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BRAINCASE MORPHOLOGY OF *BAPTANODON NATANS* (REPTILIA: ICHTHYOSAURIA)

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ABSTRACT

Two recently discovered specimens of *Baptanodon natans* provide information on the morphology of the braincase. They are from the same location northwest of Kaycee, WY, from the Redwater Shale (Jurassic, Oxfordian) of the Sundance Formation. One specimen has a completely articulate braincase, preserved in three dimensions; the second has isolated bones from the braincase, also preserved in three dimensions. This new material points out differences between *B. natans* and the closely related *Ophthalmosaurus icenicus*. They can be distinguished by the shape of the foramen magnum, and the morphologies of the supraoccipital, basioccipital, and basisphenoid. A second taxon is probably present in the Sundance Formation based on a third basioccipital from the Redwater Shale that is different from those described here for *B. natans*.

INTRODUCTION

Baptanodon natans is an ophthalmosaurid ichthyosaur from the Jurassic of North America. Previously referred to as *Ophthalmosaurus natans* (McGowan and Motani, 2003; Massare et al., 2014), some recent phylogenetic analyses suggest that the genus name '*Baptanodon'* should be retained (e.g., Campos et al., 2020; Fernández et al., 2021; Cortés et al., 2021), and that is the name that will be used in this paper. Specimens of *Baptanodon natans* have been collected on the eastern side of the Cordillera, from a pocket sea preserved as the Sundance Formation in Wyoming and northern Colorado. The Sundance Formation ranges in age from the Middle to Upper Jurassic (Kvale et al., 2001). The ichthyosaurs are found only in the Redwater Shale (Upper Jurassic, Oxfordian), the uppermost member of the Sundance Formation (Massare et al., 2014).

This research describes the braincase elements of two ichthyosaur specimens that were recently collected and prepared by the staff and volunteers of the Tate Geological Museum, Casper, WY. Braincase material from Sundance Formation ichthyosaurs has not been described since the work of Gilmore more than a century ago (Gilmore, 1906). The specimens described here indicate some inaccuracies in his reconstruction of the posterior view of the skull (Gilmore, 1906, plate IX). These specimens also illustrate some features that distinguish *B. natans* from the closely related *Ophthalmosaurus icenicus*, and add to our knowledge of the braincase morphology of ophthalmosaurid ichthyosaurs in general. We also present evidence of a second ichthyosaur taxon in the Sundance Formation, represented by a third specimen that preserves a basioccipital with a distinctly different morphology.

Institutional abbreviations: **CM**, Carnegie Museum of Natural History, Pittsburgh, PA.; **TATE**, Tate Geologic Museum, Casper College, Casper, WY; **UW**, University of Wyoming, Laramie, WY.

MATERIALS AND PROVENANCE

This report focuses on two specimens of *Baptanodon natans* that were collected in 2018 from the Redwater Shale member (Jurassic, Oxfordian) of the Sundance Formation by the staff and volunteers of the Tate Geological Museum, Casper, WY. The specimens are from the same location (TATE location V201701), northwest of Kaycee, in southwestern Johnson County, WY. They were found about 20 meters apart, with TATE v9302 being stratigraphically higher than TATE v7037. Both specimens were in calcite concretions and each was collected in a single plaster jacket. The specimens were expertly prepared by Tate Geological Museum volunteer Dwaine Wagoner, who used a variety of air scribes to remove the matrix. Cyanoacrylate glue was used to repair breaks, and epoxy putty was used to fill in larger cracks that needed stabilization.

TATE v9302 was prepared within its plaster jacket. The bones are entirely exposed but still lying in their *in situ* arrangement. The specimen includes skull fragments, both forefins, scapula, both coracoids, four sections of articulated vertebrae, and numerous ribs (Figure 1). The braincase was prepared so that it can be removed from the plaster jacket. It is completely

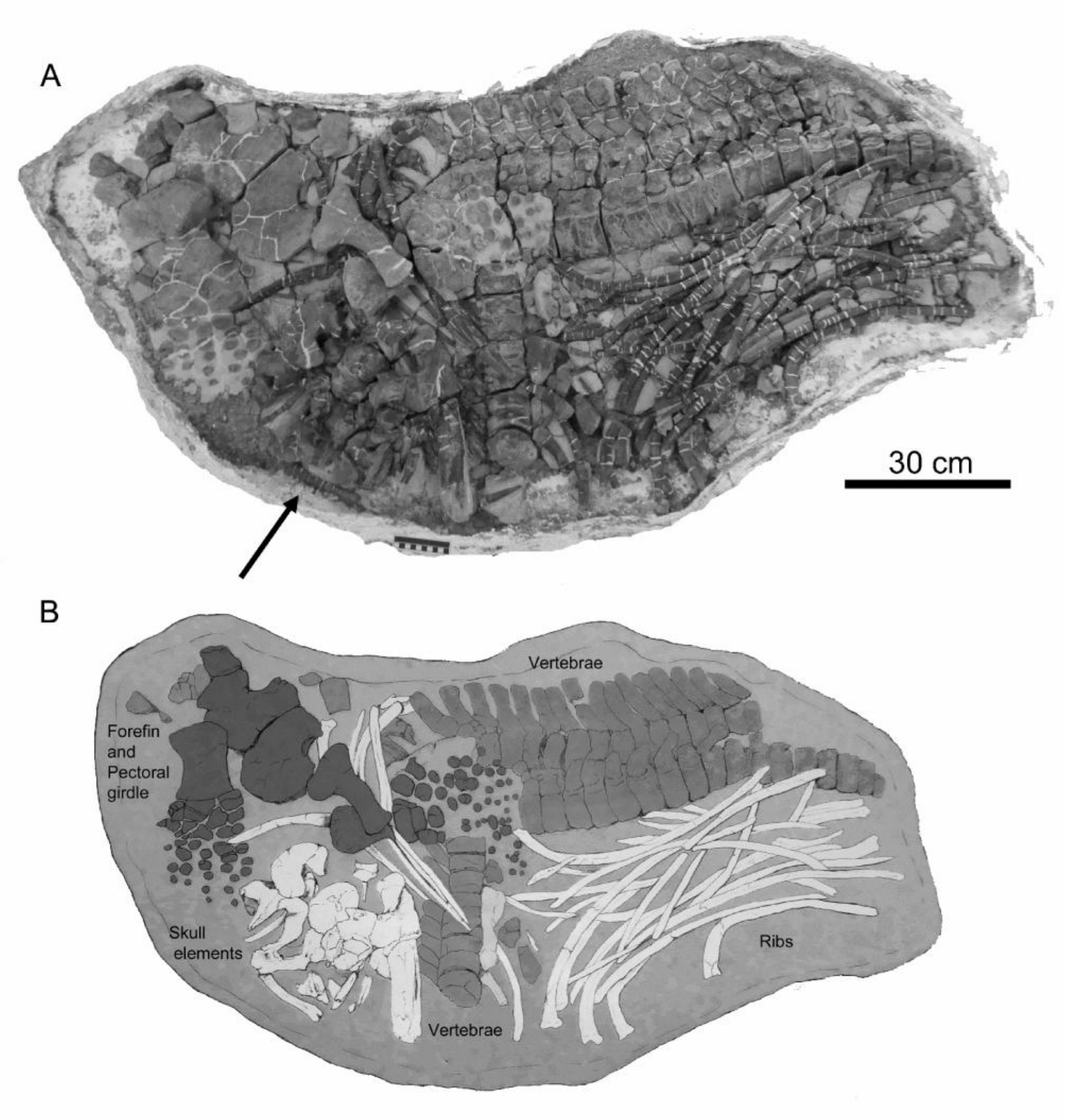

FIGURE 1: A. TATE v-9302, Kaycee specimen of *Baptanodon natans*. The braincase position (anterior view) is indicated by the arrow towards the bottom of the image. The dorsal end of the braincase is closest to the arrow. Note the left quadrate to the left of the basioccipital-basisphenoid. Scale bar = 30 cm, B. Interpretive drawing of the specimen, modified from a drawing by C. S. Worthington on display at the Tate Geological Museum and reproduced here with his permission.

articulated and laying in anterior view near the edge of the plaster jacket (Figure 1A, arrow). The left quadrate is adjacent to the articulated basioccipital and basisphenoid. The entire jacketed specimen is currently on display at the Tate Geological Museum, Casper, WY. For convenience, it will be referred to as the Kaycee specimen. Individual bones have not been given a sub-number as of this writing.

FIGURE 2: TATE v-9302, Kaycee specimen of *Baptanodon natans*, proximal portion of left forefin in dorsal view. Scale bar = 10 cm.

The forelimb (Figure 2), and in particular, the humerus, is typical of *Baptanodon natans* (Gilmore, 1906, fig. 24), the only species currently recognized from the Sundance Formation (McGowan and Motani, 2003; Massare et al., 2014). The humerus is much longer than distally wide, the shaft is relatively narrow, and the distal width is about the same as the proximal width. The ulna, radius, and an anterior accessory element are in contact with the humerus. In dorsal or ventral view, the ulnar facet is at an angle to the radial facet, whereas the facet for the anterior accessory digit is not. This is similar to the morphology of the distal end of the humerus in *Ophthalmosaurus icenicus* (Moon and Kirton, 2016, Pl. 22, fig. 1), *Arthropterygius chrisorum* (Maxwell, 2010, fig.4B, C, F) and *A. thalassonotus* (Campos et al., 2020, fig. A, B) but the humeri for those species are not as long relative to the width and have a broader shaft relative to length than for *Baptanodon*. *Bachypterygius extremis* (Kimmeridgian-Tithonian) also has three facets on the distal end of the humerus, but in that species, the radius, intermedium, and ulna articulate with the humerus, not the anterior accessory digit (Moon and Kirton, 2018, text-fig. 42a). In *Janusaurus lundi* and *Palvennia hoybergeti*, both Tithonian in age, the facet for the anterior accessory digit is at a distinct angle to the radial facet, and the humerus of the former species also has a wide shaft relative to its length (Roberts et al., 2014 fig.10A, B; Delsett et al., 2018, fig. 12). These comparisons and the analysis of Campos et al., 2021, fig. 8) suggest that the humerus morphology is sufficient to distinguish *Baptanodon* from other Middle-Upper Jurassic ichthyosaurs.

A second specimen (TATE v7037) comprises a partial skull and disarticulated postcranial material that includes an interclavicle, coracoid, limb material, and numerous vertebrae and ribs. The dermal skull bones are articulated but fractured and laterally crushed. The braincase elements are disarticulated and more weathered than those of the Kaycee specimen. They were prepared as individual bones in three dimensions, although some are fractured. Each element has been given its own sub-number (e.g., v7037-1, v7037-2, etc). The individual bones have the same morphologies as those of the articulated braincase of the Kaycee specimen, so we also identify this specimen as *Baptanodon natans*. It will be referred to as the Mayoworth specimen.

A third specimen, UW 24234, might represent a new taxon. It was collected as surface float over a few years, from a two track road across the Redwater Shale near Roughlock Hill, northern Natrona County, WY (UW location v-92066). The specimen consists of several whole centra and numerous fragmentary ones, including cervicals, dorsals, and caudals; rib fragments; a fragment of the basisphenoid; and a complete, but weathered basioccipital, which is described below. Repeated surveys of the area over the years failed to determine where the material was coming out.

DESCRIPTION

The Kaycee Braincase—The Kaycee braincase (TATE v9203) displays a typical ichthyosaurian morphology, and the following discussion points out aspects of the morphology that can be seen in posterior view (Figure 3A, B).

The parietal shelf contacts and overlaps the dorsolateral edge of supraoccipital, giving it a rounded shape in posterior view when articulated. The supraoccipital makes up the dorsal and dorsolateral margins of the foramen magnum. In *Ophthalmosaurus icenicus* (Moon and Kirton, 2016, text-fig. 16, plate 9, fig.1), the portion of the foramen magnum enclosed by the supraoccipital is much narrower laterally than the rest of the foramen magnum. This is not the case in *Baptanodon natans*. The triangular facets of the supraoccipital contact the exoccipitals ventrally. The

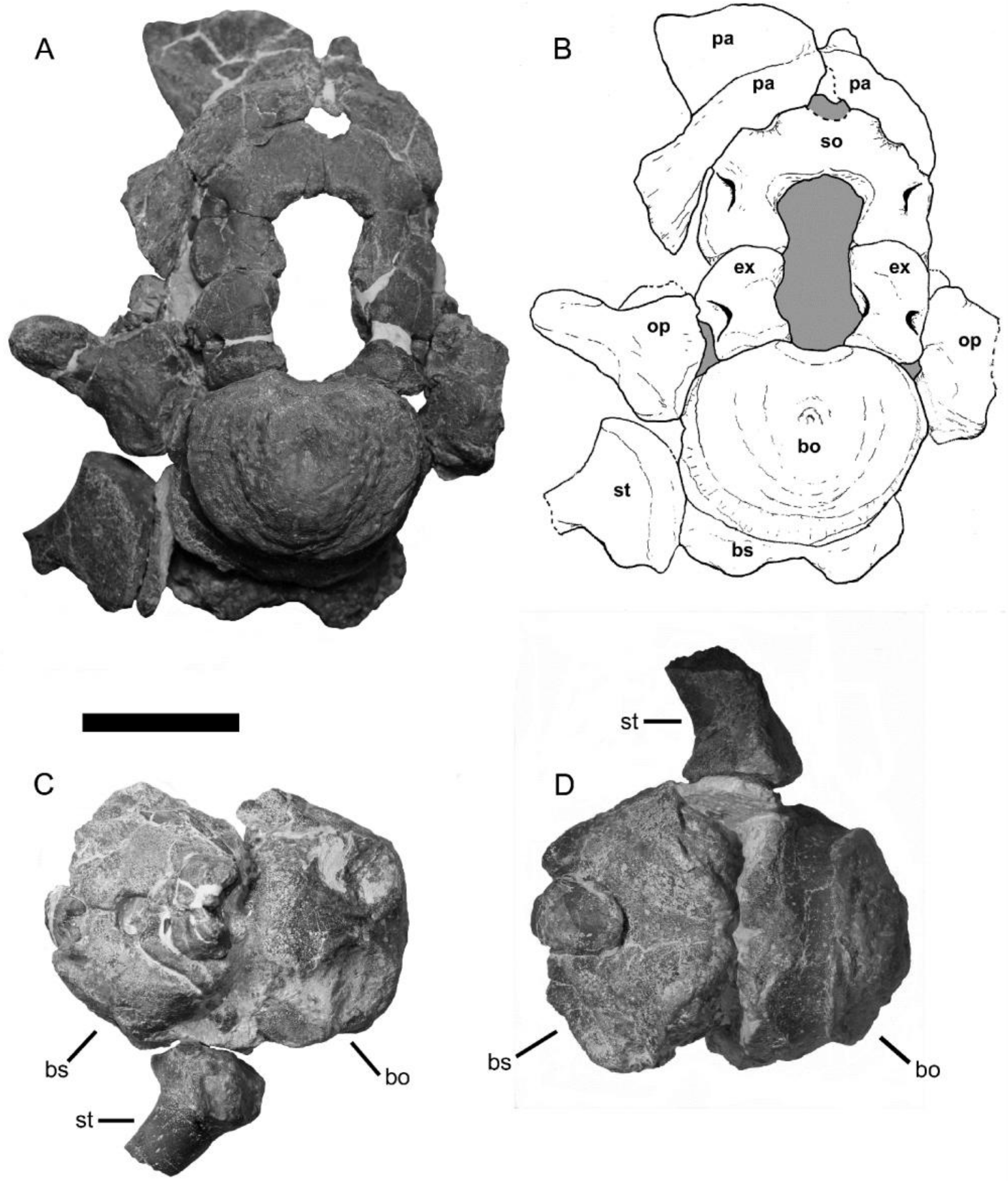

FIGURE 3: TATE v-9302, Kaycee specimen of *Baptanodon natans* A. Articulated braincase in posterior view, B. Interpretive drawing of braincase, C. Dorsal view of articulation between basioccipital and basisphenoid. D. Ventral view of braincase. Note the extent of the extracondylar area and the 'lip' that indicates the extent of the occipital condyle. The bone covering the internal carotid foramen might be an artefact of preservation, Scale bar = 5 cm. **Abbreviations**: **bo** basioccipital, **bs** basisphenoid, **ex** exoccipital, **op** opisthotic, **pa** parietal, **so** supraoccipital, **st** stapes.

exoccipitals make up aboutt 50% of the lateral edges of the foramen magnum (Figure 3A, B). In *O. icenicus*, the exoccipitals comprise well over 50% of the lateral edges of the foramen magnum (Moon and Kirton, 2016, text-fig. 16). The tall, broad foramen magnum on the Kaycee specimen is slightly constricted at the contact between the exoccipitals and the supraoccipital. The shape is almost subrectangular (Figure 3A,B), different from the somewhat pear-shaped foramen magnum of *O. icenicus* (Moon and Kirton, 2016, text-fig. 16). The exoccipitals contact the basioccipital ventrally.

The basioccipital is wider than it is high (width 8.1 cm, height 6.7 cm), and the occipital condyle itself is also wider than high (width 6.9 cm, height 5.3 cm). The notochordal pit is closer to the dorsal edge than to the ventral edge, at about the level of the maximum width of the condyle (Figure 3 A, B). The condylar surface is irregular and contrasts with the smooth surface of the extracondylar area. In posterior view, the extracondylar area forms a fairly narrow region that parallels the lateral and ventral edges of the occipital condyle (Figure 3A, B). The left ventrolateral edge of the extracondylar area is broken and the ventral edge is worn. There is no ventral notch. The convexity of the condyle decreases towards the margins. A distinct lip demarcates the condyle from the extracondylar area, best seen in ventral view (Figure 3D). Also in ventral view, the extracondylar area is extensive, comprising about half of the anteroposterior length (Figure 3D). The basioccipital and basisphenoid are about the same size (Figure 3 C, D).

The left opisthotic is complete and articulated with the rest of the braincase. It has a short, broad shaft, and a medial head with three facets of different sizes (Figure 4). In posterior view, each facet has a straight margin: a small facet located ventrally to articulate with the stapes, a larger facet dorsomedially to articulate with the exoccipital, and the largest facet medially to articulate with the basioccipital. Separating the exoccipital and basioccipital facets is a short shallow groove. The right opisthotic and both stapes are broken at the base of the shafts.

The Mayoworth Braincase—The Mayoworth braincase (TATE v7037) is entirely disarticulated with individual elements preserved in three dimensions.

Supraoccipital: A complete supraoccipital of the Mayoworth specimen (TATE v7037-126) is preserved, although it is fractured. The supraoccipital underlaps the parietals dorsolaterally and contacts the exoccipitals ventrally. The dorsal and lateral margins are straight, giving the bone an overall rectangular shape (height right side 5.9 cm; width along dorsal margin 8.2 cm) around the roughly semicircular opening for the foramen magnum (Figure 5B). The dorsolateral margins curve laterally (Figure 5A) and are covered by the parietal when articulated, so the supraoccipital appears to be a rounded arch in posterior view, as seen in the Kaycee specimen (compare Figures 3A, B to Figure 5B). A dorsoventrally elongated concavity is located on each side of the supraoccipital, at about midway between the ventral and dorsal edges (note right side of Figure 5B), although they are seen more clearly on the Kaycee braincase (Figure 3A, B). The supraoccipital widens slightly ventrally, where it contacts the exoccipitals, making the lateral margins of the foramen magnum slightly constricted at mid-height.

FIGURE 4: TATE v-9302, left opisthotic of *Baptanodon natans* (Kaycee specimen), in posterior view, oriented as it is articulated (dorsal towards the top). Scale bar = 3 cm.

In dorsal view, the supraoccipital is almost flat posteriorly but curved laterally (Figure 5A). The posterior edge is slightly higher than the anterior edge and a slight depression is in between. The facets contacting the exoccipitals are triangular, pointing anteriorly.

Exoccipital: The exoccipitals contact the left and right sides of the supraoccipital dorsally, the opisthotic ventrolaterally, and the basioccipital ventrally. The right exoccipital (TATE v7037-1) is nearly complete, but damaged laterally and anteriorly. In posterior view, the medial edge is slightly convex, and is higher than the lateral edge, which encloses a relatively large foramen (Figure 6A). In medial view, the dorsal margin is straight, with little difference in height between anterior and posterior edges. A large hypoglossal foramen is in the middle of the bone in medial view. A smaller foramen is directly anterior to it. The ventral margin curves dorsally at its anterior edge. The fairly smooth, convex dorsal surface slopes much more steeply laterally than medially, with an indistinct ridge between the two sloping surfaces. The ventral surface is very slightly convex with an irregular texture.

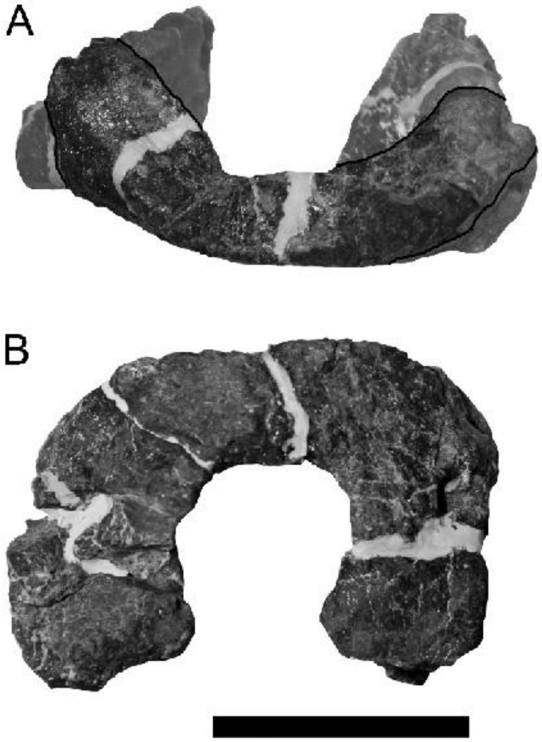

FIGURE 5: TATE v-7037-126, supraoccipital of *Baptanodon natans* (Mayoworth specimen). A. dorsal view, B. posterior view. Scale bar = 5 cm.

Opisthotic: Both opisthotics are broken at the base of the shaft, however, they allow a medial view of the bone. A V-shaped groove is clearly visible in the left opisthotic (Figure 6B).

Stapes: Both stapes are preserved in the Mayoworth specimen, but they are damaged. The left stapes (TATE v-3707-10) is missing most of the shaft, but its oval cross-section is visible, highlighting a sharp ventral ridge that extends the length of the shaft. The nearly complete shaft of the right stapes shows a similar subdued ridge that extends ventrally from the distal end of the shaft to the medial head, similar to what was described for *O. icenicus* (Moon and Kirton, 2016, text-fig 15). In posterior view, the medial head of the stapes is more than twice as wide as the shaft (right stapes: shaft diameter 2.0 cm; height of head 4.9 cm). They both have a smooth bone surface except towards the articular end of the shaft. A facet along the dorsomedial margin of the head articulates with the opisthotic and a larger facet along the medial margin articulates with the basioccipital. The facets form a broadly curved margin of the head. In medial view, the head has a broadly oval shape, with a slightly rugose, fairly flat surface. A small oval pit can be seen slightly ventromedial to the base of the shaft on the left stapes.

Basioccipital: The basioccipital is more weathered on the Mayoworth specimen than on the Kaycee specimen, and its left ventrolateral edge is damaged (Figure 7A). In posterior view (Figure 7A, B), the basioccipital is wider than high (width 8.7 cm, height 7.2 cm), with the condyle making up most of the central portion (condyle width 6.6, height 5.8 cm). The notochordal pit is an oval depression, located slightly dorsal to the middle of the condyle. It appears more dorsally located on this specimen than on the Kaycee specimen described above, but it is still a prominent depression. The condylar surface is also more rugose on the Mayoworth specimen, likely because of weathering. The extracondylar area appears narrow in posterior view, and extends continuously along the lateral and ventral margins of the condyle. The lateral margins appear curved, paralleling the condyle, whereas the ventral margin is fairly straight. However, the extracondylar surface is steeply inclined away from the condyle, and is very broad in ventral and lateral views (Figure 7 G-J), where it makes up more than half of the anteroposterior length of the bone.

In anterior view (Figure 7C, D), the basioccipital is subpentagonal with a rugose surface as in *O. icenicus*, but it lacks a ventral notch (Moon and Kirton, 2016, text-fig. 14). The maximum width is located at about the midpoint of the length, ventral to the large foramen, the notochordal tip. On the dorsal margin, the edges of the bone are inclined ventrally from the midpoint, forming a flat-topped bulge at the floor of the foramen magnum. Between the notochordal tip and the ventral edge are two low, broad, curved ridges that almost surround an elongated central depression that extends ventrally as a straight, shallow groove. The surface of the ridges is smoother than the rest of the bone. The ventral margin is nearly straight, although it is damaged.

In dorsal view, the basioccipital has a rugose surface, with the greatest width near but not at the anterior margin (Figure 7E, F). The exoccipital facets are roughly oval, with the major axis oriented anteroposteriorly. The medial and posteromedial edges of the facets are steep where they meet the floor of the foramen magnum, forming a high wall medially and to a lesser extent posteriorly. The floor of the foramen magnum, along the midline, is straight, flat, and smooth except in the posteriormost portion where it has a slight depression. A similar depression can be seen in the Kaycee specimen, but on that specimen, the floor of the foramen magnum is narrower in the middle than at either end (Figure 3C). The two rounded ridges from the anterior surface are visible along the anterior margin. Between those ridges and oriented posteriorly is the large foramen (notochordal tip).

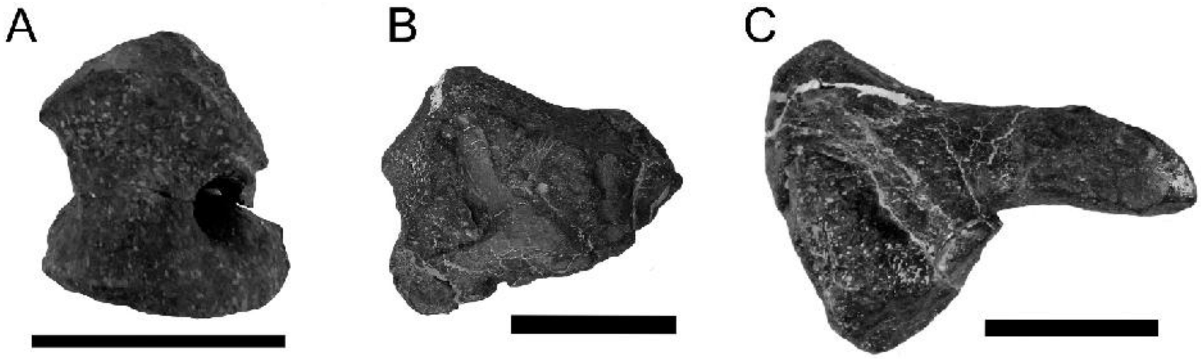

FIGURE 6: Additional braincase bones of *Baptantodon natans* (Mayoworth specimen). A. exoccipital (TATE v-7037-1) in posterior view, dorsal to the top, B. left opisthotic (TATE v-7037-39). in medial view, dorsal to the left, C. right stapes (TATE v3707-127) in posterior view, dorsal to the top. All scale bars = 3 cm.

In ventral view, the basioccipital is convex posteriorly and flares outward anteriorly (Figure 7G, H). The lip at the contact between the condyle and the extracondylar area is not as distinct on this specimen as on the Kaycee specimen (compare Figure 4D to Figure 7G); it is indicated by a change in orientation of the lateral edges. The condyle is less than half the anteroposterior length of the extracondylar area, which is extensive in this view. The extracondylar area has a smooth surface with tiny pits, different from the rugose condylar surface but not as smooth as the extracondylar area on the Kaycee specimen, probably due to weathering. At the middle of the anterior margin are two rounded ridges with a broad concavity in between them, the ventral view of the two ridges and groove on the anterior surface.

In lateral view (Figure 7 I, J), the extracondylar area is still prominent, and forms a ridge where it contacts the rugose dorsal surface. However, the contact between the condyle and extracondylar area is not clear. The dorsal surface appears strongly convex, and makes up half of the length of the bone in this view.

Basisphenoid: The basisphenoid (v7037-34) is a massive, wedge-shaped bone (Figure 8). The ventral surface is flat, the anterior surface is convex, and the posterodorsal surface is inclined for about 2/3 of its length and then flattens to almost parallel the ventral surface, best seen in lateral view (Figure 8C). The parasphenoid rostrum has broken off. On the ventral surface, flat pieces of the parasphenoid are visible at the midline anterior to the interior carotid foramen, identified by a smoother bone texture. A suture between the parasphenoid and basisphenoid is visible on the broken edge of the anterior margin, but the parasphenoid is otherwise absent. This description focuses on the ventral (Figure 8D), posterior (Figure 8B), and anterior (Figure 8A) views of the basisphenoid.

The ventral surface is flat and a roughly trapezoidal (Figure 8D). Large, triangular basipterygoid processes at the lateral edges of the anterior margin gives the margin a curved appearance. A large interior carotid foramen is at the midline, slightly posterior to the center. A short groove extends medially from the lateral margins immediately posterior to the basipterigoid processes. Two poorly defined, posterolateral facing basioccipital facets are at either end of the posterior margin. The ventral surface is 6.7 cm long along the midline, with a maximum width of 9.0 cm just posterior to the basipterygoid processes.

In posterior view, the bone surface is rugose with an irregular groove along the midline (Figure 8B). The surface of the bone is steeply inclined for about two-thirds of its length, and this is mainly what is visible in posterior view. At about 2/3 of its height, the surface bends anteriorly to become the nearly flat, dorsal plateau, almost parallel to the ventral surface (Figure 8C). The posterodorsally oriented slope gives the bone its wedge shape. Facets for the stapes are poorly defined along the dorsolateral margins. The triangular basipterygoid processes from the ventral surface are visible along the ventral margin.

The anterior surface is concave (curvature seen best in lateral view, Figure 8C) with a nearly straight ventral margin (Figure 8A). The basisphenoid is wider than high in this view (height along midline 5.4 cm; maximum width 8.5 cm), with the maximum width near but not at the ventral margin (bottom edge in Figure 8A). The lateral margins converge dorsally so that the dorsal margin is much narrower than the

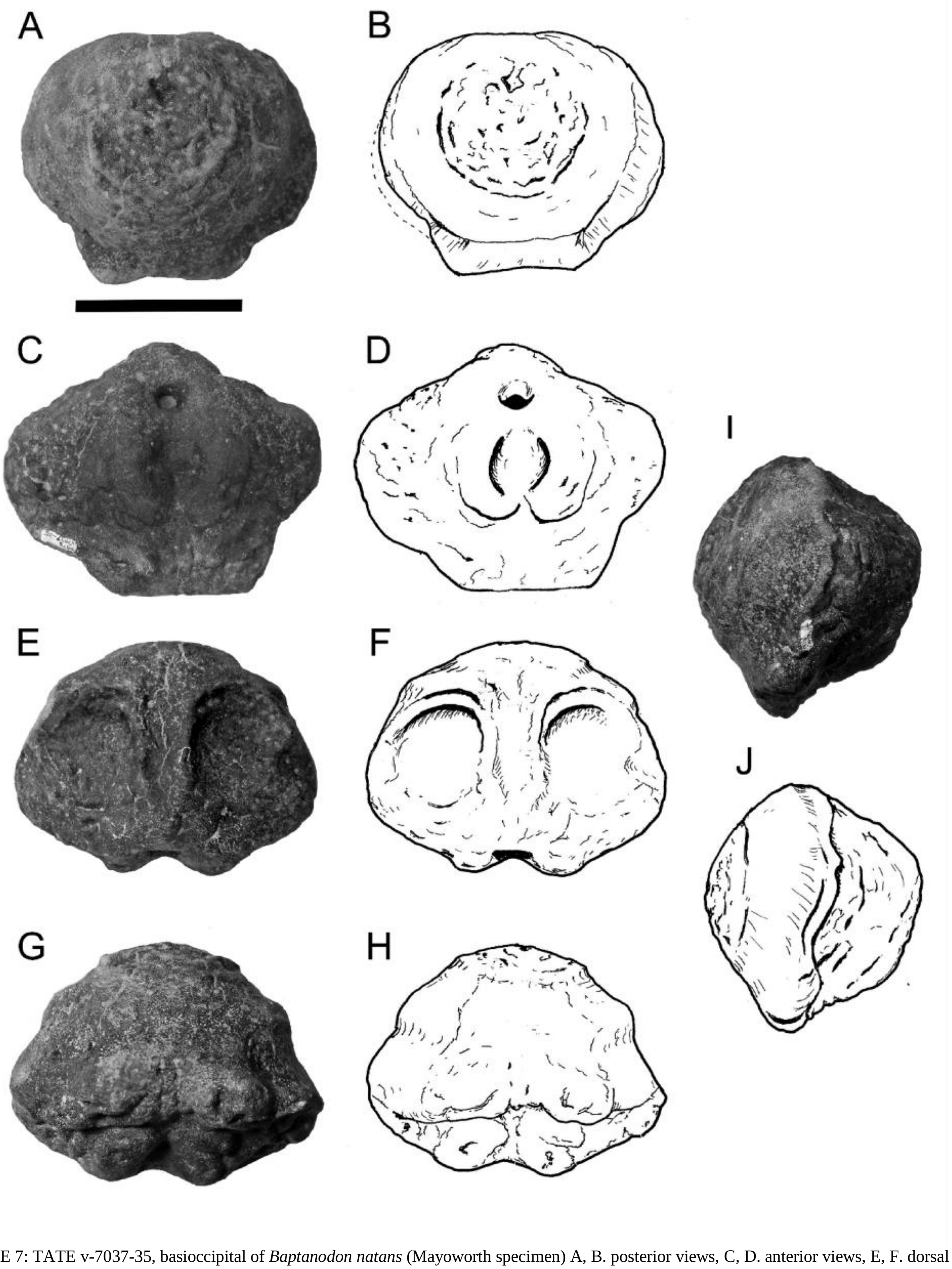

FIGURE 7: TATE v-7037-35, basioccipital of *Baptanodon natans* (Mayoworth specimen) A, B. posterior views, C, D. anterior views, E, F. dorsal views, G, H. ventral views, I, J. left lateral views. Scale bar = 5 cm.

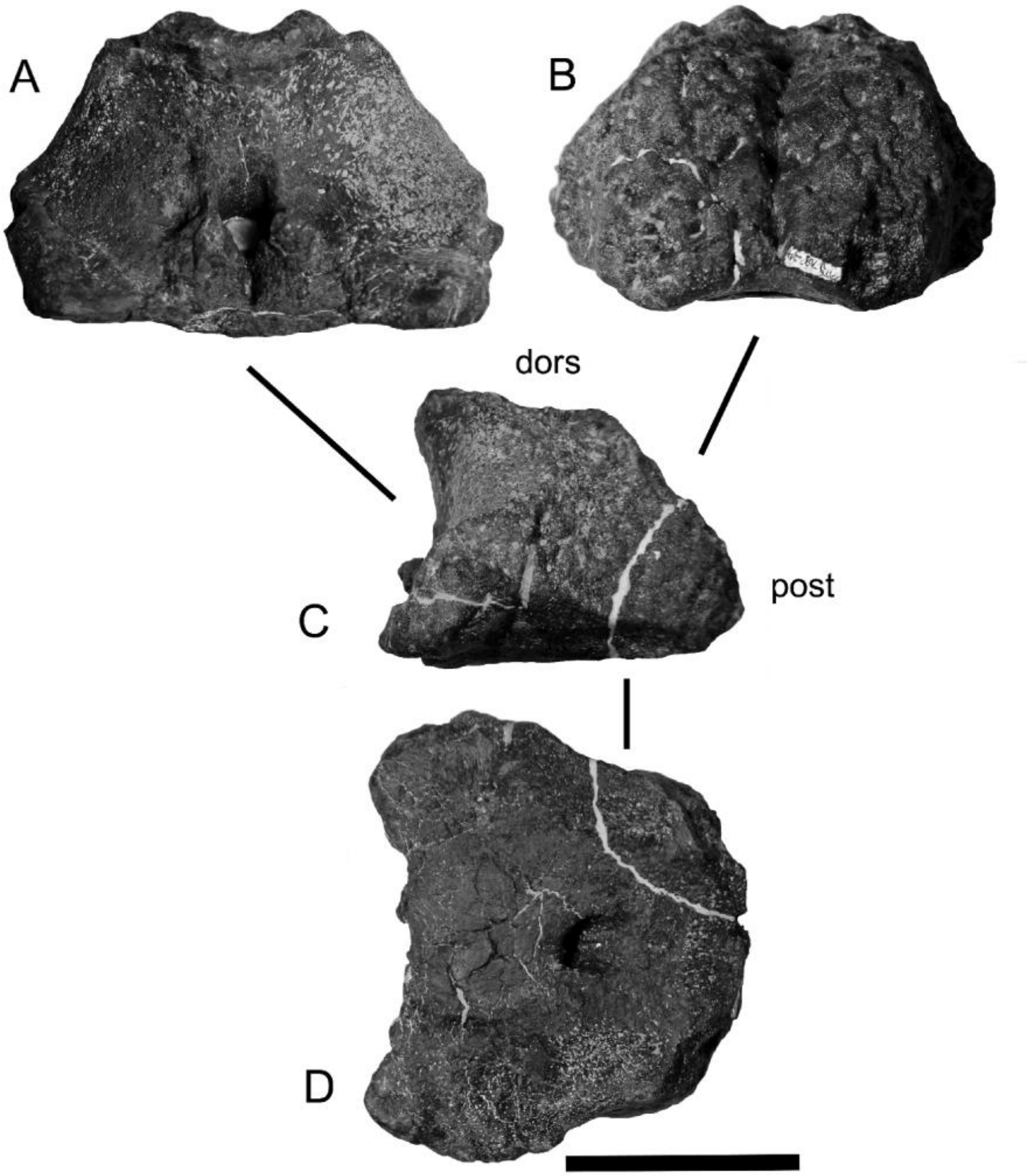

FIGURE 8: TATE v-7037, basisphenoid of *Baptanodon natans* (Mayoworth specimen). A. anteriodorsal view, B. left lateral view, C. posterior view, D. ventral view. Scale bar = 5 cm

ventral margin. Two rounded ridges are separated by a broad concavity at the dorsal margin, the *dorsum sellae* (see McGowan, 1973). A large internal carotid foramen is located along the midline, ventral to the center of the surface. A groove extends along the midline from the foramen almost to the ventral edge. Immediately lateral to the foramen are two prominent conical projections, which are medially adjacent to elongate impressions, presumably from the trabecula cartilages (McGowan, 1973; Moon and Kirton, 2016, text. fig. 14a). The projections are visible in lateral view (Figure 8C).

COMPARISON TO *OPHTHALMOSAURUS ICENICUS*

Until recently, *Ophthalmosaurus icenicus* and *Baptanodon natans* were considered congeneric (e.g., McGowan and Motani, 2003). The new material described here indicates that there are differences in braincase elements, but these features are not ones that were previously suggested (Appleby, 1956). The comparisons that follow are based on the two specimens of *B. natans* described herein and on published figures and descriptions of *O. icenicus* from Moon and Kirton (2016). Many more specimens are known for *O. icenicus*, and an evaluation of intraspecific variation in braincase elements could conceivably invalidate some the differences discussed below.

The two taxa differ in the shape of the supraoccipital in posterior or anterior view: in *O. icenicus*, it is a roughly semicircular arch (Moon and Kirton, 2016, pl. 9, fig 2), whereas in *B. natans* it is more rectangular, and overall wider than high. The supraoccipital of *O. icenicus* has broad lateral margins and a small embayment for the foramen magnum (Moon and Kirton, 2016, pl. 9, fig. 1, 2), whereas *B. natans* has narrower lateral margins and a wide, semicircular embayment for the foramen magnum (Figure 5B). In posterior view, the exoccipitals of *O. icenicus* are taller relative to the supraoccipital than those of *B. natans*. The result is that the exoccipitals comprise much more than half of the lateral margins of the foramen magnum in *O. icenicus* (Moon and Kirton, 2016, text-fig. 16), whereas they comprise only about half of the margins in *B. natans* (Figure 3A, B). Additionally, the foramen magnum is much narrower at the dorsal end in *O. icenicus*, whereas there is no dorsal constriction in *B. natans* (compare Figure 3A, B to Moon and Kirton, 2016, text-fig. 16).

The basioccipitals are similar between the taxa, and subtle differences might be difficult to recognize in isolation. Both basioccipitals are roughly pentagonal in anterior view, and have a prominent notochordal pit. However, on *O. natans* a broad notch is visible at the midpoint of the ventral edge (Moon and Kirton, 2016, text-fig 14a c, 16.), which is lacking in *B. natans*. In posterior view, both basioccipitals are wider than high, but *O. icenicus* has a prominent groove at the apex of the dorsal edge that is the floor of the foramen magnum; *B. natans* lacks this. Also in this view, the visible extracondylar area is more extensive in *O. icenicus* than in *B. natans*, especially along the ventral margins of the occipital condyle (Moon and Kirton, 2016, text-fig. 14c, 16; pl.10, fig.2). The occipital condyle itself is more flattened in *B. natans,* compared to the convex shape in *O. icenicus*, best seen in dorsal or ventral view, although this feature might be variable in the latter (compare Moon and Kirton, 2016, text fig. 14b to their pl. 9, fig. 3, 4).

Some differences also exist between the basisphenoids of *B. natans* and *O. icenicus*. In ventral view, the basipterygoid processes are longer anteriorly and larger in *B. natans*, making the anterior edge convex rather than nearly straight as it is in *O. icenicus* (compare Figure 5D to Moon and Kirton, 2016, text-fig. 10d; pl 7, fig.4). The anterior face of the basisphenoid is more convex in *B. natans*, and the two conical projections on either side of the internal carotid foramen are absent in *O. icenicus*. In posterior view, the basisphenoid of *O. icenicus* is much wider relative to its height than that of *B. natans* (compare Figure 8B to Moon and Kirton, 2016, pl. 7, fig. 2).

Postcranial features also distinguish the two taxa. As discussed above, the shape of the humerus is different, with *B. natans* having a longer humerus relative to its width and a narrower shaft compared to *O. icenicus*. The two species also differ in the pattern of shape change of centra along the vertebral column (Massare et al., 2006). The vertebral column is very regionalized in *O. icenicus* whereas *Baptanodon natans* has a less regionalized column. This is reflected in the larger height/length ratios of posterior dorsal and anterior caudal centra in *O. icenicus* compared to *B. natans* (Massare et al., 2006, fig. 4). However, measurements of individual centra are usually not sufficient to distinguish the two taxa.

A SECOND ICHTHYOSAUR TAXON IN THE SUNDANCE FORMATION

UW 24234 is a fragmentary specimen, but the weathered basioccipital is quite different from the basioccipitals described above (compare Figure 9 to Figure 7).

In posterior view (Figure 9A, B), the basioccipital is wider than high, as in *Baptanodon natans*, but the occipital condyle itself is nearly circular, with the notochordal pit slightly dorsal to the center. The condyle also differs in being strongly convex. The extracondylar area is slightly wider than on the Mayoworth and Kaycee specimens and almost uniform in width around the ventrolateral and ventral edges of the condyle. The maximum width of the basioccipital occurs at the dorsal-most extent of the extracondylar area, about midway between the dorsal and ventral edges. Unlike the *Baptanodon* specimens, there are two small ridges and a noticeable depression on the dorsal edge that marks the base of the foramen magnum. There is also a slight concavity at the midline of the ventral edge.

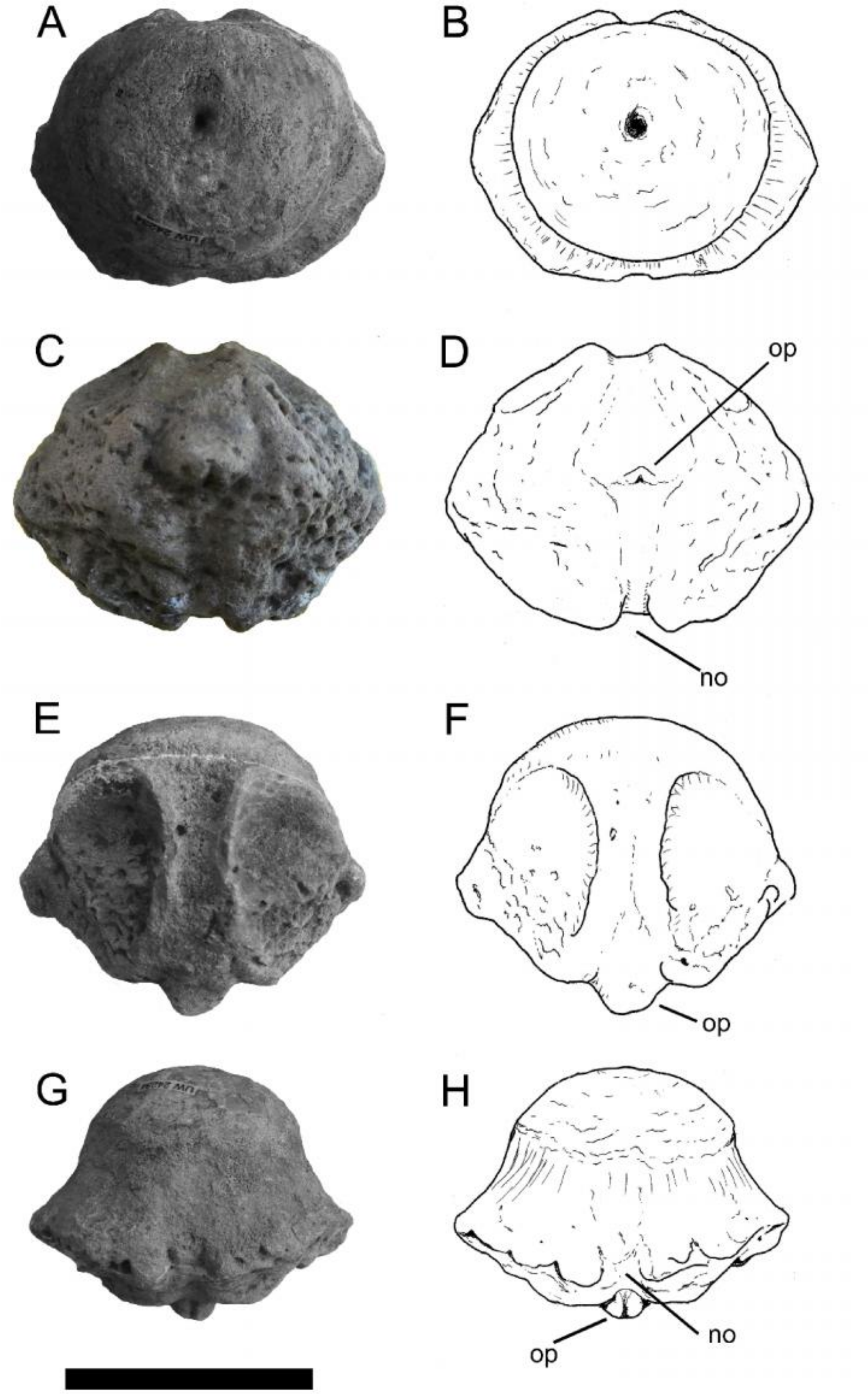

FIGURE 9: Basioccipital of UW 24234, a second species of ichthyosaur from the Sundance Formation. A., B. posterior view, C., D. anterior view, E., F. dorsal view, G, H. ventral view. Scale bar = 5 cm. **Abbreviations**: **no** ventral notch, **op** occipital peg.

In anterior view (Figure 9 C, D), the surface is rugose and lacks the large notochordal pit seen on the *Baptanodon* specimens. Instead, there is a small, triangular occipital peg at the midline, slightly dorsal to the middle of the bone. A broad groove extends from the peg to the ventral edge. As in the Mayoworth specimen, two curved ridges, smoother than the rest of the surface, are on either side of the midline, surrounding the peg, and extending almost to the ventral edge. A nearly rectangular ventral notch is visible in this view. The Kaycee and Mayoworth specimens lack a notch.

In dorsal view (Figure 9 E, F), two almost tear-drop shaped facets for the exoccipitals are oriented more laterally than in the *Baptanodon* specimens. The medial edges of the facets form ridges that define a shallow groove that is the base of the foramen magnum. Anteriorly, the groove widens and flattens, and terminates at the occipital peg. The Mayoworth specimen lacks the occipital peg and instead has a concavity at the ventral edge that reflects the presence of a large notochordal pit (Compare Figure 9 E, F to Figure 7 E, F).

In ventral view, the occipital condyle is uniformly convex, unlike that of the Kaycee and Mayoworth specimens, where the condyle flattens towards the margins (Compare Figure 9 G, H to Figure 7 G, H). In UW 24234, the exoccipital area is extensive in ventral view, similar to the *Baptanodon* specimens. The boundary between the occipital condyle and the exoccipital area is demarcated by a change in orientation of the lateral edges, as in the Mayoworth specimen. A ventral notch is at the midline, along the base of the extracondylar area, visible in ventral view (Figure 9 G, H) but more easily seen in anterior view (Figure 9 C, D). The occipital condyle and extracondylar surfaces are smooth, in spite of weathering. This contrasts with the anterior portion of the bone, which is rugose. The occipital peg is visible at the midline of the anterior edge (Figure 9 E, F).

In lateral view, the bone is strongly convex both posteriorly and anteriorly. About half of the bone length is the occipital condyle plus extracondylar area, the latter being larger than the former. The contrast between their smooth bone surfaces and the rugose surface of the anterior portion of the bone defines a distinct contact. In this view, the occipital peg is visible at the anterior edge.

The differences between this basioccipital and those of the Kaycee and Mayoworth specimens indicates that a second ichthyosaurian species, and probably a second genus, is present in the Redwater Shale. The morphology of the basioccipital of UW 24234 also has some potentially significant differences from those of other Oxfordian age ichthyosaurs. The basioccipital of *Ophthalmosaurus icenicus* from the Middle-Late Jurassic (Callovian-Tithonian) has a broad ventral notch, has less well defined facets for the exoccipitals, and has a smaller extracondylar area (relative to the size of the condyle) in ventral view (Moon and Kirton, 2016, text-fig. 14, plate 10). *Ophthalmosaurus icenicus* also lacks an occipital peg, although it can have an anterior process that might be homologous (Moon and Kirton, 2016, p. 41). The basioccipital of *Arthropterygius chrisorum* from the Late Jurassic (Oxfordian-Kimmeridgian) of Northwest Territories, Canada (Maxwell, 2010) has an incipient occipital peg, but it also has a well-defined notochordal pit on its anterior surface which UW 24234 lacks. Additionally, UW 24234 has a broader extracondylar area in posterior view than seen in *A. chrisorum*. Additional work is needed to determine if UW 24234 represents a new genus and species or a variation of a known species.

CONCLUSION

Excavation of two specimens of *Baptanodon natans* from the Redwater Shale in Johnson County, WY, has provided new information on the morphology of the braincase of the species. The morphology of the braincase of these new specimens is similar to that of the Carnegie Museum specimen (CM 878) figured by Gilmore (1906, plate XI, fig. 1), and upon which he based his reconstruction (JAM, pers. obs., 2021).

The new material indicates some inaccuracies in Gilmore’s reconstruction (1906, plate XI, fig. 2), largely due to the deformation of CM 878. The most noticeable differences are in the dorsal portion of the braincase.

1. The parietals overlap the lateral edges of the supraoccipital, they do not entirely wrap around the supraoccipital (also contrary to Appleby, 1956, who relied on Gilmore’s reconstruction).
2. The supraoccipital is wider than it is tall, and comprises about half of the lateral margin of the foramen magnum. Gilmore reconstructed it as a much taller, narrower bone that makes up much more than half of the lateral margin. This difference is probably due to the lateral compression of CMN 878, which makes the foramen magnum appear taller and the supraoccipital appear narrower, than in the undeformed state. Deformation also makes the braincase appear taller relative to its width, a feature that Appleby (1956, p. 442 and fig. 21) incorporated in his comparison of the two taxa

3. The exoccipitals are taller than shown in Gilmore reconstruction, and they comprise more of the lateral margin of the foramen magnum. They also have a more complex morphology, but the details are difficult to discern on CMN 878.

We had an advantage over Gilmore (1906) in having both a well preserved, articulated braincase as well as disarticulated elements from a second specimen. Moreover, the specimens were largely undeformed and preserved in three dimensions. We hope that these descriptions and figures will inform future analyses of the Ophthalmosauridae. Additionally, this detailed information on braincase elements of *B. natans* has led to the recognition of another ichthyosaurian taxon in the Sundance Formation, which will be the subject of future work.

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