: figs 9, 13) and *Eastmanosteus pustulosus* (Boylan, 1973). *Heintzichthys gouldii* lacks this ventral projection and its subautopalatine crista projects medioventrally, implying that the posterior superognathal articulates solely with the autopalatine and lacks any dermal support. This condition is seen in juvenile specimens of *Eastmanosteus calliaspis* (personal observation), in *Coccosteus cuspidatus* (Miles & Westoll, 1968: fig. 13) and in other aspinothoracids (*Melanosteus*, Lelièvre *et al.*, 1987: fig. 13; *Tafilalichthys*, personal observation). At present, the distribution of this character appears to be correlated with a reduction in the depth of the posterior superognathal. The unqualified use of the term 'sublinguiform process' is misleading since it is applied equally to the condition of both *Heintzichthys* and *Dunkleosteus* implying homologous states. In addition, it appears that the subautopalatine and suborbital cristae are not clearly distinguished in some cases (e.g. Long, 1988: fig. 13).

Postsuborbital (PSO). The external surface of the postsuborbital plate lacks a sensory canal. Anteriorly, there is an overlap area for the suborbital (oa.SO, Fig. 6A). The posterodorsal edge is slightly recessed, possibly to accommodate the submarginal.

Internally, the location of the quadrate is typically represented by a small ventrally placed thickening; however, the postsuborbital of CMNH 9337 shows a well developed perichondrally ossified quadrate. The condylar area is situated near the ventral edge of the plate. A detent process is present along the dorsal
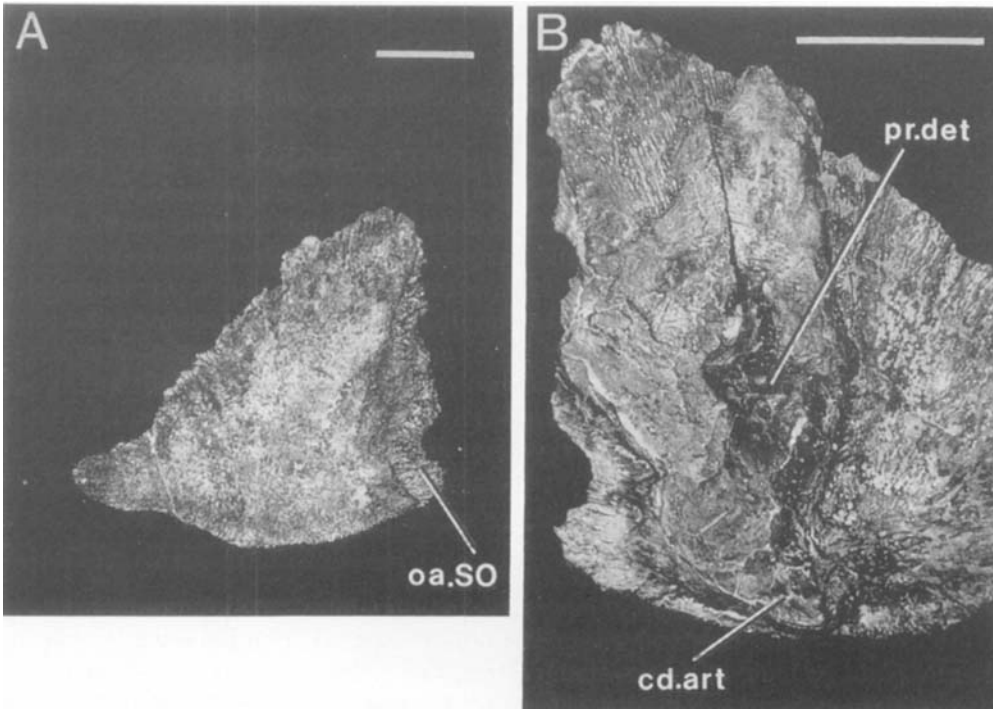

Figure 6. *Heintzichthys gouldii*. Right postsuborbital (CMNH 9337) in A, external view and B, internal view. Scale bars 2 cm.

crista of the quadrate (pr.det, Fig. 6B; this appears to be plesiomorphic at the pachyosteomorph level which assumes that the coccosteomorph and pachyosteomorph conditions are homologous).

Submarginal (SM) (Figs 2, 5C). The submarginal plate is elongate and is loosely attached to the head shield (a submarginal plate incorporated into the head shield is seen in selenosteid and camuropiscid arthrodires). Externally, it lacks sensory grooves. Internally, the submarginal is thickened by a longitudinal ridge extending from the anteroventral edge to a posterior thickened knob (k, Fig. 5C). In specimens with a complete submarginal, the dorsal part of this ridge bears a shallow groove for the hyomandibula (gr, Fig. 5C).

Gnathal plates and parasphenoid

General features. The gnathal plates include three paired elements: the inferognathals, anterior superognathals and posterior superognathals. The occlusal surfaces of these elements vary with ontogeny. The parasphenoid does not articulate with the anterior superognathal, as it does in *Dunkleosteus*.

Inferognathal (IG) (Figs 2, 7). The inferognathal can be divided into occlusal (= functional) and blade portions. The occlusal surface represents approximately one half the total length.

Adult inferognathals have a single anterior cusp and a blunt occlusal edge. The angle formed by the occlusal surface and the medial surface of the inferognathal is variable both between specimens and along the occlusal surface of a single individual. This angle ranges from 45° to 69°. CMNH 8091 and CMNH 5130 have wear striae oriented 99° and 110° respectively relative to the occlusal edge and directed anteroventrally from the dorsal edge. The orientation of the striae in these two specimens suggests that the inferognathal was displaced posteriorly relative to the posterior superognathal during closure of the mouth. This represents occlusal variation and is supported by variable wear patterns on the anterior cusp. Ontogenetic variation is evident in CMNH 8093 where the anterior cusp possesses wear surfaces oriented at two distinct angles. There is no indication of a secondary cusp as seen in *Dunkleosteus*.

Juvenile specimens possess 13 to possibly 15 large and evenly spaced denticles extending from the anterior cusp to the end of the occlusal surface (Fig. 7A). In CMNH 8038 (13 denticles) and CMNH 8037 (14 denticles) there is a small gap between the most anterior denticle and the anterior cusp (possibly a preservational artifact). These denticles are lost anteriorly to posteriorly, due to wear with age. There is no evidence for adsymphysial denticles associated with the anterior cusp and dental field (Ørvig, 1980, dfa.Ig).

Anterior superognathal (ASG) (Figs 2, 8E). The anterior superognathal possesses a posterior process (p.pro, Fig. 8E) and a lateral cusp. Unlike *Dunkleosteus*, *Heintzichthys* lacks a medial cusp (Ørvig, 1980, dfa.ASG). A depression (ch.eth, Fig. 8E) is present anterodorsally for the neurocranial ethmoid region. There are no denticles in adult forms and evidence for their presence in juveniles is unclear. The lateral face is well developed with a short shelf posterior to the cusp that opposes the inferognathal. The posterior process is poorly developed and is continuous with the lateral face as a thin lamina. These conditions are similar to those seen in *Gorgonichthys* (Dunkle & Bungart, 1946).
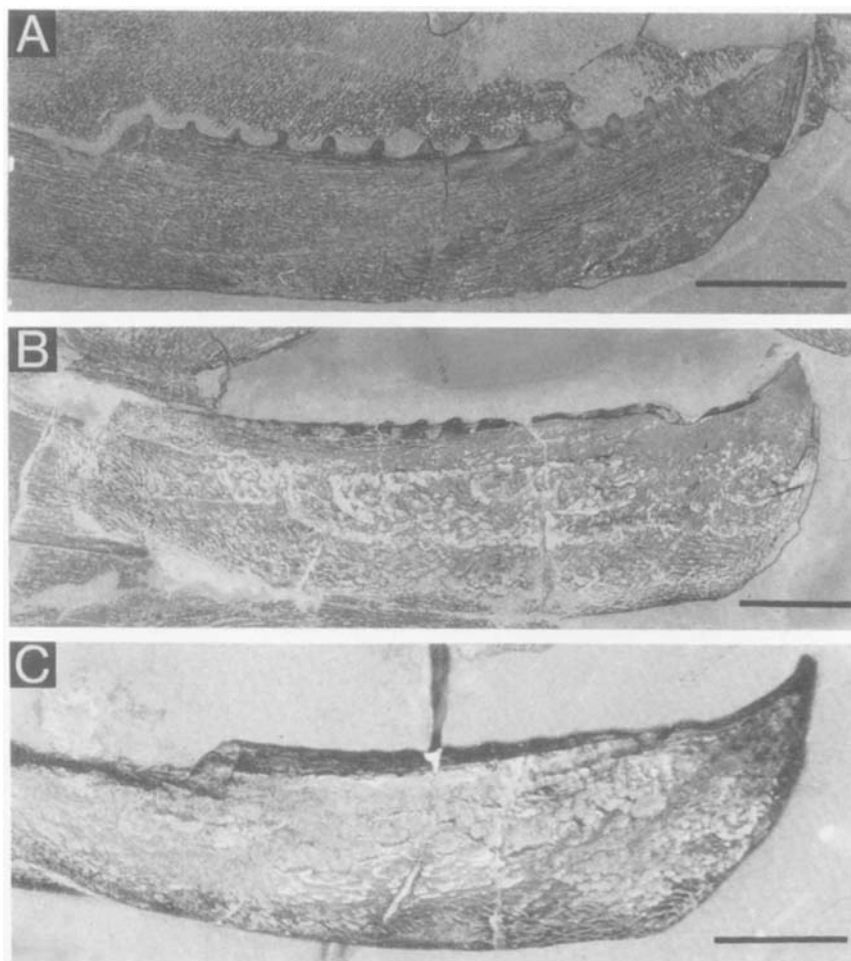
Figure 7. *Heintzichthys gouldii*. Relative ontogenetic sequence from youngest, A (CMNH 8037, type 'X'), to an intermediate age (CMNH 8056, type 'W'), and finally to an older age, C (CMNH 8057, type 'W'), showing right inferognathal in external view. Scale bars 1 cm.

Posterior superognathal (PSG) (Figs 2, 8D). The posterior superognathal is shallow and elongate and has a posterior process (p.pro, Fig. 8D). The ventral margin is denticulate in juveniles (e.g. CMNH 8038). The shape of the occlusal edge of adult posterior superognathals parallels that of the opposing portion of the inferognathals.

Parasphenoid (Figs 8A–C). The ventral surface is flattened and has a central transverse groove (tr.groove, ?CMNH, Fig. 11B, CMNH 8130). The prelepospondyl region (pre; ?, CMNH, Fig. 9, tapers to a rounded point. The parasphenoid figured by Stensio (..., pl. 15C, D) and Dunkle & Bungart (1946: Fig. 8B, C) suggests that the posthypophysial region is longer than wide; however, CMNH 9424 (Fig. 8A) has a nearly complete parasphenoid with the posterior region being wider than long. A posterolateral process (pl.pr, Fig. 9) is present (found in coccosteomorphs and pachyosteomorphs, compare with distribution noted by Gardiner & Miles, 1990, character 22.36).
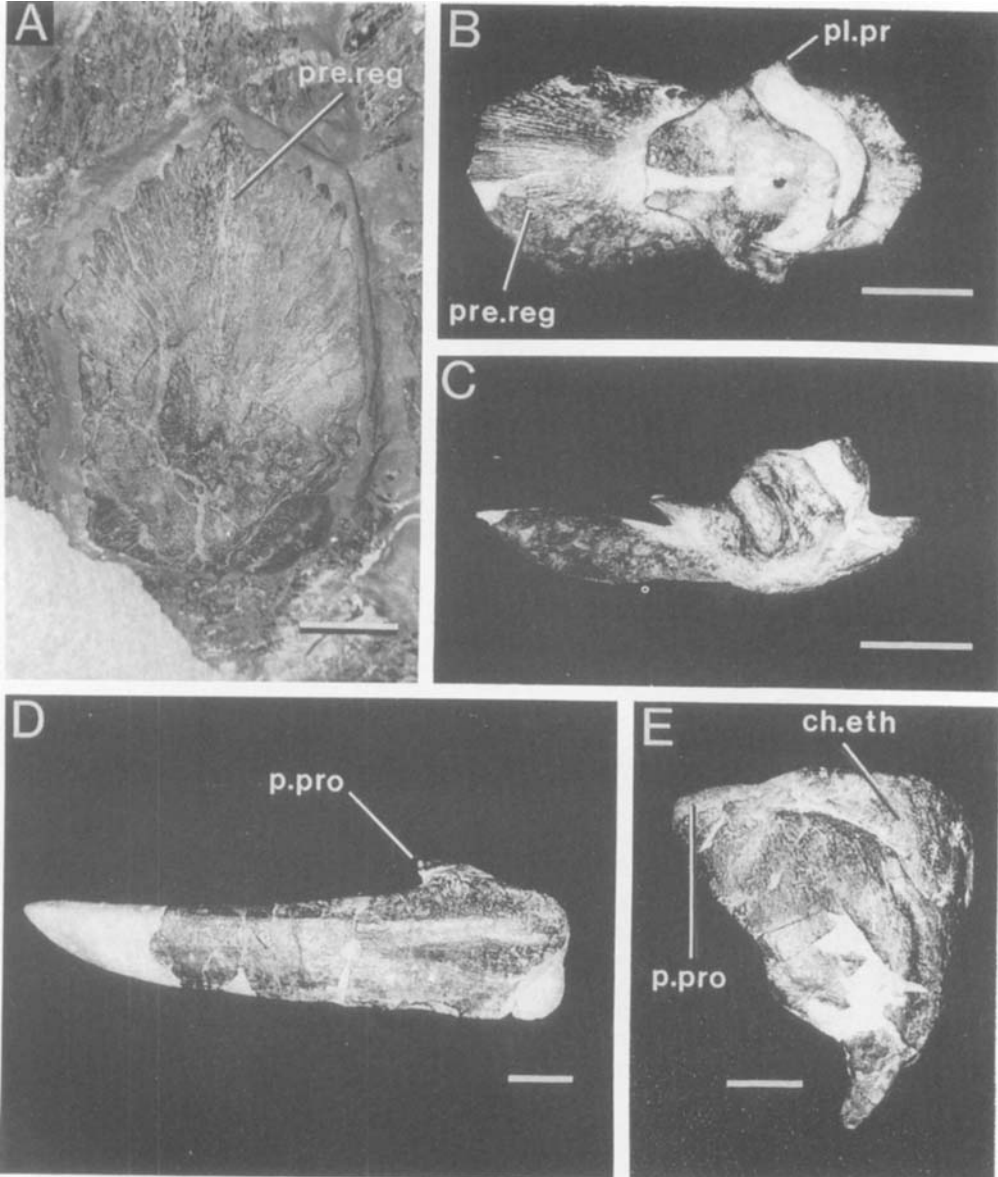
Figure 8. *Heintzichthys gouldii*. A, Parasphenoid (CMNH 9424) in ventral view. B, Parasphenoid (CMNH 5130) in lateral, and C, dorsal view. Posterior, D, and anterior, E, right superognathals in lateral view (CMNH 5266). Scale bars 1 cm.

Dermal shoulder girdle

General features. As usual in brachythoracid arthrodires, the dermal shoulder girdle is composed of 17 individual plates; three unpaired median plates (MD, AMV, PMV) and seven paired plates (ADL, PDL, AL, PL, IL, AVL and PVL). The internal surfaces of the ventral plates (AVL, PVL, AMV and PMV) show concentric growth ridges. Externally, juveniles may have a fine tuberculation near the ossification centres of these ventral plates (Dean, 1896).
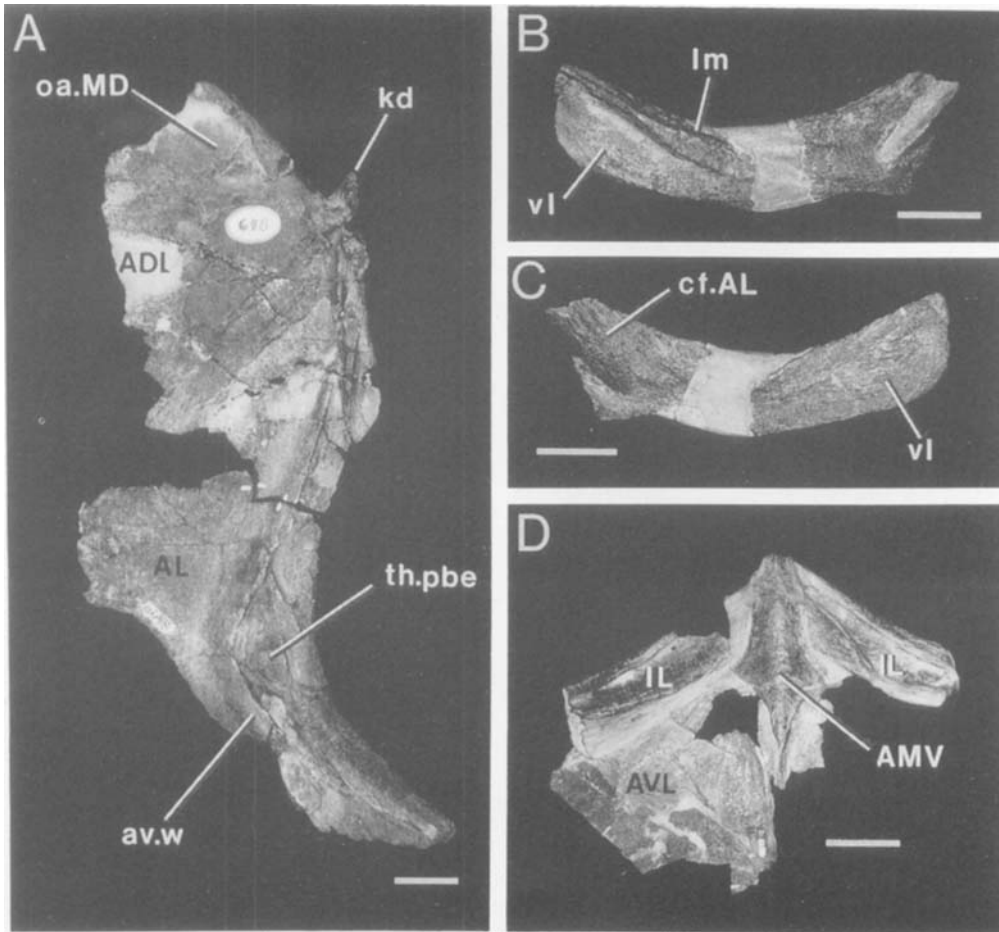
Figure 9. *Heintzichthys gouldii.* A, Right anterior dorsolateral and anterior lateral plates (CMNH 5130) in lateral view. Left interolateral plate in B, ventral and C, dorsal view (CMNH 7038). D, Anterior median ventral and interolateral plates (CMNH 5130) in ventral view. Scale bars 1 cm.

Median dorsal (MD) (Figs 1, 2, 11). The anterior margin of the median dorsal is embayed with a short, rounded, median process. The posterior margin is rounded. A carinal process (cr.pr, Fig. 2; plesiomorphic at the pachyosteomorph level) is developed and projects posterior to the edge of the plate.

Anterior dorsolateral (ADL) (Figs 1, 2, 4C, 9A, 11). Dorsally, the anterior dorsolateral plate lies deep to the median dorsal plate (oa.MD, Fig. 9A). A process of the anterior dorsolateral plate extends along the anterior edge of the median dorsal plate and forms part of the nuchal gap border. Ventrally, there is a large overlap area for the anterior lateral (Fig. 9A). Anterior to this overlap area, the plate forms part of the postbranchial embayment. The glenoid condyle (kd, Figs 4C, 9A) and the subglenoid process (pr.sg, Fig. 4C) are well developed. The groove for the main lateral line continues horizontally across the surface of this plate and ends prior to the posterior margin.

Posterior dorsolateral (PDL) (Figs 1, 2, 10A, 11). The posterior dorsolateral plate has three overlap areas on its external face; a median dorsal overlap (oa. MD,

Figure 10. *Heintzichthys gouldii*. A, Left posterior dorsolateral plate (CMNH 8056, type 'W') in external view. B, Right posterior lateral plate (CMNH 8057, type 'W') in external view. Scale bars 2 cm.

Fig. 10A), an anterior dorsolateral overlap (oa.ADL, Fig. 10A), and a posterior lateral overlap (oa.PL, Fig. 10A). Each overlap area is deeper than the preceding one giving a shingle-like effect with the median dorsal plate overlapping the anterior lateral plate and the anterior lateral plate overlapping the posterior lateral plate. No sensory line grooves are present.

Anterior lateral (AL). (Figs 2, 9A, 11). The anterior lateral plate lacks a dorsal obstantic process (Dennis & Miles, 1981: fig. 2, pro). The postbranchial embayment (Fig. 9A) extends dorsally from the obstantic thickening (th.pbe, Figs 2, 9A; = th of Heintz, 1932: fig. 51) to the anterodorsal corner of the plate. The embayment is continued on the anterior dorsolateral plate. Ventrally, the postbranchial embayment widens and is continuous with the interolateral plate. The external anteroventral wing of the plate (av.w, Fig. 9A) tapers to its ventral end. The ventral tapering of the anteroventral wing is correlated with the reduction and loss of the spinal plate. The external features of the anterior lateral plate are similar to those in *Gorgonichthys* (Dunkle & Bungart, 1946: fig. 2), *Titanichthys* (Dunkle & Bungart, 1946) and *Tafilalichthys* (Lehman, 1956: pl. 2, fig. A).

Posterior lateral (PL). The posterior lateral plate (Figs 2, 10B, 11) is dorsoventrally elongate and forms an obtuse angle which opens posteriorly. There are overlap areas for the anterior dorsolateral (oa.ADL, Fig. 10B) and anterior lateral (oa.AL, Fig. 10B) plates. The ventral portion of the posterior
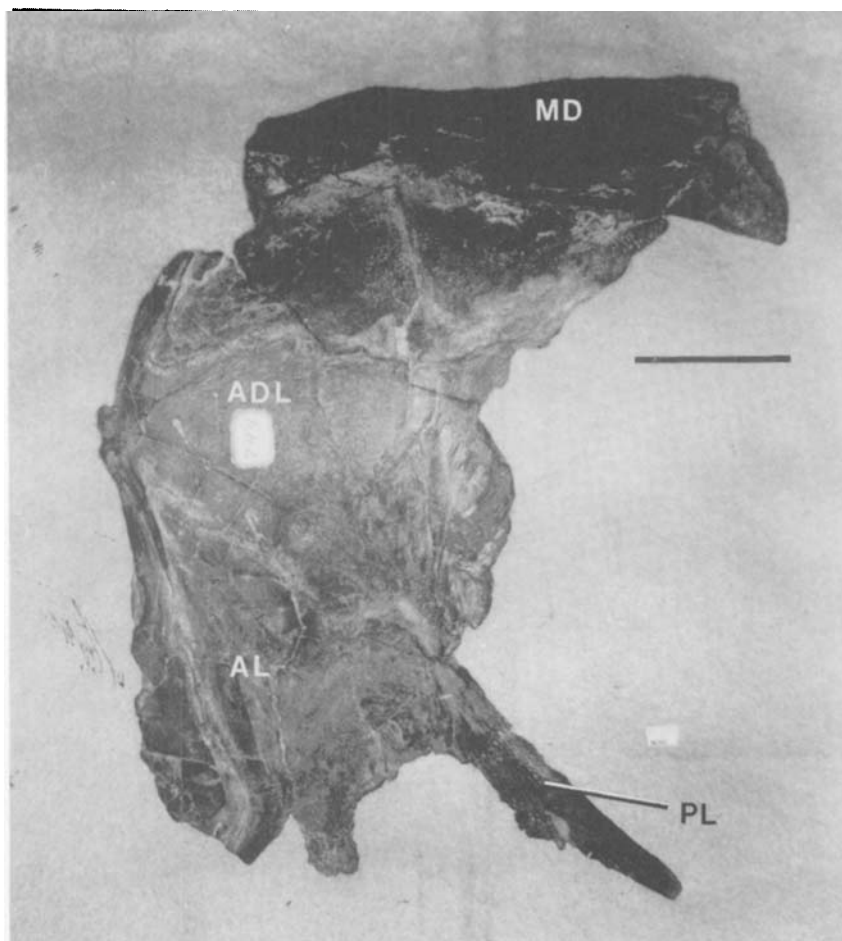
Figure 11. *Heintzichthys gouldii.* Right side of thoracic shield (CMNH 5744) in lateral view. Scale bar 5 cm.

lateral plate lacks any overlap areas and is free of contacts with adjacent plates and with the ventral shield (Figs 2, 11; diagnostic for *Heintzichthys gouldii*). This projection of the posterior lateral plate serves to enclose partially the pectoral embayment. The general form of this plate is distinct in all age classes.

Interolateral (IL). The interolateral plate (Figs 2, 9B–D) lacks an anterior ascending lamina (= postbranchial lamina, Denison, 1978), but has a well developed ventral lip (vl, Fig. 9B–D). The surface in contact with the anterior lateral plate is continuous with a thickened lower margin (Fig. 9A; Heintz, 1932). The shape of the thickened lower margin and its contact with the anterior lateral plate (cf.AL, Fig. 9C) is similar to that of *Tafilalichthys*; however, the interolateral plate of *Tafilalichthys* lacks a ventral lip (MCD 1). There is no ornamentation on the interolateral plate. The loss of ornamentation and the loss of an anterior ascending lamina represent derived features relative to basal pachyosteomorphs (*Eastmanosteus calliaspis* and *Dunkleosteus terrelli*). The orientation of the overlap area on the anterior median ventral plate (oa.IL, Fig. 12A) suggests that the interolateral plates are directed posteriorly from their
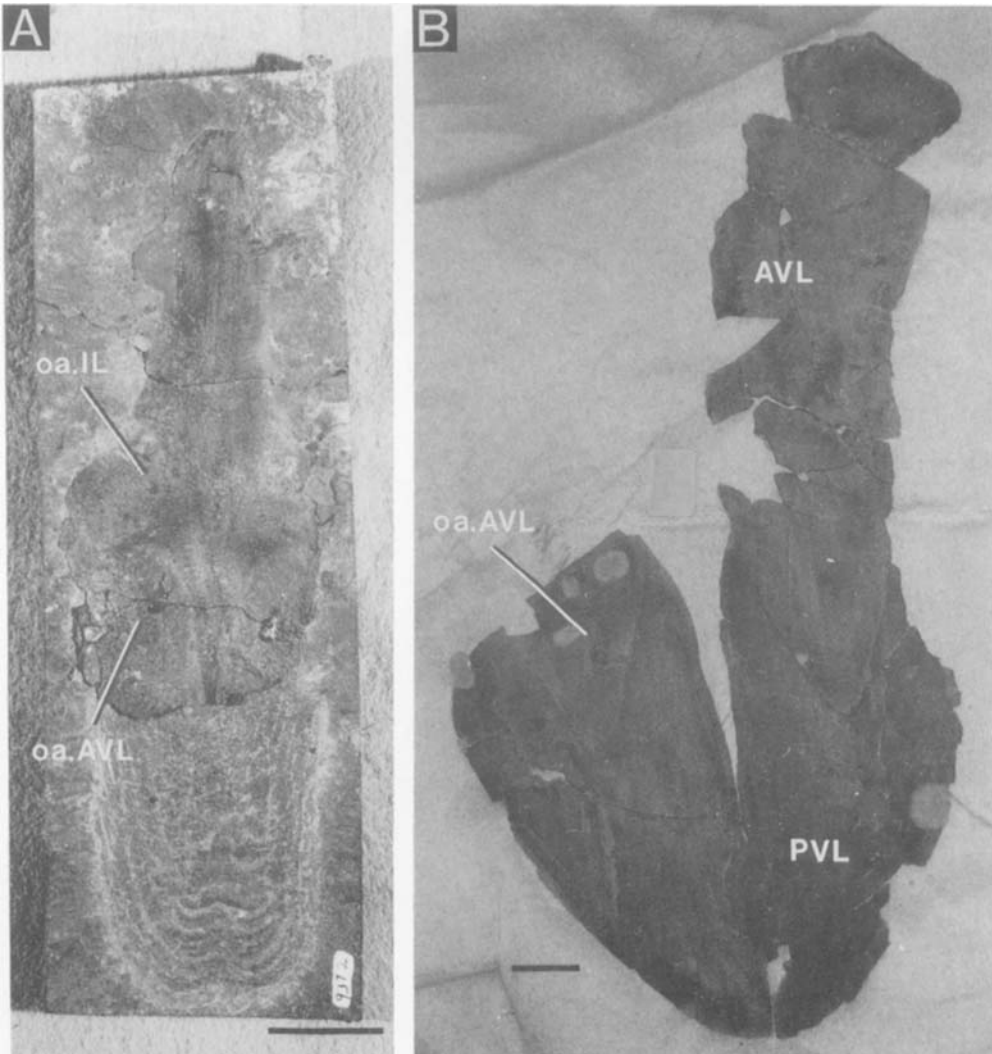
Figure 12. *Heintzichthys gouldii*. A, Anterior median ventral plate (CMNH 9372) in external view. B, Thoracic ventral shield (CMNH 8057, type 'W') in external view. Scale bars 2 cm.

medial contact with the anterior median ventral plate to their lateral contact with the anterior lateral plate at a *c*. 45° angle.

Anterior median ventral (AMV) (Figs 2, 9D, 12A). The external surface bears overlap areas for the interolateral (oa.IL, Fig. 12A), the anterior ventrolateral (oa.AVL, Fig. 12A), and the posterior median ventral plates. The anterior median ventral plate extends anteriorly beyond the anterior ventrolateral plates. This region is the site of distinct overlap areas for the interolateral ventral lip.

Posterior median ventral (PMV) (Figs 1, 13). The posterior median ventral plate has two external overlap areas; the anterior ventrolateral (oa.AVL, Fig. 13A) and the posterior ventrolateral (oa.PVL, Fig. 13A). Internally, it bears a contact face for the anterior median ventral plate (cf.AMV, Fig. 13B). Such a contact face appears to be unique in *Heintzichthys*, but the presence of this condition in
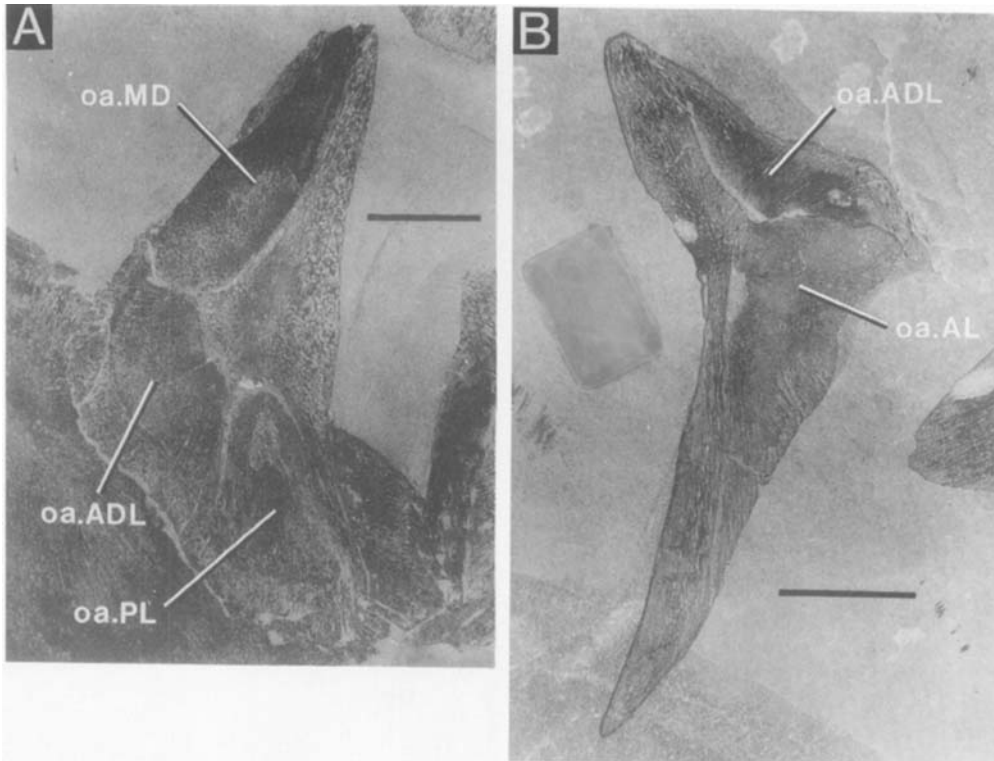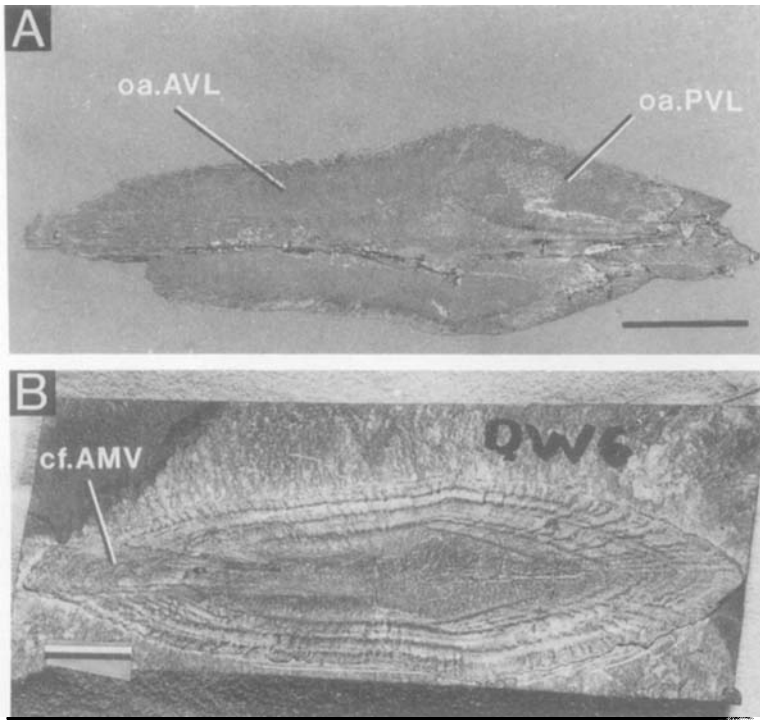
Figure 13. *Heintzichthys gouldii*. A, Posterior median ventral plate (CMNH 8056, type 'W') in external view. B, Posterior median ventral plate (CMNH 9376) in internal view. Scale bars 2 cm.

potential sister taxa is unresolved due to a lack of knowledge about the nature of these plates.

Anterior ventrolateral (AVL) (Figs 2, 12B, 14A). Internally, the anterior ventrolateral bears an anterolateral Y-shaped thickening, as noted in *Eastmanosteus calliaspis* (Dennis-Bryan, 1987). The anterior margin of the plate is oblique relative to the midsagittal plane. The V-shaped posterior part of the plate overlaps the posterior ventrolateral plate. A shallow lateral embayment for the pectoral fin is bounded anteriorly by the anterolateral corner of the plate and a distinct posterolateral angle (pl.a, Fig. 14A).

Posterior ventrolateral (PVL) (Figs 1, 2, 12B, 14B). The posterior ventrolateral plate shows an external overlap area for the anterior ventrolateral plate (oa. AVL, Fig. 12B). The right posterior ventrolateral plate may have an overlap for the opposite plate (Fig. 12B).

Pectoral and pelvic fins, axial skeleton and neurocranium

General features. A number of highly fragmented scapulocoracoids are preserved and are associated with dermal plates from *Heintzichthys* (e.g. CMNH 9437, 8242). Isolated pectoral and pelvic girdles along with vertebral arch elements are included in the Interstate 71 collection. Several of these specimens were collected from the *Heintzichthys* horizon (CMNH 9416, 9410 and 9412); however, it is not certain that this material can be assigned to *Heintzichthys*.
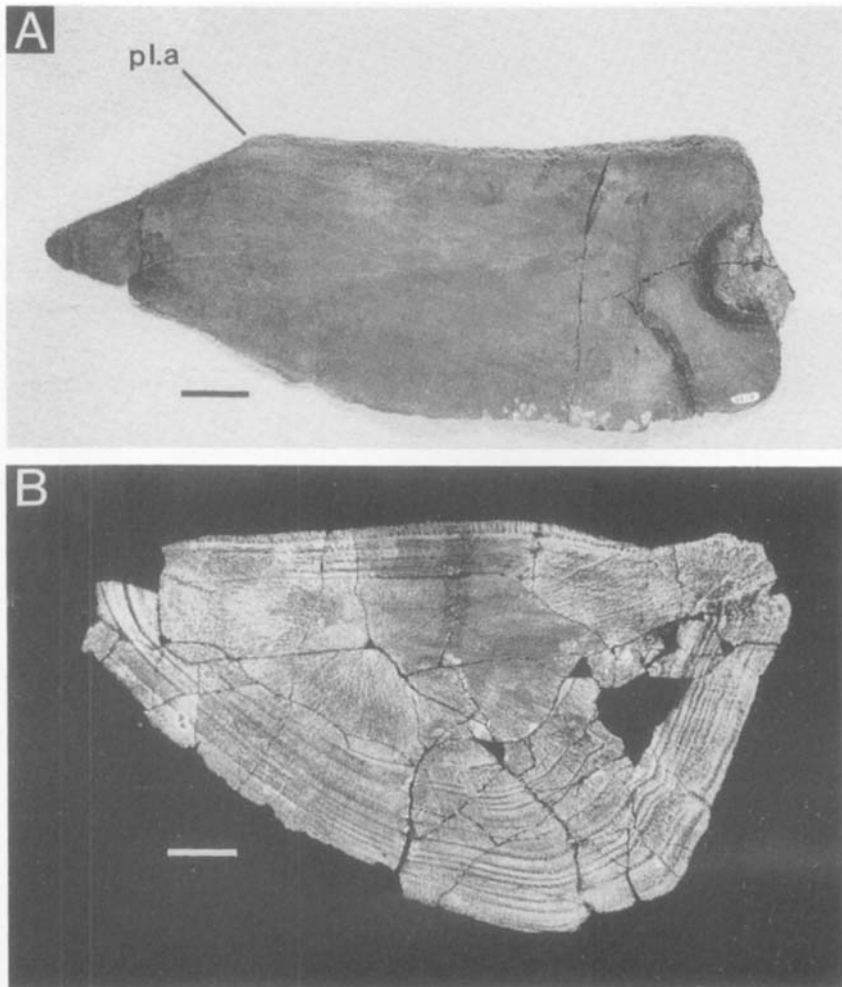
Figure 14. *Heintzichthys gouldii*. A, Anterior ventrolateral plate (CMNH 9388) in internal view. B, Posterior ventrolateral plate (CMNH 9379) in internal view. Scale bars 2 cm.

Scapulocoracoid. The scapulocoracoid (Fig. 15) is perichondrally ossified in adult specimens. Numerous neurovascular foramina are seen above and below an elongate articular ridge. The edges of the articular ridge (art.cr, Fig. 15A) are scalloped and indicate the presence of a minimum of seven anterior basals with additional posterior basals or a metapterygium; however, the exact count is unclear. The basals are perichondrally ossified and taper distally. They differ from *Dunkleosteus*, the basals of which are expanded both proximally and distally (Heintz, 1932: fig. 85). CMNH 9411 (Fig. 16A, B), an isolated group of basals from the *Heintzichthys* horizon, possesses a metapterygium (Met, Fig. 16A, B) and a minimum of eight basals. Four additional, but isolated, metapterygia are associated with *Heintzichthys* dermal plates (Fig. 16C; in addition CMNH 9354, CMNH 9416 and CMNH 9417). The scapulocoracoid bears muscle scars (m.sc, Fig. 15A) above and below the articular ridge and a number of neurovascular foramina on the anteroventral and dorsal internal surface.
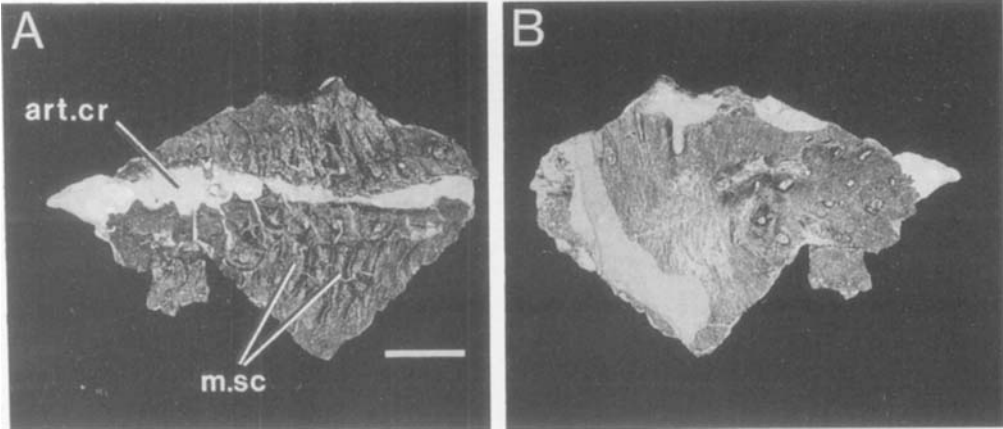
Figure 15. *Heintzichthys gouldii*. Left scapulocoracoid (CMNH 9401) in A, external and B, internal view. Scale bars 2 cm.
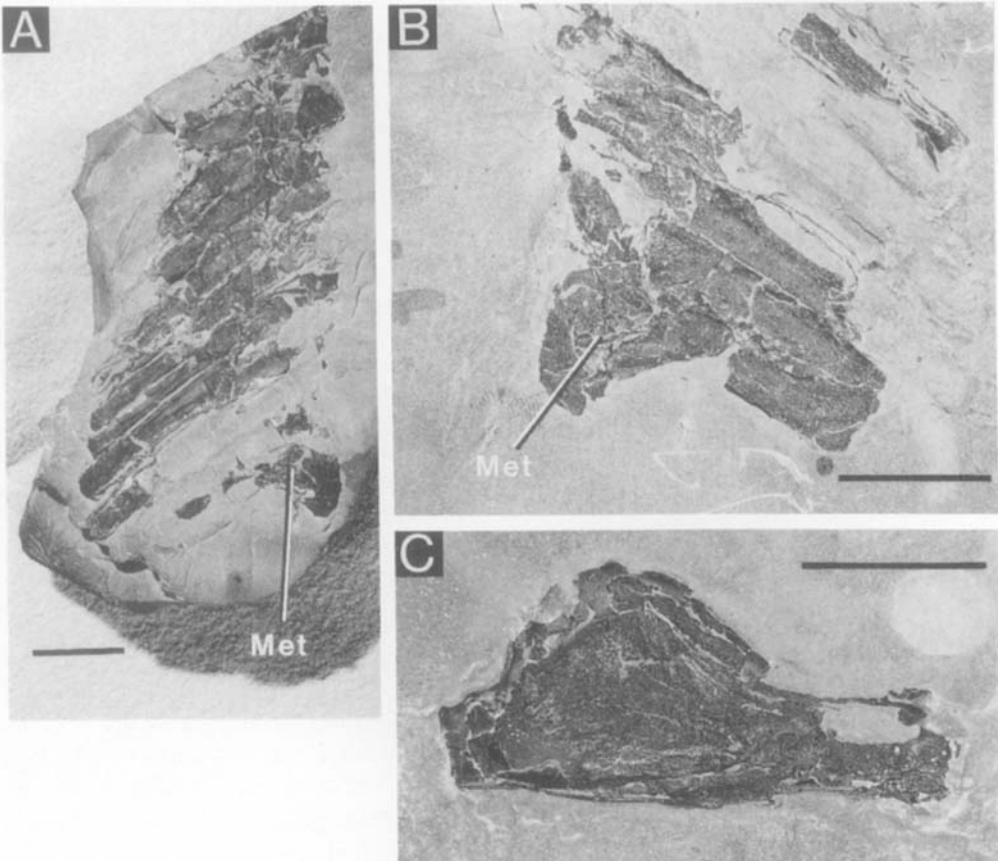
Figure 16. *Heintzichthys gouldii*. Part, A, and counter-part, B, of pectoral fin basals (CMNH 9411). C, Metapterygium (CMNH 9352). Scale bars 2 cm.
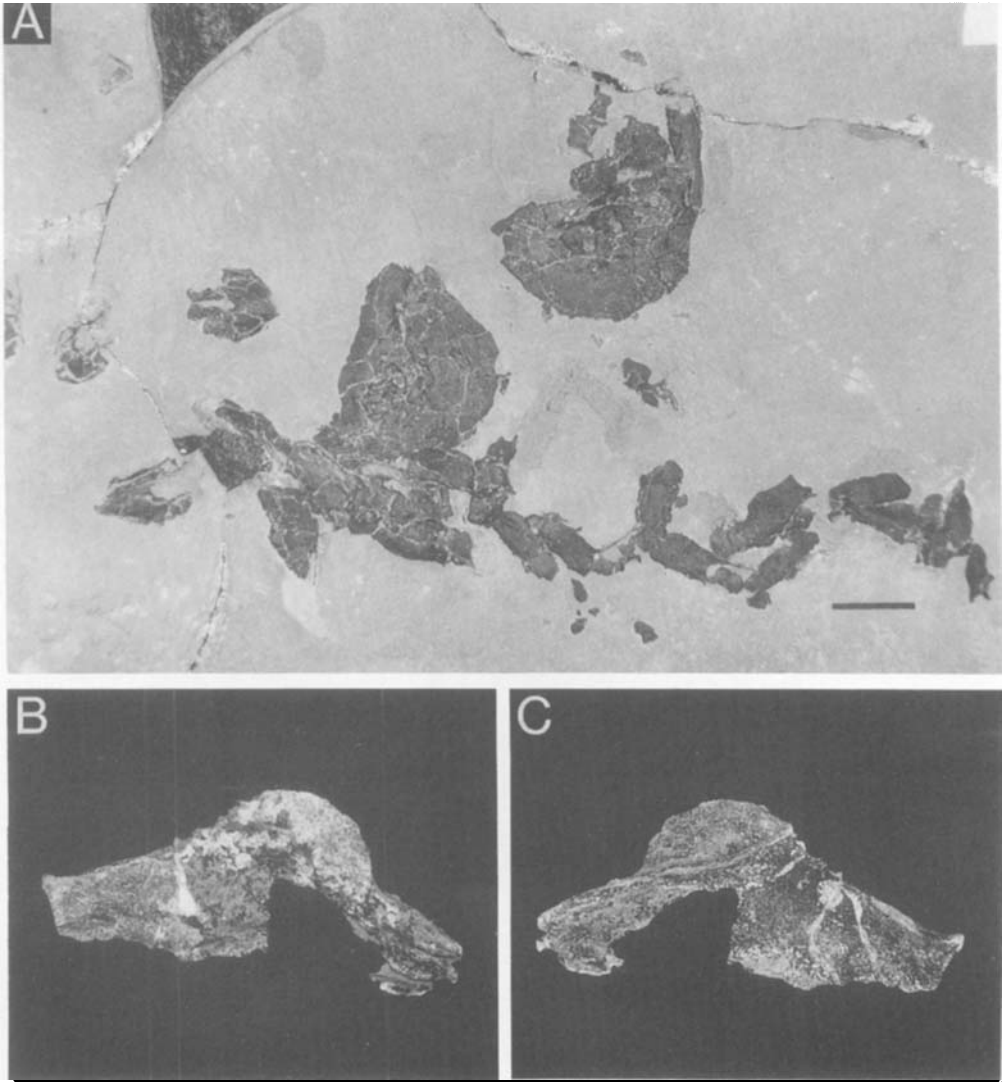
Figure 17. Unidentified brachythoracid arthrodire from the *Heintzichthys horizon*. A, Vertebral elements and pelvic girdle (CMNH 9416). *Heintzichthys gouldii*. B and C, pelvic element (CMNH 7111). Scale bars 2 cm.

Pelvic fin. A single *Heintzichthys* specimen (CMNH 7111, Fig. 17B, C) possesses a poorly preserved bone that appears to be a pelvic fin with an anterior thickened ridge and iliac process (Dennis-Bryan, 1987: fig. 30, rdg.a, pr.il). No other pelvic girdles are known from clearly identified *Heintzichthys* specimens. Within the collections from the Cleveland Museum of Natural History are two specimens of pelvic girdles associated with vertebral elements (Fig. 17A and CMNH 9412). These were collected from the *Heintzichthys* horizon and were identified in the field as belonging to *Heintzichthys*; however, the basis for this identification is unclear since no original field notes are available and the specimens are not associated with any identifiable *Heintzichthys* material. Despite
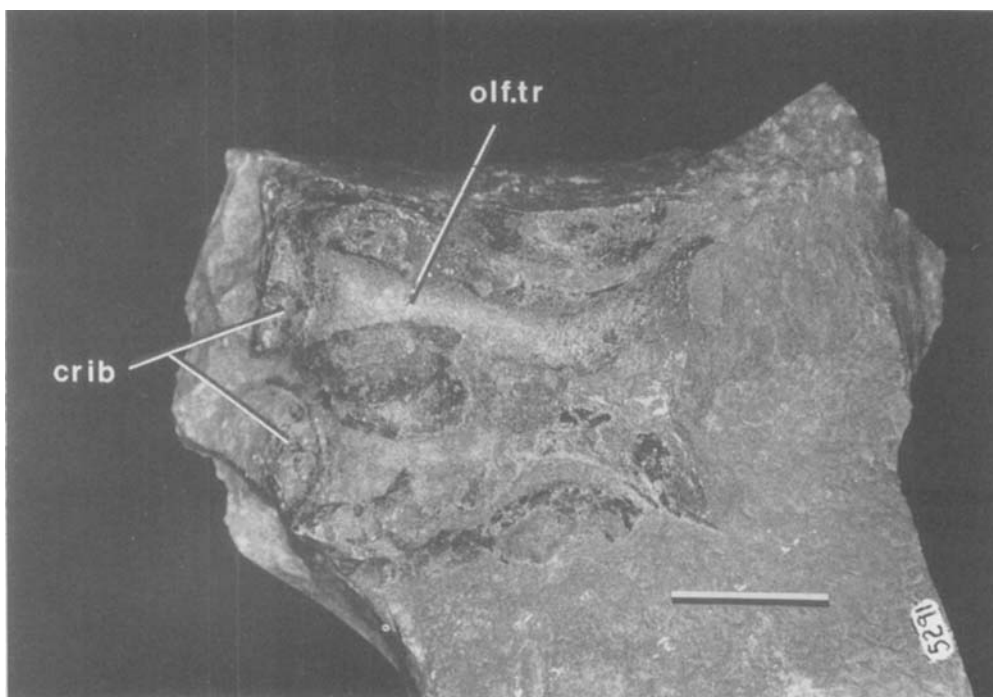
Figure 18. *Heintzichthys gouldii.* Frontal section of neurocranium and nasal capsules (CMNH 5291). Scale bar 2 cm.

the lack of evidence to associate them with *Heintzichthys*, the pelvic girdles are interesting since they consist solely of paired basal plates and lack a thickened anterior ridge and iliac process.

Vertebral elements. Vertebrae bear neural and haemal arches and spines (Fig. 17A; Dean, 1896: Plate VII); however, their detailed structure is unclear.

Neurocranium. A single neurocranium (Fig. 18) is known for *Heintzichthys* and is associated with a complete sclerotic ring. The neurocranium has been split along the frontal plane. Two medially positioned cribrosal bones (crib, Fig. 18) are present. Spaces for the olfactory tracks (olf.tr, Fig. 18) project posteriorly from the nasal capsules. Lateral to the cribrosal bones can be seen the anterolateral preorbital processes. Owing to the nature of preservation and splitting along the frontal plane, other details cannot be clearly identified at this time and must await further non-destructive analysis. Of interest to this discussion is the lack of a lateral expansion in the region of the deep recess anterior to the supraethmoid crista.

A SYSTEMATIC REVIEW OF BRACHYTHORACID ARTHRODIRES

Introduction

The systematics of brachythoracid arthrodires has been in a state of flux although the relationships of various subgroups within the Arthrodira have been studied. Topics covered were the interrelationships among the Arthrodira (Denison, 1984; Gardiner & Miles, 1990), the 'primitive' brachythoracids

(Lelièvre, 1984a, b, 1988), the eubrachythoracid arthrodires (Miles & Dennis, 1979; Dennis & Miles, 1979a, b, 1980, 1981, 1982), and the family Camuropiscidae (Long, 1988). The present study allows evaluation of *Heintzichthys* and leads to a cladistic analysis using PAUP (Swofford, 1989). Eighteen brachythoracid taxa and one phlyctaeniid arthrodiran taxon are analysed utilizing 85 characters (Appendix). *Dicksonosteus,* one of the better known phylctaeniid arthrodires (Goujet, 1984), is used as an outgroup. *Dicksonosteus* and the 'primitive' brachythoracids (*Holonema, Homosteus* and *Buchanosteus*) are included in the present analysis to establish a polarity of characters within the eubrachythoracid arthrodires. All characters are analysed as unordered. These characters are presented below and represent adult features.

Character descriptions

HEAD SHIELD

1. Nuchal plate with posterodorsally placed paired pits (f.lv of Goujet, 1984): absent (0), present on the paranuchal plate in *Holonema*; present (1).
2. Posterolateral extension of the lateral consolidated arch: extends as a distinct ridge or thickening onto postmarginal plate or to the head shield edge if the postmarginal plate is absent (0); extends onto the marginal plate (1); absent (2).
3. Triangular depression posterior to supra-orbital vault (character 14, in part, of Dennis & Miles, 1979b): absent (0); present (1).
4. Neurocranial process or thickening (character 16, in part, of Dennis & Miles, 1979b): absent (0); thickening (1); distinct process (2).
5. Rostral plate posterior development: not developed (0); subtriangular (1); T-shaped (2).
6. Anterior elongation of the rostrum (fig. 18, character 3, in part, of Dennis & Miles, 1979b; characters 4, 12, and 16, of Long, 1988): absent (0); present (1).
7. Ventrally enclosed tubular rostrum: absent (0); present (1).
8. Position of anterior edge of pineal plate: over orbit (0); anterior to orbit (1).
9. Position of posterior edge of pineal plate: over orbit (0); posterior to orbit (1).
10. Shape of the external anterior nuchal border: straight (0); convex (1); concave (2).
11. Shape of the posterior nuchal border: straight (0); convex (1); concave (2).
12. Nuchal thickening (Levièvre, 1988): discontinuous with the lateral thickening associated with the cranio-thoracic dermal articulation (0); continuous thickening across the posterior head shield (1).
13. Preorbital plate embayment of the central plate: absent (0); shallow (1); developed (2).
14. Paranuchal plate embayment of the central plate: absent (0); shallow, determined by formation of the lateral lobe and not the posterior lobe (1); developed (2).
15. Ratio for the external longitudinal lengths of the preorbital and central plates (ratio = PrO/C): subequal, i.e. $0.75 < r < 1.25$ (0); preorbital plate longer, i.e. $r > 1.25$ (1); central plate longer, i.e. $r < 0.75$ (2).

16. Postnasal plate infrafenestral process (character 22.18 of Gardiner & Miles, 1990): absent (0); present (1).

17. Preorbital plate with a dermal preorbital lamina or process (character 19 of Dennis & Miles, 1979b): absent (0); present (1).

18. Preorbital plates with a median contact (modified after character 19a of Young, 1981): contact posterior to pineal (0); contact anterior to pineal (1); pineal separates preorbital plates (2).

19. Extent of median preorbital plate contact: short (0); long, measured as the (ratio of contact length)/(PrO parasagittal length) (1).

20. Postorbital plate embayment of central plate: absent (0); shallow (1); developed (2).

21. Length of central plate contact with the nuchal plate: short (0); long, measured as greater than one half the length from the nuchal anteromedian point to the posterolateral corner of the nuchal plate (1).

22. Width of the central plate at its contact with the pineal plate: central plate tapers anteriorly to contact (0); central plate expanded laterally to produce a transverse anterior border (1).

23. Marginal plate in contact with the central plate (character 5 of Lelièvre, 1988): present (0); absent (1).

24. Extent of marginal plate along the lateral border of the head shield: less than half the length from the postorbital process to the posterolateral corner of the head shield (0); greater than half the length (1).

25. Marginal plate forms part of orbit border (character 26 of Dennis & Miles, 1979a): absent (0); present (1)

26. Postnasal plate forms part of orbit border (fig. 18, character 1 of Dennis & Miles, 1979b): absent (0); present (1).

27. Extent of postnasal involvement in the orbit border: minimal (0); developed (1).

28. Orbit size: measured as a ratio of (distance between preorbital and postorbital dermal processes)/(distance between pineal and paired condyles) small (0); intermediate (1); large (2).

29. Nuchal and paranuchal plates elongate (Lelièvre, 1984b): absent (0); present, associated with elongation of the endolymphatic canal (1).

30. Postnuchal process of paranuchal plate on dermal surface (modified after character 8, of Dennis & Miles, 1979a): absent (0); present (1), indicated by the presence of a postnuchal process on the dermal surface of the head shield.

31. Position of the central/paranuchal/marginal or postorbital triple point relative to paranuchal/central/nuchal triple point: C/PNu/M or PtO posterior to PNu/C/Nu (0); anterior (1).

32. Position of preorbital/postorbital/central triple point relative to posterior triple point (PtO/M/C or PtO/PNu/C): parallels the midline or with the anterior point lateral (0); posterior point lateral to anterior point (1).

33. Position of PrO/PtO/C triple point relative to the orbit: posterior to orbit (0); over the orbit (1).

34. Postorbital dermal process: negligible or absent (0); present (1).

35. Median dorsal plate with a ventral ridge (combination of characters 4 and 18 of Dennis & Miles, 1979a): a ventral thickening or ridge (0); posterior ridge with a posterior process, not spatulate (1); posterior process posterodorsally spatulate (2).

THORACIC SHIELD

36. Median dorsal plate shape (width/length): short and broad to equidimensional (0); body of plate long and narrow, whose measure does not include a posteriorly produced spine (1).
37. Median dorsal plate posterior border (character 18, in part, of Dennis & Miles, 1979a): rounded (0); spinous (1).
38. Anterior lateral plate/anterior ventrolateral plate contact: absent (0); present (1).
39. Anterior lateral plate/interolateral plate external contact: absent (0); present (1).
40. Interolateral/spinal lateral contact: absent (0); present (1).
41. Pectoral dermal enclosure: fenestra (0); embayment open posteriorly (1).
42. Posterior lateral plate and posterior dorsolateral plate overlap (Vézina, 1988): simple overlap (0); insertion (1).
43. Posterior lateral plates forms part of closed pectoral fenestra: absent (0); present (1).
44. Posterior lateral plate ventral lamina (character 22.13 of Gardiner & Miles, 1990): absent (0); present (1).
45. Spinal plate (Stensio, 1959); absent (0); present (1).
46. Spinal plate spinal pit (character 22.32 of Gardiner & Miles, 1990): absent (0); present (1). Gardiner & Miles distinguish between the presence of a reduced spinal pit ('pseudo-spinal' of Miles, 1971) and the presence of a developed pit which both represent the site of a lateral pre-pectoral endochondral process (e.spi, Stensio, 1959). The latter condition is found in *Coccosteus* and *Harrytoombsia* and is assumed to be primitive; however, the distribution of this character in both their study and the current study suggests that the lateral pre-pectoral process in eubrachythoracids is independently derived.
47. Interolateral plate brachial lamina: absent (0); present (1).
48. Interolateral plate ventral lamina: small or absent (0); developed with either an enlarged contact with the anterior median ventral plate or an enlarged overlap with the anterior ventrolateral plate (1).
49. Interolateral plate branchial lamina ornamentation: absent (0); present (1).
50. Posterior ventrolateral plate dorsolateral contact with the lateral thoracic shield: posterior lateral plate only (0); posterior lateral and anterior lateral plates (1).
51. Posterior ventrolateral plate postpectoral lamina (character 22.8 of Gardiner & Miles, 1990): absent (0); small (1); large (2).

CHEEK AND PALATOQUADRATE

52. Suborbital dermal lamina (character 17 of Dennis & Miles, 1979a): absent (0); present (1).
53. Suborbital plate overlaps postorbital plate (character 22.9 of Gardiner & Miles, 1990): absent (0); present (1).
54. Suborbital/preorbital contact: absent (0); lateral contact (1).
55. Suborbital and marginal plates in contact (character 22.28 of Gardiner & Miles, 1990): absent (0); present (1).

56. Suborbital plate with a contact face for the PSG (cf.PSG) on the linguiform process (cr.lg): absent (0); present (1).

57. Palatoquadrate ossifications (character 21 of Dennis & Miles, 1979a): ossified as a single unit (0); autopalatine and quadrate ossifications (1).

58. Detent process on quadrate (character 22.1 of Gardiner & Miles, 1990): absent (0); present (1). Gardiner & Miles (1990) suggest that a supraglenoid process and therefore, a dentent process are present in *Coccosteus* based on the development of the articular dorsal to the inferognathal. In the present study, this character is considered as unknown. The *a posteriori* position of *Coccosteus* might suggest the presence of these processes based on a parsimony argument; however, the current morphological evidence is not clear.

59. Submarginal plate closely associated with the hyomandibular: absent (0); present, indicated by the presence of perichondral bone or the presence of an internal depression (1).

60. Form of submarginal plate: broad (0); elongate (1).

61. Length of cheek and head shield contact: long (0); short, measured as the contact being less than one third of the length measured from the anterior suborbital plate to the posterior cheek/head shield contact (1).

62. Development of cheek/head shield overlap: loose contact (0); well bound contact, indicated by the interdigitation of plates or their complete fusion (1).

PARASPHENOID AND GNATHAL ELEMENTS

63. Inferognathal with a developed blade portion (modified after character 13 of Dennis & Miles, 1979a): absent (0); present (1).

64. Inferognathal anterior dental field developed anteriorly of the cusp region: absent (0); present (1), indicated by a projection of the inferognathal anterior to dorsal functional region.

65. Adsymphyseal (anterior dental field) denticles: absent (0); present (1).

66. Anterior superognathal cusps: none (0); lateral (1); lateral and anterior (2).

67. Anterior superognathal plate with an enclosed lateral face: absent (0); present (1).

68. Anterior superognathal plate with a dorsal process (character 22, in part, of Dennis & Miles, 1979a): absent (0); present (1).

69. Dorsal process of the anterior superognathal plate forms an open ring (modified after character 4, of Lelièvre *et al.*, 1981): ring open, measured as greater than 90° (0); ring forms a *c.* 90° angle (1); ring closed, measured angle less than 90° (2).

70. Posterior superognathal plate with a dorsal process (character 22, in part, of Dennis & Miles, 1979a): absent (0); large (1); small (2).

71. Width/length ratio for the parasphenoid pre- and posthypophysial shelf: prehypophysial shelf width greater than length, posthypophysial shelf width greater than length (0); prehypophysial shelf width less than length, posthypophysial shelf width greater than length (1); prehypophysial shelf width greater than length, posthypophysial shelf width less than length (2); prehypophysial shelf width less than length, posthypophysial shelf width less than length (3).

72. Parasphenoid posterolateral process (character 22.36 of Gardiner & Miles, 1990): absent (0); present (1).

73. Median hypophysial vein foramen (character 22.7 of Gardiner & Miles, 1990): absent (0); present (1).

74. Parasphenoid ventromedian crest (character 22.27 of Gardiner & Miles, 1990): absent (0); present (1). Gardiner & Miles presented this feature as a synapomorphy of the coccosteomorph arthrodires; however, Dennis & Miles did not note this feature in their descriptions of *Camuropiscis* (Dennis & Miles, 1979a), *Rolfosteus* and *Tubonasus* (Dennis & Miles, 1979b). In addition, this feature is also present in *Eastmanosteus calliaspis* (Dennis-Bryan, 1987, cr.m, fig. 17).

SENSORY CANAL GROOVES

75. Angle between the postorbital and otic branches of the infraorbital sensory canal groove (modified after character 5 of Lelièvre *et al.*, 1987): open posteriorly, i.e. the formed angle is greater than 90° (0); partially closed, i.e. the formed angle is between 45° and 90° (1); closed, i.e. the formed angle is less than 45° (2).

76. Central canal groove meets supraorbital groove: absent (0); present (1).

77. Ventral groove of the main lateral line on the anterior dorsolateral plate (lc.vl of Miles, 1971: fig. 108): absent (0): present (1).

78. Dorsal groove of the main lateral line on the posterior dorsolateral plate (ld of Miles, 1971: fig. 108): absent (0); present (1), distinguished from the main lateral line groove by its dorsal trajectory or its continuation onto the median dorsal plate.

79. Main lateral line groove on the posterior dorsolateral plate (lc of Miles, 1971: fig. 108): present (0); absent (1).

80. Dorsal groove of the main lateral line on the median dorsal plate (ld of Miles, 1971: fig. 108): absent (0); present (1).

81. Postorbital sensory line groove on suborbital plate (character 1 of Lelièvre, 1988): absent (0); present (1).

82. Angle between the suborbital and postorbital branches of the infraorbital sensory line groove (Lelièvre, 1984a): open (0); closed, measured as less than 90° (1).

83. Postorbital branch of the infraorbital sensory line groove and supraoral sensory groove confluent (Lelièvre, 1984a): discontinuous (0); continuous (1).

84. Supraorbital canal extended onto central plates: absent (0); present (1).

85. Postmarginal canal: absent (0); present (1).

Algorithm parameters and results

Analysis using PAUP ('hold trees' set at ten) gives seven equally parsimonious trees. A strict consensus tree is presented in Fig. 19A. These results are dependent upon choice of outgroup and choice of algorithm parameters; however, Fig. 19B represents a strict consensus summary of all possible combinations using 'primitive' brachythoracids (*Holonema*, *Buchanosteus* and *Homosteus*) and *Dicksonosteus* as outgroups. In the latter tree, the aspinothoracid arthrodires and the camuropiscid (Long, 1988) arthrodires plus *Incisoscutum* and
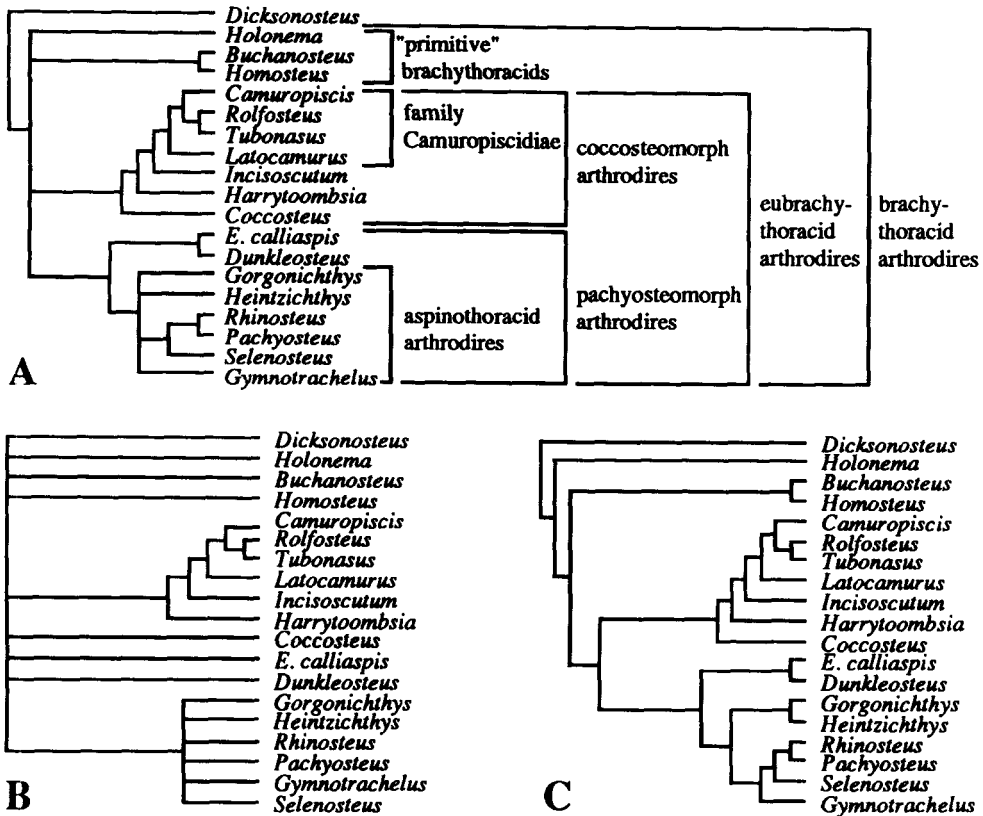
Figure 19. Cladograms showing various hypotheses of relationships as outlined in text. A, Strict consensus tree based on seven cladograms derived from PAUP. B, Strict consensus tree utilizing all possible combinations of the four outgroups (*Dicksonosteus, Holonema, Buchanosteus* and *Homosteus*). C, Fully resolved hypothesis of relationships.

Harrytoombsia remain monophyletic despite the choice of outgroup. Utilizing PAUP's default parameters ('hold trees' set as one) an additional six equally parsimonious trees are retrieved.

The analysis represented in Fig. 19A leaves the relationship of *Holonema* and the homosteids-buchanosteids unresolved. Five alternative hypotheses of relationship are apparent from this analysis: (1) *Holonema* as the sister group to the homosteids-buchanosteids and eubrachythoracid arthrodires (Fig. 20A); (2) homosteids-buchanosteids as the sister group to *Holonema* and eubrachythoracid arthrodires (Fig. 20B); (3) homosteids-buchanosteids as the sister group to pachyosteomorph arthrodires (Fig. 20C); (4) homosteids-buchanosteids as the sister group to *Holonema* and coccosteomorph arthrodires (Fig. 20D); and (5) *Holonema* as the sister group to homosteids-buchanosteids and coccosteomorph arthrodires (Fig. 20E). Figure 20F–H represents equally parsimonious resolutions to the additional unresolved portions of Fig. 19A within the aspinothoracid arthrodires. These cladograms are taken from the seven trees used to generate Fig. 19A and are consistent with the six additional equally parsimonious trees. A fully resolved hypothesis of relationships is presented in Fig. 19C. The systematic discussion that follows is based on Fig. 19A, C.
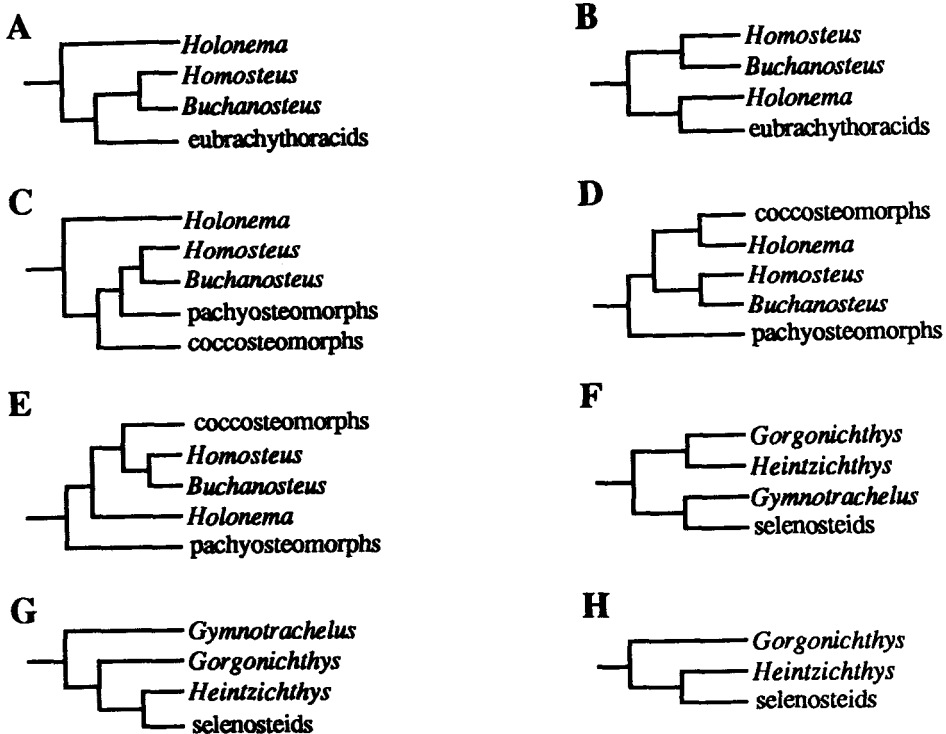
Figure 20. Equally parsimonious resolutions to unresolved portions of Fig. 19A. Cladograms represent portions of seven trees derived from PAUP analysis.

Brachythoracid arthrodires

The inclusion of *Holonema* within the brachythoracid arthrodires was proposed by Miles (1973), Miles & Dennis, (1979), Goujet (1984), Lelièvre (1984a, b) and Gardiner & Miles (1990); however, Denison (1978) and Young (1981) regarded *Holonema* as a phlyctaeniid arthrodire. Lelièvre argued for a sister-group relationship between holonematids and homosteids-buchanosteids (= 'primitive' Brachythoraci–Lelièvre, 1984a, b, 1988). This relationship was supported solely by the presence of a postsuborbital sensory line groove on the suborbital plate and was evaluated in the absence of any outgroup analysis. The relationship of *Holonema*, as presented in this paper, is in conflict with both a phlyctaeniid and a 'primitive' brachythoracid assignment. Lelièvre (personal communication) recently suggested that *Holonema* represents the sister group to the remaining 'primitive' brachythoracids–eubrachythoracids. The homosteids-buchanosteids and eubrachythoracid arthrodires are characterized by (1) the development of a lateral consolidated part of the internal surface of the head shield with the presence of an inframarginal crista (character 2); (2) a lateral displacement of the dermal cranio-thoracic articulation (Goujet, 1984: 246); (3) the reduction of the submarginal plate (character 60); (4) the development of a posterior process on the anterior superognathal (character 70); and (5) the loss of a sensory groove for the main lateral line on the posterior dorsolateral plate (character 79, reestablished in the eubrachythoracid arthrodires). The

monophyly of the homosteids-buchanosteids is supported by characters 29, 31 and 82.

Eubrachythoracid arthrodires

The diagnosis of eubrachythoracid arthrodires has been debated by Dennis & Miles (1979a, b, 1980), Denison (1978), Young (1981) and Gardiner & Miles (1990). This debate centres on a number of anatomical arguments and on the definition of various character states. A variety of characters has been proposed as diagnostic for the eubrachythoracid arthrodires. These include: (1) a trilobate central plate (character 19b of Young, 1981); (2) an inferognathal with co-ossified blade and occlusal regions (character 14 of Miles & Dennis, 1979); (3) a lateral consolidated region on the internal surface of the head shield (character 15 of Miles & Dennis, 1979); (4) a small submarginal plate closely associated with the cheek region (character 16 of Miles & Dennis, 1979); (5) a supraorbital vault (character 17 of Miles & Dennis, 1979); (6) a suborbital plate with a dermal suborbital lamina (character 18 of Miles & Dennis, 1979); (7) internal laminae on the suborbital plate (character 21 of Miles & Dennis, 1979); (8) a carinal process on the internal surface of the median dorsal plate (character 19 of Miles & Dennis, 1979); (9) a preorbital plate with a dermal preorbital lamina (character 20 of Miles & Dennis, 1979); (10) separate autopalatine and quadrate ossifications of the palatoquadrate (character 22 of Miles & Dennis, 1979; Young, 1981); and (11) the presence of posterior processes on the superognathals (character 23 of Miles & Dennis, 1979). A number of these putative synapomorphies are dependent upon a concise definition. The purpose of this discussion on proposed synapomorphies for the eubrachythoracid arthrodires is not to reject these characters, but to further point out the need for clarification.

Trilobate centrals are difficult to evaluate. The coccosteid-type of trilobate central possesses an embayment by both the preorbital and paranuchal plates. In addition, there is a posterior expansion of the central plate between the nuchal and paranuchal plates. It is important to differentiate variable development of the three lobes within the central plate. Miles & Dennis (1979) evaluated the utility of this character in their discussion of Denison's (1975) description of the Coccosteina.

In the present study, the trilobate central is considered to be a composite of several features and is subdivided into a number of discrete characters (e.g. characters 13, 14 and 21). The subdivision of this character provides greater information; for example, the presence of a preorbital embayment characterizes the coccosteomorph arthrodires (Fig. 19A).

Use of a co-ossified blade and occlusal region as a synapomorphy for eubrachythoracid arthrodires implies that 'primitive' brachythoracid, phlyctaeniid and actinolepid arthrodires either lack an ossified blade or that the two regions are present, but are independently ossified. Two questions arise in analysing this character: (1) the presence of a single ossification or co-ossified components in the inferognathal and (2) the phylogenetic level where an inferognathal blade first appears.

Ørvig (1980) argued for the presence of two ossification centres within the inferognathal, one forming the non-biting region or blade and one forming the biting or 'functional' region. Heintz (1932), Miles & Westoll (1968) and Miles

(1969) presented arguments for the presence of a single ossification. It appears that the inferognathal is a single ossification with the development of a blade portion appearing early among brachythoracid arthrodires. A single ossification is clearly seen in *Selenosteus* (Ørvig, 1980: figs 52–54) with the ossification centre located below the anterior cusp. The anterior location of ossification often makes it difficult in many forms to visualize the continuity between the occlusal portion and the blade.

The definition of a blade and the phylogenetic level of its occurrence is unclear. Lelièvre (1984b) noted the presence of a posterior non-masticatory region in *Antineosteus* and in *Goodradigbeeon* (see also White, 1978). Denison (1958: fig. 101D, F) figured two actinolepid inferognathals possessing a posterior non-biting region. As further noted by Lelièvre (1984b) the posterior regions in these forms are characterized by a deep ventral or ventrolateral groove bounded laterally and medially by dermal laminae. Eubrachythoracid arthrodires and *Homosteus* may be characterized by the loss of the lateral lamina and the development of the lamina medial to Meckel's cartilage with an inferognathal blade representing an enhancement of the medial lamina. In *Homosteus* the presence of a laterally placed shallow ridge on the inferognathal (h, Heintz, 1934: fig. 27) may mark the boundary of Meckel's cartilage. Evaluation of the appearance of this character is difficult since inferognathals are unknown in several of the 'primitive' brachythoracids (*Buchanosteus, Errolosteus, Taemasosteus, Arenipiscis and Tityosteus*; Lelièvre 1988).

Development of a lateral consolidated arch on the internal surface of the head shield is seen in several 'primitive' brachythoracids (*Homosteus*, Heintz, 1934: fig. 2; *Antineosteus*, Lelièvre, 1984b: fig. 3), which differ from eubrachythoracid arthrodires only in the degree of development.

The submarginal plate as characterized by Miles & Dennis 1979) also occurs in *Homosteus* (Heintz, 1934: figs. 24, 25). A small submarginal plate with overlap areas for the suborbital and marginal plates is found in *Antineosteus* (Lelièvre, 1984b; Fig. 12). This character appears to diagnose a homosteid-eubrachythoracid grouping (Fig. 19A, includes the 'primitive' brachythoracids of Lelièvre, 1988, with the exception of *Holonema*).

A supraorbital vault is bounded typically by the lateral consolidated arch in the orbital region. Anteriorly, this boundary is part of the internal thickening of the preorbital dermal lamina. A posterior supraorbital crista (= postorbital crista [cr.po] of Young, 1979) extends laterally from the lateral consolidated arch and forms the posterior boundary of the supraorbital vault. In *Dunkleosteus*, the neurocranial process extends medially from the posterior supraorbital crista. A triangular depression is often associated with this posterior boundary (e.g. *Eastmanosteus calliaspis*, tri, Dennis-Bryan, 1987). Miles & Dennis (1979) correlated the development of a supraorbital vault with large laterally facing orbits. *Homosteus* has a very small supraorbital vault that lacks a posterior supraorbital crista (Heintz, 1934; Stensio, 1963: fig. 113D). In *Antineosteus*, the supraorbital vault is confined to the postorbital plate and is bounded by a low ridge (Lelièvre, 1984b: fig. 3). The medial boundary of the *Antineosteus* vault is not continuous with the lateral consolidated arch. *Buchanosteus* possesses both a supraorbital vault and a posterior supraorbital crista (Young, 1979: fig. 2). In the evaluation of the brachythoracid condition it is clear that a supraorbital vault is present but varies from the derived eubrachythoracid condition in the

level of development of the vault. At the eubrachythoracid level and within *Buchanosteus*, the vault is intimately associated with the lateral consolidated arch and possesses a posterior supraorbital crista.

Antineosteus lacks a suborbital dermal lamina; however, it is present in *Homosteus* (Heintz, 1934: fig. 23) and in '*Parabuchanosteus*' (White & Toombs, 1972: figs 14, 15). Although the suborbital of *Homosteus* does not participate in the border of the orbit, it is clearly associated with the autopalatine. The internal pattern of cristae is similar to that seen in typical eubrachythoracid arthrodires. A subautopalatine crista, autopalatine depression, postocular crista (R1) and posteroventral crista (R4) are present. The absence of a suborbital crista can be explained by the dorsomedian shift of the orbits.

Internal laminae on the suborbital plate have been interpreted in a number of ways and some confusion exists as noted above in the description of the suborbital plate for *Heintzichthys gouldii*. Only *Eastmanosteus* and *Dunkleosteus* have a contact face for the posterior superognathal on the linguiform process. This may represent either a synapomorphy for these two forms or a synapomorphy appearing at the eastmanosteid level (the group containing *Eastmanosteus* and *Dunkleosteus* being paraphyletic) and lost within the aspinothoracid arthrodires.

A carinal process on the internal surface of the median dorsal plate with a concave posterior face occurs in *Buchanosteus* (Young, 1979) and '*Parabuchanosteus*' (White & Toombs, 1972: fig. 17). Young (1979) used this character to diagnose brachythoracids (excluding *Holonema*).

The dermal preorbital lamina of the preorbital plate forms the anterodorsal border of the orbit when present. Internally, the lamina is thickened and forms the anterior boundary for the supraorbital vault. Medially, this internal thickening often possesses a depression for the preorbital process of the neurocranium and a depression lateral to the rhinocapsular region of the neurocranium. The preorbital plate in *Antineosteus* does not form part of the orbit border and lacks an internal thickening and distinguishable depressions. In contrast, *Buchanosteus* and *Homosteus* have internally thickened preorbital plate laminae. Each of these forms possesses a depression for the preorbital process of the neurocranium that is associated with the internal thickening. The depression lateral to the rhinocapsular region is present in *Homosteus*, but is lacking in *Buchanosteus* where the rhinocapsular region is anteriorly displaced.

Young (1979: fig. 16A, gr.mp) noted that *Buchanosteus* had a ventral groove on the autopalatine that he interpreted as the contact face for the posterior process of the posterior superognathal. The presence of a ventral groove in *Buchanosteus* suggests that the posterior process of the posterior superognathal is possibly plesiomorphic at the eubrachythoracid level. The posterior superognathals remain unknown.

In the present study, the following characters are considered diagnostic of eubrachythoracids (Fig. 19A, C): (1) separate autopalatine and quadrate ossifications within the palatoquadrate (character 57); (2) development of a continuous thickening across the posterior margin of the head shield (character 12); and (3) a supraorbital vault developed as part of the lateral consolidated arch and posteriorly bounded by the posterior supraorbital crista (a subjectively defined character not utilized in the current PAUP analysis).

Two subgroups of eubrachythoracid arthrodires are presented in Fig. 19A, C: coccosteomorph arthrodires and pachyosteomorph arthrodires. The first group

includes the camuropiscids, *Incisoscutum*, *Harrytoombsia* and *Coccosteus*, while the second group includes the dinichthyid and aspinothoracid arthrodires. The relationships of a number of basal eubrachythoracid arthrodires (*Coccosteus*, *Eastmanosteus calliaspis* and *Dunkleosteus*) remain ambiguous and are dependent on the choice of outgroups (Fig. 19B). The cladogram in Fig. 19A is further supported by Gardiner & Miles (1990) in their evaluation of a number of North American and Australian coccosteomorph taxa. Further analysis is needed in light of additional morphological evidence and additional taxa.

Dinichthys hertzeri, *Eastmanosteus pustulosus* and *Eastmanosteus magnificus* (*Dinichthys magnificus*, Hussakof & Bryant, 1918) have been excluded from this analysis and represent forms requiring additional study. North American *Eastmanosteus* species share a number of primitive coccosteomorph-pachyosteomorph characteristics; however, they have been included traditionally in the family Dinichthyidae (Obruchev, 1964; Schultze, 1973; Denison, 1978). The holotype for *Eastmanosteus pustulosus* is a left, poorly preserved anterior dorsolateral plate (MCZ 1381). The preservation of the type specimen suggests that *Eastmanosteus pustulosus* may be a *nomen dubium*. Boylan (1973) attempted a reanalysis of the material assigned to *Eastmanosteus pustulosus*, but it is not clear whether the genus or the species represents a paraphyletic grouping based on shared primitive features. Fundamental to the phylogenetic analysis of these forms is the reanalysis of *Dinichthys* as suggested by Schultze (1973).

Coccosteomorph arthrodires

Miles (1969) suggested that a coccosteomorph level of organization includes those brachythoracid arthrodires which retain a closed pectoral fenestra. The order Coccosteomorphi, as originally described by Stensio (1944) is paraphyletic. A restricted use of the term coccosteomorph is commonly applied to the monophyletic group containing *Coccosteus* (equivalent to Denison's order Coccosteoidea, 1984). A potential relationship between *Coccosteus* and the pachyosteomorph arthrodires is consistent with a number of interpretations of the interrelationships among arthrodires (Boylan, 1973; Miles, 1969; Miles & Dennis, 1979; Dennis & Miles, 1979a, b). Boylan (1973) noted that *Coccosteus*, *Eastmanosteus* and *Dunkleosteus* were related; however, he removed the latter two taxa from the pachyosteomorph arthrodires and assigned them to the coccosteomorph arthrodires. A number of authors supported the derivation of *Dunkleosteus* from *Coccosteus* or from a *Coccosteus* level of organization. These interpretations are consistent with a sister-group relationship between *Coccosteus* and remaining pachyosteomorph arthrodires; however, the present analysis suggests that the coccosteomorph arthrodires are monophyletic. The coccosteomorph arthrodires (Fig. 19A) are characterized by (1) the preorbital plate embayment of the central plate (character 13, independently derived in *Eastmanosteus calliaspis*); (2) a reduction in the medial contact between the preorbital plates (character 19; however, this character remains ambiguous since taxa adjacent to the coccosteomorph arthrodires lack a medial contact); (3) a spinous posterior border on the median dorsal plate (character 37); (4) a posterior lateral plate lamina (character 44); (5) a pronounced posterior ventrolateral plate lamina (character 51); and (6) a median hypophysial vein foramen on the parasphenoid (character 73).

Coccosteus is the sister group to the remaining coccosteomorph arthrodires (Fig. 19C). Characters 23 (marginal and central plates in contact) and 39 (contact between the anteroventral wing of the anterior lateral plate and the interolateral plate) diagnose the clade (*Harrytoombsia* (*Incisoscutum*, camuropiscids)). *Rolfosteus* and *Tubonasus* share the unique development of a ventrally enclosed tubular rostrum. *Tubonasus* retains plesiomorphic features of the occlusal portion of the inferognathal with *Rolfosteus* possessing durophagus dentition.

Pachyosteomorph arthrodires

The pachyosteomorph arthrodires include the dinichthyid and aspinothoracid arthrodires. This group is characterized by (1) the loss of the paranuchal embayment of the central plates (character 14); (2) a reduction of the contact between the nuchal and central plates (character 21); (3) the formation of a lateral contact between the suborbital and preorbital plates (character 54); and (4) the loss of the groove for the ventral portion of the main lateral line on the anterior dorsolateral plate (lc.vl, character 77). Character 14, a synapomorphy for the pachyosteomorph arthrodires, is dependent upon the monophyly of *Eastmanosteus calliaspis* and *Dunkleosteus* which are united by (1) the position of the posterior border of the pineal plate posterior to the orbits (character 9); (2) the insertion of the posterior lateral plate into a fossa within the posterior dorsolateral plate (character 42); (3) the presence of a contact face for the posterior superognathal on the linguiform process of the suborbital plate (character 56); (4) the presence of a groove for the main lateral line (lc, Miles, 1971: fig. 108) on the posterior dorsolateral plate (a synapomorphy if this groove is interpreted as an extension of the main lateral line and not the dorsal branch of the lateral line (ld, Miles, 1971: fig. 108); considered as unknown in *Dunkleosteus* for this analysis); and (5) the presence of anterior and lateral cusps on the anterior superognathal (character 66).

Family Dinichthyidae

Dunkleosteus and *Eastmanosteus* are members of the family Dinichthyidae (Newberry, 1885). Denison (1978) placed *Heintzichthys* and *Gorgonichthys* within the family Dinichthyidae; however, this placement was not based on any clearly defined derived characters. *Heintzichthys* and *Gorgonichthys* share a number of characters with the aspinothoracid arthrodires. The validity of the family Dinichthyidae is not clear since *Dinichthys hertzeri* is poorly known and additional analysis of *Eastmanosteus pustulosus* is required.

Aspinothoracid arthrodires

The Aspinothoracidi, originally proposed by Stensio (1959) and later modified by Miles & Dennis (1979), is retained and diagnosed by the following characters: (1) a reduction in the lateral consolidated part of the head shield (character 2); (2) an anterior shift of the preorbital/postorbital/central plate junction to a

position over the orbit (character 33); (3) the loss of the spinal plate (character 45); and (4) the closure of the angle between the postorbital and otic branches of the infraorbital sensory canal associated with an enlargement of the orbits (character 75).

Denison (1984) assumed that the loss of spinal plates was independently derived in a number of families (Heterosteidae, Brachydeiroidea, Rhachiosteidae, and in some Dinichthyidae). He argued (p. 410) that these losses precluded the use of this character in diagnosing relationships. Denison further argued that using the loss of spinal plates would place members of the family Dinichthyidae in different suborders; however, he did not demonstrate the monophyly of the Dinichthyidae. As noted above, there are no derived characters that unite *Heintzichthys* and *Gorgonichthys* with *Eastmanosteus* and *Dunkleosteus* which were included by Denison within the family Dinichthyidae.

Heintzichthys and *Gorgonichthys* share a specialization of the anterior superognathal (character 67) and a loss of adsymphysial denticles on the inferognathal (character 65). The anterior superognathals in these taxa possess both the development of a lateral face and a short shelf posterior to the lateral cusp. Analysis of additional dinichthyids and further revision of the North American aspinothoracid arthrodires may help to resolve the relationships within the basal aspinothoracids.

Selenosteid arthrodires

Dean's original description of the Selenosteidae (1901) included only North American taxa and was based solely on primitive characters. Lelièvre *et al.* (1987), attempted a cladistic analysis of the Selenosteidae and related outgroups. They concluded that the Selenosteidae was the sister group to the Brachydeiridae; however, there is only a single character that unites members within Selenosteidae. This character is the closed posterior angle between the postorbital and otic divisions of the infraorbital sensory canal (Character 75). A closed angle between the two divisions of the infraorbital canal is also found in Trematosteidae (*Belosteus*, Denison, 1978: fig. 73C; *Cyrtosteus*, ·Denison, 1978: Fig. 73D), Leiosteidae (*Erromenosteus*, Denison, 1978: fig. 72B), *Heintzichthys* (Fig. 2) and Pholidosteidae (*Pholidosteus*, Denison, 1978: fig. 64A). The posteriorly directed postorbital division of the infraorbital canal is correlated with enlarged orbits. It is not clear whether this condition represents a plesiomorphic state or is independently derived in each of these groups. A similar condition is approached independently in large-eyed camuropiscids from the Gogo Formation, Australia. Assignment of taxa to the family Selenosteidae differs among authors (Dean, 1901; Obruchev, 1964; Denison, 1978; Lelièvre *et al.*, 1987).

Selenosteus is the sister group to the European selenosteids (*Pachyosteus* and *Rhinosteus*, Fig. 19A, C) which share an enlarged orbit (character 28) with closure of the angle between the postorbital and otic branches of the infraorbital canal groove (character 75). Future analysis of *Gymnotrachelus* and *Selenosteus* spp. based on material from the Interstate 71 Paleontological Salvage Project and additional preparation of the type specimens of *Selenosteus brevis* (AMNH 7312) and *Stenosteus glaber* (AMNH 7313) are needed in order to revise the North American selenosteids.

CONCLUSION

Cladistic analysis of 19 taxa using 85 characters suggests: (1) *Holonema* is neither a phlyctaeniid nor a 'primitive' brachythoracid. Analyses by Lelièvre (personal communication) and Gardiner & Miles (1990) suggesting that *Holonema* is the sister group to the 'primitive' brachythoracids-eubrachythoracids are supported by the present analysis. (2) *Homosteus* and *Buchanosteus* are retained as members of the 'primitive' brachythoracids. (3) The Coccosteomorphi, as established by Stensio (1944), are paraphyletic. A restricted use of this term is supported by the present work and that of Gardiner & Miles (1990), but some ambiguity remains as to the position of *Coccosteus* based on the choice of outgroups (Fig. 19B). (4) *Heintzichthys* and *Gorgonichthys* are more closely related to other aspinothoracid arthrodires than they are to remaining members of the family Dinichthyidae. (5) A re-evaluation of the family Dinichthyidae would be useful. This analysis must await the preparation of additional *Dinichthys* material and the reanalysis and further preparation of the *Eastmanosteus pustulosus* material described by Boylan (1973). (6) Finally, a re-evaluation would be useful for several aspinothoracid arthrodiran families (e.g. Selenosteidae, Bungartiidae, Titanichthyidae, Mylostomatidae, Trematosteidae, Leiosteidae, Leptosteidae and Brachydeiridae).

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ABBREVIATIONS USED IN TEXT AND FIGURES

a.Au	depression for autopalatine	dp.m.cu	depression for cucularis muscle
ADL	anterior dorsolateral plate	gr	groove
AL	anterior lateral plate	IG	inferognathal
AMV	anterior median ventral plate	IL	interolateral plate
art.cr	articular crest	ioc.ot	otic branch of infraorbital canal
ASG	anterior superognathal	ioc.sb	suborbital branch of infraorbital
a.th	anterior thickening		canal
AVL	anterior ventral plate	k	knob
av.w	anteroventral wing	kd	glenoid condyle
C	central plate	laf	lateral articular fossa
cd.art	region of articular condyle	lc	main lateral line
cf.AL	contact face for anterior lateral	lm	thickened lower margin
	plate	M	marginal plate
cf.AMV	contact face for anterior median	m.sc	muscle scar
	ventral plate	Met	metapterygium
cf.P	contact face for pineal plate	MD	median dorsal plate
cf.PSG	contact face for posterior	m.sept	median septum
	superognathal	n.th	nuchal thickening
ch.eth	channel for ethmoid region of	Nu	nuchal plate
	neurocranium	oa.ADL	overlap area for anterior dorsal
ch.pro.pr	channel for dorsal aspect of		lateral plate
	preorbital process of neurocranium	oa.AVL	overlap area for anterior lateral
crib	cribrosal region of neurocranium		plate
cr.inf	inframarginal crista	oa.AVL	overlap area for anterior ventral
cr.po	postocular crista		lateral plate
cr.pr	carinal process	oa.IL	overlap area for interolateral plate
cr.pso	posterior supraorbital crista	oa.MD	overlap area for median dorsal plate
cr.sau	subautopalatine crista	oa.PL	overlap area for posterior lateral
cr.seth	supraethmoid crista		plate
cr.so	subocular crista	oa.PVL	overlap area for posterior ventral
csc	central sensory canal		lateral plate

oa.SO   overlap area for suborbital plate
olf.tr   olfactory tract
P   pineal plate
pap   occipital para-articular process
PDL   posterior dorsolateral plate
p.emb   pectoral embayment
PL   posterolateral plate
pl.a   posterolateral angle
pl.pr   posterolateral process
PM   postmarginal plate
pmc   postmarginal canal
PMV   posterior median ventral plate
PNu   paranuchal plate
p.pr   median posterior process
p.pro   posterior process
pre.reg   prehypophysial region
pr.det   detent process

PrO   preorbital plate
pr.sg   subglenoid process
PSG   posterior superognathal
PSO   postsuborbital plate
PtO   postorbital plate
pt.u   paired pits on visceral surface of nuchal plate
PVL   posterior ventrolateral plate
R   rostral plate
SM   submarginal plate
SO   suborbital plate
soc   supraorbital sensory canal groove
sorc   supraoral sensory canal groove
suo.v   supraorbital vault
th.pbe   prebranchial thickening
vl   ventral lamina

APPENDIX

Character data matrix for 19 arthrodiran taxa. For explanation of characters, see text

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Dicksonosteus	1	2	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1
Holonema	0	2	0	0	2	0	0	0	1	1	1	0	1	1	0	?	0	2	?	0	0
Buchanosteus	?	0	?	0	?	0	0	?	0	0	1	0	0	1	2	?	0	0	1	0	0
Homosteus	1	0	0	0	0	0	0	1	0	0	0	0	0	1	2	?	1	2	?	0	0
Rolfosteus	?	1	1	1	0	1	1	0	0	0	0	1	1	0	1	0	1	1	1	0	1
Tubonasus	?	1	?	?	0	1	1	0	0	2	2	1	1	1	1	0	1	1	1	0	1
Camuropiscis	0	1	1	1	0	1	0	0	0	0	2	1	1	1	1	0	1	1	1	0	1
Incisoscutum	?	1	1	1	1	0	0	0	0	0	2	1	1	1	0	0	1	1	0	0	1
Latocamurus	1	1	1	1	0	0	0	1	0	2	2	1	1	1	1	0	1	1	0	0	1
Harrytoombsia	1	0	1	1	2	0	0	0	0	0	0	1	1	1	?	0	1	2	?	0	1
Coccosteus	1	0	0	0	2	0	0	0	0	{02}	0	1	1	2	0	1	1	{02}	0	0	1
E. calliaspis	0	0	1	0	2	0	0	0	1	2	0	1	1	2	0	1	1	2	?	?	1
Dunkleosteus	1	0	0	2	1	0	0	0	1	1	2	1	0	0	0	1	1	2	?	0	1
Gorgonichthys	1	1	0	0	1	0	?	1	0	1	0	1	1	0	2	?	1	2	?	1	1
Heintzichthys	1	1	?	0	1	0	0	0	0	1	2	1	1	0	2	?	1	1	1	2	1
Rhinosteus	1	?	?	?	?	0	0	0	0	1	2	?	0	1	2	?	1	2	?	1	1
Pachyosteus	?	1	?	?	1	0	0	0	0	1	2	?	0	1	2	?	1	2	?	1	1
Gymnotrachelus	1	?	?	?	1	0	0	1	0	0	2	?	0	0	2	?	1	2	?	1	1
Selenosteus	?	?	?	0	?	0	0	0	0	1	2	?	0	0	2	?	1	2	?	0	1

	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Dicksonosteus	?	1	0	0	1	1	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0
Holonema	0	0	0	0	0	?	1	0	0	0	1	0	?	1	1	0	0	1	1	0	?
Buchanosteus	?	1	1	0	?	?	0	1	1	1	1	0	?	2	1	?	0	0	?	?	?
Homosteus	0	1	1	0	?	?	0	1	0	1	1	?	?	0	0	?	0	0	1	1	?
Rolfosteus	0	0	0	0	1	1	1	0	1	0	1	0	?	2	1	0	1	1	0	0	?
Tubonasus	0	0	0	0	1	1	1	0	1	0	1	1	?	2	1	?	1	1	0	0	?
Camuropiscis	0	0	1	0	1	1	1	0	1	0	1	0	0	2	1	1	1	1	0	0	1
Incisoscutum	1	1	0	0	1	0	1	0	0	0	1	0	1	2	1	1	0	1	1	1	1
Latocamurus	0	0	1	0	1	1	1	0	0	0	0	1	0	2	1	1	0	1	1	0	?
Harrytoombsia	0	0	0	0	0	?	1	0	1	0	0	0	1	2	1	1	0	1	1	0	?
Coccosteus	1	1	1	0	0	1	1	0	1	0	1	0	0	2	0	1	0	0	1	0	1
E. calliaspis	1	1	0	1	0	?	1	0	1	0	1	0	1	2	1	0	0	0	0	0	?
Dunkleosteus	1	1	1	0	0	?	0	0	0	0	1	0	1	2	0	0	0	1	1	1	1
Gorgonichthys	1	0	0	0	?	?	1	0	1	0	1	1	1	2	0	0	0	0	1	1	?
Heintzichthys	0	0	1	0	0	?	2	0	0	0	1	1	0	2	0	1	0	0	1	1	0
Rhinosteus	0	1	1	1	0	?	2	0	1	0	0	1	0	?	0	0	0	0	0	1	?
Pachyosteus	0	0	?	1	0	?	2	0	1	0	1	1	0	?	?	?	?	?	?	1	?
Gymnotrachelus	1	0	?	?	?	?	2	0	1	0	1	1	?	1	1	0	0	0	?	1	?
Selenosteus	0	{01}	?	1	?	?	2	0	1	0	1	1	?	?	1	?	0	0	0	1	?

APPENDIX *continued*

	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Dicksonosteus	0	0	1	1	1	1	1	0	0	1	0	0	0	0	?	?	1	0	0	0	?
Holonema	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0
Buchanosteus	?	?	1	0	?	?	?	?	?	0	1	0	0	0	0	0	1	1	0	0	?
Homostius	?	?	1	1	1	1	?	?	?	1	0	0	1	?	?	?	?	0	0	0	1
Rolfosteus	1	1	1	1	1	?	?	0	2	1	1	0	1	0	?	1	?	0	0	1	1
Tubonasus	1	1	1	1	?	1	1	0	2	1	?	0	1	0	1	?	?	0	0	1	1
Camuropiscis	0	1	1	1	1	1	1	1	2	1	0	0	1	0	1	1	?	1	0	1	1
Incisoscutum	?	?	1	1	1	0	1	?	0	1	0	0	0	0	1	1	?	0	0	0	1
Latocamurus	0	1	1	1	1	1	1	1	2	1	0	0	1	0	1	1	?	0	0	0	1
Harrytoombsia	1	1	1	?	1	?	?	?	2	1	?	1	0	0	1	?	?	1	0	0	1
Coccosteus	0	0	1	0	1	0	?	0	2	1	1	0	0	0	1	1	1	1	0	0	1
E. calliaspis	?	0	1	0	1	1	?	?	1	1	0	1	0	1	?	1	1	0	0	0	1
Dunkleosteus	?	0	1	0	1	0	0	?	?	?	?	0	0	?	1	?	?	0	?	0	1
Gorgonichthys	?	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
Heintzichthys	?	1	0	?	1	0	?	?	1	1	0	1	1	0	?	1	1	1	1	0	1
Rhinosteus	?	0	0	?	0	?	?	?	?	1	?	1	1	?	?	?	0	0	1	1	1
Pachyosteus	?	?	?	?	?	?	?	?	?	1	?	1	0	0	?	?	?	?	?	?	1
Gymnotrachelus	?	?	0	?	?	?	?	?	1	1	?	1	?	0	1	?	0	?	1	1	1
Selenosteus	?	?	0	?	?	?	?	?	0	1	?	1	?	0	1	?	0	1	1	1	1

	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85
Dicksonosteus	?	?	?	?	?	?	0	0	0	0	?	0	0	0	(01)	1	0	1	0	0	0	0
Holonema	?	?	?	?	?	?	0	?	?	?	?	0	0	1	(01)	1	(01)	1	0	0	0	1
Buchanosteus	?	?	?	?	0	?	1	1	?	?	0	0	0	1	?	?	0	1	1	0	1	1
Homostius	?	?	?	0	1	?	?	?	?	?	?	0	0	1	1	0	0	1	1	0	0	1
Rolfosteus	0	?	?	0	1	0	1	?	1	1	1	1	(01)	1	0	0	1	0	0	0	1	0
Tubonasus	0	?	0	0	1	0	1	?	1	1	1	1	0	1	0	0	0	0	0	0	1	0
Camuropiscis	0	?	0	0	1	0	1	1	1	1	1	1	1	1	0	1	0	0	0	1	1	0
Incisoscutum	0	1	0	0	1	0	1	1	1	1	1	1	1	(01)	(01)	(01)	1	0	0	(01)	1	0
Latocamurus	0	1	0	0	1	0	1	3	1	1	1	1	0	1	0	0	0	0	0	1	1	1
Harrytoombsia	0	1	0	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1
Coccosteus	0	1	0	0	1	1	1	0	0	1	1	0	0	1	1	0	1	0	0	1	1	1
E. calliaspis	0	1	(12)	0	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	1	1
Dunkleosteus	0	0	2	0	1	1	1	1	1	0	0	0	0	0	?	1	0	1	0	0	1	1
Gorgonichthys	0	0	1	1	1	0	?	?	?	?	?	1	0	0	?	?	0	?	?	0	1	1
Heintzichthys	0	0	1	1	1	0	0	0	1	1	?	1	0	0	?	0	0	0	0	0	0	1
Rhinosteus	1	1	1	?	?	?	2	?	1	?	?	2	0	0	0	0	0	0	0	1	1	1
Pachyosteus	?	?	0	0	?	?	?	?	?	0	?	2	0	?	?	0	?	0	?	?	1	1
Gymnotrachelus	?	1	1	0	0	?	0	?	?	?	?	1	0	1	0	0	0	0	0	0	1	1
Selenosteus	1	1	?	?	?	?	?	?	?	1	?	2	?*	?	?	?	?	0	0	?	1	?