

THE OCCIPITAL-SYNARCUAL COMPLEX IN *NEFUDINA QALIBAHENSIS* (PLACODERMI)

HERVÉ LELIÈVRE¹ and ROBERT K. CARR^{*2}; ¹Muséum National d'Histoire Naturelle, Département Histoire de la Terre, Paléobiodiversité et Paléoenvironnements, 8 rue Buffon, CP 38 F-75231, Paris cedex 05, France; ²Department of Biological Sciences, Irvine Hall, Ohio University, Athens, Ohio 45701 U.S.A., carr1@ohio.edu

The placoderms represent the phylogenetic sister group to remaining gnathostomes (Fig. 1) and as such the anatomical patterns within this group are important in recognizing the polarity of character states within gnathostomes in general. This is especially critical in the analysis of soft tissues or poorly preserved osteological features (e.g., perichondral ossifications of the endoskeleton) where data is often limited. In many cases, the interpretation of these features is limited to osteological correlates (sensu Witmer, 1995). Ritchie (2005) noted the rare detailed preservation of occipital and synarcual (fused anterior vertebrae) perichondral ossifications in an ontogenetic series of *Cowralepis mclachlani* (Phyllolepidia). However, due to the otherwise depauperate fossil record for this anatomical region it is important to document additional examples when they are discovered. Lelièvre et al. (1995) described *Nefudina qalibahensis* (Rhenanida) from Saudi Arabia and mentioned 'other material' that included a synarcual. The synarcual and occipital ossifications are described below with an update on our current knowledge of the occipital-synarcual complex in placoderms.

MATERIAL

The holotype of *Nefudina qalibahensis* Lelièvre, Janvier, Janjou, Halawani 1995 is based on a neurocranium with attached palatal plates (no. 1992-1, Lelièvre et al., 1995:pl.1, figs. 1, 2) from the Hammamiyat Member of the Jauf Formation (Emsian). Other material from this locality includes two incomplete right sub-orbital plates (no. 1992-2 and no. 1992-3, Lelièvre et al., 1995:pl. 1, figs. 3, 4 and 5, 6, respectively), an incomplete thoracic shield (no. 1992-4, Lelièvre et al., 1995:pl. 1, figs. 7, 8), and a synarcual (no. 1992-5, unfigured). An additional unprepared fragment (not included in the original description) represents the occipital region (new number—no. 1992-6). The specimens as originally numbered are provisionally housed at the Muséum National d'Histoire Naturelle, Paris.

SYSTEMATIC PALEONTOLOGY

PLACODERMI McCoy 1848

RHENANIDA Broili 1930

NEFUDINA QALIBAHENSIS Lelièvre et al. 1995

(Figs. 2, 3)

DESCRIPTION

Occipital Ossification

The occipital fragment (Figs. 2A–C, 3D) represents the posterior floor of the neurocranium. In ventral view (Fig. 2A) the ossification possesses a central depression that is bounded laterally by thickenings (th). The thickenings are in line with the occipital glenoid processes (f.art.oc) and may have provided support for the head-thoracic joint. The hourglass-shape of the thickenings is comparable to the reinforcement of the occiput

seen in the phyllolepid *Cowralepis mclachlani* although *Nefudina* lacks the detailed ridges and struts seen in *Cowralepis* (Ritchie, 2005:fig. 13). The glenoid facet (Fig. 2A, C) is visible in ventral view and its face is obliquely oriented to the frontal plane (about 64°, the acute angle formed by the facet-ventral surface angle). Each facet is nearly 2.5 times wider than high and the surfaces are fragmented. The flattened fragmented surface lacks a convex shape that would complement the concave form of the synarcual suggesting either some bone loss or that the condyle of the glenoid process consisted mostly of cartilage in life. The ventral orientation of the facet, despite a possible loss of bone, is comparable to the angle of the articular fossae on the synarcual (they form geometrically opposing angles). On the ventral surface, between the glenoid processes, is a small raised area (the notochordal ridge of Stensiö, 1963, Goujet, 1984; r.ch, Fig. 2A) with a central depression (gr.da) that extends for about 8 mm along the ridge.

The dorsal surface possesses a complex topography (Fig. 2B). Associated with the glenoid processes are bilateral thickenings (th.oc). These may represent structures analogous to the dermal occipital arch of other placoderms, but unlike the latter they are part of the neurocranial ventral floor supporting a neurocranial-vertebral joint rather than a thickening in the overlying dermal skeleton supporting the dermal joint (at the present time, there is no direct evidence for a dermal articulation in rhenanids, which functionally might explain the elaboration of a neurocranial support for the neurocranial-vertebral articulation; "the probable absence of a cervical [dermal] joint may be a secondary state, related to extension of the tesserated areas," Goujet, 1984:231). The neurocranial thickenings in *Nefudina* are marked by several depressions. Between these thickenings is a shallow midline groove (gr.med) that extends the length of the occipital ossification from its posterior border to an anterior ventral 'step.' The groove is at the dorsal-ventral level of the spinal cord as it continues forward from the neural canal of the synarcual. The anterior 'step' represents an erosion artifact. Supporting this interpretation is the observation that when the ventral floor of the endocranium is known, there is no equivalent structure (*Bolivosteus chacomensis*, a rhenanid, Goujet et al., 1985:fig. 3B lacks a 'step' as do *Kujdanowiaspis* and *Dicksonosteus*, actinolepid and phlyctaeniid arthrodires, respectively; Goujet, 1984:figs. 26, 27).

The posterior view of the occipital ossification (Fig. 2C) is dominated by the facets of the glenoid processes. Of interest is a small pit between the two facets in the mid-thickness of the neurocranial floor that lies directly dorsal to the notochordal ridge and represents the anterior continuation of the notochord (c.nch).

Synarcual

The synarcual (Fig. 3) consists of two regions, a reinforced anterior basal region that forms the articulation with the neurocranium and a neural region that extends from the articulation to posterior of the basal region.

The longitudinal axis of the base (Fig. 3C, dashed line) and thus the articulation surface, are angled approximately 23 degrees above horizontal (conferrable with the oblique ventrally

*Corresponding author.

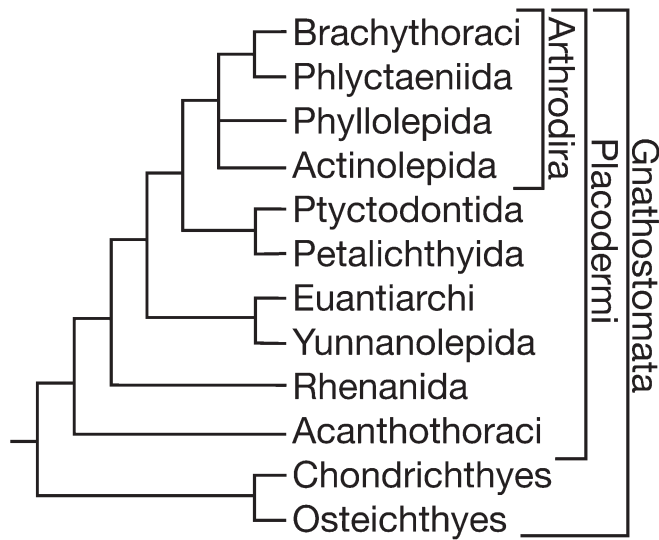


FIGURE 1. Cladogram of hypothesized relationships among gnathostomes and placoderm interrelationships (after Goujet and Young, 2004).

directed glenoid facet of the occipital). The articular fossae (f.art.s, Fig. 3F), like the glenoid facets, are approximately twice as wide as high and are separated by only 2 mm at the midline. The surfaces of the fossae are fully formed, but porous, suggesting a thin cartilaginous covering (unlike the fragmented surfaces of the occipital facets). In the space between the two fossae a small foramen represents the restricted notochord (c.nch). The fossae are backed by an apparently solid ossified basal element. The base is 45 mm wide at the fossae and tapers posteriorly to about 38 mm (over a parasagittal distance of about 23 mm). The height of the base is greatest at the fossae and decreases by approximately 50% before its end. The posterior end of the base is fragmented suggesting it is incomplete, but a narrowing and thinning trend is obvious and it is doubtful that the structure extended much farther posteriorly. On the posterior face an opening for a restricted notochord is present (Fig. 3E). The diameter of the opening is about half the diameter of the neural canal (the diameter is greater than the more restricted anterior opening). On the dorsal surface of the base are several oblique ridges. The grooves (gr.spi, Fig. 3A) between these ridges are continuous with foramina for the spinal nerves (c.spi, Fig. 3B) and thus mark the path of individual nerves.

Extending from the dorsomedial edges of the fossae, a neural arch (n.a, Fig. 3) encloses the neural canal (cn) and is intimately connected to the base. The canal is perichondrally ossified consisting of an inner lamina (lam.int) that lines the neural canal and an outer lamina (lam.ext) that anteriorly is continuous with the base. Five spinal nerve foramina are present over the base (the last is indicated only by its dorsal arch over the foramen). The anterior foramen is elongate and on the right side of the base are indications of two grooves leading away from the foramen (one obliquely posterior paralleling the other grooves, and one obliquely anterior). The two grooves suggest that the anterior foramen contained two spinal nerves. Thus the base represents the fusion of 6–7 vertebrae. The neural canal posterior to the base is incomplete ventrally (whether unossified or lost is unclear) so additional foramina are not preserved. The external perichondral ossification of the neural canal is continuous (Fig. 3A, B, D, E) indicating that developmentally the cartilaginous neural arches had completely fused into a single unit before the onset of perichondral ossification.

DISCUSSION

The formation of a synarcual (a functional fusion of the anterior vertebrae) is only seen among extant fishes in the chimaerids (Holocephali, Didier, 1995:fig. 18), skates and rays (Batoidea, Cappetta, 1987:fig. 10), and pipefishes (Syngnathiformes, Bertin and Arambourg, 1958:fig. 1690) and in the extinct placoderms. Our knowledge and understanding of the occipital-synarcual complex in placoderms is limited. Examples of synarcuals are documented in only three orders of placoderms (Fig. 1; Rhenanida, Ptyctodontida, and Arthrodira) and these are represented by limited examples (*Nefudina*, *Gemuendina*, and *Jagorina* among rhenanids; *Ctenurella* among the ptyctodonts; and *Erromenosteus*, *Trematosteus*, *Belosteus*, and the phyllolepid *Cowralepis* (sensu Dupret, 2004, Ritchie, 2005) among the arthrodirans). Denison (1978) speculated that vertebral fusion to form a synarcual might have occurred in each of the placoderm orders related to formation of a vertically acting joint. He noted that examples of vertebral fusion range from three to possibly twenty vertebrae.

In all cases where known or where the posterior neurocranium is preserved, the vertebral or synarcual articulation with the neurocranium is a paired articulation with occipital glenoid processes located ventrolateral to the foramen magnum. These articulations, in most cases appear to be lateral to an anterior extension of the notochord often indicated by a midline ventral ridge (Goujet, 1984:fig. 50) that extends anteriorly to the otic region of the neurocranium. Denison (1978:7) stated, “as far as known, the notochord is persistent and unconstricted in all Placodermi,” which is consistent with the relatively common appearance of a notochordal ridge. In the case of an ossified centrum, which appears to be the situation in the rhenanid synarcual, Denison (1978:8) further noted, “the dorsal and ventral arches are fused around the notochord to form ring-shaped vertebrae, but bony centra are probably absent.” This pattern is seen in the phyllolepid *Cowralepis* where neural and haemal pedicles laterally fuse to form an apparent cylindrical structure (Ritchie, 2005:fig. 13).

The condition in *Nefudina qalibahensis* directly contradicts two of the generalizations for the condition in placoderms. First, the notochord is clearly constricted by the formation of the synarcual. At the posterior end of the basal portion of the synarcual, the notochordal canal (Fig. 3E) is only about half the diameter of the neural canal. Anteriorly, the notochordal canal is only about a third the diameter of the neural canal. A notochordal ridge is present on the ventral surface of the occiput, but it is low and only extends 12 mm anteriorly, stopping well short of the otic region. Second, the basal region is fully ossified.

Assuming that the occipital thickenings (Figs. 2, 3) on the holotype and isolated occiput are equivalent structures, the occipital region in *Nefudina qalibahensis* is relatively long compared to other rhenanids. In *Bolivosteus chacomensis* (Goujet et al., 1985:fig. 3) the mid-otic capsule is located posteriorly approximately 71% the preserved length of the neurocranium (rostrum-to-mid-otic capsule distance / rostrum-to-condyle distant X 100). In reconstructions of other rhenanids (*Jagorina* and *Gemuendina*) the otic capsule is situated between 57–63%. In the holotype of *Nefudina* (with an assumed complete posterior region) the otic capsule is placed about 53%. Although atypical among rhenanids, an anterior position (less than 50%) is seen in petalichthyids (*Macropetalichthys*) and basal brachythoracid arthrodirans (e.g., *Buchanosteus* and *Homostius*, the latter based on the position of the endolymphatic thickening of the head shield). An elongation of the occipital region in *Nefudina* may indicate that the ventral groove on the notochordal ridge (Fig. 2A) represents a groove for the dorsal aorta (as hypothesized for *Macropetalichthys*, Young, 1980:fig. 26A), in contrast to paired grooves for lateral dorsal aortae in taxa with a shorter occipital region (e.g., *Dicksonosteus*, Goujet, 1984:fig. 51).

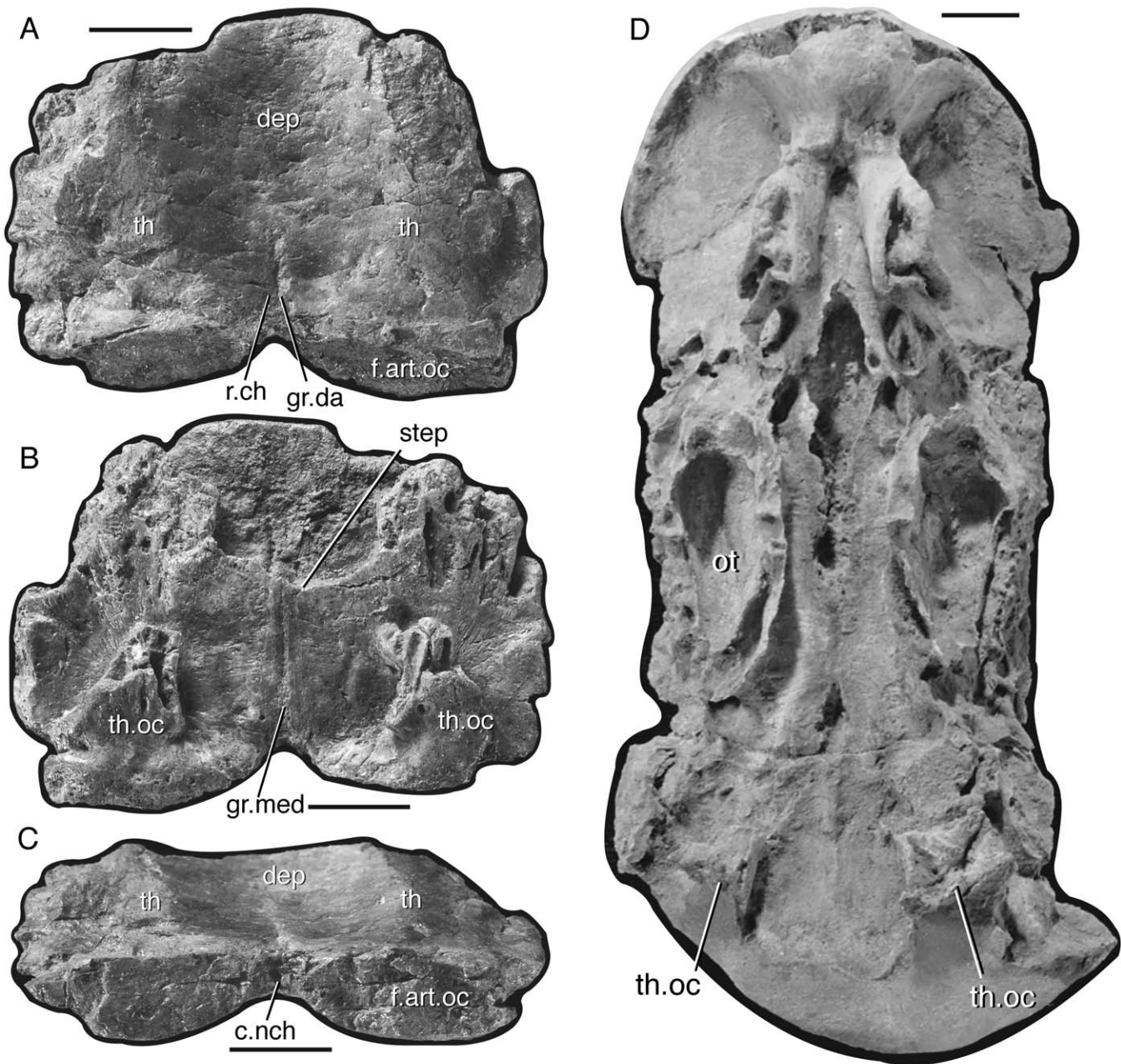


FIGURE 2. *Nefudina qalibahensis*. Occipital ossification (no. 1992-6) in **A**, ventral; **B**, dorsal; and **C**, posteroventral oblique views. **D**, neurocranium (no. 1992-1) in dorsal view. **Abbreviations:** **c.nch**, canal for the notochord; **dep**, depression; **f.art.oc**, articular facet of the occiput; **gr.med**, groove for the medulla oblongata; **gr.da**; groove for the dorsal aorta; **ot**, otic capsule; **r.ch**, notochordal ridge; **step**, an erosion artifact in floor of neurocranium; **th**, thickening; **th.oc**, internal occipital thickening of the neurocranium. Scale bars equal 1 cm.

Reconstruction of the occipital-synarcual complex shows that the longitudinal axes for the neural canal (spinal cord) and the occipital articulation are not in alignment. These axes intersect at a low angle (about 23° , Fig. 3C, the angle between the dashed line and the horizontal or axis of the neural canal) such that when the head is in alignment with the neural axis it is positioned below the axis of the joint. If the range of motion for the head is equal above and below the axis of the synarcual base (its articular surface is symmetrical above and below this axis, Fig. 3C solid lines) then the implications of this angulation is that the head can

be raised higher relative to horizontal. Such a range of motion is consistent with benthic suction feeding where ventral expansion of the oropharyngeal chamber is ventrally restricted due to proximity to the substrate. Structural reinforcement of the occipital-synarcual joint (ossified centra, complete synarcual fusion, hourglass-shaped and internal thickenings within the occiput) is indicative of the forces generated at this joint. Additionally, reduction of the notochord would likely increase the flexibility across the joint. Among the phyllolepid, a suction feeding behavior can be hypothesized for these dorsoventrally compressed

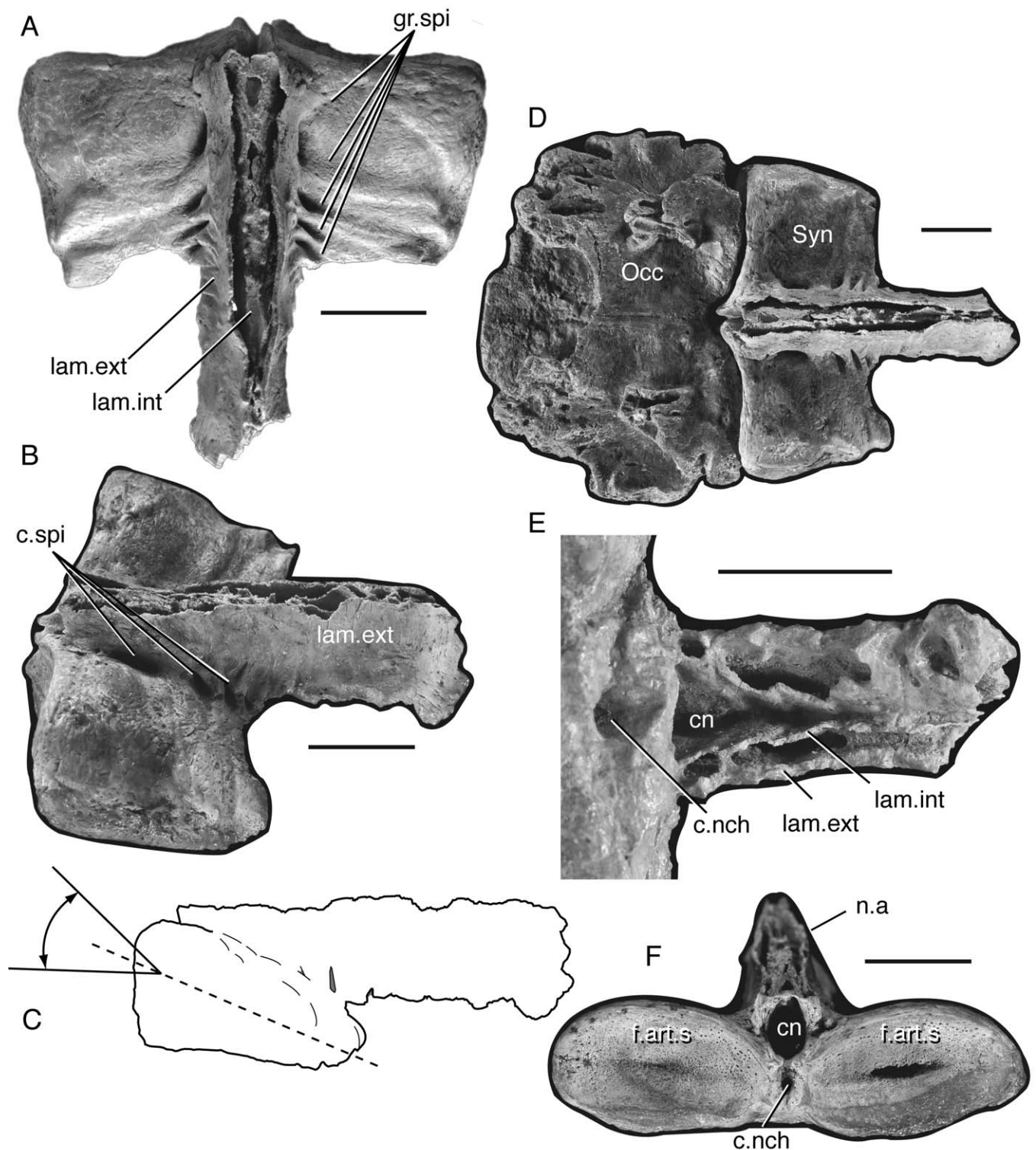


FIGURE 3. *Nefudina qalibahensis* (no. 1992-5). Synarcual in **A**, dorsal view; **B**, oblique left dorsolateral view; **C**, schematic of synarcual in left lateral view. Dashed line indicates the axis of the synarcual base and articular fossae. Arrow and solid lines indicate a possible symmetrical range of motion about the axis. Note the increased range of motion above horizontal suggesting a greater biological role for elevation of the head. **D**, occipital (no. 1992-6) and synarcual articulated in dorsal view; **E**, neural canal posterior to the base of the synarcual in ventral view; and **F**, synarcual in anterior view. **Abbreviations:** **c.nch**, canal for the notochord; **c.spi**, canal for spinal nerve; **cn**, neural canal; **f.art.s**, articular fossa of the synarcual; **gr.spi**, groove for spinal nerve; **lam.ext**, external lamina of the neural arch; **lam.int**, internal lamina of the neural arch; **n.a**, neural arch; **Occ**, occipital ossification; **Syn**, synarcual. Scale bars equal 1 cm.

placoderms (based on *Cowralepis*, where Ritchie (2005) demonstrated cannibalism by a large specimen upon a smaller one, with suction feeding a common pattern seen among macrophages, Bone et al., 1995). The phyllolepid placoderms share with *Nefudina* a structural reinforcement of the occipital-synarcual joint; however, joint alignment is horizontal in the former. In *Cowralepis* there is evidence of muscular hypertrophy of the hypobranchial musculature (Carr et al., 2009) that in modern sharks has been positively correlated with suction feeding (Motta & Wilga, 1999).

CONCLUSION

The occipital-synarcual complex in the rhenanid *Nefudina qalibahensis* consists of 6–7 fused centra, a greater number of neural arches, and a structurally reinforced occiput that form a robust functional joint. Alignment of the component parts are consistent with a hypothesis of suction feeding in this dorsoventrally compressed fish. Contrary to the hypothesized pattern for most placoderms, the condition in *Nefudina qalibahensis* clearly documents ossified centra and a restricted notochord. Both of these conditions may be functionally correlated with specializations related to its feeding strategy. Thus, the evolution of specialized feeding strategies, i.e., suction feeding, is documented among basal placoderms.

ACKNOWLEDGMENTS

We would like to thank an anonymous reviewer and G. Young for their comments. Additional thanks are extended to the Bureau de Recherches Géologiques et Minières, Jeddah, Saudi Arabia, for their assistance in organizing the 1992 Saudi Arabian field trip. The junior author thanks the Muséum National d'Histoire Naturelle, Paris, for the opportunity to work on this material and for their support during a 2007 visit.

LITERATURE CITED

- Bertin, L., and C. Arambourg. 1958. Super-ordre des Téléostéens; pp. 2204–2500 in P.-P. Grassé (ed.), *Traité de Zoologie, Anatomie, Systématique, Biologie*, Tome XIII (III), Agnathes et Poissons, Anatomie, Ethologie, Systématique.
- Bone, Q., N. B. Marshall, and J. H. S. Blaxter. 1995. *Biology of Fishes*. Blackie Academic & Professional, London, 332 pp.
- Broili, F. 1930. Über *Gemündina stürtzi* Traquair. *Abhandlungen der Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche*, München 6:1–24.
- Cappetta, H. 1987. Chondrichthyes II, Mesozoic and Cenozoic Elasmobranchii; in H.-P. Schultze (ed.), *Handbook of Paleichthyology*, Volume 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.
- Carr, R. K., Z. Johanson, and A. Ritchie. 2009. The phyllolepid placoderm *Cowralepis mclachlani*: Insights into the evolution of feeding mechanisms in jawed vertebrates. *Journal of Morphology* DOI: 10.1002/jmor.10728.
- Denison, R. 1978. Placodermi; in H.-P. Schultze (ed.), *Handbook of Paleichthyology*, Volume 2. Gustav Fischer Verlag, Stuttgart, 128 pp.
- Dupret, V. 2004. The phylogenetic relationships between actinolepids (Placodermi: Arthrodira) and other arthrodirids (phlyctaeniids and brachythoracids). *Fossils and Strata* 50:44–51.
- Didier, D. A. 1995. Phylogenetic systematics of extant chimaeroid fishes (Holocephali, Chimaeroidei). *American Museum Novitates* 3119:1–86.
- Goujet, D. 1984. Les Poissons Placodermes du Spitsberg. Arthrodirés Dolichothoraci de la Formation de Wood Bay (Dévonien Inférieur). *Cahiers de Paléontologie*, Centre National de la Recherche Scientifique, Paris, 284 pp.
- Goujet, D., P. Janvier, and M. Suarez-Riglos. 1985. Un nouveau rhénanide (Vertebrata, Placodermi) de la Formation de Belén (Dévonien Moyen), Bolivie. *Annales de Paléontologie* 71:35–53.
- Goujet, D., and G. Young. 2004. Placoderm anatomy and phylogeny: New insights; pp. 109–126 in G. Arratia, M. V. H. Wilson, and R. Cloutier (eds.), *Recent Advances in the Origin and Early Radiation of Vertebrates*. Verlag Dr. Friedrich Pfeil, München.
- Lelièvre, H., P. Janvier, D. Janjou, and M. Halawani. 1995. *Nefudina qalibahensis* nov. gen., nov. sp. un rhenanide (Vertebrata, Placodermi) du Dévonien Inférieur de la Formation Jauf (Emsien) d'Arabie Saoudite. *Geobios* 19:109–115.
- McCoy, F. 1848. On some new fossil fish of the Carboniferous period. *Annals and Magazine of Natural History* 2:1–10.
- Motta, P. J., and C. D. Wilga. 1999. Anatomy of the feeding apparatus of the nurse shark *Ginglymostoma cirratum*. *Journal of Morphology* 241:33–60.
- Ritchie, A. 2005. *Cowralepis*, a new genus of phyllolepid fish (Pisces, Placodermi) from the Late Middle Devonian of New South Wales, Australia. *Proceedings of the Linnean Society of New South Wales* 126:215–259.
- Witmer, L. M. 1995. The extant phylogenetic bracket and the importance of reconstructing soft tissues in fossils; pp. 19–33 in J. Thomason (ed.), *Functional Morphology in Vertebrate Paleontology*. Cambridge University Press, Cambridge.
- Young, G. 1980. A new Early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontographica A* 167:10–76.

Submitted April 1, 2008; accepted June 19, 2008.