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ONTOGENY OF THE BRAINCASE IN *STENOPTERYGIUS* (REPTILIA, ICHTHYOSAURIA) FROM THE LOWER JURASSIC OF GERMANY

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ABSTRACT—The fossil record of the ichthyosaur genus *Stenopterygius* comprises a large number of specimens of all ontogenetic stages. This makes the taxon a good model for ontogenetic studies in a Mesozoic marine reptile. Here, we describe the morphology of the braincase elements of *Stenopterygius* over ontogeny and compare it with that of other known ichthyosaur braincases. Substantial ontogenetic changes were observed in most elements. These included negative allometry of the exoccipitals relative to the basioccipital, changes in the morphology of the parabasisphenoid and proportional reduction of the ridge separating the right and left internal carotid arteries, variable relative length of the paroccipital process of the opisthotic in juvenile specimens, and relative ossification of the basioccipital peg. Furthermore, we observed variability in relative braincase ossification between embryos within a single gravid female.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Ichthyosauria is a diverse group of marine reptiles with a stratigraphic range spanning the Early Triassic to the Late Cretaceous (e.g., Motani, 2005). Multiple adaptations to a secondarily aquatic habitat are symplesiomorphic for the group (e.g., Motani et al., 2014: *Cartorhynchus*), and later members of the clade became increasingly specialized for a pelagic way of life. It is very likely that all ichthyosaurs were viviparous, based on many adult individuals associated with embryonic remains, from the Early Triassic to the Cretaceous (e.g., Maxwell and Caldwell, 2003; Motani et al., 2014; Boyd and Lomax, 2018). The best record of ichthyosaurian embryonic material originates from the Lower Jurassic of Holzmaden, Germany, which is famous for exceptional preservation of marine reptile material. In particular, large numbers of gravid females of the common ichthyosaur genus *Stenopterygius* are available in museum collections. Large numbers of juvenile *Stenopterygius* specimens are also available, forming a relatively complete ontogenetic series and allowing detailed observations regarding growth and development in ichthyosaurs. For instance, allometric growth (McGowan, 1973a), changes in limb-bone shape and number (Johnson, 1977; Caldwell, 1997; Maxwell et al., 2014), and changes in diet and tooth morphology (Dick and Maxwell, 2015; Dick et al., 2016) over ontogeny have all been investigated in this genus. However, the ontogeny of other aspects of skeletal morphology has received much less attention.

The braincases of ichthyosaurians have long been the subject of study (Huene, 1949; McGowan, 1973b; Kear, 2005) and differ from those of other diapsids in that the individual bones remain unfused in adults. In addition, the basioccipital of most ichthyosaurs, except some basal forms, lacks basal tubera, which are widely distributed in other diapsids (Camp, 1980; Maisch and Matzke, 2006; Evans, 2008; Gardner et al., 2010). Braincase morphology has also been used as a source of characters in phylogenetic analyses of ichthyosaurian ingroup relationships. Features such as the shape of the quadrate, the relative size of the extracondylar area of the basioccipital, the shape of the medial head of the stapes, the shape of the parabasisphenoid, and the relative contribution of the supraoccipital to the dorsal and lateral edges of the foramen magnum, among others, are thought to vary across the clade (see Moon, 2017). Detailed morphological studies have been carried out on reconstructed braincases of Jurassic ichthyosaurs such as *Ichthyosaurus* (McGowan, 1973b), *Ophthalmosaurus icenicus* (Moon and Kirton, 2016), *Hauffiopteryx* ?*typicus* (Marek et al., 2015), and more recently *Protoichthyosaurus prostaxalis* (Lomax et al., 2019). A digital reconstruction has also been made of the braincase of the Cretaceous ichthyosaur *Platypterygius australis* (Kear, 2005). Studies of braincase morphology have been primarily focused on presumably adult individuals, with one exception: the braincase of an embryo of *Platypterygius australis* has been studied in detail (Kear and Zammit, 2013). Although the braincase is historically viewed as slowly evolving and relatively invariant in ichthyosaurs (e.g., McGowan, 1972), this is not necessarily the case (Maisch, 1997). Potential bias introduced by computed tomography (CT)-based studies drawing conclusions on single, potentially immature, individuals has not been investigated comprehensively. In particular, the studies of *Hauffiopteryx* featured a suspected juvenile (Marek et al., 2015).

In this study, we qualitatively describe ontogenetic variation in the braincase of the Jurassic parvipelvian ichthyosaur

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Stenopterygius, including the description of braincase elements in embryonic material. Our study involved all three Early Jurassic species currently considered valid (Maxwell, 2012) but is in most part based on the most abundant species of *S. quadriscissus* and to a lesser degree *S. triscissus*. We included one specimen of *S. uniter* to highlight its adult opisthotic morphology. Understanding ontogenetic variability in this genus will aid in recognizing ontogenetic variation in more poorly known ichthyosaurian taxa. It will also likely improve character definitions and scoring in phylogenetic analyses of the clade.

METHODS

We studied 35 *Stenopterygius* specimens from the collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS), in which all or some of the braincase elements were exposed; four of these were gravid females in which the embryonic braincases could also be observed (see Table S1 in Supplemental Data). We assigned adult and juvenile specimens to species following Maxwell (2012). Most adult individuals in the study were referable to *S. quadriscissus*, but some specimens referred to *S. triscissus* and a single *S. uniter* were also included to the analysis, as well as some material that was specifically indeterminate. All specimens are from the early Toarcian (Early Jurassic) Posidonienschiefer Formation, excavated from quarries located around the village of Holzmaden, Germany. Due to the mode of preservation and preparation, the elements were studied mostly in two dimensions and in only one view. Orientation and preservation can affect interpretation of morphology, which is why multiple views and individuals were examined whenever possible. Linear measurements were taken as well as detailed photographs. Because *Stenopterygius* does not show lines of arrested growth (LAGs) in the limb bones, it is very difficult to assess an individual's ontogenetic age (Houssaye et al., 2014). We used mandible length as a proxy for age. We distinguished between sexually mature adults and juveniles based on the mandibular length of the smallest known gravid specimen, which is ca. 400 mm (McGowan, 1979). We further subdivided the juveniles into small (<300 mm lower jaw length) and large (300–399 mm lower jaw length) size classes, following Dick et al. (2016). We also defined two embryonic stages based on mandible length and vertebral centrum ossification; we refer to these as early and late embryonic stage, respectively. Because both of these stages fall toward the end of the embryonic period, well after the onset of ossification of most of the skeleton, the terms 'early' and 'late' are relative only to each other (see Table S1).

RESULTS

The results and observations will be presented as follows: We first remark upon the general morphology of the element across adults the species, then on any ontogenetic variation visible. The ontogenetic remarks are in principle applicable to both *S. quadriscissus* and *S. triscissus* unless stated otherwise. Because there was no juvenile or embryonic material for *S. uniter* available, we cannot conclusively state that the general ontogenetic observations are also valid for this species. Because the primary purpose of this paper is to describe braincase ontogeny in *Stenopterygius*, we make only basic comparisons with adults of other ichthyosaurian species, unless pertinent to understanding homology or intraspecific variation.

Basioccipital

The basioccipital is the largest element in the braincase of *Stenopterygius*. In posterior view, it consists of a large occipital condyle, which articulates with the atlas-axis complex, and the extracondylar area. On the condyle, the notochordal pit is visible. Dorsally, the basioccipital has facets on either side of the foramen magnum floor for the exoccipitals and, more laterally, slightly protruding facets for the opisthotics. The exoccipital and opisthotic facets have a smooth surface. The floor of the foramen magnum is in adults demarcated by slight ridges laterally and is hourglass-shaped in dorsal view (see SMNS 58881 and SMNS 81961; Fig. 1E). Its texture is smoother than the other dorsal areas of the basioccipital. In the basioccipitals of adults, in anterior or posterior view, the foramen magnum floor would be visible because the ridges are raised above the dorsal surface of the basioccipital (e.g., SMNS 50187; Fig. 1J). Anteriorly, the element has a distinct basioccipital peg, which is broad and anteriorly rounded in dorsal view (SMNS 58881 and SMNS 81961; Fig. 1E), contrary to basioccipitals of more derived ophthalmosaurids (e.g., Fischer et al., 2012; Moon and Kirton, 2016). Moreover, the extracondylar area of *Stenopterygius* is more prominently visible than in the latter clade. Although some individuals, such as SMNS 50165, have a slight notch in their extracondylar area ventrally, this is not seen in all adult individuals. Anteroventrally, the basioccipital has a facet for articulation with the basisphenoid. The basisphenoid facet bears a groove in the sagittal plane ventral to the basioccipital peg (as in SMNS 50376) and is rugose even in large adults.

The extracondylar area and basioccipital condyle of *Stenopterygius* ossify prior to birth. This is visible in embryos associated with specimens SMNS 50007 (*S. triscissus*) and SMNS 80234 (*S. quadriscissus*; Fig. 1F, G). The extracondylar area and the condyle of *S. quadriscissus* are relatively similar in size in embryonic specimens. In the embryonic stage, where ossification is present, they both have a sandpaper-like or rugose surface texture. However, the condyle is substantially more rugose (material associated with SMNS 80234; Fig. 1F, G). The rugose surface of the condyle is still present in neonates and small juveniles, e.g., SMNS 51959 and SMNS 81806 (Fig. 1H), but is replaced by a smooth surface in large juveniles, as seen clearly in SMNS 80062 (Fig. 1I). The extracondylar area displays a smooth surface earlier in ontogeny than the condyle due to ossification of the perichondrium. In large juveniles, SMNS 80062 (Fig. 1I) and SMNS 51551, the extracondylar area still appears smoother than the condyle, which retains a rugose surface. The notochord pit is easily visible on the condyle and does not shift position through ontogeny. The size of the notochord pit seems to vary somewhat isometrically with the size of the condyle over ontogeny. The dorsally projecting ridges on either side of the foramen magnum are reduced or absent in large juveniles, and in dorsal view the foramen magnum floor is relatively less hourglass-shaped in this stage, e.g., SMNS 50003 and SMNS 81958 (Fig. 1C, D). Unlike in adults, in which the floor of the foramen magnum can be distinguished from the dorsal surface of the element (SMNS 58881 and SMNS 81961; Fig. 1E), in small juveniles the floor of the foramen magnum usually cannot be differentiated from the rest of the dorsal surface of the basioccipital, although one specimen, SMNS 56615, has a groove between the exoccipital facets. It has previously been noted that the relative development of the ridges on either side of the floor of the foramen magnum vary with ontogeny in *Stenopterygius* (Hungerbühler, 1991). The protrusion of the opisthotic facets is less prominent in juveniles relative to adults; see SMNS 81958 (juvenile; Fig. 1D) and SMNS 81961 (adult; Fig. 1E). In large juveniles, the basioccipital peg is relatively narrower than in adults, e.g., SMNS 50003 and SMNS 81958 (Fig. 1C, D). In embryos, the basioccipital peg is not present and an anterior notochordal pit is present instead (material associated with SMNS 80234; Fig. 1A). This anterior notochordal pit persists in very small juveniles (e.g., SMNS 12821).
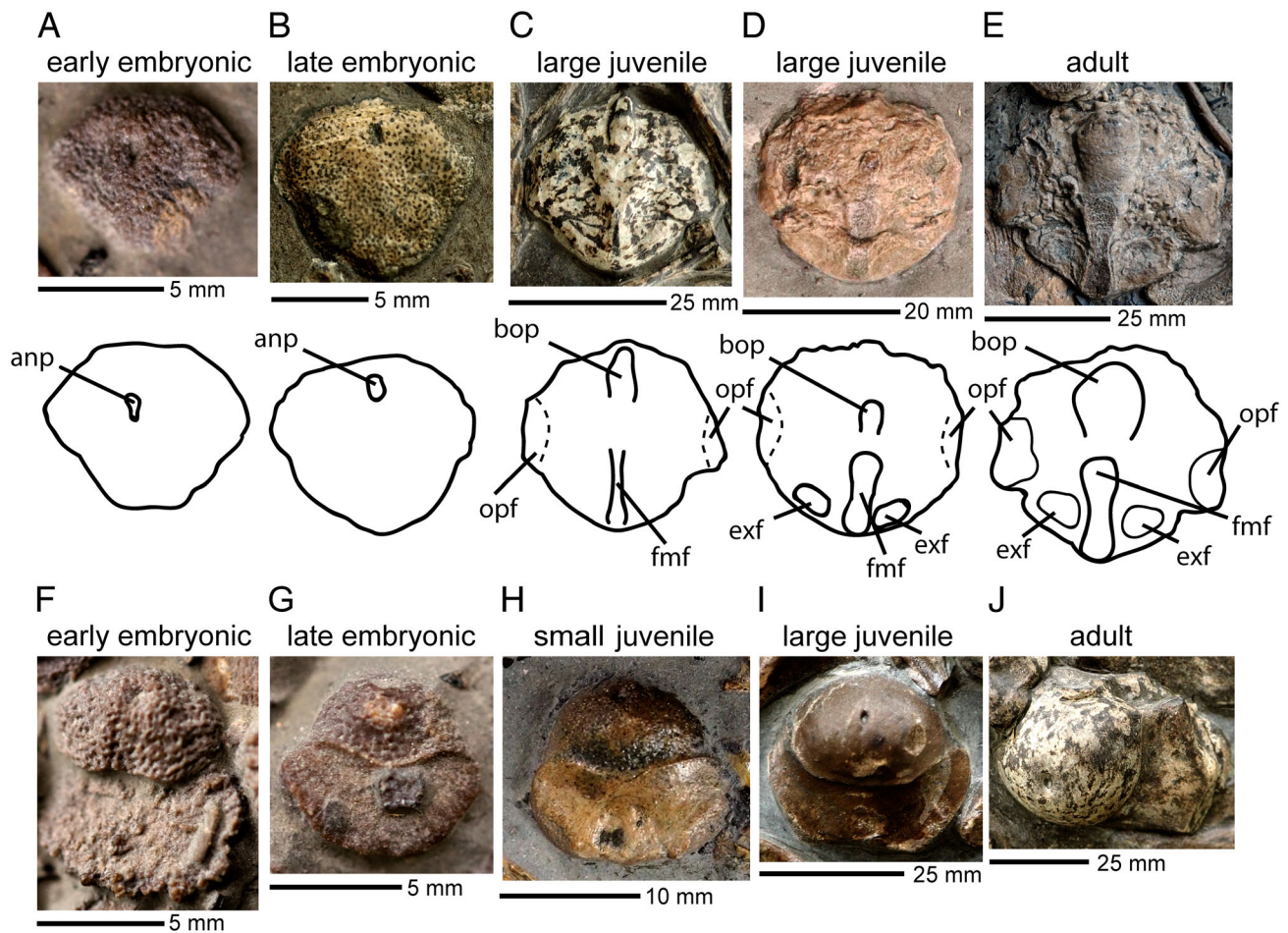
FIGURE 1. *Stenopterygius* basioccipitals in dorsal (**A–E**) and posterior (**F–J**) views in order of increasing ossification. **A–E**, anterior is toward the top of the page; interpretive drawings below the images. **A**, embryo *S. quadriscissus*, SMNS 80234; **B**, embryo *S. quadriscissus*, SMNS 54064; **C**, juvenile *S. quadriscissus*, SMNS 50003; **D**, juvenile *S. quadriscissus*, SMNS 81958; **E**, adult *S. quadriscissus*, SMNS 81961; **F**, embryo *S. quadriscissus*, SMNS 80234; **G**, embryo *S. quadriscissus*, SMNS 80234; **H**, juvenile *Stenopterygius* sp., SMNS 81806; **I**, juvenile *S. quadriscissus*, SMNS 80062; **J**, adult *S. triscissus*, SMNS 50187. **Abbreviations**: **anp**, anterior notochord pit; **bop**, basioccipital peg; **exf**, exoccipital facet; **fmf**, floor of the foramen magnum; **opf**, opisthotic facet.

Parabasisphenoid

The basisphenoid forms the floor of the braincase of ichthyosaurs and is ventrally coossified with the parasphenoid. Posterodorsally, the parabasisphenoid is in articulation with the basioccipital. Ventrolaterally, it articulates with the pterygoids. In adults of *S. quadriscissus*, the parabasisphenoid is normally a quandrangular structure. The facet for articulation with the basioccipital as well as most of the dorsal surface are rugose, whereas the other areas, including the pterygoid facets, are smooth, as in, e.g., SMNS 80234 and SMNS 54062 (Fig. 2E, I). The basioccipital facet is divided in two along the sagittal plane. This posterior groove also partly divides the parabasisphenoid dorsally (as seen in SMNS 80234 and SMNS 54062; Fig. 2E, I). In ventral view, the internal carotid foramen is situated on the ventral surface of the parabasisphenoid. In most adults, the internal carotid foramen has an unpaired, undivided morphology, e.g., SMNS 81961, but sometimes remnants of the separating ridge are visible, as in SMNS 50376 (Fig. 2J).

Contrary to the adults, some juvenile specimens have a more wing-shaped morphology of the parabasisphenoid in ventral view, whereby the anterior part of the element is wider than the posterior edge. This could be due to the earlier development of

basipterygoid processes relative to the other parts of the parabasisphenoid (e.g., SMNS 56631 and SMNS 81958; Fig. 2H). The sagittal division of the posterior basisphenoid is already visible in the late embryonic stage (SMNS 54064 and SMNS 81961; Fig. 2B, C) and persists throughout ontogeny. The internal carotid foramen is visible throughout ontogeny in both dorsal and ventral views. In adults the internal carotid foramen sometimes appears undivided in ventral view, whereas in the embryonic and juvenile stages it has a dorsal ridge which clearly separates two channels within a single foramen in ventral view. This is clearly visible in embryonic material associated with SMNS 80234 (Fig. 2F, G) and in a large juvenile, SMNS 81958 (Fig. 2H).

Quadrate

The quadrate is a large element in the skull of *Stenopterygius*, connecting the cranium to the mandible and forming part of the jaw joint. Posteroventrally, the quadrate articulates with the articular and surangular of the mandible, and dorsally it connects to the supratemporal. The element is elongated in the dorsoventral plane and is dorsally more slender than ventrally. The dorsal half of the occipital lamella, which contacts the
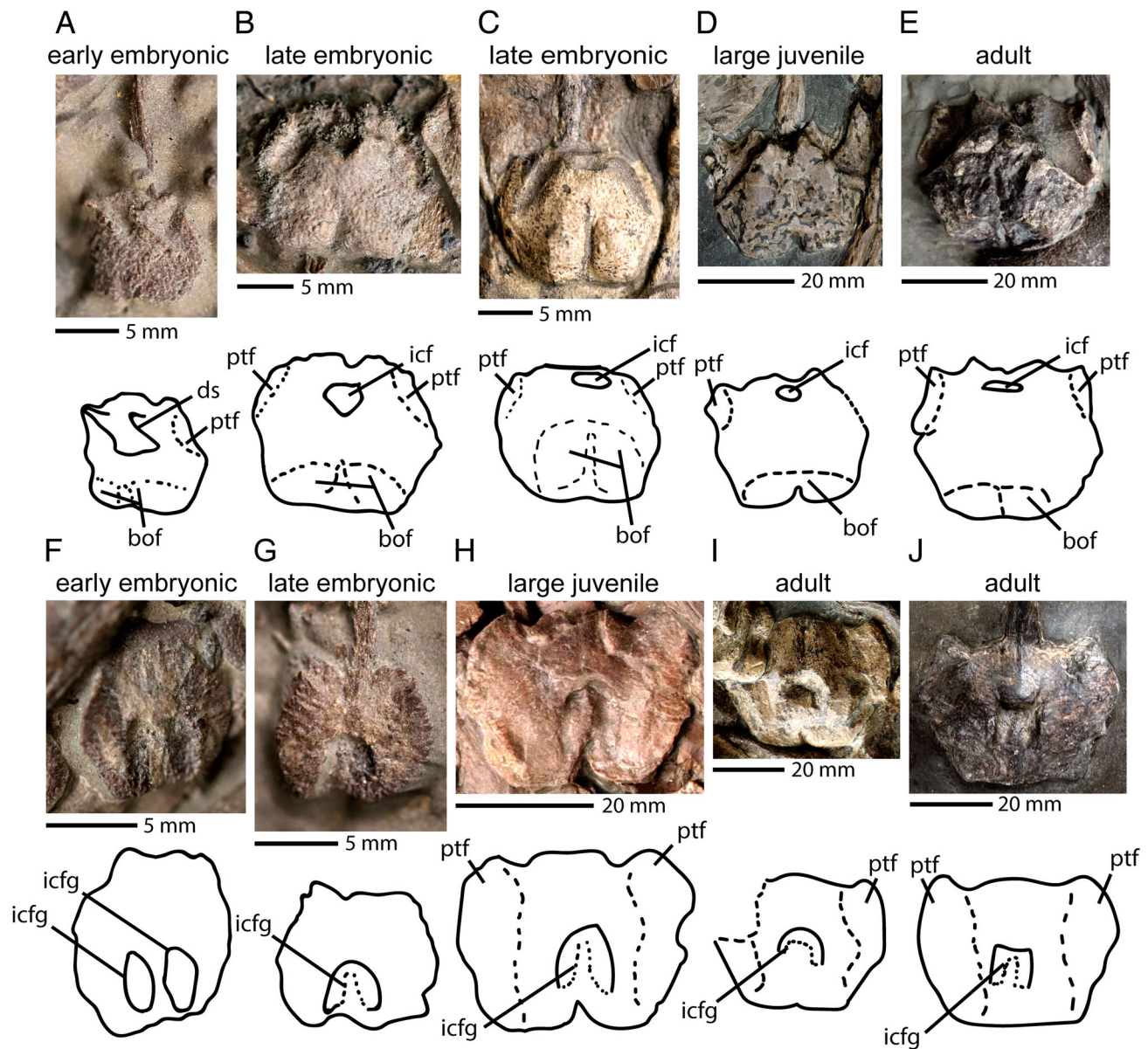
FIGURE 2. *Stenopterygius* parabasisphenoids in dorsal (**A–E**) and ventral (**F–J**) views in order of increasing ossification. Anterior is toward the top of the page. Interpretive drawings below the images. **A**, embryo *S. quadriscissus*, SMNS 80234; **B**, embryo *S. quadriscissus*, SMNS 81961; **C**, embryo *S. quadriscissus*, SMNS 54064; **D**, juvenile *S. quadriscissus*, SMNS 54026; **E**, adult *S. quadriscissus*, SMNS 80234; **F–G**, embryo *S. quadriscissus*, SMNS 80234; **H**, juvenile *S. quadriscissus*, SMNS 81958; **I**, adult *S. quadriscissus*, SMNS 54062; **J**, adult *S. quadriscissus*, SMNS 50376. **Abbreviations**: **bof**, basioccipital facet; **ds**, dorsum sellae; **icf**, internal carotid foramen; **icfg**, ventral internal carotid foramen groove; **ptf**, pterygoid facet.

supratemporal, curves slightly posterolaterally in adult *S. quadriscissus* (see SMNS 55343 and SMNS 54062; Fig. 3E). In articulated material, this curvature would create a distinct quadrate foramen (the posterior-medial opening between the quadrate and the quadratojugal; 'elliptical/oval foramen' of McGowan, 1973b), as seen in other Jurassic ichthyosaurs (e.g., *Temnodontosaurus*, *Ichthyosaurus*, *Ophthalmosaurus*, and *Undorosaurus*; McGowan, 1973b; Maisch and Matzke, 2000: fig. 13; Moon and Kirton, 2016; Zverkov and Efimov, 2019). In adults, the ovoid stapedial facet is located (postero)ventrally on the medial side of the quadrate, just dorsal to the articular condyle. The condyle is divided into two bosses of relatively similar size, with the medial of the two protruding slightly anteriorly, as seen in SMNS 55343.

In juveniles and embryos, the division of the quadrate condyle is less pronounced and the condyle is often observed as a single structure (Fig. 3A–C). Furthermore, the quadrates of adult specimens differ in external bone texture from all juvenile stages, because a lumpy texture often appears on the lamellae of the adult quadrates (SMNS 54062; Fig. 3E). This may be explained by an interaction between the pattern of ossification of the bone and taphonomic compression, as seen in the long bones of other marine reptiles (Hugi and Scheyer, 2012). In both small and large juveniles, the lateral curvature of the dorsal occipital lamellae of the quadrate is virtually nonexistent; likewise, the articular condyle protrudes less prominently (good examples include SMNS 50003, SMNS 81806, and SMNS 54026; Fig. 3C, D). This makes the quadrate look more rectangular in medial
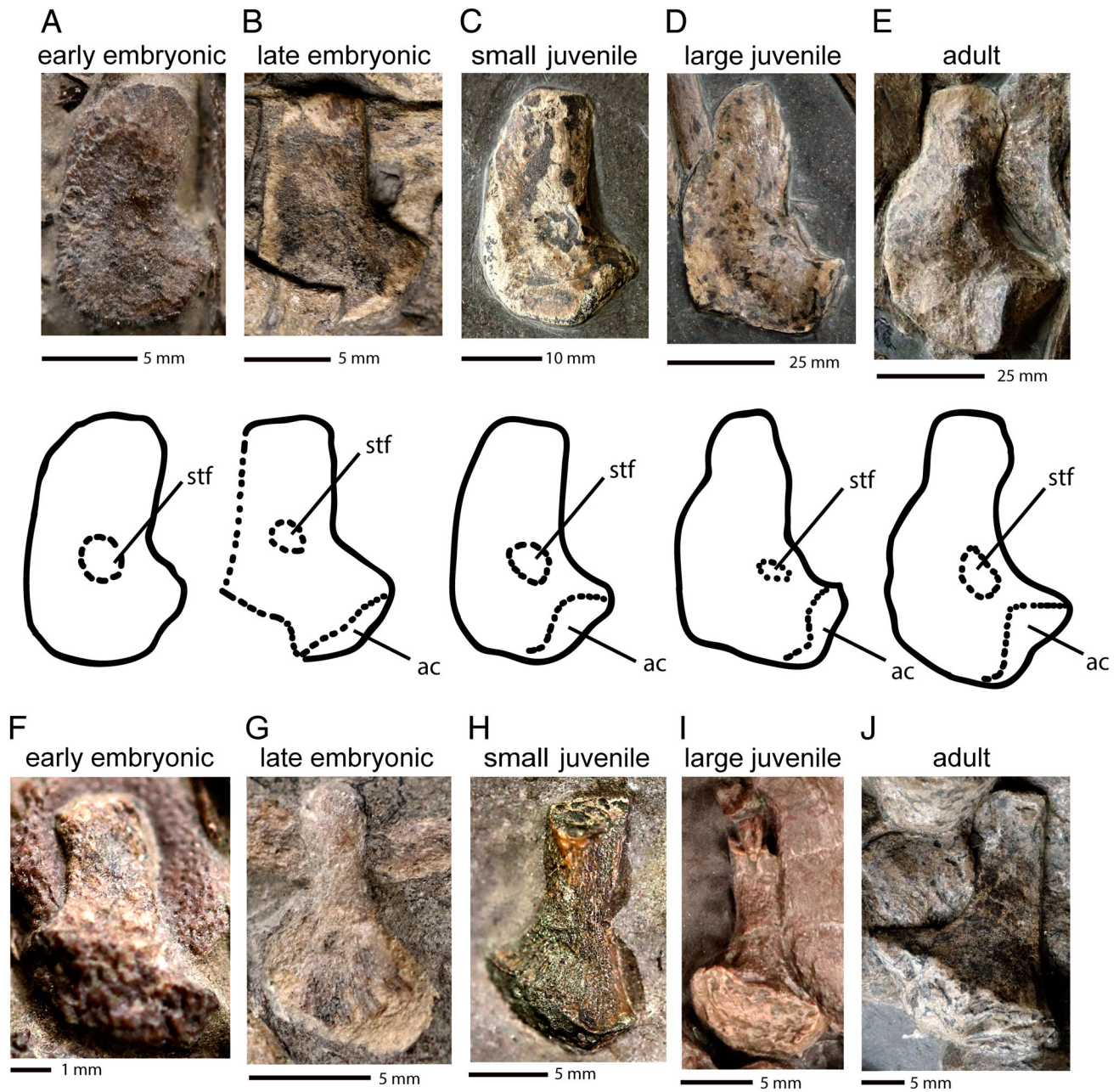
FIGURE 3. *Stenopterygius* quadrates in posteromedial view (**A–E**) and stapes in anterior (**F, J**), posterior (**G, H**), and ventral (**I**) views in order of increasing ossification. Quadrates are right quadrates except for **B** and **E**, which are mirrored left quadrates. Stapes are right stapes except **I**, which is a mirrored left stapes. For quadrates, interpretive drawings below the images. **A**, embryo *S. quadriscissus*, SMNS 80234; **B**, embryo *S. quadriscissus*, SMNS 54064; **C**, juvenile *S. quadriscissus*, SMNS 50003; **D**, juvenile *S. quadriscissus*, SMNS 54026; **E**, adult *S. quadriscissus*, SMNS 54062; **F**, embryo *S. quadriscissus*, SMNS 80234; **G**, embryo *S. quadriscissus*, SMNS 54064; **H**, juvenile *S. quadriscissus*, SMNS 51139; **I**, juvenile *S. quadriscissus*, SMNS 81958; **J**, adult *S. quadriscissus*, SMNS 54064. **Abbreviations**: ac, articular condyle; stf, stapedial facet.

or lateral view and presumably narrowed the quadrate foramen. Embryonic quadrates are likewise quadrangular in shape in medial and lateral views (Fig. 3A, B). The stapedial facet is not located as close to the articular condyle as in the later ontogenetic stages, but rather posteromedially at approximately half the height of the quadrate, on the pterygoid lamella (as seen in embryonic material associated with SMNS 80234; Fig. 3A).

Stapes

The stapes is an elongate element connecting the quadrate to the basioccipital. It has a long shaft and a bulbous head that articulate with the stapedial facet of the quadrate and the lateral basioccipital, respectively. The lateral head of the stapes of *Stenopterygius* is not expanded; in other words, the area that contacts the quadrate is not wider than the stapedial shaft. When observed in anterior or posterior view, the dorsal surface

of the shaft and the medial head lie in a horizontal plane, whereas the ventral edge curves ventrally. This morphology is observed in SMNS 55343 and SMNS 54064 (Fig. 3J).

The shaft of the stapes varies in length over ontogeny relative to the width of the medial stapes head. Both small and large juveniles have relatively longer shafts compared with the width of the medial head, whereas in adults the medial head is relatively larger. This was observed in, e.g., the large juveniles SMNS 50003 and SMNS 81958 (Fig. 3I), compared with adult specimens SMNS 55343 and SMNS 54064 (Fig. 3J). The ventral projection of the medial head of the stapes has not been observed in small juveniles or neonates. However, we do not rule out the possibility that this morphology may be present in the juveniles, given the small number of stapes that can accurately be determined to be preserved in anterior or posterior view. In general, the bone texture of the shaft of the stapes is relatively smooth starting in the late embryonic stage (material associated with SMNS 80234; Fig. 3F) and does not change over ontogeny. The medial head of the stapes starts off with a rugose texture in the embryonic material and smooths off over ontogeny, although it has still relatively rough bone texture in the adults (e.g., SMNS 54064; Fig. 3J). One large juvenile specimen, SMNS 55074, has the stapes preserved in dorsal view. In this view, the two opisthotic facets are visible, with the groove for the hyomandibular branch of the facial or glossopharyngeal nerve in between.

Supraoccipital

The supraoccipital is an arch-shaped element and the most dorsal ossified part of the braincase. The arch is dorsally overlapped by the parietals, whereas two pillars containing facets on their ventral sides articulate with the exoccipitals. In *Stenopterygius*, the supraoccipital is slightly inclined anteriorly. The parietals overlap about half of the dorsal arch of the element. This is based on two individuals (SMNS 51824 and SMNS 14846) in which the supraoccipital is preserved in life position, although caution should be used given the two-dimensional nature of their preservation. The exoccipitals exhibit a height similar to that of the lateral supraoccipital. The dorsal edge of the foramen magnum in adults is angular, as seen clearly in SMNS 58881 (Fig. 4E). Nutritive foramina are rare in the supraoccipitals in specimens of *Stenopterygius* but are found in many other ichthyosaurs, e.g., *Ophthalmosaurus* and *Ichthyosaurus* (McGowan, 1973b; Moon and Kirton, 2016). Such foramina have been observed in one specimen of *S. triscissus* (SMNS 14846) and in an isolated skull at the

FIGURE 4. *Stenopterygius* supraoccipitals in anterior view (**A–E**) and exoccipitals in medial view (**F–J**) in order of increasing ossification. Exoccipitals are all left exoccipitals except **I** and **J**, which are right exoccipitals mirrored. For supraoccipitals, interpretive drawings below the images. **A**, embryo *S. quadriscissus*, SMNS 80234; **B**, embryo *S. quadriscissus*, SMNS 81961; **C**, juvenile *S. quadriscissus*, SMNS 51139; **D**, juvenile *S. quadriscissus*, SMNS 81958; **E**, adult *S. quadriscissus*, SMNS 58881; **F**, embryo *S. quadriscissus*, SMNS 80234; **G**, embryo *S. quadriscissus*, SMNS 54062; **H**, juvenile *S. quadriscissus*, SMNS 51959; **I**, juvenile *S. quadriscissus*, SMNS 51551; **J**, adult *S. triscissus*, SMNS 96899. **Abbreviation**: **ag**, anterior groove.

Urwelt Museum Hauff in Holzmaden (F.M., pers. observ.). In both cases, there was only one foramen present, contrary to the right-left symmetrical condition observed in *Ophthalmosaurus*, *Ichthyosaurus*, *Protoichthyosaurus*, and *Temnodontosaurus* (McGowan, 1973b; Maisch, 2002, Moon and Kirton, 2016; Lomax et al., 2019).

In large juveniles, the dorsal edge of the foramen magnum is more flattened, which is in contrast to the condition in adults, see, e.g., SMNS 50003 and SMNS 81958 (Fig. 4D). This gives the foramen magnum a larger appearance in juveniles. Both these juvenile specimens have a supraoccipital with a transverse groove visible in anterior view. The groove has likewise been observed in other ichthyosaurs, such as *Ophthalmosaurus* (Moon and Kirton, 2016). The exoccipital facets in most individuals tend to be oriented ventrally. This is consistent throughout ontogeny. However, two individuals, adult specimen SMNS 58881 (Fig. 4E) and large juvenile SMNS 55074, have exoccipital facets projecting more ventrolaterally. Supraoccipitals are present in embryos associated with SMNS 80234 (Fig. 4A) and SMNS 54062. In embryos and small juveniles, the supraoccipital is angular in anterior and posterior views. The lateral rami containing the exoccipital facets project ventrally at 90° from the dorsal edge of the element. The supraoccipital contribution to the foramen magnum is relatively small and angular in embryos and small juveniles, and the anterior groove on the arch appears not to be present at this stage (Fig. 4A–C). In some embryos, the supraoccipital has an angular morphology dorsolaterally, rather than the smooth arch that is present in the adults.

Exoccipital

The exoccipitals articulate with the supraoccipital dorsally and the basioccipital ventrally. These short columnar elements have a smooth dorsal supraoccipital articular facet, which is angled anteroventrally. This facet is smooth in texture and can be as compact and smooth as cortical bone in both adults and juveniles, e.g., SMNS 81958. Evidence for the presence of the hypoglossal (XII) nerve foramen can be found in both adults and embryos, and XII nerve foramina are clearly visible in both *S. quadriscissus* and *S. triscissus* specimens (SMNS 96899 [Fig. 4J]; SMNS 51824 and embryonic material associated with SMNS 80234 [Fig. 4F]). There is little variation in shape in the exoccipitals of *S. quadriscissus* and no apparent shape change through ontogeny. However, the exoccipitals are among the largest elements in the braincase early in ontogeny, whereas they become relatively smaller toward adulthood. In embryonic material (SMNS 50007) and small juvenile material (e.g., SMNS 54851), the exoccipitals are as large as the basioccipital. The exoccipitals in *Stenopterygius* are always as large or larger than the descending processes of the supraoccipital, and in both neonates and adults the supraoccipital contribution to the foramen magnum is relatively small and dorsally angular; it can be assumed that large exoccipitals reflect a proportionately larger foramen magnum in embryos and small juveniles, consistent with negative allometry of the hindbrain and the spinal cord.

Opisthotic

Due to the complex shape and number of possible angles of preservation, it is difficult to assess total morphological variability of the opisthotic in *Stenopterygius*. Generally, it consists of a medial head, which encloses part of the inner ear, and a paroccipital process, which contacts the supratemporal dorsolaterally. In medial view, the impressions of the osseous labyrinth are preserved in a 'V' shape. The impression of the posterior vertical semicircular canal is visible as the dorsal-most indentation. The impression of the horizontal semicircular canal is similar in width and length in all specimens in which it could be observed

(SMNS 58881, SMNS 80115, and SMNS 54062). The dorsal part of the impression of the posterior vertical semicircular canal protrudes outside the main body of the medial head of the opisthotic, giving the element a second distinct process in addition to the paroccipital process (Fig. 5B–E). The paroccipital process in many adults is broad and short, although there is a high amount of variability in the length of the paroccipital process (e.g., SMNS 58881 vs. SMNS 80115). In some adults, the process created by the impression of the vertical semicircular canal is so robust in width and length that it approaches the size of the paroccipital process; this is best observed in posterior view. It gives the opisthotic a more quadrangular outline with two processes; the more slender one is the process of the posterior vertical semicircular canal, which projects dorsally, whereas the other process is the paraoccipital process, which projects dorsolaterally (e.g., *S. quadriscissus* SMNS 51824, *S. triscissus* SMNS 96899, and the isolated skull SMNS 50376). However, in other adults, the paroccipital process is the larger of the two (e.g., *S. quadriscissus* SMNS 54062 and *S. triscissus* SMNS 14846; Fig. 5E), and in one adult the paroccipital process is extremely elongated (*S. uniter* SMNS 17500). The variation in paroccipital process morphology is continuously distributed, rather than there being two distinct morphotypes. In lateral view, the stapedial facets are likewise visible, as well as the groove between them interpreted in *Ophthalmosaurus* as the groove for the passage of the hyomandibular branch of the facial nerve (VII) or the glossopharyngeal nerve (IX) (clearest in SMNS 51824).

The two distinct morphologies of widened or elongated opisthotics are more prevalent in the juvenile specimens. There are those with robust, wide paroccipital processes, such as SMNS 51139 and SMNS 81806 (Fig. 5B), and juveniles with opisthotics displaying a more slender paroccipital process, such as SMNS 50003 (Fig. 5C) and SMNS 54851. In the latter opisthotics, a distinct process for the proximal impression of the posterior vertical semicircular canal is likewise absent, whereas this is present in the robust morphology. The elements displaying the slender morphology are preserved mostly in posterior view and have such a slender morphology that we initially interpreted them as stapes.

We identified one embryonic opisthotic, associated with SMNS 80234 (Fig. 5A). It was preserved in medial view. The distinctive 'V' shape of the adults (e.g., SMNS 80115) is not present within the embryonic element. In contrast, the horizontal and posterior vertical semicircular canals form a straighter 'T' shape. The impression for the sacculus and the utriculus is large in proportion to the horizontal and vertical semicircular canal impressions, in comparison with the observed adult morphology.

Prootic

The prootic is round in outline and is the anterior-most element forming the osseous labyrinth. Posteriorly, it has a 'V'-shaped indentation, which holds the semicircular canals dorsally and the sacculus and the utriculus ventrally. The dorsal indentations have been interpreted as the impressions for the anterior vertical semicircular canal laterally and the horizontal semicircular canal medially in ichthyosaurs (e.g., McGowan, 1973b; Moon and Kirton, 2016). In *Ophthalmosaurus* and *Ichthyosaurus*, the impression of the anterior vertical semicircular canal is less wide than that of the horizontal semicircular canal in adults (McGowan, 1973b; Moon and Kirton, 2016). In the prootics of adult *Stenopterygius*, this morphology is similar, because adult prootics have one indentation that is mediolaterally wider than the other (SMNS 54062, SMNS 50376, and SMNS 51843). In one specimen, the impression of the anterior vertical canal dips slightly ventrolaterally (SMNS 54062; Fig. 5J).

In the juveniles, a small ridge dividing the impressions of the anterior vertical and horizontal semicircular canals can be
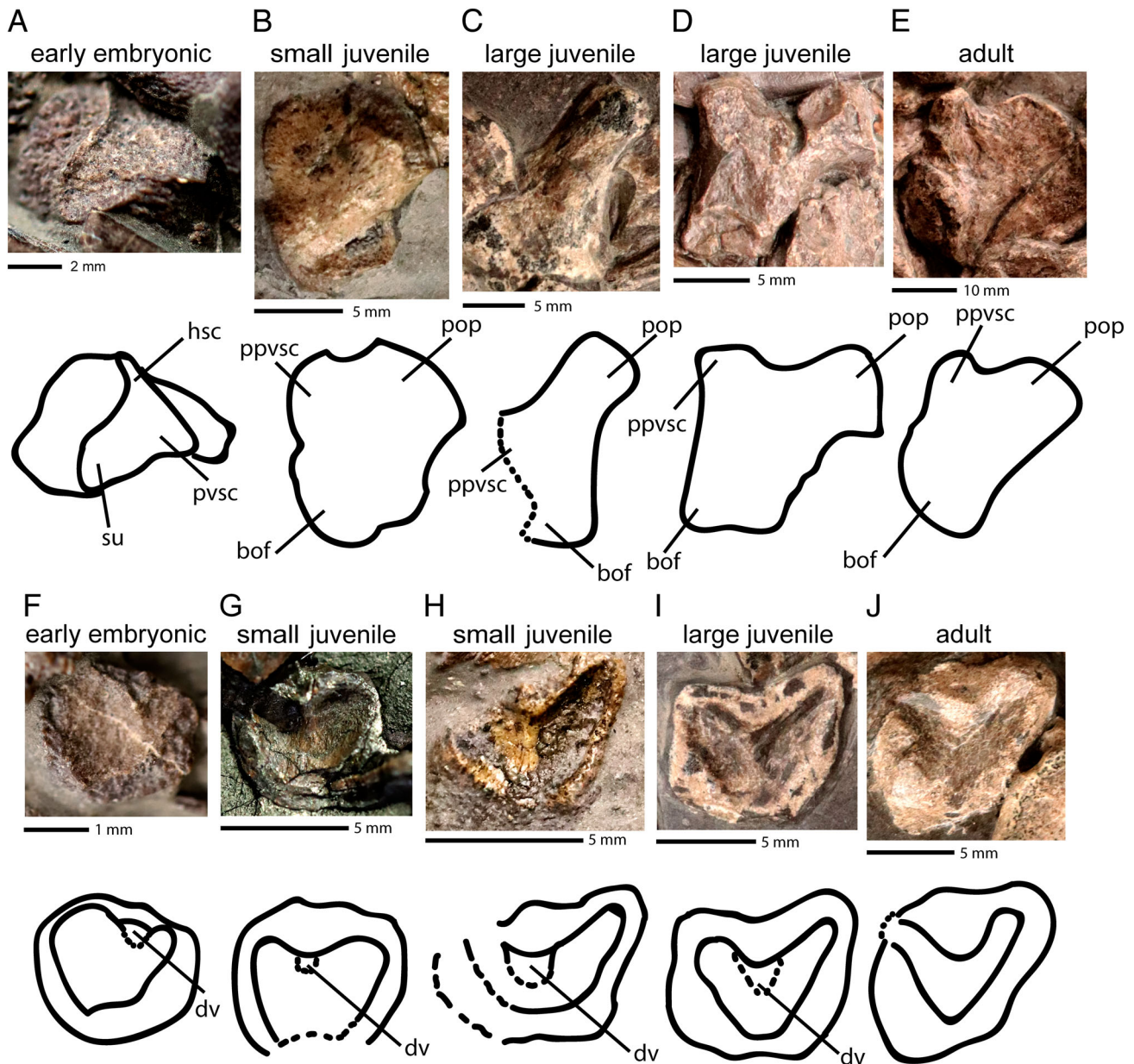
FIGURE 5. *Stenopterygius* right opisthotics (**B–E**) and prootics (**F–J**) in posterior view in order of increasing ossification, and an embryonic opisthotic in medial view (**A**). Interpretive drawings below the images. Prootics **G**, **H**, **J**, and opisthotic **C** have missing bone, indicated by dashed lines in the interpretive drawings. The position of the dividing ridge on the prootic is likewise denoted by a dashed line. All opisthotics are right opisthotics except **C** and **E**, which are mirrored left opisthotics. **A**, embryo *S. quadriscissus*, SMNS 80234; **B**, juvenile *Stenopterygius* sp., SMNS 81806; **C**, juvenile *S. quadriscissus*, SMNS 50003; **D**, juvenile *S. quadriscissus*, SMNS 81958; **E**, adult *S. triscissus*, SMNS 14846; **F**, embryo *S. quadriscissus*, SMNS 80234; **G**, juvenile *S. quadriscissus*, SMNS 51139; **H**, juvenile *Stenopterygius* sp., SMNS 81806; **I**, juvenile *S. quadriscissus*, SMNS 51551; **J**, adult *S. quadriscissus*, SMNS 54062. **Abbreviations**: **bof**, basioccipital facet; **dv**, dividing ridge; **hsc**, impression of the horizontal semicircular canal; **pop**, paroccipital process; **ppvsc**, dorsal process of the opisthotic housing the posterior vertical semicircular canal; **pvsc**, impression of the posterior vertical semicircular canal; **su**, indentation of the sacculus or the utriculus.

observed (SMNS 51551 and SMNS 81806; Fig. 5H–I). The ridge does not extend ventrally into the impression of the sacculus and the utriculus. In these specimens, the two indentations are of similar size. One embryonic prootic has been observed (material associated with SMNS 80234; Fig. 5F). The impression of one of the canals of the osseous labyrinth is much wider than the other one (likely the horizontal canal). The difference in width between the two indentations is much larger than the difference in width in adults (e.g., SMNS 54062; Fig. 5J). However, no ridge is observed in this element.

Variation between Embryonic Stages

There is distinctive variation within embryonic material in the studied collection. Most of the embryos are in the latest stages of prenatal development, e.g., the embryos of SMNS 81961, SMNS 54064, and SMNS 54062 are similar in size to the smallest juveniles and likewise have similar ossification stages. However, embryos associated with SMNS 80234 represent an earlier stage of development (compare, e.g., basioccipitals; Fig. 1A–C). In general, their ossification is less complete than in

the later-stage embryos and the smallest juveniles. This is most apparent in the larger elements such as the basioccipital, the para-basisphenoid, and the quadrate. In the basisphenoid, the dorsum sellae is not fully ossified in embryonic material associated with SMNS 80234 (Fig. 2A) but remains open, whereas it is closed in embryos associated with SMNS 81961 and SMNS 54064 (Fig. 2B, C). The connection with the palate is likewise more established in the latter embryos because the parabasisphenoids are preserved almost in articulated position with the pterygoids. The articular condyle of the quadrate is more pronounced in embryos associated with SMNS 54064 compared with SMNS 80234 (Fig. 3A, B), although neither yet displays the juvenile morphology. The supraoccipital in the embryos of SMNS 80234 is more angular dorsally than in those of SMNS 81961 (Fig. 4A, B). The latter state also very much resembles the morphology in early juveniles. The anterior dorsal groove is even faintly visible.

There is even variation within the embryos of the same mother, SMNS 80234. Two basioccipitals are preserved in posterior view (Fig. 1F, G). One of the two has a better-defined, better ossified extracondylar area. The less-ossified basioccipital is substantially larger (condylar widths of 4 and 9 mm, respectively). Likewise, two parabasisphenoids are preserved in ventral view (Fig. 2F, G) (note that there is no way of knowing whether these are from the same embryos as the basioccipitals discussed above). One has a distinct paired internal carotid foramen, not unlike that of more basal ichthyosaurs (e.g., Maisch and Matzke, 2000; Moon, 2017), whereas the other retains traces of a paired morphology, along the lines of the early juvenile stage, in which a single foramen is partially divided by a dorsal ridge, forming two channels. Of the embryonic basisphenoids, one is not more substantially ossified than the other, but the basisphenoid with the paired morphology is slightly larger (widths: 7 and 9 mm, respectively). Some embryonic quadrates within SMNS 80234 have more pronounced articular condyles and are less dorsoventrally rounded than others. Taken together, these observations might suggest that the embryos within one mother are not necessarily of the same ontogenetic stage. It is likely that there is variation in the rate or timing of the embryonic ossification of the braincase in *Stenopterygius* between embryos of similar stages or variation in stage within a litter. Alternatively, they were the result of different insemination periods or female reproductive strategies, but the fact that we observe embryos with different braincase ossification stages within one pregnant female is definitely not direct evidence of the hypothesis that the embryos were produced in different insemination periods, or that ichthyosaur females had elaborate reproductive strategies.

DISCUSSION

Variation between braincase elements of individuals of *Stenopterygius* is relatively high. However, within the adults, there are no distinct morphotypes observed and morphological variation is continuous. No differentiation in braincase morphology was observed between *S. quadriscissus* and *S. triscissus* across all the stages. In addition, no differentiation was possible between *S. uniter* and the other two species, potentially due to the small available sample sizes of this species in collections.

We observed qualitative ontogenetic shape variation in the braincase of *Stenopterygius* in most elements. Among ichthyosaurs, embryonic braincase elements are only described in *Platypterygius australis* (Kear and Zammit, 2013). Embryos of *Platypterygius australis* show weak ossification of the opisthotic and prootic, as also observed in *Stenopterygius*. The difficulty in identifying these two bones relative to the ease of identifying basioccipitals and quadrates in disarticulated embryonic material may also be a result of their poor ossification. Within *Stenopterygius*, we observed a large discrepancy between embryos and

adults in the shape of the otic capsule in the opisthotic and the prootic. These changes are less pronounced in *Platypterygius* (Kear, 2005; Kear and Zammit, 2013). The changes in morphology of the otic capsule in both the opisthotic and the prootic of *Stenopterygius* are likely due to a dissociation between growth of the membranous labyrinth and growth and ongoing ossification of the bones surrounding the inner ear, or some combination of the two processes. Other important ontogenetic changes in braincase morphology over ontogeny in *Stenopterygius* include the late ossification of the basioccipital peg, the size of the basipterygoid processes of the parabasisphenoid, the shape of the quadrate and development of the occipital lamina, the relative size of the exoccipitals, the shape of the supraoccipital, and the relative size of the medial head of the stapes. Ontogenetic changes in the size of the basipterygoid processes of the parabasisphenoid have also been noted in *P. australis* (Kear and Zammit, 2013).

Adult *Stenopterygius* have a distinct basioccipital peg. However, a basioccipital peg is not ossified in embryos and neonates and is a narrow structure in small juveniles. This is a classic ichthyosaurian phylogenetic character (character 29 of Motani, 1999; included in most subsequent analyses); thus, detection of ontogenetic variation in its presence/absence is an important result. Adults of most non-ophthalmosaurid ichthyosaurs have a distinct basioccipital peg; see, e.g., *Ichthyosaurus* (McGowan, 1973b). The basioccipital peg was lost in some ophthalmosaurids, e.g., *Platypterygius* (Kear, 2005). The evolutionary loss of the peg could therefore be a result of delayed ossification, or a part of an overall reduction in ossification of braincase elements. The retention of a notochordal pit on the anterior surface of the basioccipital, as seen in neonates and embryos of *Stenopterygius*, is also seen in the adults of some ophthalmosaurids (e.g., *Arthropterygius*; Maxwell, 2010).

In *Stenopterygius*, the internal carotid foramen on the ventral surface of the parabasisphenoid is partially divided by a ridge on the ventral surface of the basisphenoid in the embryonic and early juvenile stages, displaying a single foramen with two distinct grooves. However, in most adult specimens, a single foramen without a median ridge appears to be present. This 'ontogenetic' variation is thought to be caused by taphonomy and preparation, with the proportionately smaller median ridge in adults not visible in compressed or aggressively prepared specimens. This morphology indicates that even though a single opening is present, the right and left internal carotid arteries remain paired, with this separation being more easily observed in juveniles than in adults. In some non-ophthalmosaurid ichthyosaurian taxa, the foramina for the right and left internal carotid arteries are completely separated by bone (e.g., the Triassic genus *Phantomosaurus* [Maisch and Matzke, 2006] and the Early Jurassic *Temnodontosaurus* [Maisch, 2002]). In contrast, in Ophthalmosauridae and in the small-bodied Triassic genera *Mixosaurus* and *Chaohusaurus*, the internal carotid foramen lacks any evidence of paired arteries (Maisch, 2001; Brinkmann, 2004; Fischer et al., 2014; Moon and Kirton, 2016), even in embryonic stages (Kear and Zammit, 2013). The morphology observed in *Stenopterygius* represents an intermediate state. The paired nature of the internal carotid foramen is another character that is widely used (character 42 of Maisch and Matzke, 2000, and subsequent analyses), and based on these findings it should be further investigated to understand how widespread the discrepancy between paired arteries and an unpaired foramen is in ichthyosaurs.

It has previously has been hypothesized that the presence of a groove bisecting the basioccipital facet of the basisphenoid in *Ophthalmosaurus* might be the result of formation of this element from two lateral ossification centers (Andrews, 1910; Moon and Kirton, 2016); this groove, however, has also been identified as a notochordal structure (Fischer et al., 2012). In

Stenopterygius, this posterior groove is present in the embryonic basisphenoid but does not decrease in prominence through ontogeny, as would be expected if the underlying cause were fusion of ossification centers. Moreover, a similar groove in some turtles (e.g., Sterli et al., 2010) appears to have a demonstrable notochordal origin (Sheil, 2003). Thus, we reject the hypothesis that this groove is directly related to basisphenoid ossification centers in ichthyosaurs.

It has been likewise hypothesized that fusion between the basisphenoid and the parasphenoid could be an indicator for maturity or ontogenetic stage in the ichthyosaur *Platypterygius australis* (Fischer et al., 2011); however, embryonic material of this species has led to the rejection of this idea (Kear and Zammit, 2013). We observed complete fusion of the parasphenoid and the basiphenoid in all embryos and juveniles of *Stenopterygius*. Therefore, coossification of these elements from the earliest stages likely characterizes baracromian ichthyosaurs.

The contribution to the foramen magnum of the supraoccipital is, broadly speaking, larger in ophthalmosaurids than in the Early Jurassic ichthyosaurs (e.g., *Temnodontosaurus* [Maisch, 2002] and *Ichthyosaurus* [McGowan, 1973b], in comparison with *Ophthalmosaurus* [Moon and Kirton, 2016]). In *Temnodontosaurus*, the exoccipitals contribute almost 100% to the circumference of the foramen magnum, compared with the limited supraoccipital contribution (Maisch, 2002). In *Ophthalmosaurus icenicus*, the contributions are more equally divided between the exoccipitals and the supraoccipital (Moon and Kirton, 2016). In *Stenopterygius*, the exoccipitals are the largest contributor to the foramen magnum. However, the supraoccipital has a bigger contribution than in *Temnodontosaurus*. Such a distribution of contributions is similar to that in *Ichthyosaurus* and *Hauffiopteryx* (McGowan, 1973b; Marek et al., 2015). The supraoccipital portion of the foramen magnum is keyhole-shaped in *O. icenicus* and is hypothesized to enclose additional non-neural tissues (Moon and Kirton, 2016). The authors hypothesized the possibility of the paired cerebral veins passing through the dorsal (supraoccipital) margin of the foramen magnum, which is supported by the ventrally directed medial process dividing the dorsal-most part of the foramen magnum in this genus (Moon and Kirton, 2016). The supraoccipital of *Stenopterygius* lacks the ventrally directed median process seen in *Ophthalmosaurus*. Moreover, it does not often contain lateral foramina on the anterior or posterior surface. This is in stark contrast to the supraoccipital of other ichthyosaurs (McGowan, 1973b; Maisch, 2002; Moon and Kirton, 2016). This would suggest that the foramina on the supraoccipital transmitted either variably present or evolutionarily labile structures (McGowan, 1973b; Moon and Kirton, 2016).

The exoccipitals do not change significantly in morphology over ontogeny in *Stenopterygius*. However, the exoccipitals are proportionately much larger in the late embryonic and early juvenile stages, sometimes having the same height as the basioccipital in anterior or posterior view. This probably reflects negative allometry of the foramen magnum relative to the vertebral column. This strong negative allometry of the foramen magnum has not previously been discussed in ichthyosaurs but is logically associated with negative cranial allometry and can be expected to have implications for vertebral morphology as well as for the braincase elements.

The observed dimorphism of the paroccipital processes of the opisthotic in juvenile *Stenopterygius* is noteworthy and has not been observed in other ichthyosaurs, although small sample sizes may hinder detection. Adult *Stenopterygius* have relatively short paroccipital processes compared with most other ichthyosaurs, such as *Ophthalmosaurus* and *Phantomosaurus* (Maisch and Matzke, 2006; Moon and Kirton, 2016). The dorsal extension in posterior view corresponding to the posterior vertical semicircular canal is unique to *Stenopterygius* in the degree to which it approaches the size of the paroccipital process. However, other Jurassic taxa, such as *Ichthyosaurus* and *Temnodontosaurus*, also have a slight dorsal projection of the opisthotic associated with the posterior vertical semicircular canal (McGowan, 1973b; Maisch, 2002). In some ophthalmosaurids, the impression of the posterior vertical semicircular canal extends to the edge of the medial head of the opisthotic; this, however, does not result in a dorsal projection (Fischer et al., 2014). Non-parvipelvian ichthyosaurs have elongated, plate-like paroccipital processes, resembling the morphology in many basal and extant diapsids (Maisch and Matzke, 2006; Maisch et al., 2006).

CONCLUSIONS

The morphology of braincase elements in the genus *Stenopterygius* changes over ontogeny; however, differences in the amount of ontogenetic variation observed exist between the elements. Whereas the exoccipitals change only in size relative to the other braincase elements, the shapes of, e.g., the internal carotid foramen, parabasisphenoid outline, and basioccipital peg change in ways that could affect their reliability as characters in phylogenetic analysis of ichthyosaurian ingroup relationships. The morphology of the internal carotid foramen also appears to be strongly influenced by preservation and preparation. We observed different stages of ossification among embryos within a single gravid female, which shows either that there were embryos of different ontogenetic stages present in a gravid female or that growth and ossification of the braincase elements was variable in this genus. This study is the first to look at ontogenetic changes across braincase elements in ichthyosaurs based on a robust sample size and contributes important data on embryonic and juvenile braincase morphology in a non-ophthalmosaurid ichthyosaur.

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