REDESCRIPTION OF THE HOLOTYPE OF PLATECARPUS TYMPANITICUS COPE, 1869 (MOSASAURIDAE: PLIOPLATECARPINAE), AND ITS IMPLICATIONS FOR THE ALPHA TAXONOMY OF THE GENUS

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ARTICLE

REDESCRIPTION OF THE HOLOTYPE OF *PLATECARPUS TYMPANITICUS* COPE, 1869 (MOSASAURIDAE: PLIOPLATECARPINAE), AND ITS IMPLICATIONS FOR THE ALPHA TAXONOMY OF THE GENUS

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ABSTRACT—The fragmentary holotype and only known material of *Platecarpus tympaniticus* Cope, 1869, is redescribed and compared to other closely related plioplatecarpine mosasaurs. Re-characterization of the holotype reveals the following similarities to *Platecarpus ictericus*: exoccipital-basioccipital suture transversely oriented in condylar view; basal tubera not inflated and widely separated along ventral midline; cervical intervertebral joint surface strongly curved; seventh cervical vertebra lacking articulating intercentrum (i.e., hypapophyseal peduncle). In addition, the relatively complete right quadrate of the holotype of *P. tympaniticus* is virtually indistinguishable from those of *P. ictericus*. Quadrate characters, when combined with the four previously mentioned characters, uniquely diagnose both *P. tympaniticus* and *P. ictericus* among known mosasaur taxa. Because *P. tympaniticus* was established before *P. ictericus*, the former becomes the specific senior synonym of the latter, and is also the generic type of *Platecarpus*.

INTRODUCTION

The Late Cretaceous strata of the Western Interior Basin in North America have yielded over 3000 specimens of mosasaurs (Squamata: Mosasauridae) since the early part of the 19th century (e.g., Russell, 1967, 1988; Nicholls, 1988; Kiernan, 2002; pers. observ.). Although the earliest description of a mosasaur fossil from the continent dates back to 1834 when a partial snout was assigned to "*Ichthyosaurus*" *missouriensis* by R. Harlan (Caldwell and Bell, 2005), the vast majority of specimens were collected during the later part of the 19th century. During this time, E. D. Cope and O. C. Marsh began their famous fossil feuds, and mosasaurs figured prominently in their passion to name new fossil vertebrate taxa (e.g., Bell, 1997a; Everhart, 2005). From the late 1860s to early 1880s, a large number of mosasaur taxa were named based on inadequate and/or poorly preserved material, and with descriptions that often lacked accompanying illustrations (e.g., Cope, 1869, 1870b, 1871a, 1871b, 1874; Marsh, 1872, 1880). The holotype and only known specimen of the mosasaur *Platecarpus tympaniticus* Cope, 1869, the generic type, typifies the long-standing problems created by this clavier approach to systematics.

The type specimen of *Platecarpus tympaniticus* was collected from the Tombigbee Sand Member of the Eutaw Formation near Columbus, Mississippi, U.S.A., and is therefore middle Santonian to earliest Campanian in age (ca. 85 to 83 Ma) (Leidy, 1865; Cope, 1869; Russell, 1967; Mancini et al., 1996; Ogg et al., 2004; Mancini and Puckett, 2005) (Fig. 1). In addition to clearly plioplatecarpine cranial material and vertebrae, the holotype originally included a chelonian humerus and a phalangeal element of a non-mosasaur tetrapod (Leidy, 1865:pl. 8, figs. 1, 2, 7; Cope, 1869; pers. observ.). Leidy (1865) provided the first description of the holotype, with some specimen illustrations and various measurements, and provisionally referred it to *Holcodus acutidens* Gibbes, 1851. However, because this taxon was based on only three teeth, one of which was crocodilian (Gibbes, 1851; Leidy, 1865), Cope (1869) erected the new taxon *Platecarpus tympaniticus*, to which he assigned 'Leidy's holotype.' In proposing this new taxon, Cope (1869) devoted only half a page to the description and species diagnosis, and in this case, included neither measurements nor figures (cf. Konishi and Caldwell, 2007). Six years later, Cope (1875) figured the right quadrate of the holotype (reversed in his figure) for the first time (contra Konishi and Caldwell, 2007), but no further description was provided.

Although the holotype of *Platecarpus tympaniticus* continued to be the only specimen of the genus reported from Late Cretaceous strata of the eastern Gulf, 17 additional species of *Platecarpus* were described between 1870 and 1898, based on material collected primarily from western Kansas (Cope, 1874; Merriam, 1894; Thevenin, 1896; Williston, 1898). During this period, Cope named a total of eight *Platecarpus* species (Cope, 1874) whereas Marsh named four, although the latter used the name *Lestosaurus* (Marsh, 1872; Russell, 1967). Williston (1897:185) first addressed the taxonomic issues concerning the genus *Platecarpus*, stating that the congeneric status of *Platecarpus tympaniticus* from Mississippi with the "Kansas species" assigned to this genus had yet to be established conclusively. Williston (1897:185) based his argument on the fact that "very little of the skeleton has been described" of *P. tympaniticus*; at the same time, he also acknowledged that there is a high degree of similarity in the quadrate morphology between Mississippi and Kansas forms, and that the quadrate of *Platecarpus* is highly characteristic among mosasaurs. Subsequently, in his synthetic work on the systematics of European and North American mosasaurs, Williston (1898) reiterated these issues concerning *Platecarpus* taxonomy almost word for word, retained the genus,

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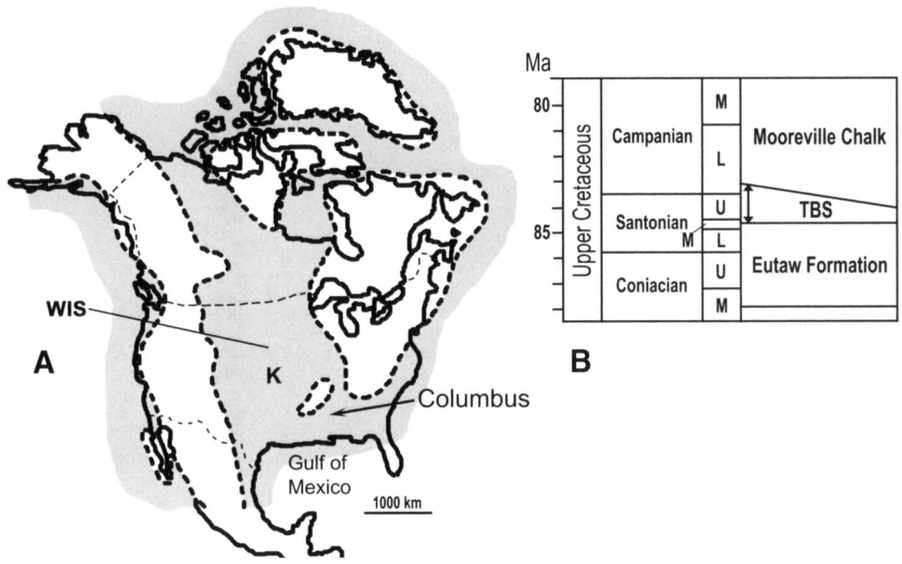


FIGURE 1. Locality and stratigraphic position of the *Platecarpus tympaniticus* Cope, 1869, holotype. **A**, paleogeographic map of North America during Campanian time. Gray areas indicate seaways. The specimen came from near Columbus, Mississippi, southern U.S.A.; **B**, section of the Upper Cretaceous chronostratigraphic column for northeastern part of the Gulf of Mexico. The holotype was collected from the Tombigbee Sand Member of the Eutaw Formation. In east-central Mississippi near Columbus, the Eutaw-Mooreville contact is earliest Campanian in age (Mancini et al., 1996), and hence the specimen is between middle Santonian and earliest Campanian in age, as indicated by the double-headed arrows. **Abbreviations**: **K**, Smoky Hill Chalk Member exposed in west-central Kansas; **L**, lower; **M**, middle; **Ma**, million years ago; **TBS**, Tombigbee Sand Member; **U**, upper; **WIS**, Western Interior Seaway. Paleogeographic reconstruction of North America modified from Hills et al. (1999). Chronostratigraphic column modified from Mancini and Puckett (2005).

and assigned a total of 14 species to it. Williston (1898:180) neither included nor redescribed *Platecarpus tympaniticus*, merely hoping that the knowledge of the eastern Gulf species would increase "in the immediate future."

Thus, the question of whether *Platecarpus tympaniticus* is congeneric with other species assigned to the genus was raised by Williston (1897, 1898), but never answered. Seventy years later, the question was revisited by Russell (1967), who recognized only five species of *Platecarpus* from North America, but considered that the fragmentary holotype and only specimen of *P. tympaniticus* was diagnostic at the generic level based on quadrate characters and general braincase and vertebral morphology. Consequently, Russell (1967) supported the nomenclatural seniority of *Platecarpus* Cope, 1869, over *Lestosaurus* Marsh, 1872 (cf. Cope, 1874; Williston, 1898). He also invalidated *Holcodus* Gibbes, 1851, stating that the only mosasaurid tooth of the *H. acutidens* holotype was characteristic of at least three plioplatecarpine genera; hence, he recognized *Platecarpus* as the oldest available generic name between the two (Russell, 1967). At the same time, Russell (1967) failed to provide a species diagnosis for *P. tympaniticus*; instead, he only suggested that *P. ictericus* (Cope, 1870a) or *P. coryphaeus* (Cope, 1871a) would become a junior synonym of *P. tympaniticus* once the "anterior portions of the skull of *P. tympaniticus* are discovered in the Eutaw Formation" in the eastern Gulf (p. 153). However, this merely indicated that the holotype of *P. tympaniticus* was not diagnostic at the species level, potentially making the taxon a nomen dubium.

Forty years later, while reviewing the taxonomy of *Platecarpus*, Konishi and Caldwell (2007) recognized the above issue and urged the redescription of the holotype of *Platecarpus tympaniticus*. This and a re-diagnosis of all other species was absolutely necessary prior to any future study addressing the nomenclatural seniority of the generic type over any other congener (see Nicholls, 1988; Bell, 1993, 1997b; Schumacher, 1993; Sheldon, 1996; Everhart, 2001; Bell and Polcyn 2005; Polcyn and Bell, 2005a). Konishi and Caldwell (2007) also concluded that *P. coryphaeus* is a junior synonym of *P. ictericus*, as they did not find Russell's (1967) proposed characters separating them to be taxonomically significant. In addition, Konishi and Caldwell (2007) suggested that another valid species of *Platecarpus* from North America, *P. planifrons* (Cope, 1874), was readily distinguishable from the holotype of *P. tympaniticus* based on quadrate characters.

Most recently, Konishi and Caldwell (2009) reported that the quadrate morphology of *Plioplatecarpus nichollsae* Cuthbertson et al., 2007, is virtually indistinguishable from that of *Platecarpus ictericus*. Following Russell (1967) and Konishi and Caldwell (2007, 2009), the quadrate of the holotype of *P. tympaniticus* could therefore diagnose *Plioplatecarpus nichollsae* as well as *Platecarpus ictericus*.

As a consequence of new perspectives and data, we here redescribe the holotype of *Platecarpus tympaniticus*, and compare it primarily with *P. ictericus*, *P. planifrons*, and *Plioplatecarpus nichollsae*, in order to determine the taxonomic validity of *Platecarpus tympaniticus*.

Institutional Abbreviations—**ALMNH PV**, Alabama Museum of Natural History, Tuscaloosa, Alabama, U.S.A.; **AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **ANSP**, Academy of Natural Sciences Philadelphia, Philadelphia, Pennsylvania, U.S.A.; **BMNH R**, The Natural History Museum, London, United Kingdom; **CMN**, Canadian Museum of Nature, Ottawa, Ontario, Canada; **FHSM VP**, Fort Hays Sternberg Museum of Natural History, Hays, Kansas, U.S.A.; **FM UC**, Field Museum, Chicago, Illinois, U.S.A.; **KU**, University of Kansas Natural History Museum, Lawrence, Kansas, U.S.A.; **LACM**, Natural History Museum of Los Angeles County, Los Angeles, California, U.S.A.; **RMM**, McWane Science Center (formerly Red Mountain Museum), Birmingham, Alabama, U.S.A.; **UW**, University of Wisconsin–Madison Geology Museum, Madison, Wisconsin, U.S.A.; **YPM**, Yale University Peabody Museum of Natural History, New Havens, Connecticut, U.S.A.

MATERIALS AND METHODS

The holotype of *Platecarpus tympaniticus* is comprised of nine numbered specimens, all attributed to a single individual (Leidy, 1865): ANSP 8484, a partial left surangular; ANSP 8487, a right quadrate; ANSP 8488, a nearly complete anterior cervical vertebra; ANSP 8491, a partial right pterygoid; ANSP 8558, a partial posterior-most cervical vertebra; ANSP 8559, a partial posterior cervical vertebra; ANSP 8562, a partial basioccipital-basisphenoid complex; and ANSP 8488, jaw fragments associated with a block of matrix. ANSP 8491, the partial pterygoid, is lost but figured in Leidy (1865:pl. XI, fig. 14; see also Konishi and Caldwell, 2007:fig. 8B). The above elements were photographed

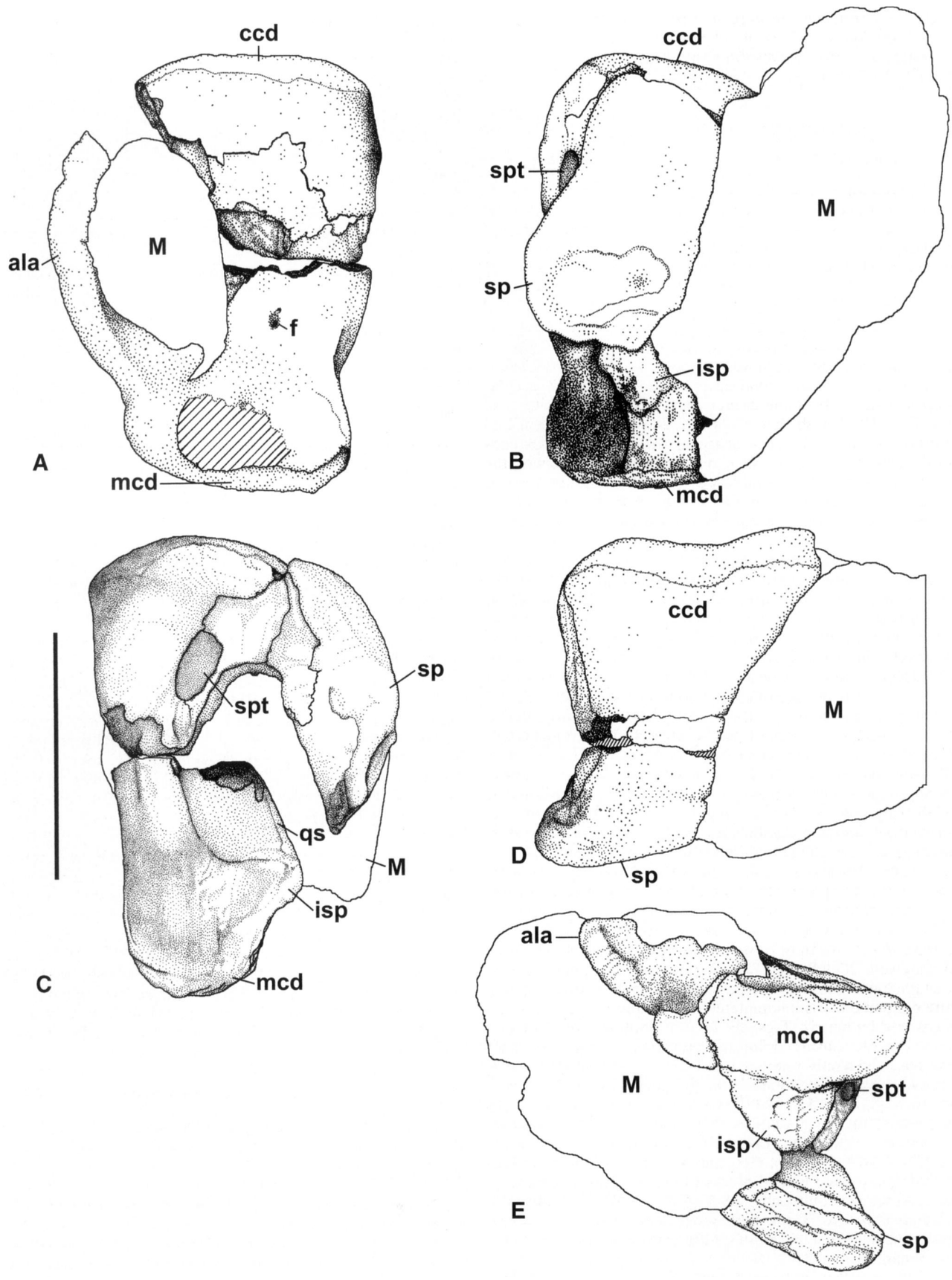


FIGURE 2. *Platecarpus tympaniticus* holotype right quadrate, ANSP 8487 (diagrams). **A**, anterior; **B**, posterior; **C**, medial; **D**, dorsal; **E**, ventral views. **Abbreviations**: **ala**, tympanic ala; **ccd**, cephalic condyle; **f**, anterior foramen; **isp**, infrastapedial process; **M**, matrix; **mcd**, mandibular condyle; **qs**, quadrate shaft; **sp**, suprastapedial process; **spt**, stapedial pit. Cross-hatched area in **A** indicates broken surface. Scale bar equals 5 cm.

and the description given here is based on observation of the material. Outline drawings of ANSP 8487 (quadrate) and 8562 (braincase) were produced from photographs using Adobe Photoshop 7.0 for Windows.

DESCRIPTIONS AND COMPARISONS

Cranial Elements

Right Quadrate—The element (ANSP 8487: Figs. 2, 3; Cope, 1875:pl. XXXVII, fig. 11) is relatively complete and undistorted. It is approximately as wide as it is long, owing mainly to the great lateral expansion of the tympanic ala (Cope, 1869; Figs. 2, 3). The suprastapedial process is laterally unconstricted and elongate, its length constituting about two-thirds the height of the quadrate shaft. The process exhibits a rounded expansion at its distal end (Figs. 2B, 3B). The anterior border of the cephalic condyle is not markedly notched posteriorly, and its anteromedial corner is gently rounded in dorsal view, similar to *Platecarpus ictericus* and *Plioplatecarpus nichollsae*, but differing from *Platecarpus planifrons* where the same corner develops into an acute crest (Figs. 2D, 3D; Konishi and Caldwell, 2007:fig. 7; Konishi and Caldwell, 2009:fig. 8E). In dorsal aspect, the quadrate ala extends laterally from the quadrate shaft, forming a right angle with the long axis of the suprastapedial process, as in *Platecarpus ictericus* and *Plioplatecarpus nichollsae* (same figure references as above). An undistorted rim of the ala describes a semicircular outline (Figs. 2A, 3A).

As in *Platecarpus ictericus* and *Plioplatecarpus nichollsae*, the quadrate bears a gently domed medial vertical ridge that extends approximately along the dorsal two-thirds of the shaft (Figs. 2C, 3C; Russell, 1967:fig. 25C; Konishi and Caldwell, 2009:fig. 8B, I). This trait differs in *Platecarpus planifrons*, where a thin, well-developed vertical crest is present instead in the same region (Konishi and Caldwell, 2007:fig. 6B). Immediately below this ridge, the medial face of the mandibular condyle is shallowly excavated, presumably for the loose ligamentous articulation with the quadrate ramus of the pterygoid. The broadly oval stapedial pit has straight lateral borders, typical of the condition in *Platecarpus ictericus* and *Plioplatecarpus nichollsae*; the pit is keyhole-shaped in *Platecarpus planifrons* (Konishi and Caldwell, 2007:fig. 6B).

In ventral view, the mandibular condyle is transversely elongate (Figs. 2E, 3E). The anterior deflection of the condylar surface has been damaged, and as a consequence the anterior condylar border is incomplete. However, the condyle probably formed a curved teardrop-shape outline similar to *Platecarpus ictericus* and *Plioplatecarpus nichollsae*. The posteroventral border of the quadrate shaft is straight in medial view (Figs. 2C, 3C; Konishi and Caldwell, 2009:fig. 7). The degree of development of the infrastapedial process is unclear, as the posteroventral portion of the tympanic ala is incomplete, and the process is also laterally covered by matrix (Figs. 2B, 3B). In both *Platecarpus ictericus* and *Plioplatecarpus nichollsae*, the infrastapedial process extends posterodorsally immediately lateral to the posteroventral corner of the quadrate shaft. In many specimens of *Platecarpus ictericus* (e.g., AMNH 1820; CMN 40914), the process is long and contacts the distolateral corner of the suprastapedial process, whereas in the well-preserved quadrate of *Plioplatecarpus nichollsae* (TMP 83.24.01), the process is small and widely separate from the suprastapedial process (compare Russell, 1967:figs. 24B, 25A; Konishi and Caldwell, 2009:figs. 7, 8D). Whether this difference is of taxonomic significance or not cannot be determined conclusively, until more specimens of the latter taxon become available.

Overall, no major features separate the quadrate morphology of the holotype of *Platecarpus tympaniticus* from that of *P. ictericus* or *Plioplatecarpus nichollsae*.

Basioccipital-Basisphenoid—Although the basioccipital-basisphenoid complex (ANSP 8562: Figs. 4, 5) is not distorted, the bone surface shows some weathering, and its dorsal portion is broken. The well-preserved ventral surface is solid except for some small foramina. The paired basal tubera are not inflated and are separated from each other, a condition more similar to *Platecarpus planifrons* and *P. ictericus* than to *Plioplatecarpus nichollsae* (Figs. 4B, D, 5B, D; Russell, 1967:fig. 17; Konishi and Caldwell, 2009:figs. 10, 11). Between the pair of posterolateral processes of the basisphenoid is a single ventral foramen with an irregular outline, situated at the sutural contact between the basisphenoid and basioccipital (Figs. 4D, 5D). Anterior to this foramen, a distinct longitudinal sulcus separates the posterolateral processes of the basisphenoid, extending forward and gradually shallowing along its course.

When viewed laterally, the distal surface of the basal tubera is notched dorsally, forming a C-shape (Figs. 4E, 5E). The descending process of the opisthotic wraps the dorsolateral portion of the tuber. Due to surface erosion, no exits for any cranial nerves can be discerned on the lateral wall of the opisthotic.

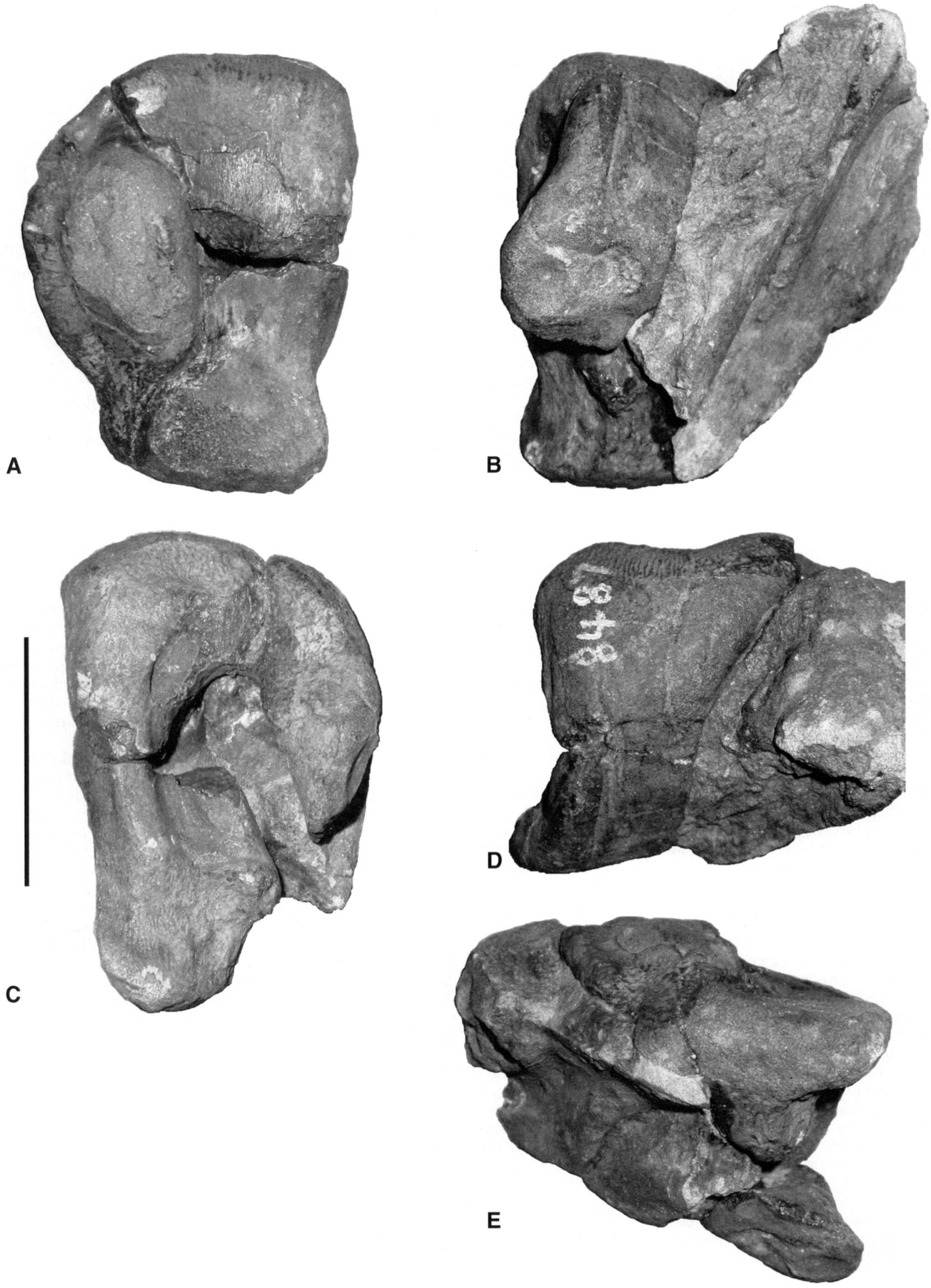
In posterior aspect, the articular surface of the occipital condyle is shallowly sulcate along the midline, but this likely reflects erosion; the same surface is strongly sulcate medially in AMNH 1820 (*Platecarpus ictericus*) and TMP 83.24.01 (*Plioiplatecarpus nichollsae*) (Figs. 4B, 5B; Konishi and Caldwell, 2009:fig. 11; pers. observ.). The orientation of the sutural surface between the basioccipital and exoccipital is horizontal, as seen in *Platecarpus ictericus* (e.g., AMNH 1820; Russell, 1967:fig. 17). In *Plioplatecarpus nichollsae* and *P. primaevus*, this suture slants lateroventrally (Konishi and Caldwell, 2009). The foramen magnum is taller than wide.

Pterygoid—The partial right pterygoid (ANSP 8491: Leidy, 1865:pl. XI, fig. 14; Konishi and Caldwell, 2007:fig. 8B), bearing five teeth and three vacant alveoli as described by Leidy (1865), is currently missing. According to Leidy (1865:72), this partial pterygoid measured "three inches [= 7.6 cm] long," comparable in size to the holotype material. The preserved pterygoid teeth have "a circular base, and are strongly curved backward" (Leidy, 1865:73). These teeth are also divided into halves by two carinae, one found on the medial and the other on the other surface of each crown (Leidy, 1865). According to Leidy (1865), the teeth were also striated on both anterior and posterior faces. These fine surface features on each pterygoid tooth crown are common to *Platecarpus planifrons*, *P. ictericus*, and *Plioplatecarpus nichollsae*. Although Leidy (1865) considered it to be the left pterygoid, his description as well as figure clearly indicates that it is the right pterygoid (a side identity supported by the position of the resorption pits) (Leidy, 1865:pl. XI, fig. 14; Konishi and Caldwell, 2007).

Surangular—The partial left surangular (ANSP 8484) deepens anteriorly as in *Platecarpus* and *Plioplatecarpus nichollsae*. The dorsal border is elevated where it meets the coronoid buttress, whereas this border remains horizontal in *Platecarpus planifrons*. The element bears a distinct, shelf-like horizontal ridge on the medial surface at about mid-height, under which the prearticular would have fitted. The lateral cortical surface is variably eroded, and the ventral, anterior, and posterior borders are all incomplete. The glenoid portion of the surangular is missing.

Postcranium

Cervical Vertebrae—The three holotype vertebrae (ANSP 8488, 8558, 8559: Leidy, 1865:pl. VII, figs. 4–7; Konishi and Caldwell, 2007:fig. 8A, C–E) are figured in Leidy (1865). ANSP 8488 and 8559 bear well-developed hypapophyses with a distinct facet for an intercentrum (= hypapophyseal peduncle). On the former vertebra, the intercentrum facet is drop-shaped with its apex pointing anteriorly, whereas the facet is smaller with a longi-



tudinally elongate elliptical outline on the latter. The synapophyseal facets are deeper in ANSP 8559 than in 8488, and thus the former most likely comes from a more posterior part of the cervical column. In ANSP 8558, although the "hypapophysis is a mere rudiment" (Leidy, 1865:38), and the vertebra apparently lacked an associated intercentrum, its articular cotyle fits well with the articular condyle of ANSP 8559, strongly indicating that they are adjoining vertebrae. Compared with a complete cervical series of *Platecarpus* sp., cf. *P. ictericus* (AMNH 2005 and YPM 24900), ANSP 8488 is probably the fourth and ANSP 8559 is either the fifth or sixth vertebra. In AMNH 2005 and YPM 24900, the last intercentrum-bearing cervical is the sixth, with the seventh exhibiting a rudimentary median ventral tuberosity (Russell, 1967:fig. 40). As ANSP 8559 most probably articulated with ANSP 8558, they are interpreted here to represent the sixth and seventh cervical vertebrae, respectively. In the holotype of *Plioplatecarpus nichollsae* (CMN 52261), the seventh cervical vertebra clearly articulated with an intercentrum (Cuthbertson et al., 2007).

In all vertebrae, the intervertebral joint surface exhibits strong curvature as in *Platecarpus ictericus*, whereas this surface is much less curved in *Plioplatecarpus nichollsae* (Leidy, 1865:pl. VII, figs. 4, 5; Konishi and Caldwell, 2009:fig. 14C, H). The articular surface is transversely oval, where the articular condyle width exceeds its height by 30% and 25% in ANSP 8488 and ANSP 8559, respectively. Hence, cervical centra are more compressed vertically towards the skull. The condyle is incomplete in the last cervical, ANSP 8558. Between ANSP 8488 and ANSP 8559, the neural spine is more erect and taller in the posterior one. A distinct rounded crest connects the well-developed prezygapophysis with the synapophysis where preserved. From the ventral corner of the synapophyseal facet, a horizontal ridge extends anteriorly to be connected with the lateroventral corner of the cotylar rim. Each postzygapophyseal facet faces lateroventrally at approximately 60 degrees from the horizontal (Leidy, 1865:pl. VII, fig. 6). The presence of zygosphenes cannot be confirmed in any vertebra due to poor preservation, but a shallow, posteriorly facing oval depression at the base of the right postzygapophysis on ANSP 8559 indicates the presence of zygantra in the posterior cervicals.

TAXONOMIC DISCUSSION

The fragmentary nature of the holotype of *Platecarpus tympaniticus* has made diagnosis relative to other plioplatecarpine species difficult (e.g., Williston, 1897, 1898; Russell, 1967; Konishi and Caldwell, 2007). No dermal skull elements such as a frontal and a parietal are preserved with the holotype material. According to our redescription, the morphology of the well-preserved right quadrate ANSP 8487 (Figs. 2, 3) cannot be discriminated taxonomically from that of *Platecarpus ictericus* (late middle Santonian to late early Campanian) or *Plioplatecarpus nichollsae* (earliest middle Campanian) (Gill and Cobban, 1965; Hattin, 1982; Nicholls, 1988; Ogg et al., 2004; Cuthbertson et al., 2007; Konishi, 2008; Konishi and Caldwell, 2009). As both the pterygoid and surangular are poorly preserved in the holotype, the partial basioccipital-basisphenoid complex (ANSP 8562) and three cervical vertebrae (ANSP 8488, 8558–59) are the only elements of the specimen useful in determining its species-level identity.

The preserved portion of the basioccipital-basisphenoid complex (Figs. 4, 5) shows at least two important characters that characterize *Platecarpus ictericus* but not *Plioplatecarpus nichollsae*. In posterior view, the suture between the exoccipital and occipital condyle is horizontal in orientation (Figs. 4B, 5B). In *Plioplatecarpus nichollsae* and *P. primaevus*, the suture is lateroventrally inclined, thereby decreasing the posterior exposure of the occipital condyle (Konishi and Caldwell, 2009:fig. 11). In *P. nichollsae*, a pair of bulbous basal tubera protrudes ventrally and towards the midline, a defining feature of this species among known plioplatecarpine mosasaurs (Konishi and Caldwell, 2009). In ANSP 8562 as well as in the holotype of *Platecarpus ictericus* (AMNH 1559), the tubera are not inflated, are widely separated from each other across the cranial midline, and project more laterally (Figs. 4, 5; cf. Russell, 1967:fig. 17).

When the general morphology of the cervical vertebrae is considered, the significant curvature of the intervertebral joint as seen in the holotype of *Platecarpus tympaniticus* is shared with *Platecarpus ictericus*, but not with *Plioplatecarpus nichollsae* (compare Leidy, 1865:pl. VII, figs. 4, 5; AMNH 1559 [*Plat. ictericus* holotype]; Konishi and Caldwell, 2009:fig. 14H [*Plio. nichollsae*]). In fact, the decrease in the intervertebral joint curvature in the cervical column appears to be a synapomorphy of the most derived plioplatecarpines, occurring in *Plioplatecarpus nichollsae* and all the other nominal *Plioplatecarpus* species (Holmes, 1996; Konishi and Caldwell, 2009; pers. observ.).

In addition, one of Russell's (1967) diagnostic characters for the genus *Platecarpus* was a total number of intercentrum-bearing cervical vertebrae of five; i.e., from the axis to the sixth vertebra. According to our comparative observations, ANSP 8558 was identified as the seventh cervical vertebra, whereas its hypapophysis is a rudimentary projection lacking a distinct articular facet for the eighth intercentrum. In contrast, a fully articulating hypapophysis is present on the same vertebra in the holotype of *Plioplatecarpus nichollsae* (Cuthbertson et al., 2007). This indicates that the holotype of *Platecarpus tympaniticus* exhibits the condition that Russell (1967) identified as diagnostic of *Platecarpus*, and that it is distinct from *Plioplatecarpus nichollsae*. Nevertheless, examination of more specimens of each taxon is required to determine the taxonomic usefulness of this trait, as the number of intercentrum-bearing cervical vertebrae is known to vary in *Plotosaurus bennisoni* (Lindgren et al., 2008).

Based on the suite of quadrate, basioccipital, and vertebral characters that we identify above, the holotype of *Platecarpus tympaniticus* is indistinguishable from *P. ictericus* but distinct from all other known plioplatecarpine mosasaurs. Based on our survey of nearly 500 plioplatecarpine specimens, little morphological evidence contradicts the synonymy of the two taxa (likewise, we find no reasonable support for distinguishing *P. ictericus* and *P. coryphaeus*; cf. Konishi and Caldwell, 2007).

This synonymy is also in accordance with the age of the holotype of *Platecarpus tympaniticus* as middle Santonian to earliest Campanian (ca. 85 to 83 Ma) (Mancini et al., 1996; Ogg et al., 2004; Mancini and Puckett, 2005). Although based on a limited sample size, Konishi (2008) suggested that in the Smoky Hill Chalk Member exposed in west-central Kansas, *P. ictericus* is known from Marker Unit 11 or above (early late Santonain to late early Campanian [ca. 84 to 81 Ma]) (Hattin, 1982; Ogg et al., 2004). *Plioplatecarpus nichollsae* occurs in the lowermost middle Campanian (ca. 80.5 Ma) (Gill and Cobban, 1965; Nicholls, 1988; Ogg et al., 2004), adding temporal support for the synonymy of *Platecarpus tympaniticus* and *P. ictericus*.

Finally, several mosasaur specimens that are morphologically comparable to the holotype of *Platecarpus tympaniticus* have

← FIGURE 3. *Platecarpus tympaniticus* holotype right quadrate, ANSP 8487 (photographs). **A**, anterior; **B**, posterior; **C**, medial; **D**, dorsal; **E**, ventral views. Scale bar equals 5 cm.

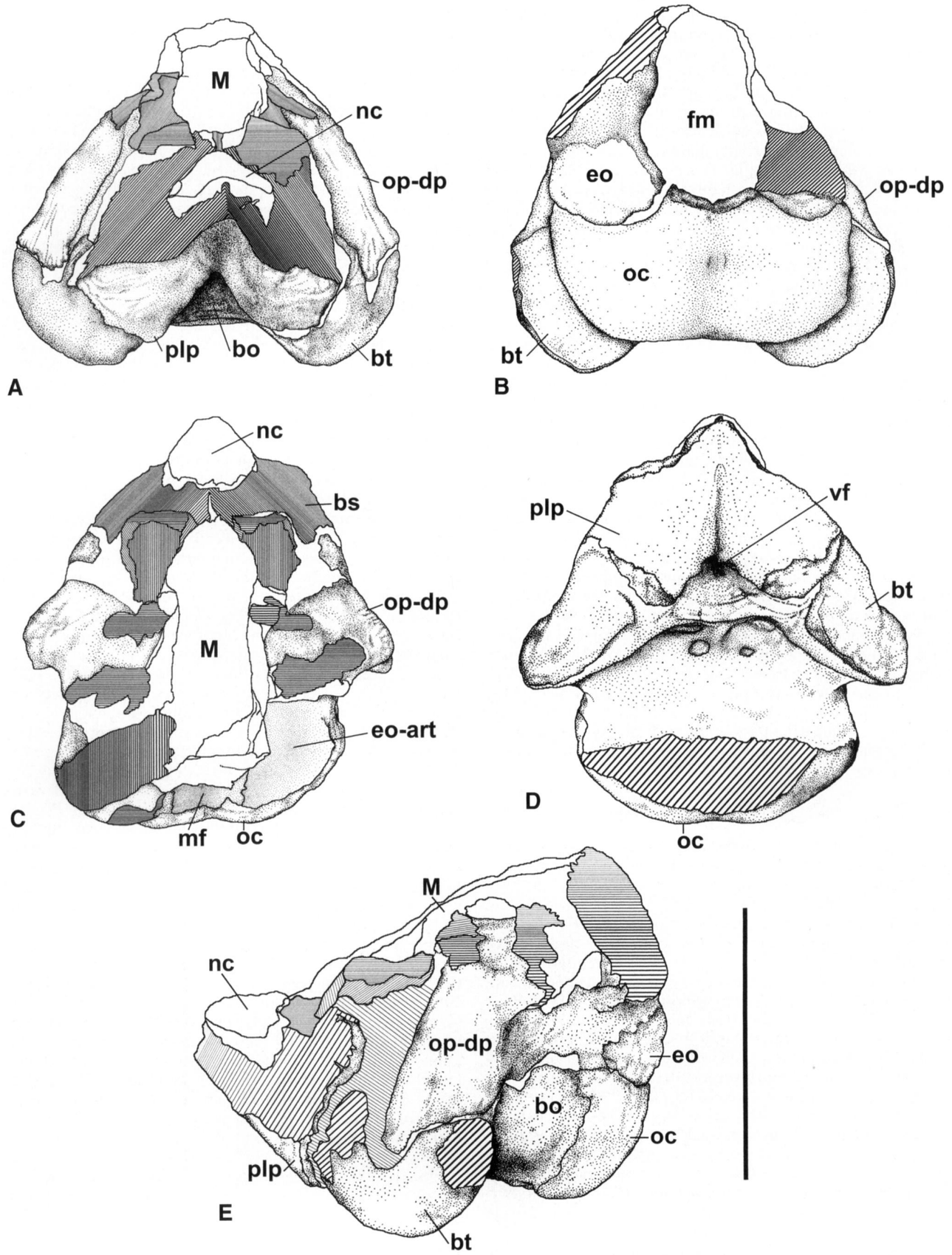


FIGURE 4. *Platecarpus tympaniticus* holotype partial braincase, ANSP 8562 (diagrams). **A**, anterior; **B**, posterior; **C**, dorsal; **D**, ventral; **E**, left lateral views. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **bt**, basal tuber; **eo**, exoccipital; **eo-art**; articulation surface for exoccipital on basioccipital; **fm**, foramen magnum; **M**, matrix; **mf**, medullary floor; **nc**, neural canal; **oc**, occipital condyle; **op-dp**, descending process of opisthotic; **plp**, posterolateral process of basisphenoid; **vf**, ventral foramen. Cross-hatched areas indicate broken surfaces. Scale bar equals 5 cm.

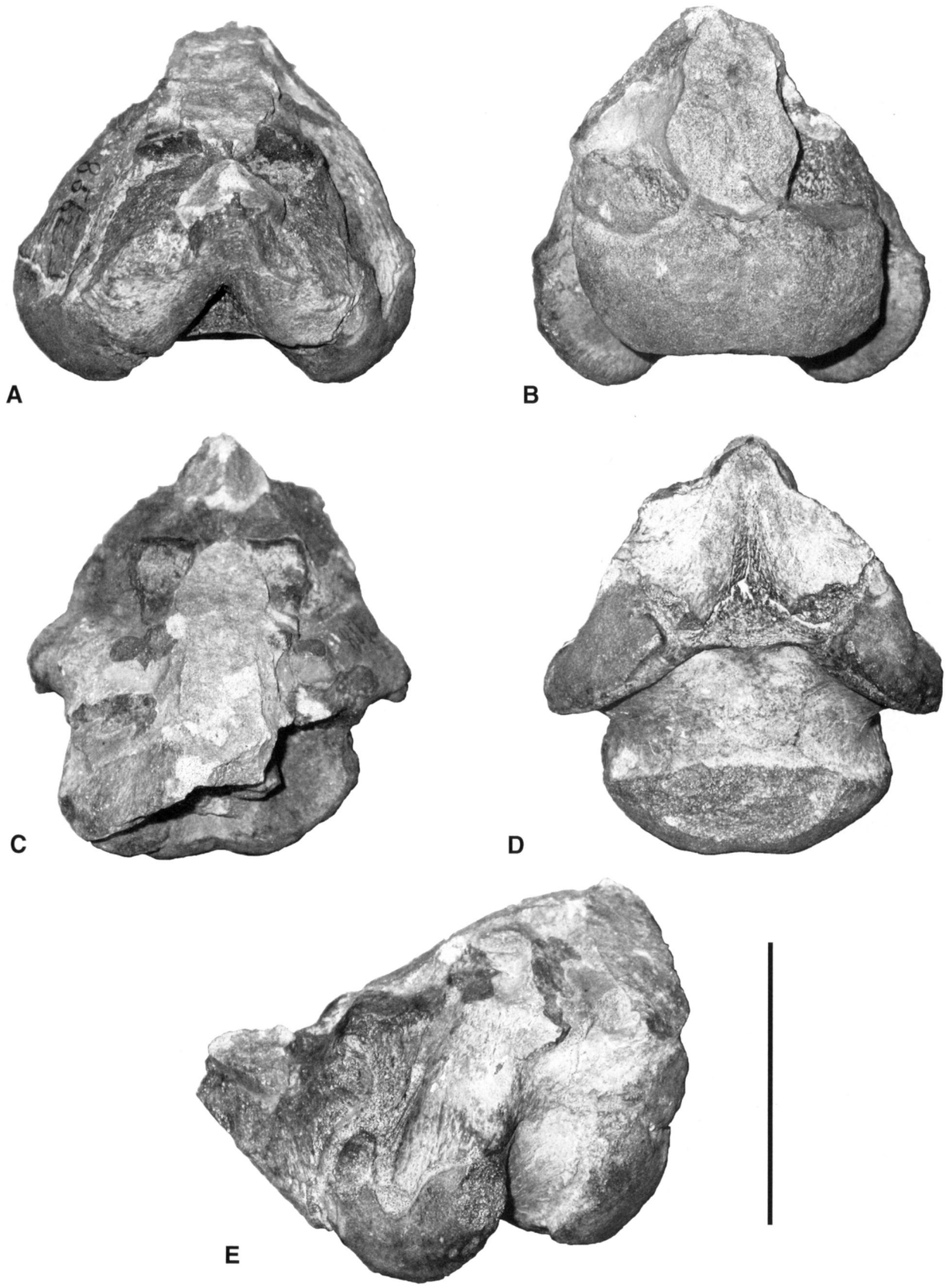


FIGURE 5. *Platecarpus tympaniticus* holotype partial braincase, ANSP 8562 (photographs). **A**, anterior; **B**, posterior; **C**, dorsal; **D**, ventral; **E**, left lateral views. Scale bar equals 5 cm.

been collected from the lowest part of the Mooreville Chalk (late Santonian to earliest Campanian [ca. 84 to 83 Ma] in age) in west-central Alabama (e.g., ALMNH PV 985.0021; RMM 1903, 7070 [in part]) (Mancini et al., 1996; Kiernan, 2002; Ogg et al., 2004; Mancini and Puckett, 2005; pers. observ.). As stratigraphically older *Platecarpus planifrons* is found in similar aged rocks in both west-central Kansas and central Alabama (Konishi, 2008), it seems likely that the later occurring *P. tympaniticus* also inhabited the Western Interior Seaway south of Kansas to the Gulf of Mexico (cf. Fig. 1). Hence, palaeobiogeographic evidence also supports the synonymy of *P. tympaniticus* and *P. ictericus*.

CONCLUSIONS

Although Konishi and Caldwell (2007) suggested that the holotype of *Platecarpus tympaniticus* may not be diagnostic, the above redescription of the holotype, and a character comparison with closely related plioplatecarpine species, indicates that the specimen exhibits characters that also diagnose *P. ictericus* to the exclusion of all other mosasaurs. As well, the stratigraphic occurrence of the Mississippi holotype conforms to the known stratigraphic range of *P. ictericus* in Kansas. We therefore conclude that *Platecarpus tympaniticus* Cope, 1869, is a senior synonym of *Platecarpus ictericus* (Cope, 1870a). Following Konishi and Caldwell's (2007) taxonomy of *Platecarpus*, and Konishi and Caldwell's (2009) suggestion that the North American material referred to *Platecarpus somenensis* should pertain to a different genus, we further conclude that there are two species of the genus present, i.e., *P. tympaniticus* (generic type) and *P. planifrons* (Cope, 1874).

SYSTEMATIC PALEONTOLOGY

REPTILIA Linnaeus, 1758
SQUAMATA Oppel, 1811
MOSASAURIDAE Gervais, 1852
RUSSELLOSAURINA Bell and Polcyn, 2005
PLIOPLATECARPINAE Dollo, 1884
PLATECARPUS Cope, 1869

Platecarpus Cope, 1869:264.
Holcodus Cope, 1871b:269.
Liodon Cope, 1871b:273 (in part).
Lestosaurus Marsh, 1872:454.
Holosaurus Marsh, 1880:87.

Generic Type—*Platecarpus tympaniticus* Cope, 1869.

Diagnosis (revised from Konishi and Caldwell, 2007)—Size moderate, mandible seldom reaching 0.7 m in length; small, acute predental rostrum on premaxilla may be present; premaxillomaxillary suture posteriorly ascending in straight line; posterior termination of the suture between second and third maxillary tooth; 12 maxillary teeth; prefrontal forming posterior one-third of lateral border of external naris; incipient supraorbital process on prefrontal; lateral margin of frontal gently curved in preorbital region; lateral borders of frontal converging anterior to orbits; ventrolateral processes of frontal running parallel with each other; frontal forming median notch to receive anterior portion of parietal table; parietal foramen ovoid; lateral margins of parietal table forming parietal crest anterior to divergence of suspensorial rami; parietal postorbital process short, not reaching anterolateral corner of upper temporal fenestra; same process not forming dorsal plateau posteriorly adjacent to frontal ala; 10 or more pterygoid teeth; ectopterygoid process projecting anterolaterally from dentigerous body of pterygoid; posteroventral jugal process acutely pointing posteriorly; suprastapedial process of quadrate elongate, more than two-thirds total quadrate height; supra- and infrastapedial process unfused; quadrate ala projecting laterally nearly perpendicular to long axis of suprastapedial process in dorsal aspect; quadrate alar surface relatively planar; large, vertically elongate stapedial pit; elongate, parallel-sided stapedial notch; mandibular condyle gently convex, transversely wide; predental projection on dentary absent; 12 teeth in dentary; no extensive edentulous portion posterior to last dentary tooth on dentary; surangular constantly diverging anteriorly, dorsal and ventral borders straight; articular portion of glenoid fossa larger than surangular portion; retroarticular process short, bearing large foramina on ventral surface; marginal teeth posteromedially recurved, possessing anterior and posterior carinae, and lingual striations and labial facets; basal cross-section of these teeth subcircular; cervical intervertebral joint strongly curved; zygosphenes and zygantra rudimentary; scapular blade anteroventral border forming obtuse angle with long axis of scapular neck; more than half the length of scapular blade posteroventral border anteriorly embayed; coracoid fan-shaped, may be notched; humerus length only slightly exceeding distal width; four or five carpals; phalanges elongate.

PLATECARPUS TYMPANITICUS Cope, 1869
(Figs. 2–5)

?*Holcodus acutidens* Gibbes, 1851: Leidy, 1865:118, pl. VII, figs. 4–7, pl. XI, fig. 14 (nomen dubium).
Platecarpus tympaniticus Cope, 1869:265.
Liodon ictericus Cope, 1870a:572 (first usage).
Liodon mudgei Cope, 1870a:572 (first usage).
Liodon ictericus Cope, 1870a: Cope, 1870b:577 (original description).
Liodon mudgei Cope, 1870a: Cope, 1870b:581 (original description).
Holcodus coryphaeus Cope, 1871a:298 (first usage).
Holcodus ictericus (Cope, 1870a): Cope, 1871a:298 (new combination).
Liodon curtirostris Cope, 1871a:298 (first usage).
Holcodus coryphaeus Cope, 1871a: Cope, 1871b:269 (original description).
Holcodus mudgei (Cope, 1870a): Cope, 1871b:273 (new combination).
Liodon curtirostris Cope, 1871a: Cope, 1871b:273 (original description).
Lestosaurus simus Marsh, 1872:455, pl. X, pl. XII, fig. 2.
Lestosaurus felix Marsh, 1872:457, pl. XIII, fig. 4.
Lestosaurus latifrons Marsh, 1872:458, pl. XIII, fig. 3.
Lestosaurus gracilis Marsh, 1872:460.
Lestosaurus curtirostris (Cope, 1871a): Marsh, 1872:461 (new combination).
Lestosaurus ictericus (Cope, 1870a): Marsh, 1872:461 (new combination).
Lestosaurus coryphaeus (Cope, 1871a): Marsh, 1872:461 (new combination).
Rhinosaurus mudgei (Cope, 1870a): Marsh, 1872:463 (new combination).
Platecarpus ictericus (Cope, 1870a): Cope, 1874:35 (new combination).
Platecarpus coryphaeus (Cope, 1871a): Cope, 1874:35 (new combination).
Platecarpus felix (Marsh, 1872): Cope, 1874:35 (new combination).
Platecarpus curtirostris (Cope, 1871a): Cope, 1874:36 (new combination).
Platecarpus simus (Marsh, 1872): Cope, 1874:36 (new combination).
Platecarpus latifrons (Marsh, 1872): Cope, 1874:36 (new combination).
Platecarpus gracilis (Marsh, 1872): Cope, 1874:36 (new combination).

Platecarpus mudgei (Cope, 1870a): Cope, 1874:36 (new combination).
Platecarpus coryphaeus (Cope, 1871a): Cope, 1875:142, pl. XV, fig. 1, pl. XVI, fig. 3, pl. XVII, fig. 6, pl. XX, figs. 4–7, pl. XXI, figs. 1, 2, pl. XXXVI, fig. 6, pl. XXXVII, fig. 9.
Platecarpus ictericus (Cope, 1870a): Cope, 1875:144, pl. XV, fig. 2, pl. XVII, figs. 3, 4, pl. XVIII, fig. 6, pl. XIX, figs. 7–10, pl. XX, figs. 1–3, pl. XXV, figs. 1–25(27), pl. XXXVI, fig. 7, pl. XXXVII, fig. 8.
Platecarpus curtirostris (Cope, 1871a): Cope, 1875:150, pl. XV, fig. 3, pl. XVI, figs. 4, 5, pl. XVII, fig. 2, pl. XVIII, figs. 7, 8, pl. XXI, figs. 7–13, pl. XXXVI, fig. 5, pl. XXXVII, fig. 10.
Platecarpus mudgei (Cope, 1870a): Cope, 1875:157, pl. XVI, fig. 2, pl. XVII, fig. 5, pl. XXVI, figs. 2, 3, pl. XXXVII, fig. 7 (reversed).
Platecarpus tympaniticus Cope, 1869: Cope, 1875:pl. XXXVII, fig. 11 (reversed).
Holosaurus abruptus Marsh, 1880:87.

Holotype—ANSP 8484 (partial left surangular), 8487 (right quadrate), 8488 (nearly complete anterior cervical vertebra), 8491 (partial right pterygoid), 8558 (partial posterior-most cervical vertebra), 8559 (partial sixth cervical vertebra), and 8562 (partial basioccipital-basisphenoid complex), and jaw fragments associated with the matrix that contains ANSP 8488. All elements are considered to be from one individual. ANSP 8491 is currently missing.

Type Locality and Horizon—From "a greenish sandstone," which most likely corresponds to the Tombigbee Sand Member of the Eutaw Formation, near Columbus, Mississippi, U.S.A. (Leidy, 1865:35) (Fig. 1). Horizon is middle Santonian to lowermost Campanian (ca. 85 to 83 Ma) (Mancini et al., 1996; Ogg et al., 2004; Mancini and Puckett, 2005).

Referred Material, Locality, and Horizon—ALMNH PV 985.0021; from Greene County, Alabama, U.S.A.; lowermost Mooreville Formation, lowermost Campanian (Mancini et al., 1996; Kiernan, 2002). AMNH 202, 1488, 1501 (*P. mudgei* holotype), 1512, 1528, 1550, 1559 (*P. ictericus* holotype), 1563 (*P. curtirostris* holotype), 1566 (*P. coryphaeus* holotype), 1820, 1821, 2005, 2006, 6159, 14788; from western Kansas (Wallace, Logan, Gove, and Lane Counties), U.S.A.; Smoky Hill Chalk Member, middle Coniacian to lower Campanian (Hattin, 1982; Ogg et al., 2004), but most likely from the upper section above the Marker Unit (MU) 11 of Hattin (1982), upper Santonian to lower Campanian (Hattin, 1982; Bennett, 2000; Ogg et al., 2004; Konishi, 2008). BMNH R-2833; from Logan County, western Kansas, U.S.A.; Smoky Hill Chalk Member, horizon as per AMNH specimens. CMN 40914; from Logan County, western Kansas; Smoky Hill Chalk Member, horizon as per AMNH specimens. FHSM VP-322, 2075, 17017; from western Kansas (Logan and Gove Counties), U.S.A.; Smoky Hill Chalk Member, horizon is upper Santonian for VP-322 (MU 12) and VP-17017 (MU 15–16), as per AMNH specimens for VP-2075 (Schumacher, 1993; Everhart, 2005). FM UC-600; from 32 km northeast of Scott City, Scott County, western Kansas, U.S.A.; Smoky Hill Chalk Member, horizon as per AMNH specimens. KU 1001, 1007, 1021, 1031, 1046, 1063, 1135, 1196, 1230, 5042, 14287, 14340, 55219, 85586, 85588; from western Kansas (Logan and Gove Counties), U.S.A.; Smoky Hill Chalk Member, horizon as per AMNH specimens. LACM 128319; from NW $\frac{1}{4}$ Section 15, T 15 S, R 34 W, Logan County, Kansas, U.S.A.; Smoky Hill Chalk Member, horizon as per AMNH specimens. RMM 1903, 7070 (in part); from western Alabama (Montgomery and Hale Counties), U.S.A.; lowermost Mooreville Chalk Formation, upper Santonian to lowermost Campanian (Mancini et al., 1996; Kiernan, 2002). YPM 884, 1112, 1114, 1175, 1256 (*Lestosaurus latifrons* holotype), 1258 (*Lestosaurus simus* holotype), 1264 (*Lestosaurus gracilis* holotype), 1267, 1269, 1277 (*Lestosaurus felix* holotype), 1284, 1350A (*Holosaurus abruptus* holotype), 3690, 3997, 4003, 24900, 24903, 24904, 24905, 24915, 24918, 24921, 24929, 24931, 40393, 40463, 40472, 40473, 40497, 40498, 40561, 40573, 40587, 40610, 40632, 40653, 40669, 40673, 40683, 40691, 40693, 40712, 40718, 40719, 40819; from western Kansas (Wallace, Logan, Gove, ?Lane, and Graham Counties), U.S.A.; Smoky Hill Chalk Member, horizon as per AMNH specimens. The above list comprises the specimens that were directly examined, and is by no means complete.

Emended Diagnosis—No predental rostrum on premaxilla; first pair of premaxillary teeth procumbent; prefrontal posteriorly contacting postorbitofrontal above orbit; frontal supraorbital border thin to slightly thickened lateral to prefrontal-postorbitofrontal contact; frontal median dorsal keel present; pair of broadly shallow parasagittal excavations extending in parallel with this keel on dorsal side; supraorbital bulge distinct; parietal foramen anterior border occurring within one foramen length from fronto-parietal suture; parietal table triangular, wider than long; parietal table lateral borders posteriorly converging with weak convexity; parietal crest typically obtuse angled; quadrate cephalic condyle anterior border straight; same condyle with round, obtuse anteromedial corner; stapedial pit oval with straight lateral borders; medial vertical ridge broadly rounded; quadrate shaft with or without slight posteroventral eminence with straight posterior border; mandibular condyle transversely wide, teardrop-shaped in outline with its apex pointing anteromedially; suprastapedial process distally terminating in rounded expansion; basal tubera moderately well developed but widely separated from each other; coronoid process moderately developed; coronoid posterior border posteriorly descending at about 45 degrees from horizontal; retroarticular process rounded; eighth intercentrum (hypapophyseal peduncle) absent on seventh cervical centrum; zygapophyses functional throughout pre-pygal series; 20 to 23? dorsal vertebrae; five to six pygal vertebrae; approximately 85 post-pygal caudal vertebrae (FHSM VP-322; LACM 128319; Williston, 1910); scapula and coracoid sub-equal in size; pectoral crest distinct but narrow; radius hatchet-shaped to nearly semicircular; carpals typically four; tarsals three; paddle broad, base of fifth digit divaricate from the others at 60 degrees or greater angle.

Taxonomic Remarks—The following *Platecarpus* taxa are considered nomina dubia, due to the lack of diagnostic characters in the holotypes. For the specimen numbers of these holotypes, see Russell (1967).

Platecarpus latispinus (Cope, 1871c): nomen dubium.
Platecarpus tectulus (Cope, 1871b): nomen dubium.
Platecarpus glandiferus (Cope, 1871b): nomen dubium.
Platecarpus affinis (Leidy, 1873): nomen dubium.

Although originally proposed as pertaining to *Platecarpus*, the holotypes of the following taxa do not possess the diagnostic features of the genus proposed here and/or they contradict them. Although formal redescription of these holotypes has yet to be conducted, it is far beyond the scope of our current study. Nevertheless, along with several former studies where applicable, we informally provide the following taxonomic designations for those species, for the sake of completeness concerning the alpha taxonomy of *Platecarpus*.

Platecarpus intermedius (Leidy, 1870): to *Globidens* sp. (Kiernan, 2002; Polcyn and Bell, 2005b; Konishi and Caldwell, 2007).
Platecarpus crassartus (Cope, 1871c): to *Plioplatecarpus* sp., cf. *P. primaevus* (Lingham-Soliar and Nolf, 1989; pers. observ.).
Platecarpus anguliferus (Cope, 1874): to *Tylosaurus* sp. (pers. observ.).

Platecarpus somenensis Thevenin, 1896: to Plioplatecarpinae, gen. et sp. indet. (pers. observ.).

Platecarpus brachycephalus Loomis, 1915: to *Plioplatecarpus* sp. (pers. observ.).

Platecarpus ptychodus Arambourg, 1952: to cf. Russellosaurina, gen. et sp. indet. (pers. observ.).

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