

The Phyllolepid Placoderm *Cowralepis mclachlani*: Insights into the Evolution of Feeding Mechanisms in Jawed Vertebrates

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ABSTRACT Remarkably preserved specimens of *Cowralepis mclachlani* Ritchie, 2005 (Proc Linn Soc NSW 126:215–259) (Phyllolepidia, Placodermi) represent a unique ontogenetic sequence adding to our understanding of anatomy, function, and phylogeny among basal jawed vertebrates (gnathostomes). A systematic review demonstrates that the Phyllolepidia are a subgroup of the Arthrodira. Consideration of visceral and neurocranial characters supports the hypothesis that placoderms are the sister group to remaining gnathostomes. Placoderms possess, as adult plesiomorphic features, a number of characters that are only seen in the development of extant gnathostomes—a peramorphic shift relative to placoderms. Developmental evidence in vertebrates leads to a revised polarity of character transitions. These include 1) hyomandibula-neurocranium and ventral parachordal-palatoquadrate articulations (vertebrate synapomorphies); 2) jointed pharynx, paired basibranchials, anterior ethmoidal-palatoquadrate articulation, short trabeculae cranii, and anterior and posterior neurocranial fissures (gnathostome synapomorphies); and 3) fused basibranchials, dorsal palatoquadrate-neurocranium articulation, loss of the anterior neurocranial fissure, elongated trabeculae cranii, and transfer of the ventral parachordal-palatoquadrate articulation to the trabeculae (crown group gnathostomes). The level of preservation in *C. mclachlani* provides the basis for a reinterpretation of phyllolepid anatomy and function. *Cowralepis mclachlani* possesses paired basibranchials allowing the reinterpretation of the visceral skeleton in other placoderms. Mandible depression in *C. mclachlani* follows an osteichthyan pattern and the ventral visceral skeleton acts as a functional unit. Evidence for hypobranchial musculature demonstrates the neural crest origin of the basibranchials and that *Cowralepis* was a suction feeder. Finally, the position of the visceral skeleton relative to the neurocranium in placoderms parallels the condition in selachians and osteichthyans, but differs in the elongation of the occiput. The cucullaris fossa of placoderms (interpreted as a site of muscle attachment) is shown to represent, in part, the parabranchial chamber. *J. Morphol.* 270:775–804, 2009. © 2009 Wiley-Liss, Inc.

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INTRODUCTION

As feeding mechanics and associated anatomy are documented in increasing numbers of extant

osteichthyans (e.g., Lauder, 1985; Westneat, 2004; Fig. 1A) and chondrichthyans (e.g., Wilga et al., 2000; Dean et al., 2005; Fig. 1A) there is an effort to model these systems and understand their phylogenetic origins. The Placodermi are a group of extinct jawed vertebrates and are currently resolved as outgroup (sister taxon) to the chondrichthyans and teleostomes (Fig. 1A). As such, placoderms are critical to our understanding of the evolution of feeding mechanics in gnathostomes. Historically, anatomical and functional models based on extant taxa have been used to interpret an imperfect fossil record. These interpretations were subsequently used to establish the polarity of character evolution in gnathostomes—a tautological approach. An increased interest in the Placodermi has provided a wealth of anatomical information allowing researchers to directly evaluate (and potentially reject) many early interpretations. As an understanding of placoderm anatomy increases, a direct comparison of fossil and extant forms can progress, both as a direct comparison of anatomy (e.g., descriptions of anatomical and functional similarities between extant fishes and placoderms, Johanson, 2003) and as an application of mechanical models (e.g., Anderson, 2005; Anderson and Westneat, 2007).

Conclusions concerning functional aspects of the placoderm suspensorium (jaws and hyoid arch including palatoquadrate, Meckel's cartilage and hyomandibula) are dependent, in part, on a clear understanding of the anatomy of the visceral

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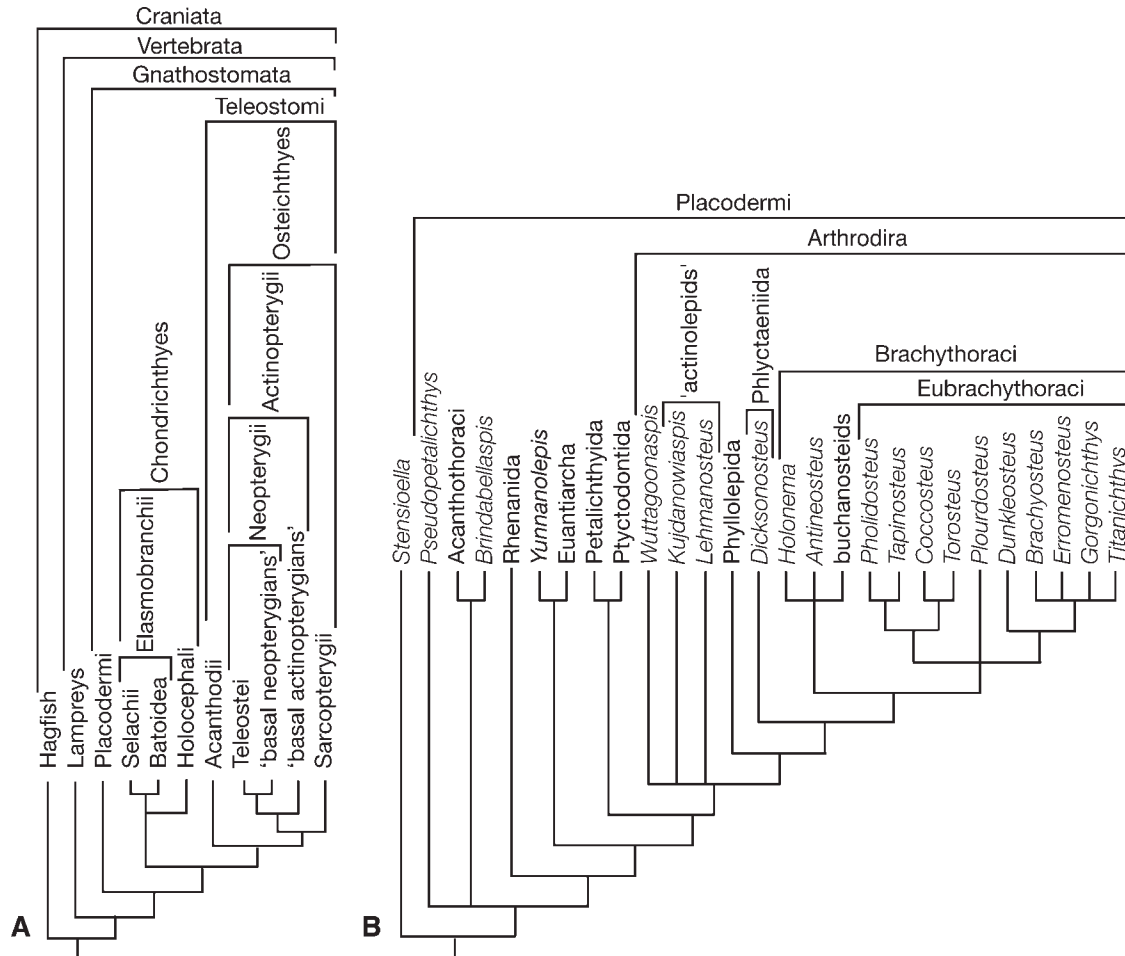


Fig. 1. Cladograms of hypothetical relationships. **A:** Phylogenetic relationships among craniates. The relationships among the chondrichthyans are simplified to reflect the Selachii (sharks) and Batoidea (skates, rays, and sawfishes). Arguments concerning the paraphyly versus monophyly of the selachians are summarized by Janvier (1996). **B:** Relationships among placoderm taxa discussed in the text (compiled from Goujet, 1984; Lelièvre, 1988; Carr, 1991; Carr and Hlavin, 1995; Goujet and Young, 1995; Dupret, 2004).

arches, which are preserved to varying degrees in the group (Denison, 1978). For example, preservation of the upper and lower jaws is relatively common, particularly in placoderm groups such as the Arthrodira (see Fig. 1), where Meckel's cartilage and the palatoquadrate can be ossified to various degrees (Young, 1986).

Ossifications associated with the hyoid arch include dorsal, ventral, and accessory structures representing basihyal, hypohyals, ceratohyals, interhyals, urohyals, epihyals (or hyomandibulae), and opercular cartilages. However, little information is available concerning the more posterior visceral (i.e., branchial) arches in placoderms. Ossified elements have been reported in stensioellids, pseudopetalichthyids, rhenanids, ptyctodontids, pholidosteid arthrodiras, and now more clearly in phyllolepidids, including *Cowralepis mclachlani* (Fig. 1B). Denison (1978) noted that our overall understanding of branchial structures in placoderms was inadequate. Given the nonpreservation

of elements even in such well-preserved specimens as those from the Gogo Formation (e.g., Dennis and Miles, 1979, 1981; Long, 1997), it seems likely that visceral elements in many cases remained cartilaginous throughout life, rather than being destroyed by postmortem taphonomic processes. Reviews of the placoderm splanchnocranium have focused mainly on the mandibular and hyoid arches, representing the suspensorium (e.g., Young, 1986).

Much of the current debate associated with reconstructing the placoderm suspensorium centers on the hyomandibula (or epihyal). Historically, interpretations have followed a chondrichthyan hyostylic model in which the hyomandibula supports the palatoquadrate on the braincase (Stensiö, 1963; Miles, 1969; Schaeffer, 1975; Young, 1986; Long, 1997). In contrast, what had been previously identified as the opercular cartilage was interpreted as the hyomandibula by Goujet (1984), Gardiner and Miles (1990), and Grogan and Lund

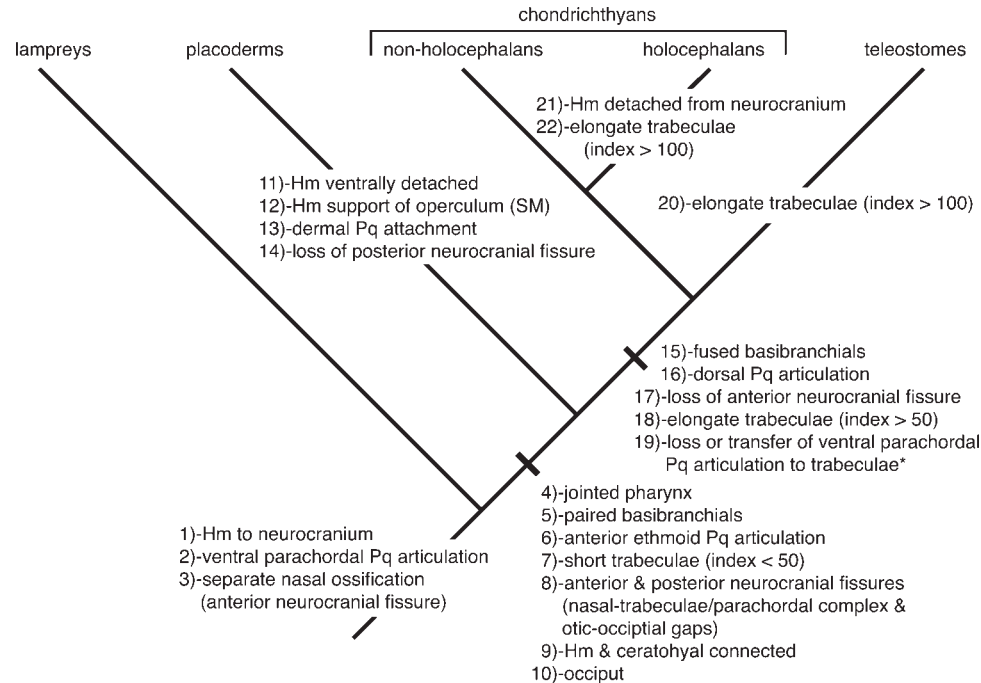


Fig. 2. Scenario for neurocranial and visceral arch character transitions in vertebrates. Trabeculae length or trabeculae-parachordal index (based on samples from published figured neurocrania) estimate the proportion of trabecular involvement in the base of the neurocranium (measured as the anterior neurocranium-to-hypophysial foramen distance/foramen-to-vagus or otic-occipital fissure distance $\times 100$). * Janvier (1996) and Grogan and Lund (2000) consider only anterior ethmoid and dorsal articulations to represent the primitive condition in chondrichthyans + teleostomes; thus basal trabecular articulations may represent independent acquisitions in chondrichthyans and teleostomes. Hm, hyomandibula (epihyal); Pq, palatoquadrate; SM, submarginal plate.

(2000), which attached to and supported the submarginal plate of the posterior cheek region. The suspensorium in placoderms is autostylic, with the palatoquadrate supported, in part, by the dermal skeleton (postorbital and suborbital plates). Here, the hyomandibula has no role in jaw support and also lacks a connection with the ceratohyal (Goujet, 1984). The presence of this condition in the phyllolepid *Austrophyllolepis* was proposed by Long (1984); however, he stated that if an epihyal was present, it extended from the postorbital plate to the "soft cheek region" (Long, 1984). Additionally, he considered the submarginal plate (analogous to an operculum) to be absent in phyllolepids.

Based in part on interpretations of the suspensorium in placoderms, it was hypothesized by Grogan and Lund (2000) that placoderms were more closely related to osteichthyans, assuming a modified form of autodiastyly in placoderms (attachment of the palatoquadrate to the braincase at two points, ethmoidal and orbital, with the hyomandibula supporting the operculum, following the early work of Stensiö [1963]). However, it is argued in following text that the suspensorium of placoderms has evolved independently relative to that of the chondrichthyans and osteichthyans, following a possible phylogenetic scenario where the primitive gnathostome condition consisted of a hyomandibula that spanned the gap between the ceratohyal

and neurocranium (Maisey, 1986; Janvier, 1996; character 1, Fig. 2). In this scenario, placoderms are characterized by a ventral detachment of the hyomandibula as it came to support the operculum (characters 11, 12, respectively, Fig. 2), correlated with a dermal support for the palatoquadrate (character 13, Fig. 2). Holocephalans (Fig. 1A), as noted by Grogan and Lund (2000), also differ from other jawed vertebrates, but possess a dorsal detachment of the hyomandibula (character 21, Fig. 2) in support of the operculum.

With this limited, and sometimes contradictory, information, the question arises as to how to best analyze the few occurrences of visceral arch preservation in placoderms. An analysis of soft tissue structures or perichondrally ossified visceral arches often destroyed by taphonomic processes involves the description of the elements themselves and/or evidence for their presence (e.g., osteological correlates for soft tissue *sensu* Witmer, [1995]). The homology of identified structures can be estimated by *a priori* estimates of similarity (Patterson, 1982; topography, ontogeny, and composition); however, an *a posteriori* test of congruence is a more robust test of homology (Patterson, 1982) with congruence based on a parsimony analysis of the interpreted structures.

An important addition to our understanding of the placoderm splanchnocranium is new phyllole-

pid material from the Middle Devonian of Australia (*C. mclachlani* Ritchie, 2005). The detailed preservation in *Cowralepis*, although incomplete, demonstrates the unique nature of the phyllolepid suspensorium and provides an important point of comparison in the understanding of the placoderm condition relative to other gnathostomes.

To make this comparison, a review of the splanchnocranium in extant gnathostomes is presented (see Background). The anatomy of *Cowralepis*, relative to this discussion, is then presented (see Results) and forms the basis for a review of the phylogenetic analyses of Goujet and Young (1995), Dupret (2004), and Dupret et al. (2007), followed by a review of gnathostome relationships and the character polarity for neurocranial and splanchnocranial features in basal gnathostomes (Phylogenetic Analysis). Supporting arguments for the interpretation of splanchnocranial and neurocranial structures in this analysis are discussed (see Discussion, under Mandibular Arch, Position of the Mandibular Joint, Hyoid Arch, Branchial Arches). Finally, with an improved understanding of the anatomy in *Cowralepis*, the visceral skeleton in placoderms is reconstructed and functional implications are evaluated (see Discussion, under Reconstruction of the Branchial Arches, Functional Implications).

MATERIALS AND METHODS

Interpretation of the splanchnocranium is based on an examination of the detailed anatomy of the structures and a comparative analysis of these elements to other gnathostomes (Fig. 1A). Where present, osteological (dermal bone) correlates to soft tissue are identified. The strength of inferences for the presence of soft tissue anatomy is evaluated following the Extant Phylogenetic Bracket (EPB) method of Witmer (1995, level I inference, fig. 2.5a, an unambiguous parsimony-based character distribution; level II, fig. 2.5b, an ambiguous character distribution; and level III, fig. 2.5c, an independent origin for the character).

Using an EPB approach to analyze placoderms is restricted, in most cases, to level II or III inferences because the closest extant outgroups to the Placodermi are sharks and bony fishes on one hand and lampreys and hagfish (jawless fish or agnathans) on the other (Fig. 1A). Limited comparisons can be made between the unsegmented agnathan branchial basket of lampreys (skeletal support external to the gill lamellae) and the segmented gnathostome condition possessed by sharks and bony fishes (skeletal support internal). The situation is not improved with the addition of bracketing fossil taxa because little is known of the condition in fossil outgroups to gnathostomes (believed to be the Osteostraci, although this is debated [Janvier, 1996; Donoghue et al., 2000]). Inferences for soft tissue structures in placoderms are complicated when the other gnathostome groups (chondrichthyans and osteichthyans) cannot be characterized by a single character state (dimorphic or polymorphic conditions for the character being analyzed in placoderms).

As a result of these restrictions, an *a posteriori* test of congruence may be equivocal, leaving us with descriptive *a priori* tests of similarity. However, it is important that we rely on any and all topographical and ontogenetic evidence to resolve the interpretation of placoderm anatomy.

Fossil material of *C. mclachlani* (Ritchie, 2005) was collected from Merriganowry quarry, NSW, Australia (Givetian; but see

Young [1999] who proposes a Frasnian age). This locality represents a lagerstätten limited to a single species. Individual specimens often include dermal elements of the head and thoracic shields along with the axial skeleton (see Fig. 3). In most specimens the dermal bones are highly weathered. In these cases, removal of the bone reveals a detailed natural mold. Latex or silicon peels provide casts demonstrating the positive relief of preserved structures.

Phylogenetic analyses were conducted using PAUP* (v. 4.0 beta 10, Swofford, 2003) with data matrices compiled using MacClade (v. 4.06, Maddison and Maddison, 2003). Reanalysis of the data matrix from Goujet and Young (1995:table 1) was completed using a branch-and-bound search option with default parameters. Reanalysis of the data matrix from Dupret (Dupret, 2004, Appendix 2) and Dupret et al. (2007) used a heuristic search with default parameters except random stepwise addition and 100 repetitions holding 100 trees. Analyses were conducted in each case with and without *Cowralepis*. Scoring for the Phyllolepidae of Goujet and Young (1995) was modified to reflect the improved understanding of phyllolepid based on *Cowralepis*.

All phyllolepid figured specimens are casts of natural molds whitened with ammonium chloride sublimate. "Corrected" figures refer to figures corrected for tectonic deformation (shear) as outlined by Ritchie (2005). Contact surfaces between adjacent dermal plates are denoted as either a contact face on the visceral surface or an overlap area on the external surface (after Dennis-Bryan, 1987). The suffix "id" when used to form taxonomic adjectives does not refer to the familial level in Linnean classification, but is used as a convenience for discussing informal taxonomic units. Abbreviations follow those of Dennis-Bryan (1987).

The abbreviations of institutions used in this article are as follows: AMF, Australian Museum, Sydney; NHM, Natural History Museum, London (formerly BMNH); WAM, Western Australian Museum, Perth.

BACKGROUND

Comparative methods have provided the basis for many of the interpretations of placoderm (see Fig. 1) morphology. In early studies on placoderms the fossil evidence was limited, necessitating a comparative approach based on a review of extant gnathostomes (Fig. 1A). This approach often resulted in an *a priori* assessment of structures. For example, Stensiö (1963) established the higher taxonomic group Elasmobranchiomorphi based on perceived similarities to the elasmobranchs (all chondrichthyans except the Holocephali; Fig. 1A). However, subsequent phylogenetic analyses have demonstrated that placoderms represent the nearest outgroup to other gnathostomes (chondrichthyans and teleostomes, Fig. 1A; Schaeffer, 1975; Young, 1986; Goujet and Young, 2004; see Janvier [1996] for a review of alternative hypotheses; Grogan and Lund [2000] have reintroduced a placoderm + osteichthyan hypothesis [see also Forey, 1980; Gardiner, 1984; Forey and Gardiner, 1986]). Despite which hypothesis of relationships is considered among gnathostomes, at present, there is little evidence to indicate the exact nature and polarity of the characters associated with the placoderm suspensorium. This is complicated by the lack of evidence for these structures in gnathostome outgroups, such as the Osteostraci, Galeaspida and

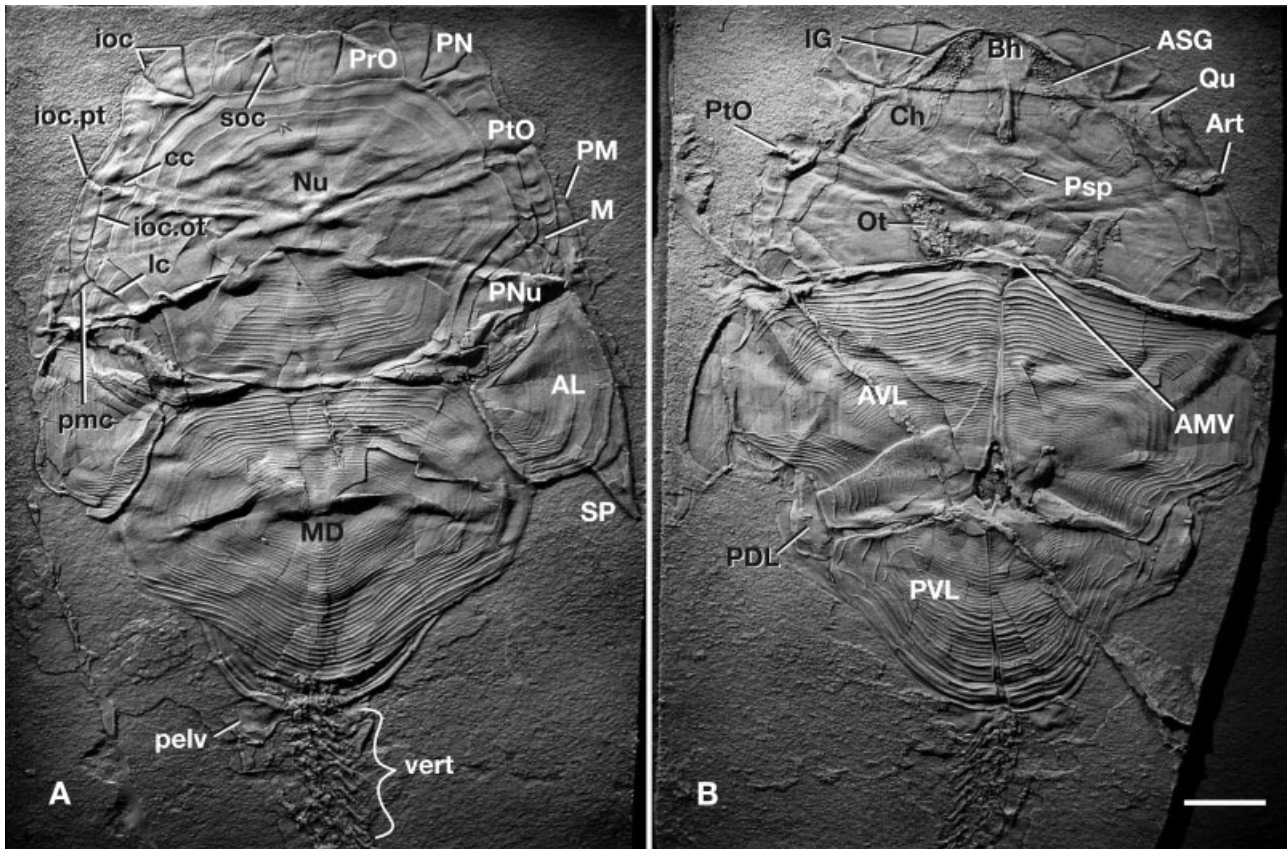


Fig. 3. *Cowralepis mclachlani*. AMF103753A, B, part and counter-part respectively. **A:** Dorsal view of head, thorax, and anterior vertebral column. **B:** Ventral view. AL, anterior lateral plate; AMV, anterior median ventral plate; Art, articular; ASG, anterior superognathal; AVL, anterior ventrolateral plate; Bh, basihyoid; cc, groove for central sensory canal; Ch, ceratohyal; IG, inferognathal; ioc, groove for infraorbital sensory canal; ioc.ot, groove for the otic branch of the infraorbital sensory canal; ioc.pt, groove for the postorbital branch of the infraorbital sensory canal; lc, groove for main lateral line sensory canal; M, marginal plate; MD, median dorsal plate; Nu, nuchal plate; Ot, otolith; PDL, posterior dorsolateral plate; pelv, pelvic girdle; PM, postmarginal plate; pmc, groove for postmarginal sensory canal; PN, postnasal plate; PNu, paranuchal plate; PrO, preorbital plate; Psp, parasphenoid; PtO, postorbital plate; PVL, posterior ventrolateral plate; Qu, quadrate; soc, groove for the supraorbital sensory canal; Sp, spinal plate; vert, vertebrae. Scale bar equals 1 cm.

Heterostraci (Janvier, 1996). In the following sections, the morphology of the mandibular, hyoid, and branchial arches is described from various gnathostome groups, followed by a comparison to the Placodermi when evidence is available.

Mandibular Arch

Among gnathostomes, two cartilages are typically found within the mandibular arch (Goodrich, 1930; de Beer, 1937; Maisey, 1989), a palatoquadrate (upper jaw) and Meckel's cartilage (lower jaw). Various authors have proposed the presence of additional elements within the mandibular arch representing vestigial serial homologues of the more posterior branchial arches (pharyngo-, hypo-, and basimandibular elements). In the summary work by Goodrich (1930), a number of elements were reported: a basimandibula in the extant elasmobranchs *Chlamydoselachus*, *Somniosus* ([*Lae-*

margus] *microcephalus* of Goodrich) and teleosts (Fig. 1A; de Beer [1937] noted the further reports of a median cartilage in holocephalans [Fig. 1A], the elasmobranch *Hexanchus*, and the tetrapods *Triton*, *Rana*, *Alytes*, and *Hyla*); hypomandibulae in *Somniosus* (*Laemargus*) and *Hexanchus*; and pharyngomandibulae preserved as the orbital process of the palatoquadrate or as dorsal cartilages in *Scaphirhynchus* and *Somniosus* (*Laemargus*). However, the validity of these identifications were questioned by Goodrich (1930) who noted the weakness in assuming the serial homology of these features to equivalent branchial arch structures, thus suggesting that these features represent independently formed structures interpreted in light of a hypothetical model for the origin of the jaws from a modified typical branchial arch. Among placoderms (see Fig. 1), a medial element in the arthrodire *Erromenosteus lucifer* (Fig. 1B) is interpreted as a basimandibula by Stensiö (1963:pls.

35–37, Bm). Alternatively, the position of this structure and its relationship to the rostral plate of the headshield might indicate that it represents a displaced internasal plate, which is commonly found among arthrodires. In an analysis of *Plourdosteus* (Fig. 1B) by Ørving (1951) it was hypothesized that a fused basimandibula-mentomandibula was present; again, however, this is not supported by evidence, i.e., either from a parsimony argument or from ontogeny, where separate elements or sites of ossification later fuse into a single structure.

As noted in aforementioned text, the branchial arch pattern is assumed to have existed throughout the visceral arches, including the hyoid and mandibular arches, based on models of visceral arch serial homology. This *a priori* imposition of a serial model of homology on the interpretation of fossils has led to the recognition of structures and patterns that are not supported by evidence. An example of this is seen in Stensiö's (1963) recognition of supra- and infrapharyngo-premandibular and mandibular elements within the neurocranium (following Jarvik, 1954), where comparisons were based on supposition alone and not on direct evidence, e.g., ontogenetic evidence suggesting the fusion of branchial elements into the adult neurocranium. Among placoderms, perichondrally ossified elements of the mandibular arch have been identified in a number of taxa. In other cases, indications of an element's presence are preserved on associated dermal bones, e.g., attachment surfaces for the palatoquadrate on the internal surfaces of the postsuborbital and suborbital plates or a groove for Meckel's cartilage on the inferognathal (osteological correlates *sensu* Witmer, 1995).

Palatoquadrate and dermal tooth plates.

The palatoquadrate is the only element recognized in the dorsal mandibular arch of placoderms and is variably ossified (one, two, or three units, Young, 1986; Goujet and Young, 1995). A single ossification, representing the primitive condition for placoderms, is seen in acanthothoracids (consisting of a single metapterygoid-autopalatine, *Romundina*, Ørving, 1975:pl. 2, fig. 5; Fig. 1B), rhenanids (*Jagorina* and *Gemuendina*, Young, 1986:fig. 10; Fig. 1B), euantiarchs (*Bothriolepis*, Young, 1984:fig. 5; Fig. 1B), and phlyctaeniids (*Dicksonosteus*, Goujet, 1975:fig. 2; Fig. 1B). Two ossification centers are seen in brachythoracid arthrodires (Fig. 1B), an anterior autopalatine and a posterior quadrate (e.g., *Torosteus pulchellus*, Gardiner and Miles, 1990:fig. 20). Ptyctodonts are characterized by the presence of three ossification centers (Young, 1986; Goujet and Young, 1995; Fig. 1B), consisting of autopalatine, metapterygoid, and quadrate ossifications ("*Ctenurella*" *gardineri*, Forey and Gardiner, 1986:fig. 3; in contrast, Long [1997] interprets the metapterygoids as nasal ossifications).

The suspension of the palatoquadrate to the neurocranium is variable among gnathostomes

(Fig. 1A) consisting of combinations of anterior (ethmoidal), dorsal (directly to the neurocranium or in connection with the hyomandibula), or ventral connections (see Janvier [1996] for a review). Placoderms are characterized by ethmoidal and ventral attachments (characters 6 and 2, respectively, Fig. 2), but uniquely possess a connection with the dermal cheek (postsuborbital and suborbital plates, character 13, Fig. 2). The connections in placoderms have been characterized as direct cartilaginous articulations, which are indicated by their lack of perichondral and endochondral ossification (Young, 1979:fig. 15, art1, art2; Young, 1980:25; Goujet, 1984:46), as entheses (thickenings or roughened areas for the potential attachment of muscle tendons or ligaments; e.g., Miles, 1971:fig. 33, daf or f.lpq; or Young, 1979:fig. 15, art3, art4), or as hypothesized attachments (not supported by direct evidence of attachment, but suggested by their assumed physical association; e.g., Stensiö, 1963:fig. 16, a.pr.ot). Articulation sites in placoderms are documented in the ethmoid region, e.g., in *Dicksonosteus* (Goujet, 1984:fig. 6, a.pr.pq) and associated with the anterior postorbital process of the neurocranium, e.g., in *Brindabellaspis* (Young, 1986:fig. 15A, art.hm; Fig. 1B). Two alternative interpretations for the anterior neurocranial articulation associated with the anterior postorbital process are actively debated, as summarized by Young (1986) and include the following: 1) a hyomandibular articulation or 2) a palatoquadrate articulation. Resolution of this debate is beyond the scope of the current study; however, the latter interpretation is accepted as the basis of the following discussion, which is based, in part, on the debate of matching three structures with only two known articulation sites and a lack of a clear co-occurrence of opercular and hyomandibular elements in any known specimen; thus the latter two are interpreted here as a single element (see Discussion, under Hyoid Arch). A hypothesis that an anterior and dorsal connection of the palatoquadrate represents the plesiomorphic condition for gnathostomes was presented by Janvier (1996) and Grogan and Lund (2000) ("ethmoid and postorbital," p. 130, and "ethmoidal and orbital," p. 238, respectively); however, they differ in their interpretation of the role for the hyoid arch (following Young's [1986] interpretation, the plesiomorphic condition may be limited to an ethmoidal articulation, while the posterior articulation is for the hyomandibula). An assumed dual connection (ethmoidal and dorsal) is derived relative to agnathan outgroups, because the putative homologue of the palatoquadrate (inner velar bar in lampreys, Mallatt, 1996; Fig. 1A) connects solely to the ventral "trabeculae" of the neurocranium in lampreys. Mallatt (1996) assumed that the lamprey trabeculae were homologous to those in gnathostomes. This was based on the ablation studies of Langille

and Hall (1988); however, more current labeling methods (e.g., DiI injection, Kuratani et al., 2004) demonstrate a lack of correspondence, with the lamprey trabeculae comparable to the mesodermal parachordals in gnathostomes. Thus, the lamprey mandibular element (or palatoquadrate homologue) is attached to the parachordals (character 2, Fig. 2). In a report by Janvier (1996:130), the placoderm condition was likened to the ventral “basipterygoid” (or “palatobasal”) attachment seen in some other gnathostomes. The basipterygoid is developmentally associated with the trabeculae and “it always lies ventrally to the head vein” (de Beer, 1937:391); thus, its relationships to the jugular in placoderms is the apparent basis for Janvier’s comparison. Basal cranial development is unknown in placoderms; however, the hypophysial foramen serves as a landmark at the junction of the trabeculae and parachordals (trabecular and basal plates; de Beer, 1937). In placoderms (e.g., *Dicksonosteus*; Fig. 4) the hypophysial foramen (or its osteological correlate, the parasphenoid in taxa where the foramen fails to perforate this dermal plate) is displaced far anteriorly relative to the basal attachment site for the palatoquadrate (at the level of the anterior postorbital process of the neurocranium). This implies an association for the palatoquadrate with the parachordals (basal plate) rather than the trabeculae. Additional landmarks (nerve foramina, J. Maisey, personal communication, 2006) associated with the pila antotica (that connects the orbital cartilage with the anterior parachordals, Goodrich, 1930) further confirm a parachordal association. Placoderms thus retain the primitive ventral attachment (parachordal, character 2, Fig. 2) seen in lampreys. Ethmoid, dorsal, and basipterygoid attachments represent derived attachment sites relative to the condition in lampreys (characters 6, 16, 19, respectively, Fig. 2).

The placoderm upper dentition is represented by dermally derived superognathal plates, varying in number among placoderms and absent altogether in antiarchs where a dermal cheek plate (homologue of the suborbital plate) forms the functional dentition (Young, 1984). In arthrodiros (Fig. 1B), which possess two superognathals, the posterior superognathal is associated with the autopalatine (e.g., *Dicksonosteus*, Goujet, 1984:fig. 50; or *Toros-teus pulchellus*, Gardiner and Miles, 1990:fig. 20, dp.PSG), whereas the anterior superognathal attaches more anteriorly to the ethmosphenoid region of the braincase (ASG, Fig. 4).

Meckel’s cartilage. Meckel’s cartilage comprises a major element of the mandibular arch. Ossification of Meckel’s cartilage is variable among placoderms (see Fig. 1) ranging from complete ossification antero-posteriorly, to separate ossifications of anterior and posterior elements, to an absence of ossification altogether (Goujet and Young,

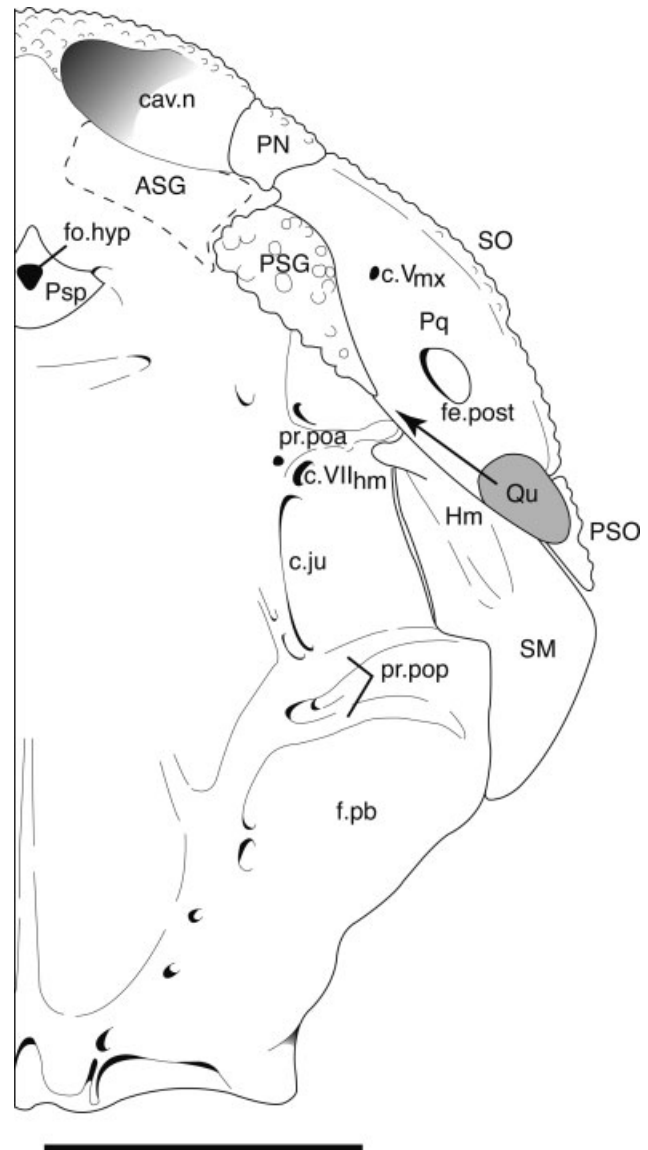


Fig. 4. *Dicksonosteus arcticus*. Reconstruction of the left half of the neurocranium and left dermal cheek (redrawn from Goujet, 1984:fig. 50). Arrow indicates the relative shift of the quadrate (gray) to achieve the condition in phyllolepid. ASG, anterior superognathal; c.ju, canal for jugular vein; c.VII_{hm}, canal for hyomandibular branch of the facial nerve; c.V_{mx}, canal for maxillary branch of the trigeminal nerve; cav.n, nasal cavity; fe.post, posterior fenestra of the palatoquadrate; fo.hyp, fossa hypophysialis; f.pb, parabranial fossa (cucullaris fossa of Stensiö, 1963); Hm, hyomandibula; PN, postnasal plate; Pq, palatoquadrate; pr.poa, anterior postorbital process of the neurocranium; pr.pop, bifid posterior postorbital process of the neurocranium; PSG, posterior superognathal; PSO, postsuborbital plate; Psp, parasphenoid; Qu, quadrate; SM, submarginal plate; SO, suborbital plate. Scale bar equals 1 cm.

1995:character 17). The latter condition could either represent missing data (not preserved) or a true failure to ossify. Complete ossification of Meckel’s cartilage is found in rhenanids (e.g., *Jagorina*, Young, 1986:fig. 10; Fig. 1B) and an

unnamed "buchanosteid" arthrodire (Young et al., 2001:fig. 4; Fig. 1B). The more basal phylogenetic position of rhenanids indicates that complete ossification is likely the primitive condition for placoderms. A posterior ossification alone (Goujet and Young, 1995) is recognized in euantiarths (although in *Bothriolepis* [Young, 1984] and *Remigolepis* [Johanson, 1997:fig. 12], the ossification extends anteriorly to the symphyseal region; Fig. 1B) and in ptyctodonts (Miles and Young, 1977; Long, 1997; Fig. 1B). The derived condition, found among brachythoracid arthrodires (Fig. 1B), consists of two separate ossifications, an anterior mentomandibula and posterior articular.

The dermal dental element associated with Meckel's cartilage is known as the inferognathal. In eubranchythoracid arthrodires (Fig. 1B) where the inferognathal is represented by ossified occlusal and non-occlusal (blade) regions (Carr, 1991:character 63), the articular is most often preserved as a perichondral ossification on the posterolateral surface of the blade region (Heintz, 1932:fig. 30, PIG; Miles and Dennis, 1979:fig. 11). In the posterior occlusal region, indication of the presence of Meckel's cartilage is limited to a ventral groove. A mentomandibular (symphyseal) ossification is often present (Miles and Dennis, 1979:fig. 11) that unites the right and left inferognathals and may form a fused symphysis.

However, in arthrodiran taxa such as *Antineoteus lehmani* (Lelièvre, 1988; Fig. 1B) and a buchanosteid (Young et al., 2001:fig. 4A–D) the non-occlusal blade region is reduced. In these cases, the ventral groove extends along most of the inferognathal, which rests entirely on the dorsal surface of Meckel's cartilage (ossified in the latter and unknown in the former taxon).

Hyoid Arch

The hyoid arch in gnathostomes (Fig. 1A) consists typically of two elements, the hyomandibula and ceratohyal. As in the mandibular arch, the number and morphology of elements varies among taxa (Goodrich, 1930; de Beer, 1937). Commonly, a basihyal or copula is well developed. Hypohyals are variably present with de Beer (1937:410) noting them in some elasmobranchs (*Somniosus* [Lae-margus], *Heptanchus*, and "perhaps in" *Squalus*; Fig. 1B) and many teleostomes (considered absent in acanthodians, Miles, 1973:93; Fig. 1B). In a study by Lauder and Liem (1983), the hypohyals were considered to be a synapomorphy of osteichthyans (Fig. 1A). In those taxa lacking discrete hypohyals it was argued by de Beer (1937) that these elements were fused to the basihyal or copula. Again, this latter statement reflects an *a priori* interpretation based on a model of serially homologous segmentation (de Beer, 1937:410, "where the hypohyals are apparently absent"; also

de Beer, 1937:62, "it seems possible that the hypohyals are fused to the basihyal"). It is more likely that the hypohyals are independently developed in osteichthyans and elasmobranchs (based on a parsimony argument following from the limited and scattered distribution for this feature).

There are two patterns for the ceratohyal and hyomandibula among extant taxa. Among chondrichthyans, these elements remain as individual chondrified structures that articulate directly with each other (character 9, Fig. 2). In contrast, teleostomes (acanthodians and osteichthyans *sensu* Lauder and Liem, 1983) possess additional elements in the hyoid arch. Teleostomes are characterized by the presence of an interhyal (Lauder and Liem, 1983:character 6, fig. 1; Gardiner et al., 1996). A symplectic is a synapomorphy of the derived actinopterygian group, Neopterygii (Lauder and Liem, 1983; Gardiner et al., 1996; Fig. 1A).

The relationship of the hyomandibula to neurovascular structures also has distinct selachian (Fig. 1A) and osteichthyan patterns. In selachians, the hyomandibula articulates with the otic region of the neurocranium medially and ventrally to the head vein, in contrast to osteichthyans where the articulation is lateral and dorsal to the head vein (de Beer, 1937). The relationship of the hyomandibula and hyomandibular branch of the facial nerve (VII_{hm}) also differs. The nerve passes anterior and dorsal to the hyomandibula in selachians whereas in osteichthyans the pattern is variable (anterior and dorsal, posterior, or forks anterior and posterior to the hyomandibula, de Beer, 1937).

The position of the foramen for the hyomandibular nerve in teleostomes was demonstrated by Goodrich (1930:fig. 446) to be either anterior, anterodorsal, or anteroventral to the hyomandibular articulation site, but in all cases anterior. Thus, it is the path of the nerve that is variable in teleostomes. Young (1986) proposed a fixed positional relationship in placoderms (see Fig. 1) for the articulation of the hyomandibula (on the anterior postorbital process) anterior relative to the foramen for VII_{hm}. In comparing the arthrodire *Kujdanowiaspis* (Goujet, 1984:fig. 10; Fig. 1B) and *Dicksonosteus* (Goujet, 1984:fig. 6; Fig. 1B) the exit for VII_{hm} is equivalent (less than a 1% difference in *Dicksonosteus*) relative to pituitary and occipital landmarks. However, the anterior postorbital process in *Dicksonosteus* has shifted anteriorly relative to *Kujdanowiaspis* (greater than a 9% difference). In *Tapinosteus* (a eubranchythoracid arthrodire; Fig. 1B) the exit for VII_{hm} is anterodorsal to the anterior postorbital process (Stensiö, 1963:fig. 46; note that the basiptyergoid process of Stensiö is interpreted here as the anterior postorbital process; thus, his anterior postorbital process is a posterior postorbital process). The nerve traverses the dorsal surface of the anterior postorbital process (Stensiö, 1963:fig. 46, gr. VII_{hm}) to a notch at the

posterior base of the process (Stensiö, 1963:fig. 46, n.VII_{hm}; unlike *Dicksonosteus*, the anterior postorbital process in *Tapinosteus* is ventrally depressed due to the development of a ventrally projecting lateral consolidated arch in the dermal headshield). As the relative position of dermal plates shifts, e.g., as seen with the relatively large orbits in *Tapinosteus*, there is also a shift in neurocranial structures (i.e., the processes) apparently independent of the organization of cranial nerves as they exit the brain. The shift of the VII_{hm} foramen between *Kujdanowiaspis* and *Dicksonosteus* represents changes in the organization of the dermal bones (relative to the process) including the submarginal plate with its hyomandibular articulation to the anterior postorbital process. Thus, contrary to Young (1986), the positional relationship between the anterior postorbital process and the foramen for VII_{hm} is not fixed, but varies with topographical changes in the dermal headshield. These differences represent character states that may have value for phylogenetic analyses.

Summaries for the reported records for elements of the hyoid arch in placoderms are noted by Denison (1978) and Janvier (1996). To date, a basihyoid (=urohyal of Forey and Gardiner, 1986), epihyals (or hyomandibulae), and opercular cartilages have been reported in the literature. Additional elements have been hypothesized to have been present, but are not supported by fossil evidence. The naming and homology of the reported elements have been debated and are discussed in following text.

Hyomandibula. The hyomandibula, as noted by Denison (1978), is unknown in antiarchs, phyllolepid, pseudopetalichthyids, acanthothoracids, and petalichthyids, but is clearly present in rhenanids and non-phyllolepid arthrodiros (Fig. 1B). The hyoid arch of ptyctodonts (Fig. 1B) was described by Long (1997) based on disarticulated specimens of *Austroptyctodus*, *Campbellodus*, *Ctenurella*, and *Chelyophorus*. Six perichondral ossifications associated with the hyoid arch were recognized by Long (based on element shape and articular surfaces) who cautioned that there is a lack of direct evidence for identification (basihyal, hypohyals, ceratohyals, interhyals, hyomandibulae, and opercular cartilages). However, there are a number of interpretations presented for the splanchnocranium in ptyctodonts (e.g., Miles and Young, 1977; Forey and Gardiner, 1986; Young, 1986; Long, 1997). Resolution of the condition in this group must await the analysis of new material preserving both the neurocranium and visceral arches (K. Trinajstić, personal communication, 2007).

Following Goujet (1984), the placoderm hyomandibula (see Fig. 4) is interpreted here as supporting the submarginal plate (character 12, Fig. 2) with its articulation to the neurocranium associated with the anterior postorbital process, in con-

trast to a separate element—the opercular cartilage—as proposed by Young (1986) (see Discussion, under Hyoid Arch). Notably, the hyomandibula lacks a connection to ventral elements in the hyoid arch (character 11, Fig. 2). In the absence of a preserved hyomandibula, a groove on the medial surface of the submarginal plate (Goujet, 1984:fig. 48:s.hm; Young, 1986) represents an osteological correlate for the presence of this visceral element. Unlike placoderms, the hyomandibula in selachians and teleostomes (Fig. 1A) extends from the neurocranium to the region of the jaw articulation (connecting to the ceratohyal or intervening elements when present). An opercular support is also seen in holocephalans (Fig. 1A), although the hyomandibula is detached dorsally from the neurocranium (character 21, Fig. 2) and a distinct opercular cartilage and hyoid rays provide additional support for the operculum (the former “formed by the fusion of dorsal hyoid rays” [Didier, 1995:70]).

Ceratohyal. A ceratohyal is reported in *Stensioella* (Gross, 1962:fig. 4C, Chy; Fig. 1B), although Goujet and Young (1995) excluded stensioellids from their placoderm analysis because they do not possess any placoderm characteristics (including character states summarized by Goujet, 2001). Also, a possible holocephalan relationship (Fig. 1A) for *Stensioellida* was proposed by Coates and Sequeira (2001). Ceratohyals are also reported in rhenanids (Denison, 1978; Fig. 1B) and ptyctodonts (Long, 1997:figs. 6, 35, CH; Fig. 1B). In the latter group, the ceratohyals are notably broad and rectangular in shape (Long, 1997).

Hypohyal. As noted in aforementioned text, hypohyal elements represent an osteichthyan synapomorphy (Fig. 1B; Lauder and Liem, 1983), although their presence in some chondrichthyans (Fig. 1A) was reported by de Beer (1937). These elements are only reported among placoderms in ptyctodonts by Long (1997:fig. 6, HH for *Campbellodus* although not reconstructed in *Austroptyctodus* Long, 1997:fig. 35; Fig. 1B).

Basihyal. The presence of a basihyal element is noted by Denison (1978) in pholidosteid arthrodiros (*Tapinosteus*, Stensiö, 1963:fig. 83; Fig. 1B) and possibly in the rhenanid *Gemuendina* (copula element of Gross, 1963:figs. 3, 4, Cp; Fig. 1B) and *Pseudopetalichthys* (Denison, 1978:fig. 12B; Fig. 1B). A basihyal is reported in ptyctodonts by several authors (Forey and Gardiner, 1986:fig. 1; Long, 1997:figs. 6, 35; Fig. 1B).

Pharyngohyal. Pharyngohyals have been described (as noted by de Beer, 1937) in holocephalans and several elasmobranchs (Fig. 1B). However, among gnathostomes, only holocephalans are reported by Didier (1995) to possess this feature. This isolated or irregular distribution (assuming de Beer's contention to be correct for elasmobranchs) is consistent with an independent origin for this element (see Maisey [1986] for a discussion

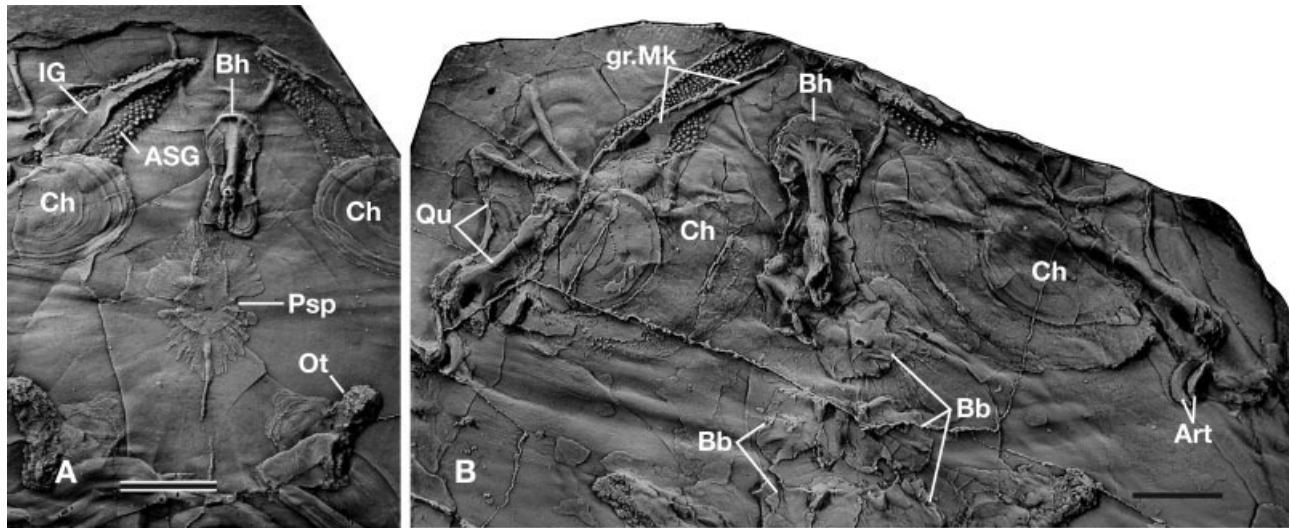


Fig. 5. *Cowralepis mclachlani*. **A:** AMF 96781, ventral view of juvenile. **B:** AMF127156 corrected, ventral view of adult. Note the differences between the juvenile and adult in the extent of ossification of the ceratohyal. Art, articular; ASG, anterior superognathal; Bb, basibranchial; Bh, basihyoid; Ch, ceratohyal; gr.Mk, groove for Meckel's cartilage on the inferognathal; IG, inferognathal; Ot, otolith; Psp, parasphenoid; Qu, quadrate. Scale bar equals 1 cm.

on the serial homology of hyoid elements to a typical branchial arch).

Branchial Arches

The pattern of a typical branchial arch for extant fishes consists of four elements (pharyngo-, epi-, cerato-, and hypobranchials) organized in a Σ -pattern in selachians and holocephalans and a $>$ -pattern in teleostomes (de Beer, 1937; Grogan and Lund [2000] note exceptions to this generalization; Fig. 1A). Basibranchials are typically fused forming a single element or copula.

In placoderms, preservation of splanchnocranial elements posterior to the hyoid arch is limited. Possibly five elements are reported by Gross (1962:fig. 4, Cb, Eb) in *Stensioella* that correspond to ceratobranchial and epibranchial elements, both extending anteromedially from their respective lateral articulations (as discussed in aforementioned text, only questionably a placoderm; Fig. 1B). Four ceratobranchial elements were figured by Gross (1963:fig. 3B, Cbr₁₋₄) in the rhenanid *Gemuendina* (also *Jagorina*, Denison, 1978:fig. 15C; Fig. 1B). *Pseudopetalichthys* (Fig. 1B) possesses what appear to be four to five ceratobranchials (Gross, 1962:fig. 7, Br; the anterior element, if associated with a basihyoid, may represent a ceratohyal). In the ptyctodont *Austroptyctodus* (Fig. 1B), two epibranchial elements were illustrated by Long (1997:fig. 35, Ep). Among arthrodires (Fig. 1B), three pairs of hypobranchial elements were identified by Stensjö (1963:fig. 83, Hbr₁₋₆) that he assumed represented the fused equivalent of six pairs of hypobranchials (not supported by the evi-

dence, but representing an *a priori* application of a chondrichthyan model; compare Stensjö's reconstruction with his figure of an extant elasmobranch, 1963:fig. 84A).

RESULTS Mandibular Arch

The mandibular arch in *C. mclachlani* (a phyllolepid, Fig. 1B) consists of both perichondral and dermal elements (see Fig. 5). With respect to the latter, two pairs of superognathals are present along with an inferognathal (IG, Fig. 5A). The anterior superognathal (ASG, Fig. 5A) in *C. mclachlani* represents the larger element with the posterior superognathal representing less than 13% the length of the former (measured from the symphysis posteriorly along the occlusal surface in AMF96783, Ritchie, 2005:fig. 9E). The inferognathal (Ritchie, 2005:fig. 10D, E) consists of two laminae, an occlusal lamina and a vertical anterolateral lamina. The ventral surface presents the shallow groove for Meckel's cartilage (gr.Mk, Fig. 5B). Anteriorly, the inferognathal tapers to a narrow point (see Fig. 5). The distribution of denticles on the upper and lower dental elements is unequal, with those on the anterior superognathal extending far medially beyond the occlusal surface of the inferognathal (Fig. 5; ASG ca. 3 times wider in some cases).

Other than the supero- and inferognathals, another ossification, a perichondral ossification, is associated with the mandibular arch, extending anteriorly from the jaw joint in *C. mclachlani*. This is identified as the quadrate (Qu, Figs. 3B

and 5B; originally identified as an “articular,” Ritchie, 2005). The quadrate ossification does not reach either the posterior superognathal or inferognathal, although it is clearly aligned with both of these elements (six specimens with PSG and IG and 28 specimens with IG and the perichondrally ossified mandibular element). The quadrate (Fig. 6A) consists of a “prominent ventral ridge” (Ritchie, 2005:230; r, Fig. 6A) and an anterior flange (fl, Fig. 6A) directed laterally and if original curvature were restored to the headshield it would be directed ventrolaterally. Posteriorly the ridge bifurcates, enclosing a large pit (pit, Fig. 6A). The depth of the pit is such that it nearly traverses the element, but does not extend to the dorsal surface in the one specimen where the dorsal surface is exposed (Fig. 7A,B). Additionally, the matrix filling the pit seen in the natural molds has no indication of anything other than a blind pit (the infilling possesses a natural curved transition from the sides of the pit to its base). This is very similar to the quadrate of *Holonema westolli* (Fig. 1B), where, in the holotype (WAM70.4.243; Fig. 6B,C), the central thickened ridge on the quadrate bifurcates posteriorly (r, Fig. 6B). A large blind pit is also situated between the limbs of this bifurcation (Fig. 6B,C).

Anteriorly, the quadrate of *C. mclachlani* is open, reflecting the expansion of perichondral ossification across a preexisting cartilaginous structure. Growth lines, when present, suggest an ossification center located at the ventral ridge just anterior to the pit. Typically, the posterior margin of the quadrate is incomplete, again suggesting a cartilaginous core. In AMF103776 (Fig. 7A), seen in dorsal view, the posterolateral edge of the quadrate possesses an indentation (indent, Fig. 7B). From this point, the quadrate expands to form a bulbous structure, the articular condyle (art.cond, Fig. 7B, although partially crushed). Posteromedially, there is an apparent unossified corner (possible site of articulation with the neurocranium or headshield). The posterolateral surface of the condyle is in contact with the articular bone (Art, Fig. 7B; “suborbital” of Long (1984) and Young (2005); “hyoid arch element?” of Ritchie (2005).

The articular (Fig. 7B) consists of two perichondrally ossified parts that are concentrically arranged and separated by a deep groove that is seen in both dorsal and ventral views. Thus, the articular consists of two laminae, a thinner one with its outer surface forming a concavity and an adjacent thicker lamina with a convex outer surface (the facing surfaces of the two laminae possess a porous texture). It is not clear whether the two elements are connected deep within the groove (an H-shape); however, the common association of both laminae indicates an osseous connection. In rare cases, the articular is represented by an isolated lamina or there is evidence of slippage

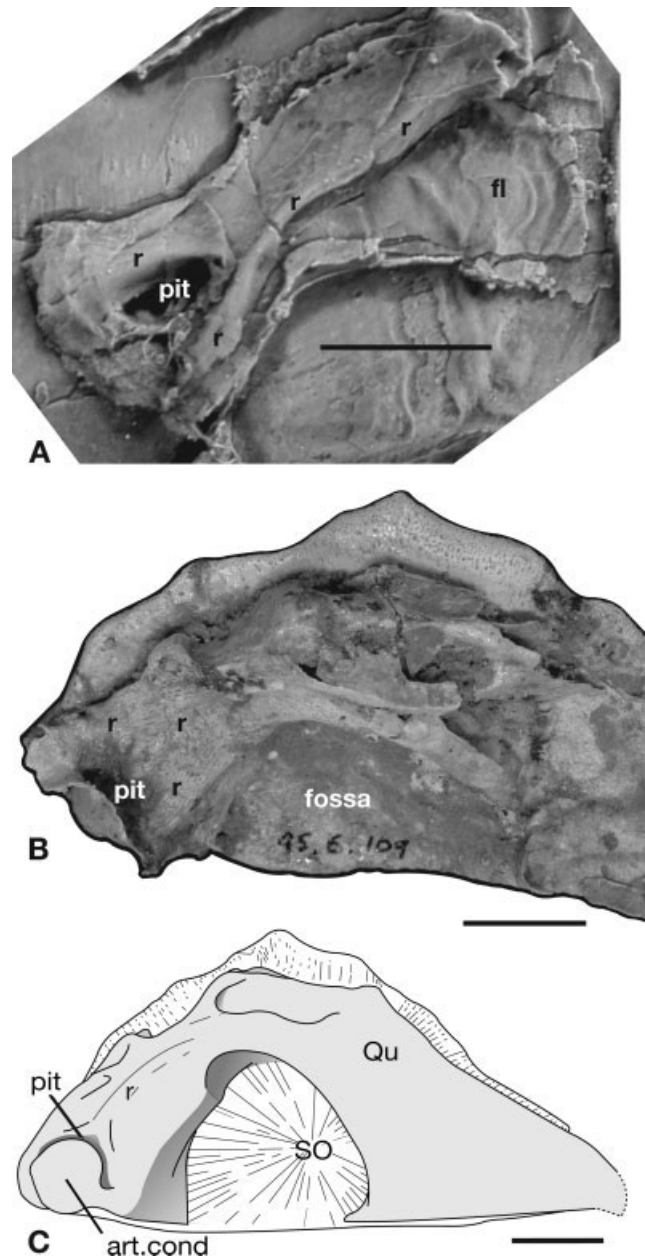


Fig. 6. Comparison of left quadrate ossifications. **A:** *Cowralepis mclachlani*, AMF96783, in medial view. **B:** *Holonema westolli*, WAM95.6.109, in oblique dorsomedial view. **C:** *Holonema westolli*, reconstruction in medial view (redrawn from Miles, 1971:fig. 33B). art.cond, articular condyle of the quadrate; fl, flange; fossa, fossa for the adductor mandibulae muscle; pit, blind pit within quadrate; Qu, quadrate; r, thickened ridge; SO, suborbital plate. Scale bar equals 1 cm.

between the two laminae. This evidence implies that an osseous connection is minimal or that (less likely) the laminae were only connected by a thin layer of cartilage. Whether the components are directly connected or separate, the articular is found in close proximity to the quadrate. The orientation of the articular in preserved specimens is

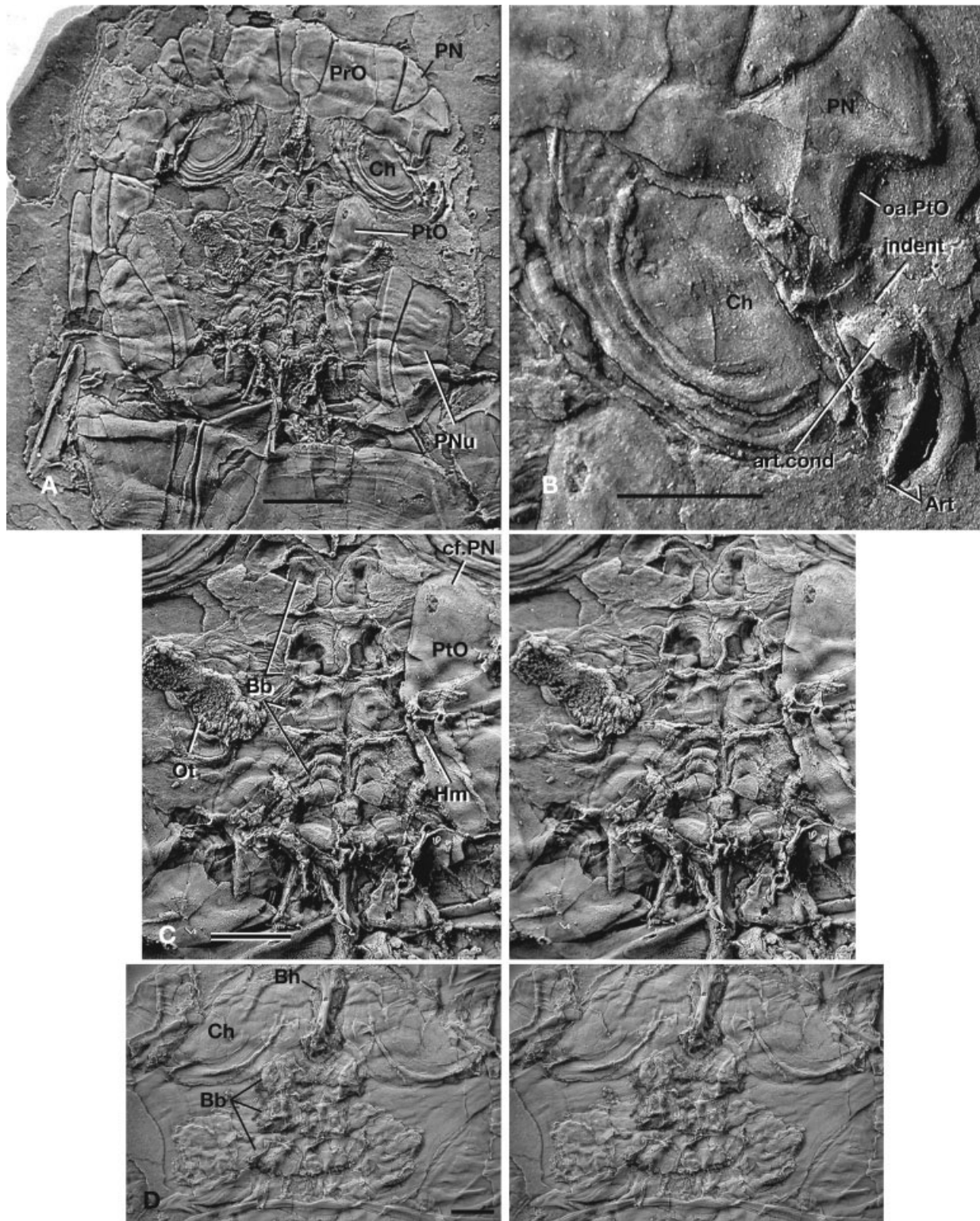


Fig. 7. *Cowralepis mclachlani*. **A**: AMF103776, visceral elements in dorsal view. **B**: Close-up of articular-quadrate complex. **C**: Stereoscopic close-up of medial elements. **D**: AMF90007, stereoscopic ventral view of visceral elements. Art, articular; art.cond, articular condyle; Bb, basibranchial; cf.PN, contact face on the postorbital plate for the postnasal plate; Ch, ceratohyal; Hm, hyomandibula; indent, indentation; oa.PtO, overlap area on postnasal plate for the postorbital plate; Ot, otolith; PN, postnasal plate; PNu, paranuchal plate; PrO, preorbital plate; PtO, postorbital plate. Scale bars in A and D equal 1 cm, B and C 0.5 cm. Stereoscopic interocular distance = 65 mm.

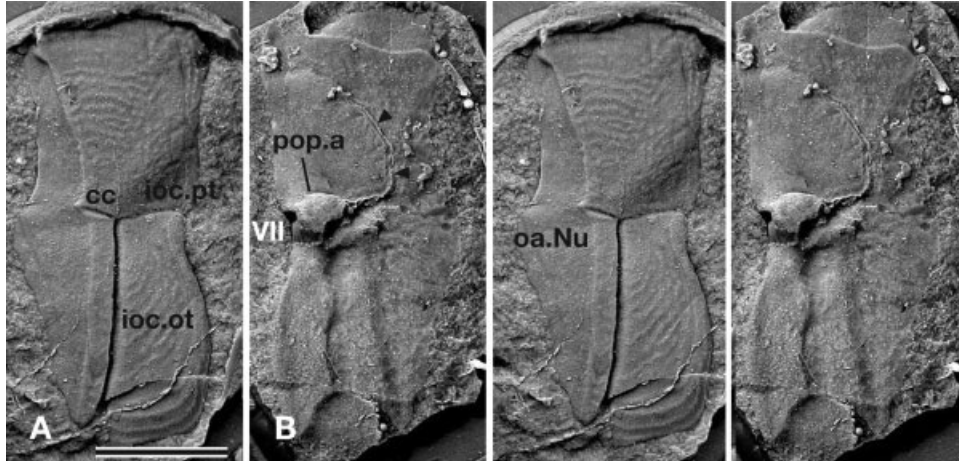


Fig. 8. *Placolepis budawangensis*. A: AMF61759A, stereoscopic external view of right postorbital plate. B: AMF61759B, stereoscopic internal view. Arrowheads indicate the neurocranial contact with the overlying dermal bone outlining the postocular cavity. cc, groove for the central sensory canal; ioc.ot, groove for the otic branch of the infraorbital sensory canal; ioc.pt, groove for the postorbital branch of the infraorbital sensory canal; oa.Nu, overlap area for the nuchal plate; pr.poa, anterior postorbital process of the neurocranium; VII, foramen for the facial nerve. Scale bar equals 1 cm. Stereoscopic interocular distance = 65 mm.

variable, ranging from the concavity facing laterally (Fig. 5B) to medially (Fig. 7B). The location of the articular and quadrate is clearly associated with the overlying postorbital plate (Figs. 3B and 7A,B) and the anterior postorbital process of the neurocranium. Traces of the anterior postorbital process or other aspects of the neurocranium on the overlying dermal plates in *C. mclachlani* are limited due to flattening and tectonic deformation (only the outline of the supravagal process is visible on the paranuchal plate).

In the phyllolepid *Placolepis budawangensis* (Ritchie, 1984:figs. 7J, H, 8D), the distal portion of the anterior postorbital process is preserved (pr.poa, Fig. 8B) and pierced by a canal that Long (1984:fig. 14) equated with the hyomandibular nerve (VII, Fig. 8B). Traces of the neurocranial contact with the overlying dermal bone are visible, outlining the posterior boundary of the postocular cavity anterior to the anterior postorbital process (Fig. 8B). The neurocranial process is located directly beneath the externally visible triple junction of the grooves for the central canal and postorbital and otic branches of the infraorbital canal (or ossification center for the postorbital plate, Fig. 8A).

Hyoid Arch

The hyomandibula in the phyllolepid *C. mclachlani* (Fig. 1B) is represented by small posteriorly-directed circular caps (Hm, Fig. 7C) located near the ossification center of the postorbital (and assumed to lie on the posterior surface of the anterior postorbital process). These caps represent perichondral ossifications of the proximal part of the hyomandibula. Among placoderms (see Fig. 1),

the hyomandibula is associated with the dermal submarginal plate (Goujet, 1984); however, Long (1984) suggested that this is phylogenetically lost in phyllolepids. The submarginal plates previously identified (Ritchie, 2005:fig. 6; Young and Long, 2005) are reinterpreted as the postmarginal plates (see following text).

The basihyal in *C. mclachlani* was described by Ritchie (2005). This structure is represented by a single midline ossification (Bh, Figs. 3B, 5, and 7D) in direct contact with the paired median branchial elements, inserting into a notch formed by the first pair (Figs. 5B, 7D, and 9C). It is physically separate from the mandibular arch and laterally in contact with the ceratohyals in mature specimens (Ch, Fig. 5B).

As noted by Ritchie (2005), the ceratohyal lies both ventral and medial to the inferognathal, extending from the region of the mandibular joint to the basihyal. It also lies ventral and medial to the quadrate (determined by overlap patterns). It is often found in close association with the quadrate. A number of specimens demonstrate a closed lateral edge on the ceratohyal indicating that it is a distinct ossification separate from the quadrate. Along the medial edge the element is open. Growth lines (Figs. 5 and 7A,B,D) demonstrate the expansion of perichondral ossification in an antero-medial direction (toward the basihyal).

Branchial Arches

The only structures that can be associated with the branchial arches in *C. mclachlani* are perichondrally ossified paired basibranchials situated along the midline. These elements are preserved in a number of specimens (Bb, Figs. 5, 7A,C,D,

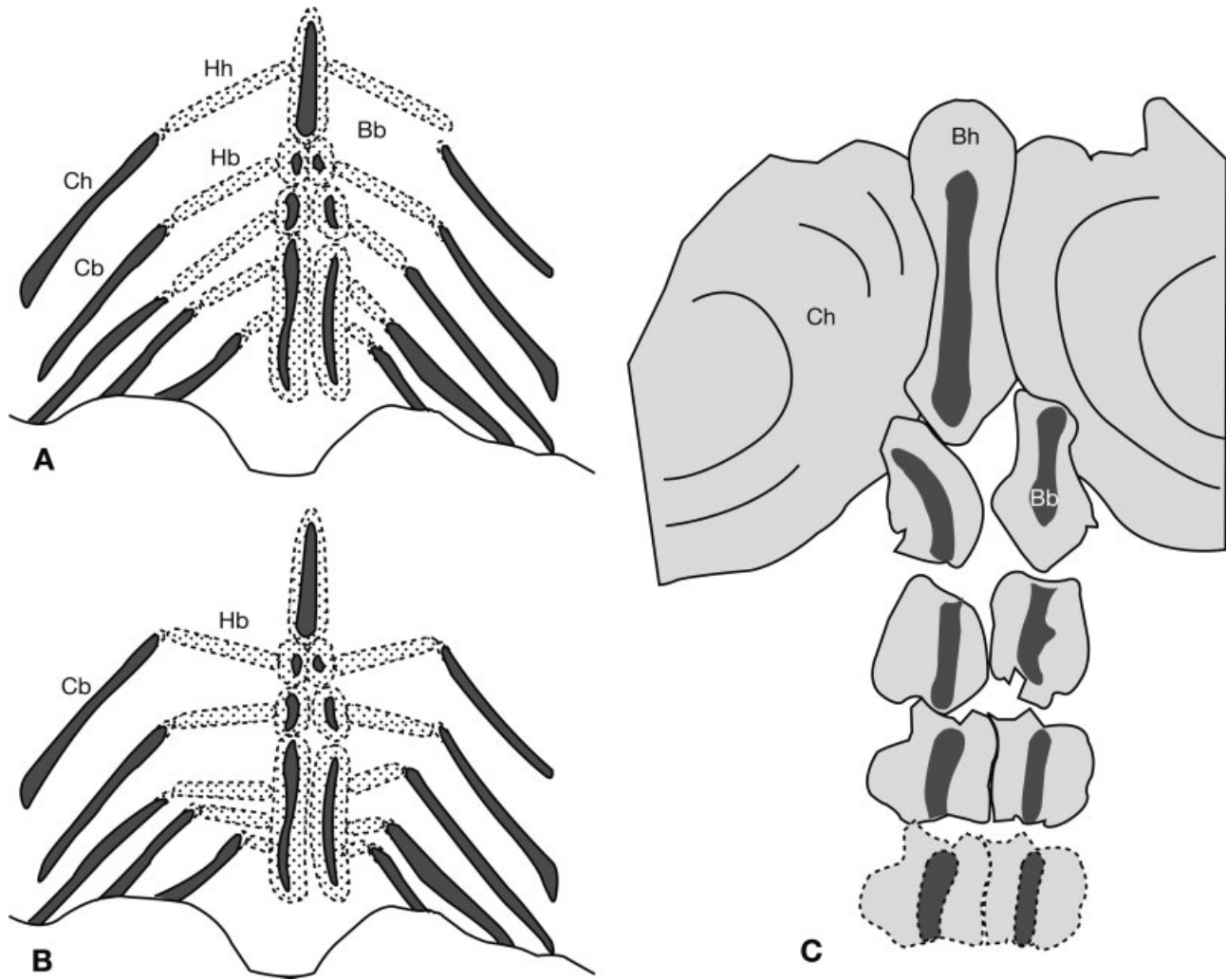


Fig. 9. Comparison of the visceral arch pattern in *Pseudopetalichthys problematica* and *Couralepis mclachlani*. Individual elements in *P. problematica* and the thickened ridges in *C. mclachlani* that represent the centers of ossification are dark gray and thin laminar perichondral ossifications light gray. **A, B:** Alternative reconstructions of missing elements in *P. problematica*. Hypothesized cartilaginous elements stippled. Preserved elements (redrawn from Gross, 1962). **C:** *C. mclachlani* (AMF 90003) perichondrally ossified elements. The posterior (fourth) pair of basibranchials is obscured from view by ventral plates, but their presence is confirmed from additional specimens. Note the similarity between the thickened ridges of *C. mclachlani* and the preserved midline elements in *P. problematica* with each arranged longitudinally. Bb, basibranchial; Bh, basihyoid; Cb, ceratobranchial; Ch, ceratohyal; Hb, hypobranchial; Hh, hypohyal.

and 9C). In AMF90007 (Fig. 7D), four pairs are present. In specimens where the fourth pair is not visible it is often discernable as a compression artifact in the overlying anterior ventrolateral plates (in ventral view). Ventrally, each element is a flattened, perichondrally-enclosed structure with rugged surface contours consisting of depressions, ridges, and pits. Some specimens retain a thickened core that is typically bounded laterally by thin laminae. In elements with cores, they are open both anteriorly and posteriorly. The outline ranges from ovoid to rectangular and each element is in close proximity with its counterpart and elements both anterior and posterior. Dorsally, the elements are not ossified (Fig. 7A,C).

Postmarginal Plate

In specimens of the phyllolepid *C. mclachlani* (Fig. 1B) with little or no displacement of plates, both the right and left postmarginal plates lie adjacent to the marginal plates (PM, M, respectively, Fig. 3A; Long, 1984:fig. 14A, PMG), near the posterolateral corner of the headshield and well separated from the anterior postorbital process (and thus far from the point of hyomandibular attachment). The ossification center of the postmarginal plate is displaced posteriorly (in AMF96779 ca. 67% of the length of the plate from its anterior point) and located in the middle of the plate (ca. 44% of the width from the lateral edge). It appears

that the ossification center is situated adjacent to the groove for the postmarginal canal on the marginal plate (pmc, Fig. 3A) The groove typically extends to the edge of the marginal plate in *C. mclachlani*, but does not extend as a groove on to the postmarginal plate (in arthrodiran taxa where the postmarginal canal groove extends on to the postmarginal plate, it passes through, or to, the plate's ossification center, e.g., *Coccoosteus cuspidatus* Miles and Westoll, 1968; Fig. 1B).

Parasphenoid and Palatal Perichondral Ossifications

In *C. mclachlani*, the large parasphenoid (Psp, Figs. 3B and 5A; "up to 1/3 the length of the headshield" Ritchie, 2005:229) and independent ossifications in the floor of the neurocranium extend from the occipital condyles to the ethmoid region of the neurocranium (median occipital and paired paraotic ossifications of Ritchie (2005) and an undescribed paired ossification that fuse in adults to cover most of the neurocranial floor posterior to the parasphenoid). Among juvenile specimens, individual ossification centers are recognizable while in mature specimens these elements fuse to form a complex palatal element. In some specimens, there are isolated denticles on the ventral surface of the ossified neurocranium in this region.

PHYLOGENETIC ANALYSIS

Character Recoding Based on *Cowralepis*

Eleven characters for the Phyllolepidia (Fig. 1B) from the phylogenetic analysis of Goujet and Young (1995) are modified to reflect the condition in *Cowralepis* (or *Placolepis*) as follows: ch. 6, suborbital, from present to absent (following Ritchie [2005]); ch. 9, opening of c.VII_{hm}/epihyal facet, from unknown to anterior; ch. 11, posterior postorbital process, from double to unknown; ch. 17, Meckel's cartilage, from unknown to posterior element only; ch. 18, ASG on endocranium, from absent to present; ch. 19, PSG on palatoquadrate, from absent to present; ch. 20, palatoquadrate, from unknown to one ossified unit; ch. 23, ventral ridge or keel on median dorsal plate of trunkshield, from unknown to absent; ch. 24, posterior dorsolateral plate of trunkshield, from absent to present; ch. 26, interolateral plate, from absent to present; and ch. 31, posterior median ventral plate of trunkshield, from present (large) to small (revised scores for all 49 characters = 1, 3, -, 0, 1, 1, 1, ?, 1, 0, ?, ?, 1, ?, 1, 0, 1, 1, 1, 0, 0, 0, 0, 0, 1, 1, 0, 0, 0, 0, 2, 0, 2, 2, 0, -, ?, ?, 1, 0, 1, 3, 1, 2, ?, 2, 1, ?, 0).

A reanalysis of the Goujet and Young data set (Goujet and Young, 1995; Fig. 10A) with the addition of *Cowralepis* using PAUP* (v. 4.0 beta 10,

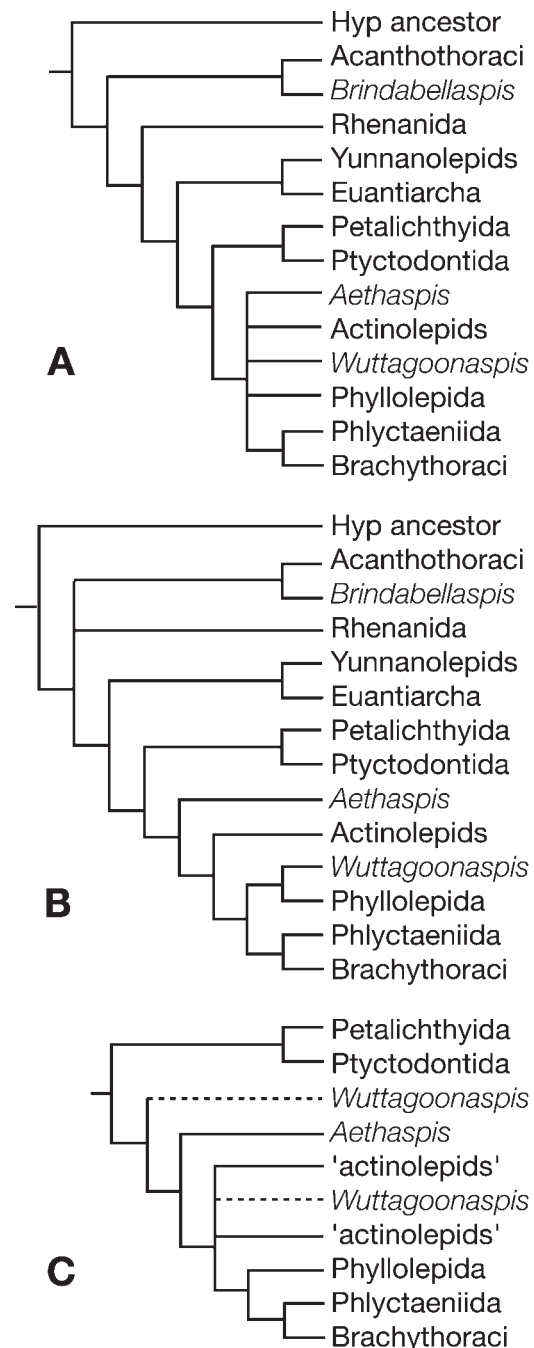


Fig. 10. Cladograms of hypothetical relationships among Placodermi. **A:** Published cladogram of Goujet and Young (1995). **B:** Strict consensus cladogram based on addition of *Cowralepis* to Goujet and Young (1995) (two trees, tree length = 105, C.I. = 0.6667, R.I. = 0.7295). **C:** Cladogram based on addition of *Cowralepis* to Dupret (2004). Tree based on strict consensus of 109 trees (tree length = 133, R.I. = 0.4286, C.I. = 0.6935) reduced to reflect the paraphyly of "actinolepids" and the relationships of phyllolepidia. Two hypotheses (dashed lines) for *Wuttagoonaspis* are presented: the sister group to other arthrodire (Dupret, 2004, and reanalysis with *Cowralepis*) and *Wuttagoonaspis* nested within the "actinolepids" based on trees of 134 steps in the reanalysis of Dupret (2004); the analysis of Dupret et al. (2007) resolves *Wuttagoonaspis* as a basal arthrodire.

Swofford, 2003) results in 13 equally parsimonious trees (Fig. 10B). A sister-group relationship between *Wuttagoonaspis* and phyllolepid is based on the assumed homology of the central-nuchal complex with its associated sensory line grooves converging on the nuchal plate. *Wuttagoonaspis* + phyllolepid and phlyctaeniids + brachythoracids are united based on the absence of dermal elements in the pelvic girdle and the loss of body scales. A phylogenetic analysis with the addition of *Cowralepis* to the published matrix of Dupret (2004) results in a similar hypothesis of relationships for phyllolepid (Fig. 10C; scores for *Cowralepis* = ?, ?, ?, ?, -, -, -, -, 0, 1, 0, 1, 0, 0, 0, -, -, 0, -, 1, -, 0, 1, -, 1, 1, -, -, 1, ?, 0, 1, -, 0, -, 0, -, 0, 1, 0, 0, 0, 0, 0, 0, -, 0, 0, 1, 1, ?, 0, ?). *Wuttagoonaspis* retains its sister-group relationship to other arthrodires, although only a single step differentiates the hypotheses of *Wuttagoonaspis* as the sister group to other arthrodires and *Wuttagoonaspis* as nested within a paraphyletic grouping of "actinolepid" arthrodires. Reanalysis of Dupret et al. (2007) gives the same results, in regards to phyllolepid, as the earlier Dupret (2004) analysis. One difference in the later analysis is the resolution of *Wuttagoonaspis* as the sister group to other arthrodires (with the exception of *Antarctaspis mcmurdoensis* that was not included in the earlier Dupret analysis, Dupret et al., 2007:fig. 12).

Phylogenetic Resolution of the Phyllolepidia

A detailed phylogenetic review of basal arthrodires (Fig. 1B) is beyond the current scope of this paper (refer to Dupret et al. [2007] for a recent review). Our goal here is to clarify questionable or unknown characters in previously published phylogenies (e.g., Goujet and Young, 1995; Dupret, 2004; Dupret et al., 2007). Goujet and Young (1995) noted a 5-way polytomy between *Aethaspis*, actinolepids, *Wuttagoonaspis*, Phyllolepidia, and Phlyctaeniida + Brachythoraci (Fig. 10A). The inclusion of *Cowralepis* to their analysis resolves the polytomy as follows: (*Aethaspis* (actinolepids ((*Wuttagoonaspis* + Phyllolepidia) (Phlyctaeniida + Brachythoraci))). The sister-group relationship between *Wuttagoonaspis* and phyllolepid is based on a single character (homology of the central-nuchal plate complex). Diagnosing the clade (*Wuttagoonaspis* + phyllolepid) + (phlyctaeniids + brachythoracids) is, as noted in aforementioned text, the absence of dermal elements in the pelvic girdle and the loss of scales covering the body.

Although the phylogenetic position of *Wuttagoonaspis* is debated (proposed outgroup to other arthrodires [Dupret, 2004]; summarized by Ritchie [2005]; and reevaluated by Dupret et al. [2007]), it is the position of phyllolepid that is important to this discussion. The current revision of the analy-

sis by Goujet and Young (1995; Fig. 10B) results in a hypothesized sister-group relationship between phyllolepid and Phlyctaeniida + Brachythoraci (consistent with Dupret [2004] and Dupret et al. [2007], although differing in the disposition of *Wuttagoonaspis*). A reanalysis of the data matrix from Dupret (2004) (including *Cowralepis*; Fig. 10C) results in a hypothesized sister-group relationship between phyllolepid and Phlyctaeniida + Brachythoraci with *Wuttagoonaspis* either as an unresolved member of the paraphyletic actinolepid or as the sister group to other arthrodires; the latter hypothesis is supported by the more recent analysis of Dupret et al. (2007).

Not considered in the analysis of phyllolepid by Goujet and Young (1995), nor considered by Dupret (2004) or Dupret et al. (2007), was the location of the anterior postorbital process relative to the postorbital plate, the number of spino-occipital nerves in the neurocranium, and the development of muscle attachment sites along the anterior trunk shield (the clavobranchialis of Johanson [2003]; see Discussion, under Functional Implications). The anterior postorbital process, as noted in aforementioned text, is located beneath the ossification center for the postorbital plate and the laterally directed postorbital branch of the infraorbital sensory line groove in *Dicksonosteus* (Goujet, 1984:fig. 32) and phyllolepid (*Cowralepis* and *Placolepis*) whereas in actinolepid (*Kujdanowiaspis* and *Lehmanosteus*) it is posteriorly displaced under the postorbital plate (although in *Lehmanosteus* the sensory groove is anterolaterally directed leaving the postorbital plate far anteriorly). In *Wuttagoonaspis*, the junction of the submarginal plate with its perichondrally ossified hyomandibula and the postorbital plate indicates that the anterior postorbital process is situated anteriorly under the postorbital (derived relative to the actinolepid condition; based on analysis of Young and Goujet [2003:figs. 4, 6, 7C,D]). It is worthwhile to note that this character, although potentially useful in closely related taxa is less reliable across major clades with the process being displaced posteriorly, as a derived condition, in eubrachythoracids with a posterior shift or enlargement of the orbit (e.g., *Tapinosteus*, Stensiö, 1963:fig. 47).

Reconstructions of the neurocranium in *Dicksonosteus* and *Kujdanowiaspis* (Goujet, 1984:figs. 26, 27, c.spio.a-c, respectively) indicate the presence of three spino-occipital nerves. In brachythoracids there are an increased number of these nerves implying a phylogenetic expansion of the occipital region of the neurocranium (e.g., *Buchanosteus confertituberculatus* with seven nerves [Young, 1979:fig. 6, spio1-7] and *Erromenosteus* [*Paraleisteus*] *diensti* with nine nerves [Stensiö, 1963:fig. 94, c.spio₁₋₉]). A preliminary analysis of the occiput in *Cowralepis* indicates that it may possess the derived condition, i.e., an increased number of

spino-occipital nerves (work in progress). The strength of the phylogenetic signal from this character is unclear at present; Young (1980) notes the presence of five spino-occipital nerves in the acanthothoracid *Brindabellaspis* (Fig. 1B).

These three characters illustrate that phyllolepidids (Fig. 1B) are derived relative to actinolepidids in terms of the position of the anterior postorbital process, derived relative to actinolepidids and phyllolepidids in terms of development of the occiput (increased spino-occipital nerve number), and retain the primitive condition of feeding mechanics (presence of coracobranchialis muscles) relative to the condition in phlyctaeniids and brachythoracids (presence of clavobranchialis muscles). However, the distribution of these characters is insufficiently known at present (soft tissue and neurocranial characters are either excluded from analyses or represent missing data). It is hoped that recent and on-going studies of basal arthrodires along with an improved understanding of the anatomy of the neurocranium, visceral elements, and feeding mechanics will lead to a better understanding of arthrodiran relationships and their evolution.

Gnathostome Relationships

The relationship of placoderms to other gnathostomes (chondrichthyans and osteichthyans, Fig. 1A) has been vigorously debated with all three possible phylogenies for this tricotomy proposed (summarized by Goujet [2001] with Grogan and Lund [2000] adding recent arguments for a placoderm + osteichthyan hypothesis [see also Forey, 1980; Gardiner, 1984]).

Recent phylogenies utilize new information on the anatomy of the neurocranium and visceral skeleton. However, these features are often the least known when considering Paleozoic vertebrates (Fig. 1A). In Goujet's (2001) analysis of placoderms, two alternative phylogenetic hypotheses were proposed: 1) autapomorphic features characterize placoderms or 2) placoderms retain in the adult primitive features only seen in the ontogeny of extant gnathostomes (a peramorphic shift in the latter). The latter pattern was proposed by Goujet (2001) for aspects of the neurocranium and the pectoral girdle.

The neurocranium in placoderms consists of two ossification centers that primitively were loosely connected—the “loose snout problem” summarized by Jarvik (1980). The details of this connection are described by Goujet (1984), who later hypothesized (Goujet, 2001) that the temporal and spatial differences in the development of the nasal region in extant taxa (Thorogood, 1993) relative to the basal trabeculae-parachordal complex may indicate that the placoderm anterior fissure is a generalized feature (a retention of a separation between developmental units that are ontogenetically fused in

chondrichthyans and teleostomes). A similar temporal difference is seen in lampreys (Fig. 1A) where Johnels (1948) noted chondrification of the nasal cartilage after formation of the cranial basal elements, suggesting a wider vertebrate condition. If the primitive condition in gnathostomes were represented by separate elements in early development with subsequent fusion in the adult, then the placoderm condition would represent a paedomorphic event. In contrast, if primitively separate, then the extant condition (fusion) represents a peramorphic change with placoderms retaining the plesiomorphic condition (characters 3, 17, Fig. 2; the polarity of this character is ambiguous [level II or III inference] pending further study of the fossil aganthan condition).

A similar heterochronic argument can be extended to the pectoral fin. A single proximal element in the pectoral fin represents a gnathostome plesiomorphy (present in the osteostracan outgroup, Carr et al., in press). Subdivision of this element into multiple elements (basals or primary radials) is seen in chondrichthyans, osteichthyans, and as a derived condition in placoderms (Goujet, 2001; Goujet and Young, 2004). Developmental studies in actinopterygians and sarcopterygians (Fig. 1A) demonstrate the formation of basal elements from a single mesenchymal anlage, thus representing a heterochronic shift from the plesiomorphic gnathostome condition (Goujet, 2001; Carr et al., in press). The argument of a heterochronic shift can now be extended to the retention of paired basibranchial elements in the visceral skeleton of placoderms (thus, the fusion of basibranchials or its fusion as an adult feature represents a synapomorphy for chondrichthyans + osteichthyans; character 15, Fig. 2).

As proposed by Grogan and Lund (2000), the plesiomorphic condition for the hyoid arch in gnathostomes consisted of an arch with articulating ceratohyal and epihyal elements (character 9, Fig. 2) with the dorsal elements supporting an opercular cover and with the jaw being supported by separate attachments to the neurocranium (thus hyostyly represents a derived condition). The condition in placoderms is unique relative to this proposed primitive condition in other gnathostomes. Although the hyomandibula of placoderms does support the submarginal plate (=operculum; character 12, Fig. 2), the hyomandibula dorsally articulates with the neurocranium and lacks a connection to the ceratohyal (following Goujet, 1984; character 11, Fig. 2) in contrast to the condition in chondrichthyans + osteichthyans proposed by Grogan and Lund (2000).

Contrary to published scenarios for the suspension of the palatoquadrate in gnathostomes (e.g., Janvier, 1996; Grogan and Lund, 2000), developmental evidence leads to a revised polarity of character transitions (see Fig. 2). The primitive condi-

tion for suspension of the palatoquadrate, represented by the condition in lampreys, is attachment of the mandibular element to the parachordal (character 2, Fig. 2). Placoderms, the immediate outgroup to other gnathostomes, retain this condition. An ethmoidal attachment is a synapomorphy for gnathostomes (correlated with the origin of neural crest trabeculae; character 6, Fig. 2). The anterior position of the hypophysial foramen in placoderms is consistent with relatively short trabeculae (character 7, Fig. 2; trabeculae-parachordal index measured as the anterior neurocranium-to-hypophysial foramen distance/foramen-to-vagus or otic-occipital fissure distance $\times 100 < 50$ based on samples of published figured neurocrania; e.g., compare figured neurocrania in Janvier, 1996:fig. 4.27). Uniting the chondrichthyans and teleostomes (Fig. 1A) is a dorsal attachment for the palatoquadrate (character 16, Fig. 2; consistent with Janvier [1996] and Grogan and Lund [2000], but reversing placoderms with a derived condition to representing the primitive condition). The loss of a parachordal articulation or its transfer to relatively posterior expanded trabeculae is seen in chondrichthyans and osteichthyans (character 19, Fig. 2; trabeculae-parachordal index >50 in the chondrichthyan neurocranium in Paleozoic taxa including stem-group chondrichthyans, character 18, Fig. 2; index >100 in osteichthyans [Janvier, 1996:fig. 4.27D1, E1] and among chondrichthyans in higher nested selachians [de Beer, 1937] and in holocephalans [de Beer, 1937:plate 23]; characters 20 and 22, respectively). The limited preserved distribution of a basiptyergoid (palatobasal) articulation and the uncertainty for phylogenetic relationships among basal non-placoderm gnathostomes prevent a determination of homology for this character.

A discussion of the origin of the trabeculae and changes within the trabeculae-parachordal complex is not complete without a consideration of the polar cartilages. Among extant gnathostomes there appear to be two patterns of landmarks for the presence of a polar cartilage. In chondrichthyans, as noted by Maisey (2005) after de Beer (1937), there are two landmarks for the polar cartilage, the foramina for the efferent pseudobranchial artery and the pituitary vein (anterior and posterior landmarks, respectively [Maisey, 2005:figs. 9, 10]). In osteichthyans, as noted by de Beer (1937), an anterior landmark includes the presence of a notch (and subsequent foramen, de Beer, 1937:pl. 35, fig. 2) between the polar and trabecular cartilages for the internal carotid artery. Posteriorly, the polar cartilage is bounded by the foramen of the palatine branch of the facial nerve (e.g., *Amia*, a basal neopterygian, de Beer, 1937:pl. 35, fig. 2; Fig. 1A). The basis for these different patterns is, in part, due to the path of the internal carotid artery. In chondrichthyans, the internal carotid artery enters

the neurocranial cavity and travels dorsal to the trabecula where it gives off an efferent pseudobranchial artery (Goodrich, 1930:figs. 246, 247; Maisey, 2005) that then exits the neurocranium. In osteichthyans, the internal carotid artery gives off an efferent pseudobranchial artery ventral to the neurocranium before penetrating the neurocranial cavity (Goodrich, 1930:fig. 284, *Lepidosteus*, a basal neopterygian, and *Amia* embryo; Fig. 1A).

The arthrodire *Kujdanowiaspis* was interpreted by Stensiö (1963:fig. 22) using a chondrichthyan model. However, studies by Young (1980:fig. 26) clearly demonstrate an osteichthyan pattern in placoderms with the efferent pseudobranchial artery as a branch of the internal carotid artery ventral to the trabeculae (preserved as grooves on the ventral surface of the neurocranium in several placoderms). Recognition of a polar cartilage, using an extant model, is dependent upon which model is used and on specific interpretations within each model. In placoderms, in lateral view, the efferent pseudobranchial artery is ventral to the pituitary vein (e.g., *Buchanosteus*, Young, 1979:fig. 4, the former vessel is seen between a.pq₂ and a.pq₃) suggesting (using a chondrichthyan model) the potential absence of a polar cartilage or at least that it is greatly reduced. In contrast, the internal carotid foramen is well separated from the foramen for the palatine branch of the facial nerve suggesting (using an osteichthyan model) the presence of a polar cartilage comparable in size to Paleozoic sharks (after Maisey, 2005).

Our current knowledge of the developmental anatomy for this region is limited, e.g., the early pattern in the holocephalans is unknown in a form where the adult lacks an internal carotid artery. It was noted by de Beer (1937:72) that the internal carotids in holocephalans degenerate and do not penetrate the cranial cavity. The condition in *Polypterus* (a basal actinopterygian, de Beer, 1937; Fig. 1A) includes the lack of a discernible polar cartilage (de Beer, 1937), the efferent pseudobranchial artery is lost, and the internal carotid artery passes dorsal to the trabeculae (the latter an atypical osteichthyan condition; however, de Beer [1937] notes the lack of early developmental stages to establish the primacy of this condition).

Thus, it can be said with confidence that placoderms do not share with chondrichthyans (as proposed by Stensiö [1963]) the pattern of the internal carotid and efferent pseudobranchial arteries, but follow the general pattern as proposed for osteichthyans (Goodrich, 1930; de Beer, 1937). Recognition of a polar cartilage in placoderms is equivocal (pending a better understanding of the polarity and pattern of anatomical landmarks in extant taxa).

Although the picture is incomplete, new evidence based on the endoskeleton (visceral, neurocranial, and pectoral girdle elements) lends sup-

port to the hypothesis that placoderms are the sister group to remaining gnathostomes (Figs. 1A and 2).

DISCUSSION

Reports on the splanchnocranium in phyllolepid (Fig. 1B) are limited, with Long (1984:fig. 14) reporting the presence of a quadrate and metapterygoid in *Austrophyllolepis*, Young (2005:figs. 5E, 7E) reporting a quadrate in *Cobandrahlepis*, and Ritchie (2005:fig. 15) reporting articular, ceratohyal, basihyal, hypobranchial, and unidentified hyoid elements in *Cowralepis* (note that the metapterygoid and quadrate of Long were re-identified by Ritchie as ceratohyal and articular elements, respectively, and the latter element re-identified here as the quadrate, following Long's original identification). As noted by Ritchie (2005), *Cowralepis* is represented by numerous articulated specimens (see Fig. 3) forming an ontogenetic sequence. In addition to the preservation of portions of the splanchnocranium, specimens also preserve the complete dermal skeleton, parasphenoid, posterior portions of the neurocranium including otoliths, synarcual, pelvic girdle, and a complete vertebral column with caudal fin. Although our understanding of the anatomy in this taxon is still incomplete, the vast amount of material has shed new light on the splanchnocranium in phyllolepid and demonstrates a unique feeding mechanism in this group. It also forms the basis of a reinterpretation of the branchial elements in basal gnathostomes (Figs. 1A and 2).

Mandibular Arch

In the mandibular arch of arthrodires, Meckel's cartilage lies ventral to the occlusal (biting) region of the inferognathal, as in the phyllolepid *Cowralepis*. In arthrodires that possess a dermal non-occlusal region (a blade), Meckel's cartilage extends from the occlusal region lateral to the blade. Extending forward from the quadrate, the palatoquadrate continues anteriorly to the posterior superognathal (with this element articulating to the autopalatine part of the palatoquadrate). The anterior superognathal lies ventral to the ethmoid region of the neurocranium. Meckel's cartilage and the palatoquadrate both extend from the mandibular joint forward to their respective gnathal plates. Because the plates are in occlusion with each other (upper and lower elements), the arches that support these elements are also aligned one over the other.

In *Cowralepis*, a single perichondrally ossified element extends from the jaw joint and is in alignment with, but does not reach either the superior or inferognathals. This mandibular element was identified by Long (1984:281) as the quadrate

based on its position relative to the superognathal and its morphology (it possesses a ridge similar to that seen in the quadrate of other euarthrodires) and on the association of the "metapterygoid" ("firmly attached") with the quadrate. Subsequently, the structure was identified by Ritchie (2005) as the articular bone, with Ritchie noting its close relationship to the ceratohyal that clearly lies ventral to the inferognathal and proposed that given these relationships, neither element could represent elements of the palatoquadrate. It is the positional association between the two elements that Long (1984) and Ritchie (2005) considered to be important (metapterygoid or ceratohyal and quadrate or articular); however, they differ in whether these elements are attached. It is now clear that these are separate elements. Regarding the quadrate or articular interpretation, positional evidence is equivocal. An alternative criterion to distinguish articular and quadrate ossifications is the morphology of the element.

If this element were an articular, or Meckel's cartilage, there are some peculiarities when comparing to other arthrodires. First is the large pit located posteromedially (Fig. 6A). No instances of such a pit are reported among placoderms for Meckel's cartilage. A groove was reported by Young et al. (2001:fig. 4F, gr) along the medial posterior surface of the ossified Meckel's cartilage in an unnamed buchanoosteid (Fig. 1B). Based on their figure, this is a superficial structure quite unlike the pit in *Cowralepis*.

The second peculiarity of this element is the lateral flange (Fig. 6A). If a Meckelian element, the flange is reminiscent of a coronoid process; however, such a structure is only known in the arthrodire *Brachyosteus* (Fig. 1B) where it is part of the dermal inferognathal (Denison, 1978:fig. 67L). To be effective as a site of muscle attachment (i.e., coronoid process) the element or its flange would have to be rotated dorsolaterally in order to be available as an attachment site of a potential adductor mandibularis muscle, rather than its proposed ventrolateral position.

Alternatively, a lateral flange is seen on the posterolateral corner of the Meckelian ossification of *Bothriolepis* (Young, 1984:fig. 4, a.sh; Fig. 1B). The posterior inferognathal covers most of this flange, although space is available laterally for adductor muscle attachment. Supporting this functional interpretation in *Bothriolepis* is the robust nature of the flange seen in cross section (Young, 1984:fig. 4C). In contrast, the flange in *Cowralepis* is thin—a construction that seems counterintuitive for the support of muscular forces acting perpendicular to the flange, and would be prone to breakage.

By comparison, if this element represents a palatoquadrate ossification, a pit, foramen, or canal is known in the palatoquadrates of several other taxa. *Dicksonosteus* (Fig. 1B) possesses two neuro-

vascular foramina (see Fig. 4), the unidentified buchanosteid of Young et al. possesses a canal (2001:fig. 1, c.ext.), and, as noted in aforementioned text, *Holonema* (Fig. 1B) possesses a canal (Miles, 1971:fig. 34, mc) and an undescribed pit (Fig. 6B,C). In *Holonema westolli*, the posterior descending arm of the palatoquadrate bifurcates into anterior and posterior thickenings that are connected above a shallow depression (Fig. 7B). The dorsal aspect of this depression is visible in the figured specimens of Miles (1971:figs. 23, 33); however, the photographed specimen is incomplete. The reconstruction provided (Miles, 1971:fig. 33; Fig. 6C) hints at the continuation of the depression as a closed recess (represented by shadowing anterodorsally to the articular condyle, cd.art). In the holotype (WAM70.4.243; BMNH P50984 after Miles, 1971), the depression separating the anterior and posterior thickenings ends in a distinctive blind pit comparable to the condition in *Cowralepis* (compare Fig. 6A with 6B,C; not figured in Miles, 1971). Given this similarity, we propose this element in *Cowralepis* represents the quadrate or posterior portion of the palatoquadrate (Figs. 3B, 5B, 6A, and 7A,B,D).

A single specimen (Fig. 7A,B) may resolve any remaining uncertainty concerning the identification of the articular-quadrate complex. Seen in dorsal view, the postorbital plate of the headshield is dislodged revealing the ceratohyal, articular, and "hyoid accessory element" of Ritchie (2005:fig. 14B, Chy, Art, and hae?, respectively). The posterior quadrate is complete; possessing a bulbous articular condyle that is in contact with the element that we now propose represents the articular bone (originally interpreted as the suborbital by Long [1984] and Young [2005] and as a "hyoid arch element?" by Ritchie [2005]).

The two perichondrally-ossified parts of the articular are separated by a groove (the sensory canal groove in the suborbital plate interpretation, e.g., Long, 1984); however, unlike the condition in the dermal suborbital plate the articular groove is seen in both internal and external views. Its common association with the quadrate and its direct articulation in the one specimen with an intact condyle on the quadrate supports the interpretation of this element as the articular. No other ossification of Meckel's cartilage is preserved in *Cowralepis*. The orientation of the articular varies, ranging from the concavity facing laterally (Fig. 5B) to medially (Fig. 7B). In the derived condition in the eubranchyarthrodires (Fig. 1B), the quadrate faces medially on the surface of the postorbital plate and the articular faces laterally on the blade portion of the inferognathal. The variable orientation of the articular in preserved specimens of *Cowralepis* relative to the quadrate might indicate an original anterodorsal orientation of the articular surface, such that minor taphonomic dis-

placements might account for its variably preserved positions.

If the phyllolepid quadrate was found associated with dermal suborbital and postsuborbital plates it would easily be interpreted as a palatoquadrate, by comparison to other placoderms. In *Cowralepis*, the palatoquadrate extends from the site of articulation anteriorly to the posterior superognathal, possesses a ventrally directed fossa (formed by the body of the element and the flange), and a deep blind pit. What is unusual in *Cowralepis* (and assumed for other phyllolepids) is that this element is associated with the dorsal plates of the dermal headshield, rather than those of the cheek (e.g., suborbital and postsuborbital plates, Fig. 4) and it lacks the typical Ω -shape described for palatoquadrates in other arthrodires.

Thus, the palatoquadrate of *Cowralepis* consists of a perichondrally-ossified quadrate with the autopalatine region unossified (ossification does not continue under the posterior superognathal). The ossified portion is represented by a single ossification (unlike the distinct quadrate, metapterygoid, and autopalatine ossifications in ptyctodonts, Goujet and Young, 1995:character 20). A quadrate was identified by Young (2005) in the phyllolepid *Cobandrahlepis petyrwardi*; however, its level of preservation limits its direct comparison to the quadrate in *Cowralepis*, but it also is a single ossification. The ossification of Meckel's cartilage is limited to the articular, specifically the site of articulation (and its secondary lamina).

Position of the Mandibular Joint

Despite any uncertainty in the interpretation of the quadrate-articular complex, its location in phyllolepids (Fig. 1B) is clearly associated with the postorbital plate and the anterior postorbital process of the neurocranium (*Cowralepis*, Fig. 3B; *Placolepis*, Fig. 8). The condition in *Placolepis budawangensis* sheds light on the phyllolepid condition where the anterior postorbital process is pierced by the hyomandibular nerve (Fig. 8B) and the process is situated beneath the ossification center of the postorbital plate (site for the confluence of the grooves for the central canal and postorbital and otic branches of the infraorbital canal, Fig. 8A).

The plesiomorphic location for the quadrate-articular complex is on the medial surface of the dermal cheek (suborbital and postsuborbital plates, character 13, Fig. 2), occurring in all known placoderm groups, including the antiarchs (Fig. 1B) where a homologue to the suborbital plate forms the upper gnathal unit (Young, 1984). In phyllolepids this dermal support for the quadrate-articular complex is absent. To retain the placoderm autostylic condition in phyllolepids, the complex would have to acquire neurocranial or

other dermal support (the dermal headshield in this case). To achieve this, the complex would have to migrate anterodorsally with the phylogenetic loss of the dermal cheek resulting in the quadrate-articular complex being located anterior to the anterior postorbital process of the neurocranium (see Fig. 4). Whether the quadrate was directly attached to the postorbital plate (similar to the condition where the quadrate is associated with the postsuborbital plate) or to the anterior postorbital process (or both) is not clear. A spatial relationship between the palatoquadrate and the anterior postorbital process is consistent with Goujet's (1975, 1984) interpretation of a contact between the palatoquadrate and the anterior surface of the anterior postorbital process of the neurocranium (e.g., as interpreted in *Kujdanowiaspis*, Stensiö, 1963:fig. 43B, a.pr.ot). That is, with loss of a dermal cheek the posterior support for the palatoquadrate has shifted from the postsuborbital plate to its neurocranial connection (or association) with the anterior postorbital process.

Hyoid Arch

Alternative hypotheses for the interpretation of the hyoid arch center on the discussion of whether separate opercular and hyomandibular cartilages are present in placoderms (see Young [1986] for a detailed review of the arguments). As noted by Goujet (1984), the hyomandibula is attached to the submarginal plate (character 12, Fig. 2) with no role in jaw support (character 11, Fig. 2) such that placoderms possess an autostylic suspension (also Grogan and Lund [2000], in contrast to a hystylic model of Stensiö [1963] as the plesiomorphic state among placoderms). In *Dicksonosteus*, a single articulation is present on the posterior aspect of the anterior postorbital neurocranial process, assumed by Goujet (1984:fig. 6, f.a.hm, and reconstructed in fig. 50; Fig. 4) to represent the articular site for the hyomandibula. By comparison, in *Kujdanowiaspis*, where two articulation sites are hypothesized, Goujet (1975) proposed that the anterior articulation is for the palatoquadrate, following an earlier interpretation by Stensiö (1963:fig. 16, a.pr.ot.).

Two elements were recognized by Young (1986) that articulated to the anterior postorbital process, the opercular cartilage posteriorly and the hyomandibula anteriorly. This interpretation was supported by Young (1986) noting that the trajectory of the hyomandibular nerve in *Brindabellaspis* (Fig. 1B) and the petalichthyid *Macropetalichthys* (Fig. 1B) is directed anteriorly toward the anterior articulation site associated with the anterior postorbital process. Thus the submarginal plate is not associated with the hyomandibula, but with an opercular cartilage. He further provided a functional argument for the presence of a hyomandibu-

lar suspensorium to support lateral expansion of the mandibular joint (Young, 1986:39). As noted by Young and Zhang (1992), an opercular support that articulates with the neurocranium is a unique feature of placoderms. This uniqueness was used by Gardiner and Miles (1990) as an argument against the presence of a separate opercular element in placoderms. An additional argument, in their reconstruction of the arthrodire *Torosteus* (Gardiner and Miles, 1990:fig. 20, hm), was that there is insufficient room for a second element between the supporting element for the submarginal plate and the palatoquadrate—thus, their proposal for the presence of a hyomandibula alone.

As noted by Long (1984), the submarginal plate is phylogenetically lost in phyllolepid and any operculum would be composed of soft tissues. The submarginal plates previously identified (Ritchie, 2005:fig. 6; Young and Long, 2005) are reinterpreted as the postmarginal plates (Long, 1984:fig. 14A, PMG).

The presence of a hyomandibula in other placoderm taxa is typically confirmed by indications of its presence on the internal surface of the submarginal plate. In the absence of a submarginal plate, the presence of a hyomandibula is limited to evidence of its attachment to the anterior postorbital process. In *Cowralepis*, this is limited to the small posteriorly-directed circular caps (Fig. 7C) situated near the ossification center of the postorbital plate and representing perichondral ossifications of the proximal part of the hyomandibula. From this point, the hyomandibula is assumed to have supported the fleshy opercular flap and is directed posteriorly relative to the quadrate-articular complex. It thus has no role in support of the mandibular arch.

Basihyal. The basihyal in the phyllolepid *Cowralepis* was described by Ritchie (2005) who noted its separation from the inferognathals and its association with the ceratohyals. As an anterior median element, two interpretations are plausible, either as a basihyoid, or alternatively, as a mentomandibula. The mentomandibula in arthrodires is a paired ossification of the anterior portion of Meckel's cartilage (at the symphysis). It is typically unossified where it continues posteriorly with Meckel's cartilage and at its midline contact with its antimere. On occasion, the right and left elements may fuse at the symphysis (occasionally seen in *Dunkleosteus terrelli*, Fig. 1B; RKC, personal observation). However, none of these conditions can be identified in the median element in *Cowralepis*. Aside from the contact with the ceratohyals, the basihyal is in direct contact with paired median basibranchials, inserting into a notch formed by the first pair (Figs. 7D and 9C). Confirming the interpretation of a basihyal is the fact that no known gnathostome possesses a skeletal connection in the midline between Meckel's car-

tilage (or mentomandibula if present) and the branchial arches.

Ceratohyal. The ceratohyal in *Cowralepis* extends from the mandibular joint to the basihyal and is positioned ventral and medial to the quadrate. The close association between the ceratohyal and quadrate leads to several alternate interpretations, dependent on whether these elements could have ossified from the same cartilaginous element (e.g., palatoquadrate or Meckel's cartilage).

A closed lateral edge on the ceratohyal rules out a cartilaginous connection to the identified quadrate. The common overlap pattern of the quadrate dorsal to the ceratohyal of Ritchie (2005) means that the ceratohyal could represent either a Meckelian or hyoidean element, which both lie ventral to the palatoquadrate. The critical evidence in *Cowralepis* against identification of a Meckelian ossification is the association of this element with the basihyal (discussed in aforementioned text). Along with its ventral position and location between the mandibular joint and the basihyal it is most reasonably interpreted as a ceratohyal.

The common association of the ceratohyal to adjacent elements in the mandibular arch indicates that it may have been ligamentously connected in life (i.e., a mandibulohyoid ligament; see Functional Implications). This association begins early in ontogeny (Fig. 5A), when the ceratohyal lacks the bony connection to the basihyal that occurs later in larger specimens as perichondral bone develops (note rings of concentric bone growth; Fig. 5B), and often persists even when the ceratohyal has become displaced.

Branchial Arches

The basibranchials in *Cowralepis* (Figs. 5B, 7A,C,D, and 9C; Carr et al., 2007) consist of four pairs of elements that meet along the midline (this interpretation is contrary to that of Ritchie [2005]). This arrangement raises two possible questions: "If these elements are homologous to the hypobranchials of other gnathostomes then are the basibranchials lost in *Cowralepis*?" or, "If these elements are homologous to basibranchials then how do we reconcile this with the unpaired basibranchials seen in other gnathostomes?" The latter interpretation may contradict the pattern known in other gnathostomes. However, developmentally, neural crest contributes to branchial arch development, and as neural crest streams extend down the left and right sides of the head towards the midline, it could be predicted that midline elements such as the basibranchials would initially be paired, with a contribution from each of these streams. Questioning this scenario are recent studies on the ontogeny of pharyngeal elements in tetrapods (i.e., the toad *Bombina*), where Olsson and

Hanken (1996) report that the median basihyoid and the basibranchials are not derived from primary neural crest, although they note that the origin of these structures is unknown. However, in a study by Creuzet et al. (2005:fig. 3) it was shown that neural crest contributes to basihyoid and basibranchial homologues in the chick. The absence of a primary neural crest origin in *Bombina* may be a derived condition among tetrapods representing modification of the pattern for neural crest dispersal as noted by McCauley and Bronner-Fraser (2003:2326) in their comparison of lamprey (Fig. 1A) and gnathostome patterns ("constraints to migration [referring to the condition in gnathostomes] may be a later innovation"). Arguments by Kimmel et al. (2001) for the homology of the branchial elements in lampreys and gnathostomes were based on their "outside-in" hypothesis that equates the lamprey lateral arches with the medial arches in gnathostomes. This relationship is further supported in the recognition that single gene mutations, e.g., *edn1* (previously *sucker*, *suc*, or *et-1*), in zebrafish (a teleost, Fig. 1A) result in reduction of anteroventral pharyngeal elements and fusion with their dorsal counterparts, potentially explaining the dorsal-ventral jointed patterning seen in gnathostomes (Miller et al., 2000; character 4, Fig. 2). Developmental studies addressing the origin of basibranchials in teleosts include neural crest ablation and knockout/down studies that provide indirect evidence of origin. However, direct labeling with neural crest markers is limited to early streaming of neural crest or if extended, labeled elements are not identified. At present, the definitive origin of the basihyoid and basibranchial elements in zebrafish remains unknown (C. Miller, personal communication, 2008).

As noted by Goodrich (1930), a paired neural crest origin for the basibranchials was proposed along with arguments that the single medial elements in the visceral skeleton may represent a secondary event in ontogeny (character 15, Fig. 2) and that the developmental primordia are originally paired (character 5, Fig. 2). Supporting this interpretation with evidence from several chondrichthyan taxa (Fig. 1A) was Holmgren's (1940) report on the presence of paired copula primordia in 40 mm *Raja clavata* (Holmgren, 1940:fig. 127; a batoid) and an anteriorly divided copula in 27 mm *Urolophus halleri* (Holmgren, 1940:fig. 170; a batoid) that secondarily fuses in the 49 mm embryo. This ontogenetic evidence supports the hypothesis that midline basal elements were primitively paired among gnathostomes. A paired origin might extend to the basihyal where de Beer (1937:62), in referring to the selachian *Scyllium* (Fig. 1A), suggested that this element might have been originally paired based on the presence of a foramen for the duct of the thyroid gland that pierces the element (de Beer, 1937:plate 14.5, tf). Addi-

tional support for a neural crest origin of the paired basibranchials in *Cowralepis* is the attachment of hypobranchial muscles to these elements (discussed further in the Functional Implications section). As noted by Köntges and Lumsden (1996:3240), “strict skeletomuscular specificity” exists between the branchial and hypobranchial muscles and their attachment sites—the muscular connective tissue and the attachment sites are neural crest. This specificity of attachment to neural crest is independent of the attachment site (dermal or endoskeletal, cranial or pectoral girdle, Matsuoka et al., 2005; see Olsson et al. [2001] for a discussion of amphibian patterns of specificity; we assume that this pattern extends to placoderms).

Interpreting the condition of these paired branchial elements in placoderms cannot be established, at present, through a parsimony argument (level II inference or level III depending on the distribution of ontogenetic information among chondrichthyans and teleostomes, Fig. 1A, and the extension of neural crest marker studies to non-tetrapods). The paired-element argument cannot be tested through outgroup analysis as a sufficient fossil record for visceral arches in agnathans such as the Osteostraci and Thelodonti is lacking and the branchial skeleton, where known in agnathans, is a single unit (i.e., unjointed; Janvier, 1996).

Preserved basal elements in placoderms (see Fig. 1) are limited to *Pseudopetalichthys problematica* (Gross, 1962:fig. 7), *Tapinosteus heintzi* (Stensiö, 1963:fig. 83, Hbr₁₋₆) and *C. mclachlani*. As interpreted by Stensiö (1963), the *T. heintzi* elements were reconstructed as a median basihyal and three pairs of fused hypobranchials (homologous to the six pairs in some extant selachians). His illustration of these elements shows some preservational displacement; however, he reconstructed the paired elements as being further separated by unpaired basibranchials. This is clearly an interpretation based on a chondrichthyan model, consistent with his concept of the group Elasmobranchiomorphi.

In *Pseudopetalichthys problematica* there is a single unpaired median element and three sets of paired elements. These structures are elongated longitudinally. Lateral to these there is a gap and then a set of possibly five pairs of oblique rod-like structures. The paired medial elements are unlike the hypobranchials in extant and fossil teleostomes and chondrichthyans where they are organized obliquely between the midline and the ceratobranchials. A traditional interpretation (*sensu* Stensiö, 1963) of the condition in *P. problematica* is the presence of unossified basibranchials, uniquely oriented paired hypobranchials, an unexplained gap, and then paired ceratobranchials. An equally plausible argument (if not more parsimonious; Fig.

9A,B) is the presence of paired basibranchials, unossified hypobranchials, and ossified ceratobranchials. There is an interesting resemblance between the elements in *P. problematica* and the elongate and longitudinal ridges in the branchial elements of *Cowralepis* (representing the ossification centers for these elements; compare Fig. 9A,B with 9C). In the latter, thin perichondral laminae extend outward from the ossification centers filling the space between ridges to meet along the midline.

In *Cowralepis* there is a single anterior median element (the basihyal as in other gnathostomes) and up to four sets of paired elements. The anterior pair is in direct contact with the basihyal. In specimens with minimal displacement, the right and left elements of each arch meet at the midline, indicating a lack of space available to reconstruct unpaired medial elements.

The anatomical evidence indicates that placoderms (based in particular on *Cowralepis* and likely *Tapinosteus* and *Pseudopetalichthys*) possessed paired basal elements for the branchial arches and combined with extant developmental evidence, implies that these represent the basibranchial elements rather than hypobranchials. If a primitive gnathostome character (character 5, Fig. 2, in contrast to an autapomorphy for Placodermi or individual placoderms), then the chondrichthyan and teleostome condition represents a secondary fusion of these elements (character 15, Fig. 2, a heterochronic shift from a primitive paired condition).

Reconstruction of the Branchial Arches

The organization of the branchial arches and their relationship to neurocranial and dermal elements remains unclear among placoderms. In analyses by Stensiö (1963), the gills were reconstructed beneath the neurocranium; however, Stensiö noted that in forms with a short occipital region, the branchial skeleton extended posterior to the dermal articulation between head and thoracic shields. A similar proposal by Denison (1978:7) stated that the gills opened into “gill chambers” beneath dermal operculae (=parabranchial chambers, formed by the dermal cheek bones). In selachians (Fig. 1B; e.g., *Squalus acanthias*, Fig. 11B), the pharyngobranchial elements of the branchial skeleton extend from the epibranchials posteromedially ventral to the vertebral column and are contained within the space between the glossopharyngeal (IX) nerve foramen (posterolateral corner of the chondrocranium) and the seventh vertebra. A superficial comparison between the condition in chondrichthyans and arthrodires (see Fig. 11) indicates a similar condition; however, the occipital region of the neurocranium in arthrodires extends posteriorly for the equivalent of three to

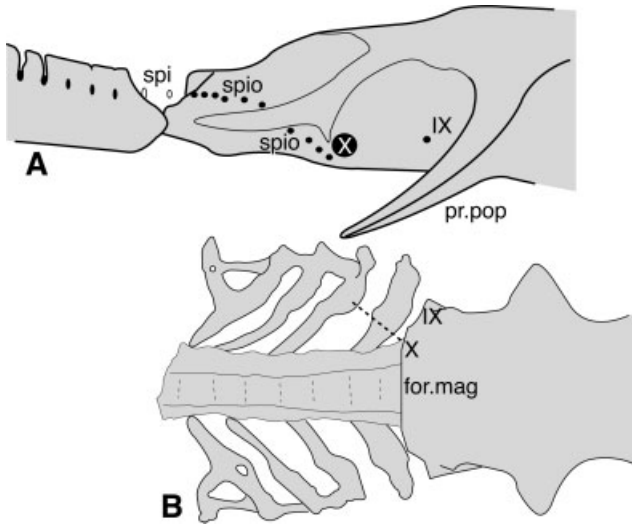


Fig. 11. Comparison of shark and placoderm neurocrania and axial skeletons. **A:** *Erromenosteus (Paraleisosteus) diensti*, posterior neurocranium and anterior synarcual in right lateral view (redrawn from Stensiö, 1963:fig. 93). **B:** *Squalus acanthias*, posterior neurocranium, anterior vertebral column, and dorsal elements of the branchial arches in dorsal view (redrawn, in part, from Gans and Parsons, 1964:plate 4) and preserved specimens. The dashed line indicates a possible trajectory for the vagus nerve if the occiput is posteriorly expanded (as in placoderms). Foramina indicated in black. Hypothesized foramina (i.e., not preserved) indicated as outlines. for.mag, foramen magnum; IX, glossopharyngeal nerve foramen; pr.pop, posterior postorbital process of the neurocranium; spi, spinal nerve foramina; spio, spinal-occipital nerve foramina; X, vagus nerve foramen. Not to scale.

nine vertebrae (the fusion of vertebrae to the occiput is species dependent and the number of vertebrae can be based on the presence of spino-occipital nerves incorporated into the neurocranium). Given this comparison, the parabranial chamber in arthrodires would lie between the extended occipital region and the anterolateral positioned posterior postorbital process of the neurocranium (pr.pop, pierced by the IX nerve foramen, Fig. 4; Fig. 11A). This space is routinely interpreted as the site for extension of a cucullaris-like muscle from the thoracic shield to the dermal headshield (Heintz, 1932:fig. 79; Stensiö, 1963:fig. 112, dp.m.cu; Goujet, 1984:fig. 32, d.mc; f.pb, Fig. 4), but notably, attachment surfaces for the branchial arches have been identified at the base of the postorbital process in arthrodire taxa such as *Dicksonosteus* (Goujet, 1984:fig. 6, a.pr.br). Even if the intent of the aforementioned authors was not to consider this space as purely for muscle attachment, the continued use of the term cucullaris fossa has functional implications for those unfamiliar with the details of arthrodiran anatomy. The recent declaration that the bite of *Dunkleosteus* (Fig. 1B) “is the greatest of all living or fossil fishes” (Anderson and Westneat, 2007:76) was based on muscle casts “to fit the muscle cavities”

(Anderson and Westneat, 2007, Supplemental Material, p. 1) of the adductor mandibularis and cranial depressor (“cucullaris”). The latter would represent a clear overestimate of muscle mass if the entire fossa were used in their calculations. The presence of denticles (an epithelial-dermal phenomena; AR and RKC, personal observation) in this region of *Cowralepis* provides the first direct evidence for the interpretation of this space (at least in part) as the parabranial chamber.

In *Amia calva* (a basal actinopterygian, Fig. 1A), the parabranial chamber in the posterior otic region and at the level of the exit for the vagus nerve (X) extends dorsally beneath the dermal skeleton (opercular bone), well above the upper pharyngeal elements to a mid-frontal-plane level of the neurocranium (Jarvik, 1980:fig. 12). In the actinolepid arthrodire *Kujdanowiaspis* sp. (Stensiö, 1963:fig. 35C; Fig. 1B) the dermal cover for the space between the body of the neurocranium and the posterior postorbital process extends from a dorsal position comparable to that in *Amia* ventrally to a position below the level of the neurocranium.

Differences in the position of the branchial skeleton between placoderms and most other gnathostomes is most easily explained as differences in the extent of the occipital region (Fig. 11; an exception is seen in holocephalans where the branchial arches are displaced anterior to the vagus nerve, de Beer, 1937:plate 22). Occipital elongation in placoderms places the branchial skeleton beneath the neurocranium; however, the relationship between the branchial skeleton and neural landmarks (e.g., the glossopharyngeal and vagus nerves) is conserved among placoderms, selachians, and osteichthyans. The presence of a functional dermal and axial articulation would imply a posterior limit for the branchial skeleton in contrast to the proposal by Stensiö (1963:34) that the branchial skeleton extends posterior to the articulation in forms with a short occipital region. This latter interpretation would require a dorsal-ventral flexion within the branchial basket (or a hinge-like movement within the basket paralleling the dorsal-ventral movement of the head)—a condition not seen in any other vertebrate.

Functional Implications

The rare preservation of visceral skeletal elements in placoderms has limited our understanding of feeding mechanics in this group and the organization of these visceral elements within the oropharyngeal cavity. Initial hypotheses regarding feeding were based primarily on the spatial relationships of dermal bones and in the case of the inferognathal, the recognition of its unique suspensorium associated with the dermal cheek (the fused quadrate and postorbital plate, e.g., Miles, 1969).

A phylogenetic hypothesis for the origin and modification of jaw depression mechanisms in gnathostomes was proposed by Wilga et al. (2000:fig. 7). In their hypothesis the depression mechanism included a coracomandibularis associated with the mandible and coracohyoideus with the hyoid, with each muscle originating from the pectoral girdle (refer to their tables 1 and 2 for a synonymy of muscle names across gnathostomes). Additionally, a mandibulohyoid ligament was recognized that connected the hyoid and mandible. In distinguishing the function of this system in extant gnathostomes, Wilga et al. (2000:figs. 5, 6) noted that in sharks (selachians, Fig. 1A), the coracomandibularis coupling operates independently from the coracohyoideus coupling. That is, mandibular depression associated with motor activity of the coracomandibularis occurs prior to coracohyoideus activity rather than as a consequence of the latter. In contrast, in osteichthyans (Fig. 1A) it is the activity of the coracohyoideus mechanically transferred through the mandibulohyoid ligament that lowers the jaw. The selachian condition was extended to placoderms, but Wilga et al. (2000:181) noted that the condition in placoderms remains ambiguous. The homology of these muscles among extant taxa is based on the development, topography, and innervation patterns (Edgeworth, 1935), although, extension to fossil taxa is limited to topographical arguments. Differences in the nature of attachment sites (dermal versus endoskeletal, e.g., the dermal attachments to the thoracic shield in placoderms versus the cartilaginous endoskeleton of chondrichthyans) are shown by Matsuoka et al. (2005) to be potentially variable between homologous muscles. They reject the historical argument that a dermal or endochondral attachment of muscles is key in determining homology by identifying that muscles directly connect to skeletal tissue of the same genetic identity independent of whether the attachment site is endoskeletal or exoskeletal.

The condition in placoderms was reviewed by Johanson (2003) who proposed a potential mix of chondrichthyan and osteichthyan feeding mechanics within the group; a selachian-like coracomandibularis and coracohyoideus originating from the dermal bones of the trunk shield (Johanson, 2003: fig. 10A, c.mand, c.hyoide) and an osteichthyan-like clavobranchialis originating from the anterior surface of the lateral margin of the trunk shield to insert on the ventral branchial elements (Johanson, 2003:fig. 10A, clavo). This dual pattern is apparent in phlyctaeniid and brachythoracid arthrodires (Fig. 1B). Phyllolepidi variably have been considered as the outgroup to arthrodires (as discussed in aforementioned text) or more deeply nested within basal arthrodires (compare Denison, 1978; Dupret, 2004; Goujet and Young, 2004; Ritchie, 2005; Dupret et al., 2007). With their rela-

tively extensive preservation of visceral elements, where do phyllolepidi fit in terms of their feeding mechanics?

In *Cowralepis* (and presumably other phyllolepidi) the floor of the branchial basket, formed by the basihyal and basibranchials, must have functioned as a single unit (effectively comparable to a fused copula). This is seen in the close approximation of elements; the fit of the posterior basihyal into a notch formed by the first pair of basibranchials and the close packing of the basibranchials to adjacent elements (Figs. 7D and 9C). It seems doubtful that individual arches moved independently of their neighbor. The basihyal in combination with the paired ceratohyals forms an estimated 40% of the surface area of the floor of the branchial basket (area covered by hyoid and branchial elements). An unusual feature in *Cowralepis* is the expansion of the ceratohyals ventral to the mandibular elements. This would preclude an independent depression of the mandible without affecting the hyoid and subsequent arches. This is contrary to the condition seen in selachians (Wilga et al., 2000) where, as noted in aforementioned text, mandibular depression precedes, and is independent of, hyoid depression. Given the close association of the ceratohyal and the site of the mandibular articulation throughout ontogeny and despite displacement of other elements (as described in aforementioned text), it is possible that a mandibulohyoid ligament connected these. Given the restricted movement of the mandible and the presence of this ligament, we propose that mandible depression in *Cowralepis* would have paralleled that in osteichthyans, where retraction of the hyoid imparts rotational forces on the mandible via a mandibulohyoid ligament (otherwise speculative at present until the distribution of this ligament among placoderms is better known [Johanson, 2003]).

Evidence of the musculature driving this system is limited to extrapolation of known muscle patterns to the preserved visceral and dermal elements in phyllolepidi. The origin (posterior attachment) of potential hypobranchial musculature in *Cowralepis* is limited to the dermal interolateral plates of the trunkshield as hypothesized by Johanson (2003) for the coracomandibularis and coracohyoideus in other arthrodires. At present there is no indication, in preserved specimens, of a more dorsal, potential attachment site on the lateral trunk shield for clavobranchialis musculature as seen in phlyctaeniid and brachythoracid arthrodires (Johanson, 2003:fig. 9). Thus, the phyllolepidi retain a primitive muscle pattern of hypobranchial muscles that parallels the condition in sharks (coracomandibularis, coracohyoideus, and coracobranchialis muscles).

In *Cowralepis*, there is evidence of robust insertions for the tendinous attachments (entheses) of the hypobranchial muscles to hyoid and branchial

elements (Fig. 7D). This consists of the strongly ossified ventral surfaces of the basal elements with rugged surface contours consisting of depressions, ridges, and pits, which are analogous to patterns of elevations and pits seen in entheses in diapsids (Hieronymus, 2006), mammals (Benjamin et al., 2002), and in attachments between dermal elements and bone in mammals (Hieronymus and Witmer, 2004). As noted by Motta and Wilga (1999), hypertrophy of the coracohyoid and coracobranchial muscles in the nurse shark (*Ginglymostoma cirratum*, a selachian) equate with specialization for suction feeding. The number and robust nature of attachment sites in *Cowralepis* indicates a vigorous depressor mechanism connected to the midline elements of the branchial basket.

This pattern differs from selachians where the coracobranchialis muscles insert more laterally along hypobranchial and ceratobranchial elements, e.g., as seen in *Squalus acanthias* (Gans and Parsons, 1964), *Scyliorhinus canicula* (Hughes and Ballintijn, 1965), and *Ginglymostoma cirratum* (Motta and Wilga, 1999). In *Squalus*, the copula, which constitutes a large percentage of the midline of the branchial basket, is located in the roof of the pericardial cavity implying that most of the expansion within the posterior branchial basket is accomplished by rotation and depression of lateral elements around a fixed base resulting in an expansion of the "oro-branchial and parabranchial cavities" (Hughes and Ballintijn, 1965:365; more current studies of muscular activity in chondrichthyans have been limited to anterior visceral elements, e.g., Wilga et al., 2000). In contrast, the brachial basket in placoderms is displaced anteriorly (relative to the heart) with the pericardial cavity located posterior to the potential origin of the hypobranchial muscles (posterior to the post-branchial lamina formed by the anterior lateral and interolateral plates; Stensiö, 1959:fig. 1, d.perc). This distribution would eliminate any potential interference of the ventral expansion of the pharynx on the pericardial cavity.

In the mandibular arch of phyllolepid, there is no evidence of muscle attachments at the symphysis, primarily because no mentomandibular ossification is known and the phyllolepid inferognathals taper anteriorly to a narrow point (see Fig. 5). Reduction of anterior jaw/muscle mass is consistent with a rotational system where the moment arm for depression of the mandible is posterior to the fulcrum and is relatively short, as is the case in arthrodires where the attachment site for a mandibulohyoid ligament is known (Johanson, 2003:fig. 4, mand.hy?). In forms such as *Dunkleosteus terrelli* or *Gorgonichthys clarkii* (Fig. 1B) the inferognathals are extremely massive with relatively well-ossified mentomandibular elements at the symphysis. The lever-advantage in an osteichthyan-style depressor system here would be minimal; instead,

jaw depression would be more effective through the direct action of a coracomandibularis (Anderson and Westneat [2007] propose an expansion rate in *D. terrelli* comparable to modern suction feeders). However, in phyllolepid evidence for the greatest muscle mass is in the depressor system for the hyoid and branchial midline elements (working as a functional unit). Reduction of the anterior portion of inferognathals implies a relatively small coracomandibularis. Thus in phyllolepid, it is likely that an osteichthyan-style depressor system was present resulting in jaw depression through the mechanical linkage of the mandible to the hyoid via a mandibulohyoid ligament. The limited space in the headshield for the orbit and the palatoquadrate with its adductor mandibularis might indicate that depression serves the greater biological role in phyllolepid in contrast to piscivores like *D. terrelli* where large shearing forces are generated at the anterior cusp of the inferognathal as the jaw is elevated by the adductor mandibularis muscle (estimates for bite forces are quantified by Anderson and Westneat [2007]).

Our interpretation of the feeding mechanism in phyllolepid is that of a suction feeding gulper capable of capturing prey items up to 50% their own body width (based on the relative proportions of predator and prey in AMF90011 [Ritchie, 2005:fig. 19], a large *Cowralepis* that swallowed a juvenile). The pattern of dentition is consistent with this interpretation. The distribution of denticles on the anterior superognathal extends far medially beyond the occlusal surface with the inferognathal (Fig. 5; ASG ca. 3 times wider in some cases). This implies that beyond the partitioning and processing of small prey items, the expanded denticles may serve as a holdfast for larger items. Potentially correlated with this feeding strategy is the ossification of the palate. The palate (dorsal roof of the oropharyngeal cavity) consists of a large parasphenoid anteriorly and independent ossifications in the floor of the neurocranium that extend from the occipital condyles to the region of the parasphenoid (median occipital and paired paraotic ossifications of Ritchie [2005] and an undescribed paired ossification that fuse in adults thus covering most of the neurocranial floor posterior to the parasphenoid). In some specimens, there are isolated denticles on the ventral surface of the neurocranium in this region. The condition of a complete palatal ossification is comparable to that seen in the rhenanid placoderm *Nefundina qalibahensis* (Lelièvre et al., 1995; Fig. 1B), a dorso-ventrally flattened form hypothesized to be a suction feeder (Lelièvre and Carr, in press).

CONCLUSIONS

The detailed preservation of *C. mclachlani* provides valuable information on the visceral skeleton

in phyllolepid and on the primitive condition of visceral elements in gnathostomes (jawed vertebrates, Fig. 1A). Visceral ossifications in *C. mclachlani* include quadrate and articular ossifications of the mandibular arch; hyomandibula, ceratohyal, and basihyal ossifications of the hyoid arch; and paired basibranchial ossifications. The presence of paired basibranchial elements adds support to Goodrich's (1930) original contention that paired elements represent the primitive condition among gnathostomes. It also provides the basis for reinterpretation of paired elements in other placoderms (*Pseudopetalichthys* and *Tapinosteus*) as basibranchials. The presence of paired basibranchials with attachment sites for hypobranchial musculature leads to the hypothesis that these elements are derived from neural crest (the origin of these elements have not been explicitly documented in extant non-tetrapods).

A review of the systematics of placoderms (based on published analyses with a revision of phyllolepid character states; Fig. 10) confirms phyllolepid as arthrodires. Phyllolepid represents a sister group to phlyctaeniids + brachythoracids. The proposed relationships of *Wuttagoonaspis* (Fig. 10B,C) vary from a hypothesis that they are the sister group to phyllolepid (the current analysis of Goujet and Young [1995] including *Cowralepis*) to the hypothesis that they are the sister group of other arthrodires (Dupret, 2004 and Dupret et al., 2007, with inclusion of *Cowralepis*; although, the latter study includes *Antarctaspis* as the most basal arthrodire).

Recent challenges to the phylogenetic position of placoderms as the sister group to remaining gnathostomes (Grogan and Lund, 2000), based in part on interpretation of the suspensorium, increases the importance of understanding the condition in placoderms. Gnathostomes possess a hyoid arch that primitively connected the ceratohyal to the neurocranium via the hyomandibula (Maisey, 1986; Janvier, 1996; hyomandibular attachment to the neurocranium is also the case for its homologue in lampreys, Grogan and Lund, 2000:fig. 16; character 1, Fig. 2) and was connected to the mandibular arch via a mandibulohyoid ligament (serving as a functional linkage in jaw depression among osteichthyans in contrast to chondrichthyans, Wilga et al., 2000). Evolutionary modification of this pattern included a ventral detachment of the hyomandibula in placoderms for support of the operculum (submarginal plate; characters 11, 12, respectively, Fig. 2) correlated with a dermal support of the palatoquadrate (post-suborbital and suborbital plates; character 13, Fig. 2). Among the chondrichthyans, the holocephalans achieved an opercular support via a dorsal detachment of the hyomandibula from the neurocranium (such a derived condition is in contrast to the polarity of characters proposed by Grogan and Lund

[2000]; character 21, Fig. 2). Placoderms retain a number of plesiomorphic conditions of the neurocranium and visceral skeleton, whereas chondrichthyans and osteichthyans share modifications for some of these features. The placoderm plesiomorphic features include: 1) a neurocranial articulation for the hyomandibula (Janvier, 1996; character 1, Fig. 2), a gnathostome plesiomorphy (present in lampreys) that is modified in holocephalans with hyomandibular dorsal detachment to support the operculum (Didier, 1995; character 21, Fig. 2); 2) the presence of paired basibranchials (character 5, Fig. 2), a gnathostome synapomorphy (absent from the lamprey branchial basket), which in chondrichthyans and teleostomes are single midline elements or further fused to form a copula (paired condensations are transitory in the ontogeny of some chondrichthyans, Holmgren, 1940; character 15, Fig. 2); 3) an ethmoidal attachment for the palatoquadrate, a gnathostome synapomorphy (Janvier, 1996; associated with the origin of trabeculae; character 6, Fig. 2); 4) a ventral attachment for the palatoquadrate to the parachordal portion of the neurocranium (character 2, Fig. 2), a gnathostome plesiomorphy that is either lost or transferred to the trabeculae in chondrichthyans and teleostomes (character 19, Fig. 2); 5) an anterior neurocranial fissure (Goujet, 2001; character 3, Fig. 2), a gnathostome synapomorphy that is only seen as an ontogenetic feature in non-placoderm gnathostomes (an anterior fissure represents a gnathostome feature because the trabeculae associated with the anterior fissure are a gnathostome synapomorphy; characters 8, 17, Fig. 2); and 6) relatively short trabeculae (character 7, Fig. 2), the plesiomorphic character state for the trabeculae that expanded posteriorly in chondrichthyans and teleostomes (character 18, Fig. 2) and is correlated to a shift of the basal articulation to the basiptyergoid, when present. Further expansion of the trabeculae (trabeculae-parachordal index >100) is seen independently in chondrichthyans and osteichthyans (characters 22 and 20, respectively, Fig. 2).

Derived features for the placoderms include the following: 1) the dermal support for the palatoquadrate (character 13, Fig. 2); 2) an operculum supported by the hyomandibula (character 12, Fig. 2) that retains the primitive connection to the neurocranium, but is ventrally detached from the remaining hyoid arch (character 11, Fig. 2; in contrast to the holocephalan opercular support, Grogan and Lund, 2000); and 3) loss of the posterior neurocranial fissure (character 14, Fig. 2), which may be related to the expansion and fusion in the occipital region in this group and related to the functional axial and dermal joints between the head and thoracic regions. The polarity of this feature is ambiguous with extant agnathans lacking an occiput (de Beer, 1937:383) and some fossil

agnathans possessing an occipital region (Wängsjö, 1952:86).

Finally, we hypothesize a suction feeding and gulping behavior in phyllolepid that parallels that seen in the extant angel shark (*Squatina*, a selachian). This behavior in phyllolepid may represent an autapomorphic specialization of the feeding mechanics in these dorsoventrally flattened fishes (whereas the musculature and their attachments retain the plesiomorphic gnathostome condition). The spatial organization of the ventral hyoid arch (the expansion of the ceratohyal laterally beneath the inferognathal) and basibranchials (their intimate connection to their antimeres and the basihyoid) indicates that the floor of the branchial basket operated as a functional unit. Associated with these midline elements are indications of substantial muscular attachments indicating the biological importance of depression of the oropharynx. Depression of the mandible is most likely hyoid-driven via a mandibulohyoid ligament connecting the ceratohyal and mandible (based on a rotational system with reduced mass of the anterior inferognathal and a short depressor lever posterior to the fulcrum—unlike chondrichthyans where the mandible depression is independent and prior to hyoid depression [Wilga et al., 2000]). Presence of a mandibulohyoid ligament is considered by Wilga et al. (2000) as a plesiomorphic condition in gnathostomes with its presence in arthrodires documented by Johanson (2003); however, she noted uncertainties in its distribution and thus its functional interpretation among placoderms.

The excellent preservation in *C. mclachlani* has shed new light on the suspensorium and splanchnocranium in arthrodires allowing a reinterpretation of the placoderm and basal gnathostome conditions. Character recoding for phyllolepid has stabilized their phylogenetic position as arthrodires. Preservation of an ontogenetic sequence of neurocranial and vertebral elements (including a synarcual) can form the basis for a comparison of these regions to other gnathostomes. Finally, our improved knowledge of phyllolepid anatomy has enabled an interpretation of feeding mechanics in this Devonian group, demonstrating an early occurrence of suction feeding among basal gnathostomes.

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