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Morphology of the anterior vertebral region in elasmobranchs: special focus, Squatiniformes

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Abstract

The morphology of extant and extinct Squatiniformes is well conserved within this lineage, but differences are of consequence to character interpretations for phylogenetic analyses. Investigation of the extinct taxon †*Pseudorhina alifera* (Münster, 1842) from the Late Jurassic of Solnhofen with extant species of *Squatina* provide new evidence that members of Squatiniformes possess a basioccipital fovea. Presence of a basioccipital fovea is the ancestral condition in Neoselachians and hypothesized to be lost in members of Hypnosqualea. In addition, species of *Squatina* all posses a reduced occipital hemicentrum while the occipital hemicentrum in †*Pseudorhina* is unreduced, indicating the condition in *Squatina* is an example of postdisplacement heterochrony. Pristiophoriformes and Batoidea also are characterized by a lack of a basioccipital fovea and hemicentrum. However, extinct members of Batoidea, such as †*Spathobatis*, and modern taxa do possess a distinct notch in the posterior basicranium ventral to the foramen magnum. Except for the lack of an associated occipital hemicentrum, this notch is similar to the basioccipital fovea, but its homology is not yet addressed. Furthermore, within all species of Squatiniformes and Pristiophoriformes, as well as some members of Orectolobiformes and Carcharhiniformes, basiventral cartilages are laterally expanded, contributing to a broad articulation with the occipital condyle. The disparate taxa with modifications to the basiventral cartilages suggest a significant functional, rather than phylogenetic, signal for this feature.

Key Words

Introduction

Fishes are known to have a great deal of variability in their vertebrae especially near the occipital region. Despite this observed variability, there is new and compelling evidence for developmental conservatism in the region for actinopterygians (Bemis & Forey 2001; Britz & Johnson 2010; Johnson & Britz 2010). Authors have even hypothesized that the occiput could be homologous among chondrichthyans (Britz & Johnson 2010). This study is a first attempt at characterizing the ontogeny of the occipito-vertebral region, specifically in the derived chondrichthyans, Squatiniformes.

Squatiniformes is a group of dorsoventrally-flattened cartilaginous fishes with shark and batoid-like morphology. These fishes were shuffled among many branches of elasmobranchs; sometimes aligned closely with ba-toids, sometimes squaloids, and sometimes both depending on the study (Seret 1986; Shirai 1992a, 1992b, 1996 and references therein). Most recently two well supported but drastically different competing hypotheses based on morphology and molecules posit batoids as derived sharks closely related to angel sharks and saw-sharks (Shirai 1992a, 1992b, 1996; Carvalho 1996), or as the sister group to a monophyletic group of sharks with no relationship to angel sharks respectively (Douady et al. 2003; Winchell et al. 2004; Heinicke et al. 2009, Vélez-Zuazo & Agnarsson 2011) (Fig. 1).

The superficially similar morphology of angel sharks to batoids prompted our new investigation of both extinct and extant squatiniform-taxa, with particular emphasis placed on the anterior portion of the axial skeleton. This region of the axial skeleton is of particular interest because of its possible functional and systema-

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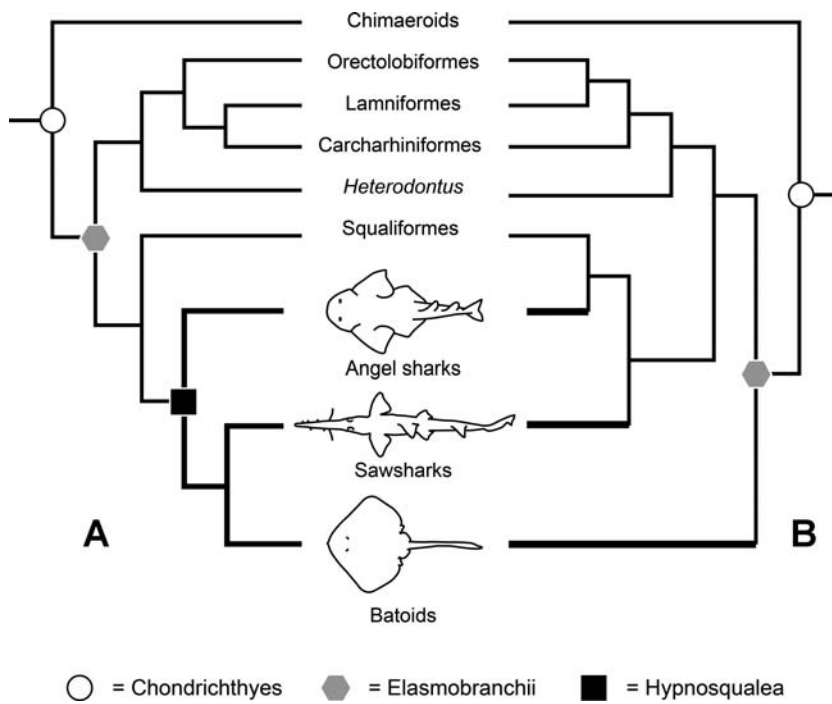
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Figure 1. Hypotheses of Elasmobranch Phylogenetics. **A.** Morphological hypothesis modified from Shirai (1996, fig. 2); **B.** Molecular hypothesis modified from Douady et al. (2003, fig. 1). "Hypnosqualean" taxa are bold faced. Molecular hypothesis predicts a monophyletic shark group that is sister to a monophyletic batoid group.

tic implications among elasmobranchs (Melouk 1949; Shirai 1992a, 1992b). Functionally, the morphology of the anterior axial skeleton is similar to taxa such as *Sphyrna*, which have a propensity to move swiftly from side to side (Melouk 1949). Recently the occipital was demonstrated to play an essential role in the morphologically driven hypotheses of elasmobranch systematics (Carvalho 1996; Carvalho & Maisey 1996; Shirai 1996). In particular, the reduction of a vertebral hemicentrum and the lack of a basioccipital fovea were considered more batoid in nature than shark-like. This region therefore warrants further inquiry. We provided a detailed description of the region in fetal through mature squatiniform specimens. New data are further compared to other groups of neoselachians, such as Pristiophoriformes and Orectolobiformes, which are known to have similar morphology, as well as taxa that do not have a similar morphology such as Lamniformes.

Material and methods

Materials examined

Valid taxon names, authorship, and accompanied references listed according to the California Academy of Sciences, Catalogue of Fishes.

Squatiniformes
†*Pseudorhina alifera* (Münster, 1842): BSP AS I 817; BSP AS I 1367; BSP AS I 1368; CMNH 4052; CMNH 4054; NHM P8535; NHM 37013; *Squatina californica* Ayres, 1859: *AMNH 55686 (#2 of 3); *Squatina dumeril* Lesueur, 1818: MCZ 39903; MCZ 39913; MCZ 40156; MCZ 40372; MCZ 40386; TNHC 42086; TNHC 42087; *Squatina guggenheim* Marini, 1936: ZMB 33877; *Squatina japonica* Bleeker, 1858: FMNH 89926; *Squatina punctata* Marini, 1936: ZMB 33878; *Squatina squatina* (Linnaeus, 1758): ZMB 33873; ZMB 33874; ZMB 33875.

* This is an additional specimen of *S. californica* from the same lot that provided the AMNH 55686 specimen figured by Carvalho et al. (2008, fig. 4).

Comparative sharks
Chiloscyllium arabicum Gubanov, 1980: MCZ 46564; *Isurus oxyrinchus* Rafinesque, 1810a: MCZ 37994; *Orectolobus maculatus* (Bonnaterre, 1788): MCZ S972; *Pristiophorus japonicus* Günther, 1870: MCZ 1045-s; MCZ 1283; *Pristiophorus schroederi* Springer & Bullis: 1960, FLMNH 24621; †*Pristiophorus tumidens* Woodward, 1932: MNHN SHA 1593a,b (1946–18–66); *Schroederichthys bivius* (Müller & Henle, 1838): NMNH 114726; *Sphyrna* sp. Rafinesque, 1810b: NMNH 264341; *Sphyrna lewini* (Griffith & Smith, 1834): NMNH 170556; NMNH 295163; *Sphyrna zygaena* (Linnaeus, 1758): NMNH 51289; NMNH 51291; *Stegostoma fasciatum* (Hermann, 1783): MCZ S1027; MCZ S55.

Comparative batoids
Gymnura micrura (Bloch & Schneider, 1801): UF 26491; *Narcine brasiliensis* (Olfers, 1831): TNHC 18512_A–C; *Raja inornata* Jordan & Gilbert, 1880: FMNH 2754_A–G; †*Spathobatis bugesiacus* Thiollière, 1854: CM 5396; CM 4409; NHM P0299; NHM P10934; NHM P12067.

Preparation methods

Fossil specimens were observed with the aid of a hand lens or under a dissecting microscope and were drawn using camera lucida. Comparative extant shark data were gathered by examining previously exposed radiographs or skeletonized specimens. Batoid data are from personal observations of complete and disarticulated specimens. In addition to radiographs or skeletons, taxa were quantified based on published literature. †*Protospinax* was observed only from the literature.

Two extant specimens of *S. squatina* housed at ZMB were cleared and double-stained using a modified version of the protocol published by Dingerkus & Uhler (1977) and later disarticulated. One cleared and stained specimen of *S. japonica* from the FMNH was also examined. Radiographs were taken at the MCZ of five specimens of *S. dumeril*. Additional skeletal specimens of *S. dumeril* were prepared at

the North East Fisheries Science Center in Woods Hole, Massachusetts and at The University of Texas at Austin. Those skeletons were deposited at the TNHC.

One specimen each of *S. guggenheim*, *S. punctata*, and *S. squatina* from ZMB was examined using microfocus computed tomography (CT) and 3D reconstruction at the HZB. CT scans were performed using a microfocus x-ray tube (Hamamatsu, L8121–03) with a maximum 150 keV. The acceleration voltage was set to 60 keV and the electron beam current was 500 μA in middle spot mode (focus: 20 μm). A 1 mm aluminum plate served as a beam filter. The x-ray detector was a flat panel sensor (Hamamatsu, C7942SK-05) with 2316×2316 pixel and a resolution of 50 μm. Exposure time was approximately 0.8 sec. For each scan, 500 projections were measured over an angular range of 360°. The magnification ratio was 1.55 and corresponds to an effective voxel size of 32 μm for the specimens. The cone beam reconstruction was executed with the software package Octopus (Institute for Nuclear Sciences, Ghent, Belgium). Resulting digital thin sections were processed using the volume rendering program VG StudioMax version 1.2 (Volume Graphics, Heidelberg, Germany).

Comparative methods

The squatiniform specimens were also compared to several additional taxa that were chosen based on prior hypotheses of phylogenetic relationships and functional correlates. Due to a small sample size of comparative, non-batoid elasmobranchs, a new phylogenetic analysis was not performed. However, based on our comparative descriptions, we modified two characters from Shirai (1996) and proposed two additional characters (Appendix). We then mapped states onto two trees modified from the phylogenetic hypotheses proposed by either morphological (Shirai 1992a, 1992b, 1996; Carvalho & Maisey 1996) or molecular data (Douady et al. 2003; Winchell et al. 2004). Characters were mapped using MacClade 4.08 (Maddison & Maddison 2005).

Anatomical abbreviations

bof – basioccipital fovea of Shirai (1992a, 1992b); **bv** – basiventrals; **dubv** – dorsally up-turned basiventrals; **fm** – foramen magnum; **oc** – occipital condyle; **och** – occipital hemicentrum; **sl** – synarcual lip; **vc1** – first vertebral centrum; dashed curved line marks the basioccipital fovea.

Institutional abbreviations

Institutional acronyms follow Leviton et al. (1985) except for the following acronyms; **BSP** – Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **HZB** – Helmholtz Zentrum Berlin, Berlin, Germany; **NHM** – Natural History Museum, London, England; **TMM** – Texas Memorial Museum, Austin, Texas; **TNHC** – Texas Natural History Collection, Austin, Texas; **UTCT** – The University of Texas High Resolution Computed Tomography Laboratory, Austin, Texas.

Results

Comparative anatomy

Basioccipital fovea (character 20 of Shirai 1996)

The basioccipital fovea of Shirai (1992a, 1992b, 1996) and the occipital cotylus of Maisey (1982, 1983) are both described as an unpaired concavity ventral to the foramen magnum. However, no clear distinction can be

made between the two morphologies. Statements herein for the concavity will use basioccipital fovea and, as per Claeson (2008), statements will reserve the term occipital cotyle for the structure on the batoid synarcual that articulates with the occipital condyle of the skull.

The absence of a 'basioccipital fovea' was first hypothesized to unite Squatiniformes with Pristiophoriformes and batoids as members of Hypnosqualea (Character 52, Shirai 1992a) and the relationship was formally established by Carvalho & Maisey (1996). However, a distinct unpaired cavity, which we consider to be the basioccipital fovea, was observed in all fetal specimens of *Squatina,* regardless of preparation method (Figs 2, 3A). A relatively smaller basioccipital fovea was also observed in more mature skeletal specimens of *S. dumeril* (Fig. 3B) and *S. californica* (AMNH 55686, not shown). It is not possible to judge if the basioccipital fovea is present in specimen of *S. californica* figured by Carvalho et al. (2008, fig. 4) because the label for the foramen magnum is directly over the region of interest.

The partly calcified occipital hemicentrum of fetal specimens detaches easily from the basioccipital fovea and remains articulated with the vertebral column (Fig. 3A). In volume-rendered fetal specimens the occipital hemicentrum is loosely situated in the basioccipital fovea. Because soft tissue was not rendered in volume models, the hemicentrum appears to float in that space (Fig. 2). In more mature specimens, the occipital hemicentrum is more tightly associated with the basioccipital fovea and instead detaches from the vertebral column and remains in the skull (Fig. 3B). A dense, un-tessellated, fibrous tissue partially covers the hemicentrum and slightly obscures the margin of the basioccipital fovea, which is still present (Fig. 3B). Previously, cartilage was observed to 'grow back' over the first vertebral centrum (Melouk 1949). It was not clarified by Melouk if this cartilage was tessellated or not, but his description of position is similar to our observation of untessellated fibrous tissue overlaying the occipital hemicentrum.

Evidence of a basioccipital fovea is present in several other elasmobranch taxa, including the extinct species †*Pseudorhina alifera*, the relatively primitive *Heterodontus*, and the derived orectolobiform, *Orectolobus*, and carcharhiniform, *Sphyrna* (Figs 4–6). Margins of the basioccipital fovea are barely discernable in †*Pseudorhina*, but can be traced (Figs 4B–D). The overall size and position of the occipital hemicentrum in the skull supports the presence of a basioccipital fovea. Furthermore, the extinct taxon †*Protospinax* (a close outgroup to Squatiniformes) is also known to have a basioccipital fovea (Carvalho & Maisey 1996). The fovea is easy to recognize in *Orectolobus* and *Sphyrna* (Fig. 5) and other non-batoid elasmobranchs, as it is further emphasized by a slight posterior extension of the occipital condyles over the first complete centrum (Figs 5B, D) (Melouk 1949).
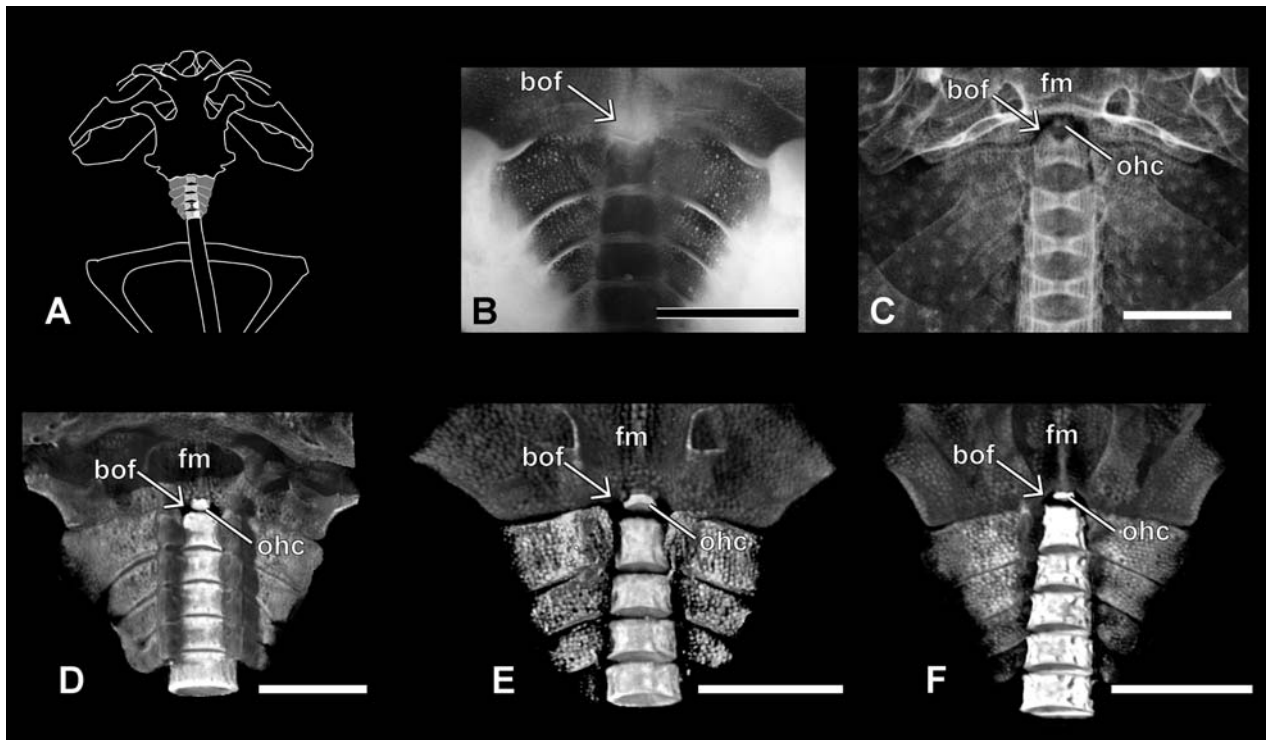
Figure 2. Cranial-vertebral articulation in *Squatina*. **A.** Schematic drawing of *Squatina* with region of interest filled in gray; **B.** Ventral view of *S. japonica* Bleeker, 1858, C&S specimen FMNH 89926; **C.** *S. dumeril* Lesueur, 1818, radiograph of specimen MCZ; **D.** Dorsal view of *S. punctata* Marini, 1936, CT model of specimen ZMB 33878; **E.** Dorsal view of *S. squatina* (Linnaeus, 1758), CT model of specimen ZMB 33875; **F.** Dorsal view of *S. guggenheim* Marini, 1936, CT model of specimen ZMB 33877. Arrowheads point to margin of bof. Scale bars = 2.5 mm.

A basioccipital fovea does not appear to be present in *Pristiophorus* (Shirai 1992a, 1992b, 1996; Carvalho 1996; Carvalho & Maisey 1996). Observable in radiographs, there is a small V-shaped notch present at the back of the skull (Fig. 6B), and resembles the minute basioccipital fovea of *Schroederichthys*. Batoids also potentially lack a basioccipital fovea, although, upon inspection of several early forms of batoids (e.g., †*Spathobatis* and †*Asterodermus*) and even modern ones, (e.g., *Torpedo*, *Rhinobatos*, and *Gymnura*) a notch is present in the base of the skull ventral to the foramen magnum (Figs 6D–E). This notch varies in size and shape, but typically conforms to the shape of the synarcual lip (Claeson 2010). In Rajidae (e.g., *Raja*) the synarcual lip rests above the ventral rim of the foramen magnum (Claeson 2008).

Occipital hemicentrum (character 21 of Shirai 1996) and other centra

In both extinct and extant squatiniforms, an occipital hemicentrum is present and inserts into the basicranium (Figs 2–4). In all species of *Squatina* examined, the hemicentrum is spherical and significantly smaller than the vertebral centra that immediately follow it. By comparison, the occipital hemicentrum of †*Pseudorhina* is somewhat cylindrical, not greatly tapered and it is roughly the same diameter as the vertebral centra that

are immediately posterior to it (Fig. 4). The first complete centrum in all squatiniforms examined is tapered anteriorly. In species of *Squatina*, the first complete centrum is anteroposteriorly longer than more posterior vertebrae. This is also the case in †*Pseudorhina*, however, to a lesser degree.

Comparatively, most other non-batoid elasmobranchs also possess a distinct occipital hemicentrum. This is generally close in diameter to more posterior vertebrae and with the exception of it being only half a centrum, it does not appear greatly reduced in size (Figs 5B, D). Two exceptions were observed for *Schroederichthys bivius*, which has a reduced hemicentrum, and *Pristiophorus*, in which the hemicentrum is absent (Fig. 6B) (Shirai 1992a, 1992b, 1996; Carvalho 1996; Carvalho & Maisey 1996). The first vertebral centrum is greatly tapered in *Pristiophorus* – so much so that it actually looks like the hemicentrum in *Schroederichthys* – except that a pair of basiventral cartilages surrounds it.

Members of Batoidea also lack an occipital hemicentrum, however they do have a synarcual lip. This lip is vaguely similar to the dens or odontoid process, which is long-considered the developmental fusion of the first vertebral body to the second vertebral body in other vertebrates such as birds and mammals (Murray & Drachman 1969; Jenkins 1969; Moritomo et al. 2001). This is present in all clades within Batoidea, including primitive taxa such as †*Spathobatis* (Figs 6D–E), although it is shorter than in extant taxa. The synarcual
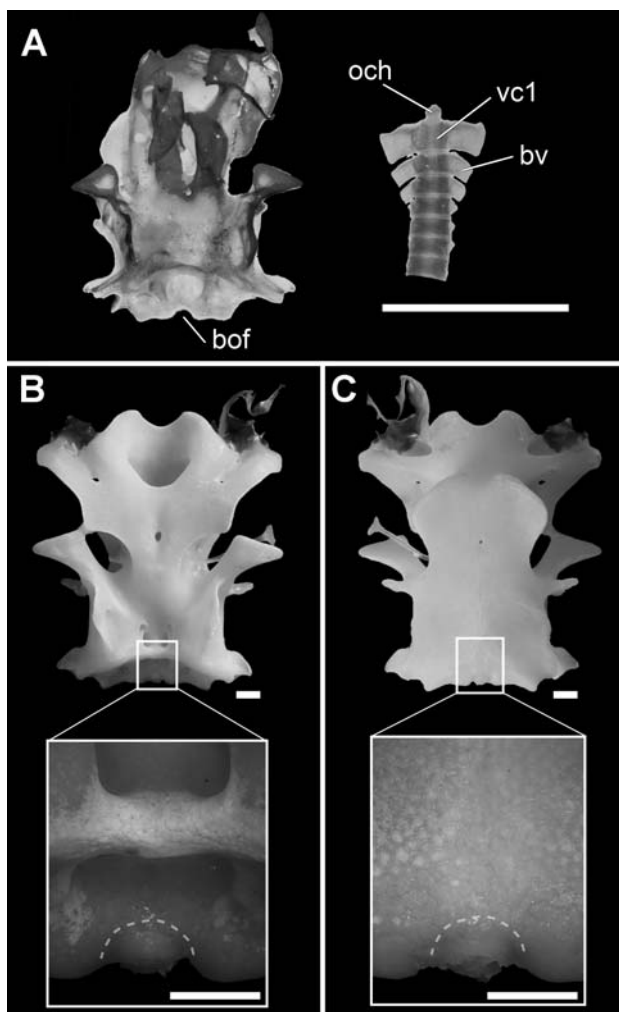
Figure 3. Basicranial-occipital hemicentrum relationship. **A.** Skull (left) and anteriormost vertebrae (right) of cleared and stained *Squatina squatina* (Linnaeus, 1758) (ZMB 33874). Darkest region of skull is uncalcified cartilage; **B.** Dorsal view of skull of *S. dumeril* Lesueur, 1818 (TNHC 42086) with close-up of basioccipital fovea in white box; **C.** Ventral view of skull of *S. dumeril* Lesueur, 1818 (TNHC 42086) with close-up of basioccipital fovea in white box. Anterior is to top of page for all images. Scale bars = 1 cm.

lip is composed of tessellated cartilage and is therefore not likely to represent a remnant hemicentrum. Remnants of a notochord are present however in the synarcual lip of some skates (Claeson 2010, in press).

Basiventrals

In Squatiniformes, the basiventrals are typically dorsoventrally flat across the length of the vertebral column. Basiventrals in combination with the median vertebral centra contribute to the rigidity of the anterior vertebral column. Typically, there is no fusion among and between the cartilages (as in the synarcual of batoids). We observed one exception of fused basiventrals in a specimen of *S. californica* (AMNH 55686 – #2 of 3). In the specimen of *S. californica* figured by Carvalho

et al. (2008) no fusion is present among basiventrals. Reference to fused basiventrals (two segments) of *S. californica* also was made by Compagno (1977, p. 314).

The anterior basiventral pairs (of varying number) also are modified in, *Pristiophorus*, Orectolobiformes (e.g., *Orectolobus* and *Chiloscyllium*), Carcharhiniformes (e.g., *Schroederichthys* and *Sphyrna*), and all batoids (Figs 5–6). Except for the batoids, all groups possess laterally expanded anterior basiventrals. Squatiniforms have at least three expanded basiventral pairs and *Orectolobus* and *Sphyrna* have at least two (Figs 2–5). A maximum of four expanded basiventral pairs were observed in species of *Squatina* as well as †*Pseudorhina*, not ten expanded basiventrals as depicted by Melouk (1949, fig. 2). *Pristiophorus* has at least five expanded basiventral pairs (Fig. 7). In batoids the basiventrals and basidorsals fuse together early in ontogeny (around day 35; Miyake 1988; Claeson 2010, in press) and are thus not directly comparable to nonbatoid elasmobranchs (Figs 5F–G) (Garman 1913; Claeson 2008, 2010).

In species of *Squatina*, the anteriormost basiventral pair is distinctly larger than basiventrals that are more posterior and they are correlated to the elongate first complete centrum (Figs 2–3). The anteriormost basiventral pair is also relatively larger in †*Pseudorhina*, though less so than in *Squatina* (Figs 2–4). In *Pristiophorus*, the anteriormost basiventral pair is actually shorter than the more posterior basiventrals (Fig. 5D). The anteroposterior length of the first several basiventrals is otherwise relatively uniform in comparative taxa (Fig. 5).

Distal margins of individual basiventrals are wedge-shaped ancestrally and do not articulate to form a continuous smooth edge. In squatiniforms, the distal margins of the anteriormost basiventrals taper from anterior to posterior creating a smooth, somewhat triangular complex. This triangular complex is similar to that observed in *Orectolobus* and *Sphyrna* (Fig. 5). In *Pristiophorus*, the distal margins are curved from anterior to posterior and the complex is more U-shaped (Fig. 6A). In addition, the lateral view of squatiniforms, the distal margins are not reflected dorsally. The distal margins, however, are reflected dorsally in *Pristiophorus* (Fig. 6).

Discussion

Ontogeny of the anterior vertebral column in Squatiniformes

By examining extant size series it is possible to assess the ontogenetic implications of the similarities and differences between extinct and extant taxa. Gadow & Abbott (1895) described the two-part nature of the elasmobranch vertebrae: a chordal component that reflects the vertebral centrum and the basal component that reflects the basiventral and basidorsal components. The distinction of these two components is important when dis-
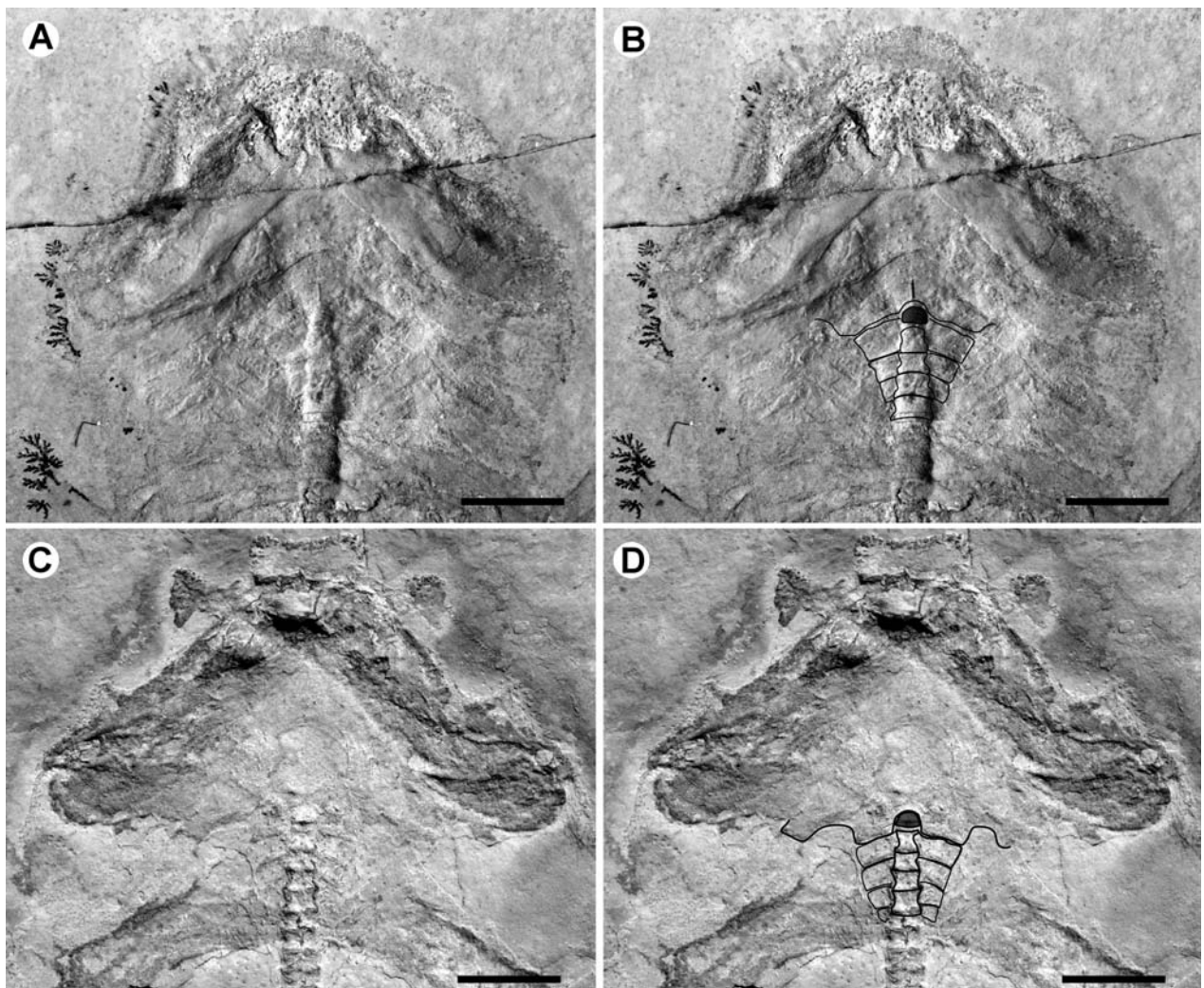
Figure 4. †*Pseudorhina alifera* (Münster, 1842). **A.** Ventral view photo-mosaic of specimen NHM P8535; **B.** Line drawing over-laying craniovertebral articulation in NHM P8535; **C.** Dorsal view of specimen NHM 37031; **D.** Line drawing overlaying cranio-vertebral articulation in NHM 37031. Dark gray shading overlies occipital hemicentrum. Border of basioccipital fovea surrounds occipital hemicentrum. Scale bars = 5 mm.
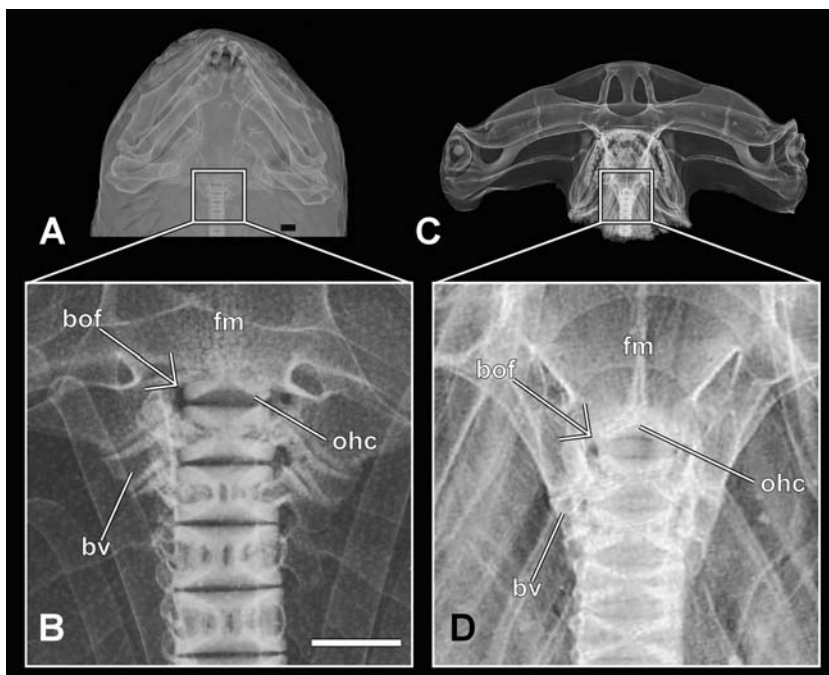

Figure 5. Comparative taxa. **A.** Radio-graph of *Orectolobus maculatus* (Bonna-terre, 1788), specimen MCZ S972; **B.** Close-up of craniovertebral articula-tion of MCZ S972; **C.** Radiograph of *Sphyrna zygaena* (Linnaeus, 1758) NMNH 51291; **D.** Close-up of cranio-vertebral articulation of NMNH 51291. Scale bars = 5 mm.
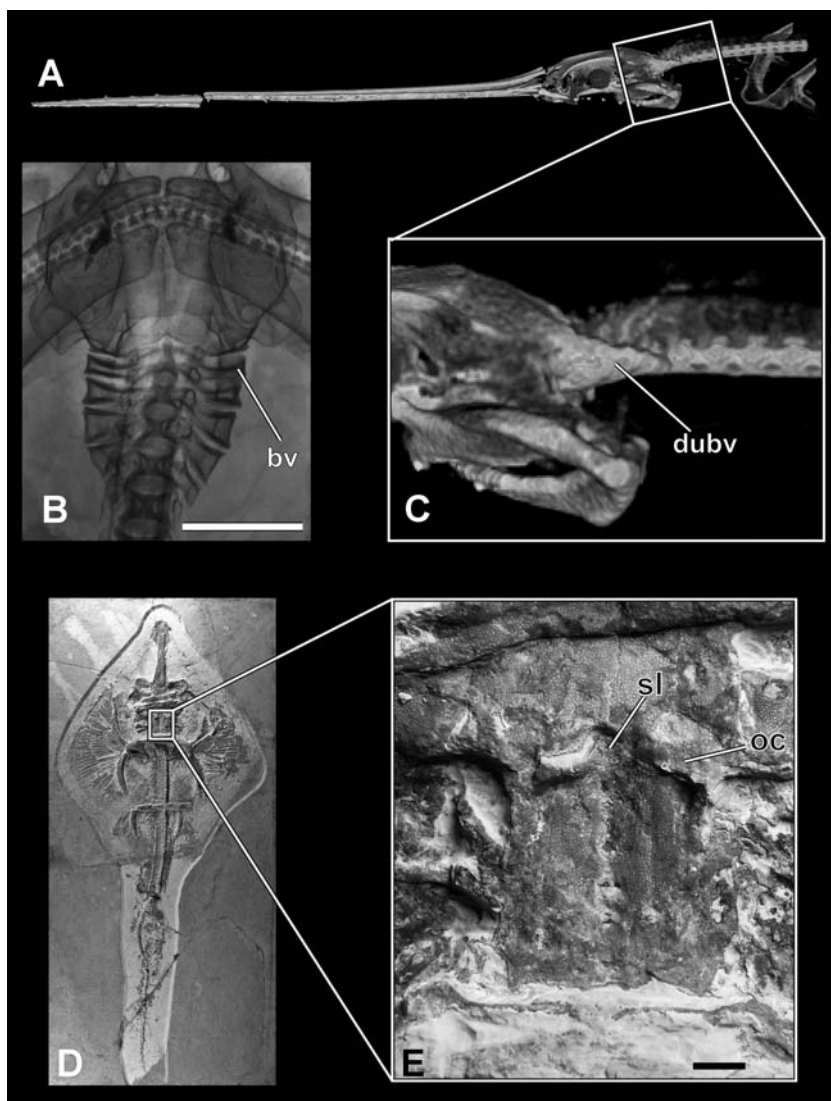
Figure 6. Comparative "hypnosqualean" taxa. **A.** Lateral view of CT model of *Pristiophorus schroederi* Springer & Bullis, 1960 specimen FLMNH 24621; **B.** Radiograph of *Pristiophorus japonicus* Günther, 1870 (MCZ 1045-s); **C.** Close-up of craniovertebral articulation of specimen FLMNH 24621; **D.** Ventral view of †*Spathobatis* NHM P10934; **E.** Close-up of synarcual in NHM P10934. Scale bars = 5 mm.

cussing the ontogeny of angel sharks as well as other elasmobranchs with modified vertebrae.

Basidorsal and basiventral cartilages in *Squatina* grow around the vertebral centrum, firmly affixing themselves to one another but not fusing with the centrum. In the youngest specimens, this connection between chordal and basal components is visibly looser than it is in adults. Additionally, the first two vertebral centra become completely engulfed by their respective basal cartilages, while more posterior centra are still quite visible.

Another ontogenetic trend observed in *Squatina* is a general decrease in the proportional lateral expansion of the first and second basiventral cartilages compared to the third and fourth basiventral cartilages. It was noted by Carvalho et al. (2008) that the basiventrals of †*Pseudorhina alifera* are more slender proportionally and shorter than basiventrals of *Squatina*. This is most obvious when directly comparing adult specimens of both *Squatina* and †*Pseudorhina*. Fetal specimens and the smallest juveniles, however, have nearly the same proportional lateral basiventral expansion (Figs 2, 4).

The decrease in size of the anteriormost basiventrals is therefore likely coupled with the tendency for the cranium to decrease in size relative to body size during development (Cloutier 2010).

In addition, the size of the occipital hemicentrum decreases relative to the neurocranium and more posterior vertebral centra. This is coincident with the size of the basioccipital fovea, which is unambiguously present in fetal specimens of all species of Squatiniformes examined for this study. The basioccipital fovea is also present in more mature specimens, though it is much smaller relative to overall skull and vertebral size than it is in fetal and juvenile specimens. During development, the lateral aspect of the squatiniform occipital region appears to retract anteriorly and the occipital hemicentrum does not grow uniformly with more posterior vertebral centra. Therefore, the region is present although it appears truncated. This contrasts the observations made by Melouk (1949) that describe a projection of the occipital regions posteriorly, past the occipital hemicentrum and overlapping the first complete centrum in other taxa such as *Sphyrna* (Figs 5C–D).

In these examples of ontogenetic shifts, there is a similar trend when comparing the same taxon at different growth stages as when comparing extinct and extant taxa at the same growth stages. While †*Pseudorhina* and *Squatina* follow the same trajectory, *Squatina* starts at a later stage. Thus, the evolution of the anatomical module of the anterior vertebral column is likely an example of postdisplacement heterochrony (Godfrey & Sutherland 1996; Cloutier 2010).

Functional Considerations

Basiventral expansion is present in members of Squatiniformes, Orectolobiformes, Carcharhiniformes, Pristiophoriformes, and Batoidea (Fig. 7), but the functional significance of this morphology is not currently known. The morphology of expanded basiventrals in these disparate taxa is highly variable; for each taxon there is a difference in the number of expanded basiventrals, the ultimate length of each expanded basiventral, and the degree and/or direction of curvature of each basiventral. The apparently independent evolution of expanded basiventrals along multiple lineages of neoselachians makes it possible to hypothesize on their functional significance, because cases of parallel evolution are presumably due to something other than shared ancestry, such as function. Developing and testing hypotheses is, however not so straight forward, because these member taxa are within clades that are known to have vastly different modes of feeding and swimming – two of the most-studied functions in neoselachians (e.g., Wilga & Lauder 2004; Motta 2004).

There are however, similarities across the different clades of neoselachians that are also observed in other vertebrate lineages. Thus, we can cautiously hypothesize about functional correlations in neoselachians, which can and should be tested in future studies. For instance, it is possible that the evolution of suction feeding in neoselachians is linked to the evolution of novel morphology in the craniovertebral region. It also is possible that the evolution of maneuverable swimming in neoselachians (i.e., anguilliform or subcarangiform swimming) is linked to the evolution of novel morphology in the craniovertebral region. We base our hypotheses on the skeletal morphology of specimens examined; therefore future investigation of the soft tissue (i.e., musculature and ligaments) at the craniovertebral joint, as well as additional behavioral observations will provide valuable information to test these hypotheses.

Neoselachians are unlike bony fishes (e.g., Osteichthyes) in that their pectoral skeleton is not attached to their skull. In most bony fishes, the pectoral girdle is fixed in place to the posttemporal bone via cleithral elements (e.g., Gregory 1933). That connection may limit the range of lateral (side-to-side) rotation, while
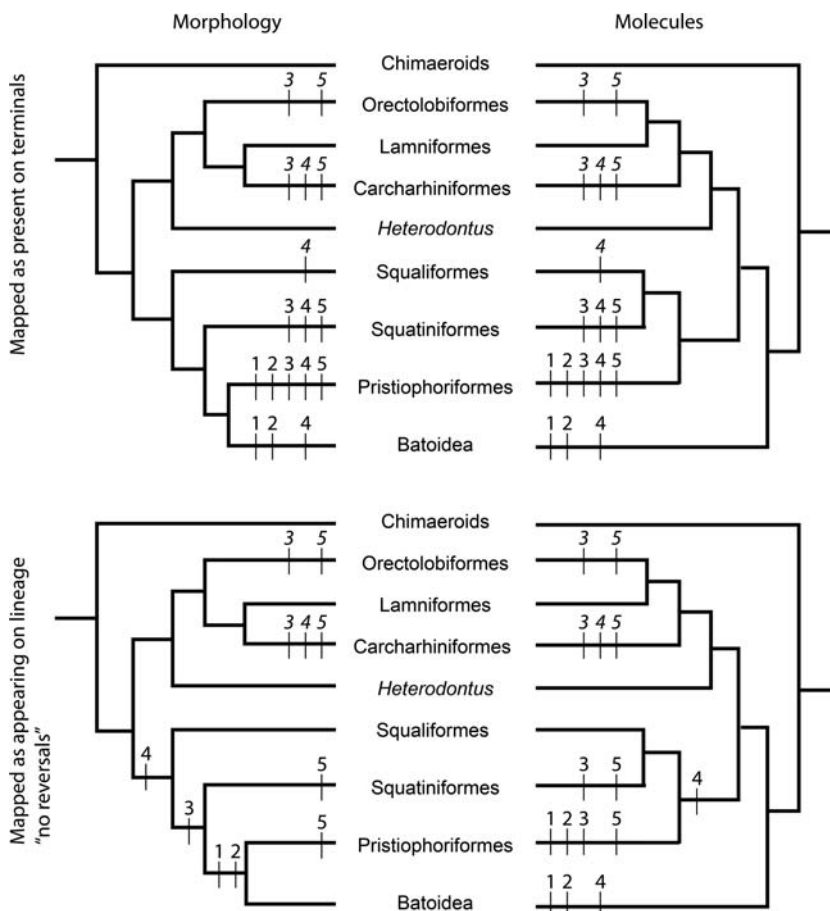

Figure 7. Mapped features on alternative hypothesis. Hypothesis from Figure 1, with morphological features described in this paper, and behaviors documented by other researchers. Numbers in italics represent occurrences in only some members of marked lineages. **1** – occipital hemicentrum absent; **2** – basioccipital fovea absent; **3** – basiventral expansion present; **4** – exhibits head elevation; **5** – exhibits lateral head movements.

at the same time facilitating dorsal/ventral flexion or rotation of the skull at the supracleithral-posttemporal joint in conjunction with the craniovertebral joint during cranial elevation (Carroll et al. 2004). In actinopterygians, cranial elevation occurs across a wide, stable axis provided by paired, lever-like supracleithral-posttemporal joints. Cranial elevation, in addition to hyoid depression, jaw opening, and jaw protrusion, is known to drive the initial phase of suction feeding in bony fishes (Lauder 1982). Despite the absence of the supracleithral-posttemporal connection, cranial elevation is also exhibited by a number of elasmobranch taxa that are known suction feeders (Fouts & Nelson 1999; Motta & Wilga 1999; Wilga & Motta 2000; Edmonds et al. 2001; Laptikhovsky et al. 2001; Motta et al. 2002; Lowry & Motta 2007; see also Motta et al. *in* Edmonds et al. 2001). Furthermore, in several of the taxa known to elevate their cranium, there are expanded basiventrals (pers. obs.). That expansion, which spans the craniovertebral joint, may help to reinforce the axis of rotation in the absence of a pectoral skeletal connection, and thus may provide more area for muscle attachment.

Placoderms, known only from the fossil record, are another group of fishes that also have a highly modified anterior vertebral skeleton, possessing a true synarcual. The development of that synarcual was recently addressed by Johanson et al. (2010). In several different placoderm taxa, the synarcual is described as "hourglass" shaped – i.e., the anteriormost portion is broad in its articulation with the occipital region of the neurocranium and narrows greatly near the mid-length of the element (Carr et al. 2009; Lelièvre & Carr 2009; Johanson et al. 2010). Researchers hypothesize that the morphology of the craniovertebral articulation in placoderms may have permitted substantial range of motions, such as head lift during benthic suction feeding (Ritchie 2005; Carr et al. 2009).

Tetrapods also lack a connection between the pectoral girdle and the skull. That dissociation is considered to be a critical change during the fish-to-tetrapod transition because it meant the head could move from side-to-side independently from the body during terrestrial locomotion (Downs et al. 2008). Considering that form and function correlation, the dissociation of the skull and pectoral girdle in neoselachians may also mean that the head can move about the craniovertebral joint freely. However, moving the head from side-to-side independently of the body underwater may pose a disadvantage.

Neoselachians have evolved several modes of swimming that involve the whole body (anguilliform), the posterior two-thirds of the body (subcarangiform), or the posterior third of the body (carangiform or thunniform) (Wilga & Lauder 2004). In carangiform-swimming taxa (e.g., Lamniformes), the anterior portion of their body is larger and stiffer than the posterior portion of their bodies. As a result, they resemble a torpedo. These taxa are known to keep their heads and mid-body stable during swimming and none of the taxa sampled

within Lamniformes exhibited basiventral expansion. Some of the anguilliform-swimmers (e.g., orectolobiform and squatiniform) do, however, have basiventral expansion and it is possible that the laterally expanded processes are involved in restricting lateral movements of the mid-body relative to the skull during swimming. This may be particularly relevant for taxa with major modifications to their anterior neurocranium, such as the hammerhead *Sphyrna* (Melouk 1949) and the sawshark *Pristiophorus* (Wueringer et al. 2009) that have significant counterweight anterior to the craniovertebral junction.

Phylogenetic Considerations

The modifications of the occipital region and vertebral column in *Squatina* were recognized by Melouk (1949), who concluded that the anterior part of the vertebral column ". . . illustrates the line of evolution of [Selachii]," specifically between the Squaliformes [Squatiniformes] and Rajiformes [Batoidea], although he excluded *Pristiophorus* (Melouk 1949, p. 48). He later provided additional support for an intermediate position of *Squatina* and stated that the occipital-vertebral region was modified but not fused (Melouk 1954, p. 154).

Among the first comprehensive modern attempts at resolving elasmobranch relationships were studies conducted by Compagno (1973, 1977) in which he divided the elasmobranchs into four groups based on overall similarity; squatinimorphs (angel sharks), squalomorphs (dogfish), batoids (skates and rays), and galeomorphs (all other sharks). In both studies, craniovertebral morphology was not used to link *Squatina* between squalimorphs and batoids. Compagno's four groups have undergone much study and revision, however, they have largely held up in numerous later studies, including one conducted by Shirai (1992a), in which the results supported a clade known as Hypnosqualea. Within the Hypnosqualea, *Pristiophorus* and batoids were more closely related to each other than either was to the squatiniforms (Shirai 1992a, p. 507). This relationship was supported in part by craniovertebral morphology. Results of additional morphological analyses by Shirai (1992b, 1996), Carvalho (1996), and Carvalho & Maisey (1996) maintained a hypnosqualean group with more support and minor changes in the characters used to infer those phylogenies. Each of those analyses cited two characters that relate to the occipital and anterior vertebral regions: the presence/absence of a basioccipital fovea and the presence/absence of an occipital hemicentrum. Our observation of a basioccipital fovea in *Squatina* and †*Pseudorhina* is contrary to prior findings and should thus be scored differently in future studies.

The small size of the occipital hemicentrum in *Squatina* (Figs 2–3) is also significant in the discussion of hypnosqualean taxa. According to Shirai (1992a, 1992b), the occipital hemicentrum was reduced in Squatiniformes and absent in *Pristiophorus* and batoids. While the occipital hemicentrum is in fact reduced in *Squa-*

tina, it is not reduced in †*Pseudorhina*. The occipital hemicentrum in †*Pseudorhina* actually is relatively larger than the hemicentrum in the extant *Schroederichthys*. If Squatiniformes is monophyletic, a hypothesis for which there is a great deal of support (Carvalho et al. 2008; pers. obs.), two possible scenarios arise when plotted on the morphological phylogeny. Either there was a reduction of the hemicentrum at the common ancestor of Squatiniformes + (Pristiophoriformes + Batoids) and a subsequent increase in hemicentrum size in †*Pseudorhina* and loss in *Pristiophorus*, or, there was one hemicentrum reduction in *Squatina* and one loss in *Pristiophorus*. The second scenario is more parsimonious, and we take it to mean that the condition in †*Pseudorhina* does not represent a reversal. A reduction seems to have also occurred in other parts of the tree (e.g., *Schroederichthys*: Carcharhiniformes) and may indicate more of a functional correlation than a phylogenetic precedence.

Molecular hypotheses of elasmobranch systematics consistently indicate that batoids are the sister taxon to modern sharks and that *Pristiophorus* and *Squalus* are more closely related to one another than either is to *Squatina* (Dunn & Morrissey 1995; Kitamura et al. 1996; Schwartz & Maddock 2002; Douady et al. 2003; Winchell et al. 2004; Heinicke et al. 2009). The continued support for a batoid-shark sister taxon relationship from those molecular analyses warrants continued investigation of characters used in modern morphological studies, like the presence or absence of a basioccipital fovea and an occipital hemicentrum. When we map the morphological observations made for this study onto molecular-based trees, we inevitably find that the absence of a basioccipital fovea requires an additional step when batoids are not closely related to sawsharks. Based on the definition of the basioccipital fovea (Maisey 1982, 1983; Shirai 1992a, 1992b, 1996), however it is possible that the feature was not lost in some (or all) batoids. Thus, if the notch in the batoid basicranium were a basioccipital fovea, the absence of a basioccipital fovea would be autapomorphic for Pristiophoriformes. One more step is also required when scoring the absence of an occipital hemicentrum for Batoidea. Interestingly, there is also an extra step added for the presence of basiventral expansion in 'Hypnosqualea' depending on the molecular phylogeny, because sometimes Squatiniformes is aligned with Pristiophoriformes, while other times it is sister to Squaliformes.

Conclusions

By comparing juvenile, fetal, and fossil specimens, we have begun to decouple ontogenetic from phylogenetic variation and in the process, we reveal evolutionarily significant shifts in developmental morphology that have the potential to change are current notions of elasmobranch systematics. Although our new observations are not included in a phylogenetic analysis, data sug-

gest that either hypothesis, morphological or molecular is plausible, and potentially reflects the conservative nature of the region. Further data collected on the fossil record and ontogeny of additional non-batoid sharks will be critical for lending more support to either phylogenetic hypothesis.

The occipital development in batoids is important to examine further detail. In prior cladistic analyses of elasmobranch systematics the craniovertebral articulation of batoids was noted to lack a basioccipital fovea and an occipital hemicentrum. However, the unpaired notch ventral to the foramen magnum that is present in the skull in several batoids more closely resembles the condition in non-pristiophoriform sharks than the pristiophoriforms. There is, however, a great deal of morphological variability of that notch within Batoidea and currently makes the presence or absence of a basioccipital fovea non-applicable for the clade as a whole.

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Appendix

Suggested characters and states for the anterior vertebral skeleton in Elasmobranchs. Modified states from previously published characters are listed in bold.

1) Occipital Hemicentrum (modified from character 21, Shirai 1996): [0] absent; **[1] present and spherical – much smaller than more posterior vertebrae (e.g., Squatina); [2] present and cylindrical – diameter equal to diameter of more posterior vertebrae (e.g., †Pseudorhina and † Protospinax).**

2) Basioccipital fovea (modified from character 20, Shirai, 1996): [0] present; [1] absent.

3) Lateral extent of anterior-most basiventrals: [0] not wider than posterior basiventrals; [1] at least first four basiventrals laterally-expanded (e.g., *Squatina* and *Pristiophorus*).

4) Contour of lateral margins of anterior-most basiventrals: [0] wedged shaped, like more posterior basiventrals; [1] flat margin that is angled/tapered anteroposteriorly (e.g., *Squatina*); [2] curved margins that are reflected dorsally (e.g., *Pristiophorus*).