Supplementary Appendix and Figures for:

Reassessing the morphological foundations of the Pythonomorph Hypothesis

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1. Supplementary Appendix 7.S1

1.1 Acknowledgments

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1.2 Institutional abbreviations

ALMNH – Alabama Museum of Natural History, Tuscaloosa, U.S.A.
AMNH – American Museum of Natural History, New York, New York, U.S.A.
ATU – Arkansas Technical University, Russellville, Arkansas, U.S.A.
BMB – Booth Museum of Natural History, Brighton, UK.
BSP – Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany.
BRV – Paleontological collections of the Department of Geosciences of the National University of Colombia, Bogotá, Colombia.
DMNH – Perot Museum of Nature and Science (former Dallas Museum of Natural History), Texas, U.S.A.
FMNH – Field Museum of Natural History, Chicago, Illinois, U.S.A.
GBA – Austrian Geological Survey, Wien, Austria.
HGM – Hobetsu Museum, Mukawa, Hokkaido, Japan.
IRScNB – Institut Royal des Sciences Naturelles de Belgique, Brussel, Belgium.
ISEM-Institute for the Study of Earth and Man, SMU, Dallas, U.S.A.

MSC – McWayne Science Center, Birmingham, Alabama, U.S.A.
MCSNT – Museo Civico di Storia Naturale di Trieste, Italy.
MSNM – Museo di Storia Naturale di Milano, Italy.
NHMM – Natuurhistorisch Museum Maastricht, The Netherlands.
NHMUK – The Natural History Museum, London, UK
NHW – Natural History Museum, Wien, Austria.
SMU – Southern Methodist University, Dallas, Texas.
TLAM – Timber Lake and Area Museum in Timber Lake, South Dakota.
TMM – Texas Memorial Museum, University of Texas at Austin.
TNHC – Texas Natural History Collections at the Biodiversity Center University of Texas at Austin, Texas, U.S.A.

1.3 Specimens examined

Acteosaurus tommasinii (MCSNT 9960)
Adriosaurus suessi (NHMUK R2867)
Aigialosaurus dalmaticus BSP 1902II501
Clidastes propython (YPM 1368)
Clidastes sp. (RMM 2479; TMM 43208-1)
Coniasaurus sp. (SMU69019, DMNH 1601)
Coniasaurus crassidens (BMB 007155; NHMUK R 3421)
Coniasaurus gracilodens (NHMUK R44141)
Dallasaurus turneri (SMU 76529, TMM 43209-1)
Dinilysia patagonica (MACN-RN 1013, MACN-RN 1014, and MUCPv 38)
Dolichosaurus longicollis (NHMUK R49002)
Eonatator cf. *E. sternbergi* (FMNH PR-186, FMNH PR-195, MSC-6890)
Phosphorosaurus ponpetelegans (HMG-1528)
Phosphorosaurus ortliebi (IRScNB R34)
Globidens alabamaensis (SMU 76241)
Haasiasaurus gittelmani (HUJI EJ 693)
Halisaurus (MSNM V3662)
Halisaurinae sp. (YPM-40383, USNM 3777)
Heloderma (TNHC 64380; Digimorph HRCT data)
Judeasaurus tchernovi (HUJI P4000)
Lanthanotus borneensis (FMNH 148589; Digimorph HRCT data)
Cylindrophis ruffus (FMNH 60958; Digimorph HRCT data)
Latoplatecarpus willistoni (FHSM 16582)
Mosasaurus cf. *hoffmanni* (TLAM NH.HR.2009.032.0001)
Mosasaurus cf. *hoffmanni* (ATU unnumbered specimen)
Najash sp. (MPCA 500, [40])
Opetiosaurus buchichii (GBA-1901-002-0001 through GBA-1901-002-0005)
Plesioplaticarpus planifrons (SMU 76516)
Plioplatecarpinae gen. et. sp. indet. (SMU 77681 and TMM43210-1)
Plotosaurus (UCMP 32778; Digimorph HRCT data)
Pontosaurus lesinensis (GBA 1873/4/2)
Pontosaurus kornhuberi (MSNM V3662)

Prognathodon saturator (NHMM 1998141)
Russellosaurus coheni (SMU73056)
Tethysaurus nopcsai (SMU-75486, GM1)
Tupinambis sp. (FMNH 22416- Digimorph HRCT data)
Tylosaurus nepaeolicus (SMU76546)
Varanus komodoensis (TNHC 95803; Digimorph HRCT data)
Varanus exanthematicus (FMNH 58299; Digimorph HRCT data)
Varanus dumerilii (SMU uncatalogued)
Varanus niloticus (SMU uncatalogued)
Varanus rudicollis (SMU uncatalogued)
Varanus saladori (SMU uncatalogued)
Yaguarasaurus columbianus (BRV-68)

1.4 Taxonomic nomenclature

In the body of the book chapter and the supplementary information below, we use the term mosasaurians (= Mosasauria) to include dolichosaurids, "aigialosaurids", and mosasaurids following Augusta et al. (this volume) and summarized in Supplementary Figure 7.S1a. We use the term "early diverging mosasaurians" for the paraphyletic non-mosasaurid mosasaurians, predominantly known from the Cenomanian-Turonian (~100–~90 Ma) and which includes dolichosaurids and "aigialosaurids"; however, we follow Bell and Polcyn [1] in considering "aigialosaurids" a paraphyletic assemblage which are likely stem mosasaurids. We use the term "early diverging mosasaurids" to include *Dallasaurus*, *Tethysaurus*, *Russellosaurus*, and *Yaguarasaurus* all of which retain (to varying degrees) plesiomorphic morphology and are known from the Turonian (~94–~90 Ma). We also include Halisaurinae in our concept of "early diverging mosasaurids" because they retain substantial plesiomorphic morphology, suggesting early divergence as recovered in numerous phylogenetic analyses; however, they are known only from the Santonian through the Maastrichtian (~86– ~66 Ma). We use the term "later diverging mosasaurids" to refer to generally more derived mosasaurids, largely known from the Coniacian through the Maastrichtian (~90–~66 Ma). See Augusta et al. (this volume) for a recent phylogenetic analysis and Supplementary Figure 7.S1a for a simplified phylogenetic tree that includes the mosasaurian taxa referenced in this study. Due to space limitations, expanded morphological descriptions, notes on other details of anatomy, and figures referred to in the main body of the text are included below.

1.5 Specimen completeness and preservation

Of the early diverging mosasaurians examined, most are preserved on platy limestone slabs and either prepared from one side, or partially embedded in resin for preparation of select anatomy from the opposite side (Supplementary Figure 7.S1b–h). Preservation is variable as is quality of preparation and/or collection. One of the best preserved is the holotype of *Pontosaurus kornhuberi* (Supplementary Figure 7.S1b), but that specimen is sheared to the right and dorsoventrally crushed, displacing a number of elements. There is also significant damage to the premaxilla and left maxilla. Some details of Caldwell's [2] interpretation of the skull elements could not be confirmed. A crack in the right maxilla was probably misinterpreted as the prefrontal suture and we interpret the maxilla ascending process is in close proximity to anterolateral frontal. The identity of the elements just anterior to the frontal are also unclear. The right ones (figured as the posterior parts of the premaxilla and the right septomaxilla by Caldwell [2], his figure 4b) may be the nasals and the left two elements labeled "?nasal" and figured as the posterior part of the left septomaxilla are likely palatal elements. If we are correct in our observations, neither the premaxilla nor the septomaxilla reach as far posterior as in Caldwell's reconstruction.

In the holotype of *Pontosaurus lesinensis* (Supplementary Figure 7.S1c, d) the skull is sheared to the right, with plastic deformation and some disarticulation (see figs. 2A and 3A in [3]). Bone surface is not as well preserved as in *P. kornhuberi*. The single specimen of *Adriosaurus suessi* (Supplementary Figure 7.S1.e) is poorly preserved and dorsoventrally crushed with many cracks. Many of the elements in the interpretative drawing of Lee and Caldwell [4] are not objectively verifiable (see Augusta et al. this volume). *Coniasaurus gracilodens* (NHMUK R44141)*, Coniasaurus crassidens* (NHMUK R3421), *Dolichosaurus longicollis* (NHMUK R49002) are all broken with minor crushing and brittle fractures, but nearly three-dimensionally preserved. These specimens were HRCT scanned to reveal portions previously embedded in matrix which led to the discovery of a number of hidden elements and previously unknown aspects of their morphology (Figs.7.1f, 7.2a–u, 7.4n–p, 7.5a–c, 7.5f–l, and Supplementary Figures 7.S2c, 7.S3f, 7.S5c–f, 7.S6, 7.S9a–b, and 7.S10). *Opetiosaurus buchichii* (Supplementary Figure 7.S1f–h) is preserved in a number of blocks, part and counterpart and taken together show a number of features of the dorsal surface of the skull and lateral mandible (in natural molds) however, many details are missing or broken (e.g., internarial bar, quadrates).

The inescapable reality is that although many of these specimens are relatively complete and articulated, they are preserved in such a way that many critical details of their anatomy remain unknown.

1.6 Narial retraction

Narial retraction in mosasaurians can be viewed as three independently evolving complexes: (1) an anterior narial complex, composed of the contacts of the premaxilla and maxillae; (2) a posterior narial complex, composed of the maxilla, prefrontals, and frontal; and (3) the internarial complex, composed of the nasal process of the premaxilla, the nasals, and the anteromedial part of the frontal.

Anterior narial retraction – In varanoids generally, the anterior maxilla is relatively broad in dorsal view compared to mosasaurians and possesses a maxillary recess ([5]; fenestra exonarina anterior of [6]) and a premaxillary fenestra (*sensu* [7]) between its anterior margin and the posterolateral premaxilla. Posteromedial closure of the premaxillary fenestra is formed by a process from the medial dental shelf, hereafter the anteromedial process. Lateral to the maxillary recess, a ridge of bone (hereafter the anterodorsal ridge) continues posteriorly forming the dorsolateral margins of the external nares and ascending process (Supplementary Figure 7.S2a–f).

Anterior narial retraction in mosasaurians is associated with vertical development and medial migration of the anterodorsal ridge of the maxilla, along with a conjugate vertical development of the posterolateral premaxilla, the two elements forming an elongate sutural contact in dorsal view (Fig. 7.1 a–d see also Supplementary Figure 7.S2a–f). Posteromedial migration of the maxillary-premaxillary contact obscures dorsal exposure of the premaxillary fenestra and the maxillary recess (if they had existed historically), and through lateral development of the base of the nasal process of the premaxilla, progressively obscures the dorsal view of the anterior septomaxilla. Ultimately, these modified relationships form the typical configuration of the anterior external nares occurring in mosasaurids such as *Yaguarasaurus* (Fig. 7.1c; see also Supplementary Figure 7.S2f). The migration of the anterior terminus of the external nares migrating to a more dorsally oriented and posterior position is seen in a number of secondarily adapted marine amniotes.

In the dolichosaurid *Pontosaurus kornhuberi* (Supplementary Figure 7.S2b), the premaxillae are small and anteriorly broad, with a narrow posterior process. Although slightly displaced in the holotype, the absence of a maxillary recess or any sign of the premaxillary fenestra suggests the maxilla and premaxilla formed an elongate dorsal sutural contact. *Pontosaurus lesinensis* (Fig. 7.1a and Supplementary Figure 7.S1c, d) is similar to *P. kornhuberi* and bears an elongate premaxillary-maxillary contact, exposing a posteromedially trending suture in dorsal view [3]. *Adriosaurus suessi* is too poorly preserved to be informative [4] (Supplementary Figure 7.S1e). The premaxilla of a *Coniasaurus* specimen from Texas (DMNH 1601), is well developed and tall, the nasal process wide, and preserves a long sutural facet for the maxilla, suggesting substantial anterior narial retraction in that taxon (Fig. 7.1h–j). In *Coniasaurus gracilodens* (Fig. 7.2c, j; see also Supplementary Figure 7.S2c), the anterodorsal ridge of the maxilla forms the anterolateral margins of the external nares posterior to the sutural contact with the premaxilla. It retains the varanoid condition of the anteromedial process (Fig. 7.2e, j) but the premaxillary fenestra would have been obscured in dorsal view; however, in ventral view, it likely maintains the primitive relationships with the premaxilla and the vomer (Fig. 7.2f).

Posterior narial retraction – Posterior narial retraction, in which the frontal participates in the narial opening, is present in early diverging mosasaurians and early diverging mosasaurids (Fig. 7.1a–d) and was likely present in their shared ancestor. In the dolichosaurids *Coniasaurus* and *Pontosaurus* the frontal is anteriorly wide and does not project into the internarial space, except for an extremely short, narrow anteromedial process (Fig. 7.1f). Mosasaurids further retract the nares at the expense of the anterolateral portion of the frontals as exemplified in *Tethysaurus* (Fig.7.1g)*,* a trend that first appears in the "aigialosaurs" *Aigialosaurus* and *Opetiosaurus* (Supplementary Figure 7.S1f), leaving the anteromedial frontal projecting into the "internarial space". In those specimens in which it can be examined, this narrowing is accompanied by a more horizontal articulation of the prefrontals underlying the frontal and an apparent lateral migration of the nasal capsule, embraced by the prefrontals laterally, posteriorly, and posteromedially. The pattern seen in *Opetiosaurus* and *Tethysaurus* is retained in *Russellosaurus* [8] and *Yaguarasaurus* (Fig. 7.1c; Supplementary Figure 7.S2f), which exhibit a trend of increasing interorbital width that continues in some more derived plioplatecarpine mosasaurids.

Internarial complex – The internarial complex in *Pontosaurus lesinensis* appears nearly identical to the varanid condition. It is composed of the elongate posterior process of the premaxilla, that apparently formed an elongate suture with the paired narrow nasals which in turn appear to contact but likely do not overlie the anteromedial frontal (Fig. 7.1a;

fig. 2A, B in [3]). This also appears to be the case in *Coniasaurus gracilodens* based on the lack of facets on the frontal (fig. 4A in [9]) which suggests the nasals articulate loosely with the anterior frontal margin and/or the anteromedial ventral process (Fig. 7.1f). The condition in *Opetiosaurus* and *Aigialosaurus* is unclear due to poor preservation. The internarial complex in some halisaurines (Fig. 7.1d) is comparable to the condition in *Varanus* and *Pontosaurus lesinensis*, the paired nasals underlying the premaxilla a long distance (e.g., YPM 40383; [10]), whereas the nasals underlie the premaxilla only a relatively short distance in others (fig. 1e in [11]). In all halisaurines examined, narrow paired nasals lie in facets on the anteromedial dorsal surface of the frontal [11–13] (Fig. 7.1d). In the early diverging mosasaurid *Tethysaurus*, the nasal process of the premaxilla slightly overlies the frontal and the nasals are reduced to narrow, short splints that span the premaxilla and frontal in a ventrolateral position (Fig. 7.3a) and are largely obscured in dorsal view. Fusion of the nasals with frontal in mosasaurs as hypothesized by Caldwell et al. [14] is rejected. Extreme elongation of the internarial process of the premaxilla also occurs in some *Varanus* species (e.g., *V. rudicollis*; Supplementary Figure 7.S2g), reaching the anterior frontal, and underlying coossified nasals posteriorly.

1.7 Premaxilla

In *Pontosaurus kornhuberi*, the premaxilla is anteriorly blunt and broad and the post-dentigerous portion projects a long narrow nasal process posteriorly (Supplementary Figure 7.S1b). The anterior dorsal surface is damaged (as is the left anterior maxilla), but appears to bear two teeth on each side of the midline. No midline teeth are present but given the size of preserved crowns, room for additional medial teeth or a single tooth is possible. *Pontosaurus lesinensis* possesses a similar morphology in dorsal view, but no premaxillary teeth or alveoli are visible and *Adriosaurus suessi* (Supplementary Figure 7.S1e) is too poorly preserved to be informative [4].

New specimens of *Coniasaurus* from North America [15] include a three-dimensionally preserved premaxilla in an association of three partial embryos and an adult animal (Fig. 7.1h–j). In dorsal view the embryonic premaxilla is broadly arcuate anteriorly, approximating a semi-circle, and possesses a broad anteriorly rounded midline boss dorsally that merges into a wide nasal process. There is no evidence of the medial ethmoid nerve entering or exiting the premaxilla. Laterally, clear facets for an elongate maxillary articulation indicate significant anterior narial retraction in this *Coniasaurus* species, a derived condition relative to *Pontosaurus*. Ventrally, an elongate incisive process bears a prominent median sulcus, but is broken posteriorly. Five tooth positions, including a median one, possess pleurodont implantation with no evidence of interdental ridges nor tooth sockets. In no respect does the premaxilla of *Coniasaurus* (DMNH-1601) or any other dolichosaurid resemble that of a snake.

In the "aigialosaurid" *Opetiosaurus,* the premaxilla is preserved only as a natural mold (Fig. 7.1h). It is broadly arcuate anteriorly in dorsal view and possesses a narrow nasal process, but no other details can be ascertained. The premaxilla in the early diverging mosasaurid, *Tethysaurus,* is broadly arcuate anteriorly with a narrow nasal process (Supplementary Figure 7.S2e) [16] and bears four teeth, the bases of which are surrounded by a low ridge of bone, the derived condition in mosasaurs. The ethmoid nerve entered the body of the premaxilla on either side of the nasal process, exposed dorsally in shallow sulci before entering the body of the premaxilla. The ethmoid nerve exited anteroventrally via two small foramina and exits on the anterodorsal surface are indistinct or not present in specimens examined. In more derived mosasaurids, the ethmoid nerve entrances take a deeper path in the premaxilla, branching internally, and exiting as distinct foramina on the dorsal, anterior, and lateral surface, a consequence of evolving a taller anterior snout. A partial premaxilla is preserved in a new specimen of *Dallasaurus* (SMU-76529; Fig. 7.1k–n), a taxon found to be a stem mosasaurine mosasaurid [1]. In dorsal view, it is broadly arcuate anteriorly, although the most lateral portion is broken and missing on both sides. A prominent dorsal boss forms the base of the internarial process, lateral to which are entrances for the median ethmoid nerve. Ventrally, two tooth bases remain, the left mostly complete, only missing the crown. There is an empty partial medial alveolus preserved. The ethmoid nerve exited ventrally via two small parasagittal foramina, one on either lateral side of the preserved tooth bases, but no exits are visible on the preserved dorsal surface. The bases of the teeth are buttressed posteriorly by a low ridge of bone that separates the dentigerous portion from the flat underside of the base of the nasal process. No incisive process is preserved.

A medial premaxillary tooth in mosasaurians is rare, but occasionally present in halisaurines (e.g., YPM-40383), mosasaurines (e.g., *Dallasaurus* SMU-76529), and some plioplatecarpines (SMU-77681 and TMM-43210-1), which retain the medial tooth well into ontogeny. Possession of a median premaxillary tooth in mosasaurs, though variable, is contrary to Lee's [17] diagnosis of Pythonomorpha. Premaxillary tooth bases surrounded by alveolar bone is common among derived mosasaurids but is absent in the dolichosaurid *Coniasaurus*.

1.8 Septomaxilla

The septomaxilla is a delicate structure and rarely preserved in fossil lizards and only reported for a handful of mosasaurids (e.g., [18, 19]). It has been reported in *Pontosaurus kornhuberi* [2], but not in other dolichosaurids. In *Pontosaurus kornhuberi* (MSNM V3662) it is badly crushed and interpretations of the extent of the element and identification of other nearby bones by Caldwell [2] are not well-supported (Supplementary Figure 7.S1b). New HRCT imaging of *Coniasaurus gracilodens* (NHMUK-R44141) allows three-dimensional observation of the vomers and maxillae (Fig. 7.2a–l), and although no septomaxilla was found, a recess on the anteromedial wall of the right maxilla dorsal to incisura Jacobsoni, between tooth positions three and five is consistent with lateral accommodation of the vomeronasal organ. Given the conjugate morphology of the vomer (Fig. 7.2b, i, j), we take the dorsal margin of the maxillary recess as the articulation of the lateral part of the cupola Jacobsoni as in other varanoids (Supplementary Figure 7.S3). This interpretation is corroborated below in *Tethysaurus* (Fig. 7.3). In *Coniasaurus gracilodens*, the narrow vomer articulates anterolaterally with the maxilla and is quite similar to that of varanids. In dorsal view, the vomer presents a channel beginning just posterior to the articulation with the maxilla, bounded by bony ridges medially and laterally. The channel deepens posteriorly to the posterior terminus of the element where it would receive a vertical narrow process of the palatine. The lateral margin of the vomer slightly widens posterior to the anterolateral articulation with the maxilla but does not meet the maxilla posterior to the incisura Jacobsoni, leaving the fenestra vomeronasalis open posteriorly, and thus exhibiting the incomplete neochoanate condition [20]. In some derived mosasaurids such as *Mosasaurus* there is evidence of vomer contact with the maxilla posterior to the incisura Jacobsoni; however, in those forms, it is the flat lateral body of the vomer and not a discreet process as in *Varanus* that makes the contact. In *Coniasaurus gracilodens,* the vomer bears two parallel ventral ridges of bone bounding an elongate sulcus as in *Varanus*. The medial ridge begins at the anterior terminus of the vomer and the lateral ridge begins just medial to the posterior articulation with the maxilla. This morphology, notwithstanding artifacts of anterior narial retraction, is similar in most respects to that of *Tethysaurus* (Fig. 7.3) described below, including the dorsal expansion of the lateral dorsal ridge of the vomer.

The three-dimensionally preserved septomaxilla in *Tethysaurus* (SMU-75486) is described from HRCT imaging (Fig. 7.3a–f). It comprises a subtriangular domed anterior cupola Jacobsoni, an elongate posteromedial process, and a shorter posterolateral process. The cupola is not as domed as in some varanoids, a result of reduced accommodation space due to anterior narial retraction and diminished olfactory sense as evidenced by the relatively narrow olfactory tract on the frontal (Fig. 7.1g). The lateral and anterolateral margin of the cupola meets the maxilla enclosing the cupola. The cupola is open medially. There is no evidence of the ethmoid nerve piercing the dorsal septomaxilla in *Tethysaurus*, but given the relatively tall anterior snout and reduced height of the cupola Jacobsoni and the dorsal position of the ethmoid nerve foramen on the premaxilla, it is likely the ethmoid nerve passed above the septomaxilla.

A mediodorsal ridge runs the length of the septomaxilla contacting the medioventral ridge of the nasal process of the premaxilla along its entire length (Fig. 7.3a). The elongate posteromedial process is vaulted its entire length (Fig. 7.3f) and overlies, but is vertically separated from a corresponding trough in the vomer that communicates anteriorly with the posteromedial, ventral part of the cupola. The lateral wall of this trough expands dorsally just posterior to the cupola, and medial to the posterior end of the incisura Jacobsoni, and meets the aforementioned corresponding descending process of the septomaxilla, forming a closed lateral wall for the vomeronasal nerve a short distance (Fig. 7.3d). Posteriorly, the dorsal trough on the vomer narrows and embraces the laterally compressed vomer process of the palatine.

Posterolateral closure of the cupola Jacobsoni is similar to the condition in *Heloderma and Lanthanotus* (Supplementary Figure 7.S3a, b), but in the latter taxon, the vomer "forms a scroll-like process" behind the incisura Jacobsoni [20]. The posterolateral process of the septomaxilla in *Tethysaurus* is a simple sheet of bone that meets the maxilla but does not significantly overlie it.

1.9 Palatine

The palatine of derived mosasaurids deviates from most squamates in the expansion of the antorbital part and reduction on the suborbital part. The palatine has reported, but has not been previously described in dolichosaurs. We describe here for the first time the palatine of the holotype of *Dolichosaurus longicollis* (NHMUK-R49002) based on HRCT imaging (Fig. 7.2s–u). In dorsal view, the palatine can be divided into anterior (antorbital) and posterior (suborbital) parts by the transverse dorsal articulation with the prefrontal. In *Dolichosaurus*, the antorbital part is elongate, and proportionally intermediate between mosasaurids and the typical varanoid condition. The floor of the anterior portion is bounded by the prefrontal articulation posteriorly, the maxillary suture laterally, and a ridge medially that continues forward as the vomer process. The floor bears two sulci, one originating in the posteromedial floor and trending anterolaterally terminating at the lateral margin about the midpoint of the maxillary suture. The second sulcus originates at about the middle of the first and trends anteriorly, terminating at the posterolateral margin of the internal choana. These sulci are present in halisaurines (Supplementary Figure 7.S4b) and other mosasaurids but we have not seen this morphology in any other squamates [however, for similar structures see [21]). Along with the antorbital expansion of the palatine these sulci may be synapomorphies of Mosasauria.

The palatine clasps the posteromedial maxilla in a deep lateral groove that originates just below the infraorbital process and continues to the anterolateral terminus of the palatine, the dorsal contribution overlying the maxillary more significant than the ventral part. The pterygoid articulates with the suborbital part, broadly underlying a triangular sutural area bounded by the posteromedial terminus, the posterolateral terminus and a point on the anterolateral margin at about the level of the prefrontal suture. Laterally, at a point above the posterior terminus of the maxillary suture, the palatine projects a distally broadened arch of bone we refer to as the lateral infraorbital process (Fig. 7.2s–u). The distal portion of this process likely contacted the maxilla as in *Phosphorosaurus ponpetelegans* [13] and along with the body of the palatine encloses the infraorbital foramen (*sensu* [21]; maxilla-palatine foramen of Russell, [22]) dorsally and medially. In *Dolichosaurus*, a second foramen just medial to the infraorbital foramen (possibly homologous with the palatine foramen of Oelrich [21]), enters the palatine via an anteromedial path, but it is not clear if it emerges elsewhere on the palatine.

Tethysaurus possesses an expanded antorbital portion of the palatine, but a small suborbital part (Fig. 7.3g–j). In halisaurines the palatine is truncated posteriorly (Supplementary Figure 7.S4b) as it is in many mosasaurids. In most mosasaurids, the anterior portion of the palatine is elongate. The morphology of the posterolateral palatine in *Clidastes* differs from that in *Dolichosaurus*, and other non-mosasaurine mosasaurids (Supplementary Figure 7.S4d, e) in that the infraorbital foramen is more medially situated and incompletely enclosed within the palatine due to the presence of a narrow ventral fissure. This also seems to be the case in *Mosasaurus* [23]; however, in that specimen the prefrontal overlaps the posterodorsal margin of the palatine obscuring relationships (Supplementary Figure 7.S3f, g). In *Clidastes*, *Prognathodon*, and *Globidens* specimens in which it is preserved, the palatine also has a second posteromedial foramen that emerges ventrally just below the anterior part of the palatine-maxillary articulation and would likely have carried the palatine branch of the maxillary artery. In *Plotosaurus* and *Mosasaurus* the branching of the palatine artery appears to have occurred anterior to the infraorbital part of the palatine, passing over the palatine dorsally and emerging at the anterior terminus of the palatine-maxillary suture and likely continued anterior in a recessed trough on the medial part of the maxilla.

The anterior expansion and suite of characters of the palatine in mosasaurs is unique. Konishi [24] hypothesized the anterior expansion of the palatine in mosasaurids may be evidence for development of salt glands, a concept consistent with other reports in other secondarily adapted marine reptiles [25–27]. The reduction of the anterolateral frontal in mosasaurids accompanied by medial expansion of the prefrontals, underlain by anteriorly expanded palatines create a deep posterior recess, open anteriorly and communicating with the infraorbital region via the small posterior lacrimal foramen. It is reasonable to interpret this region as housing salt glands which may also in part account for some of the changes seen in the lacrimal. Additionally, recruitment of nasal glands is consistent with their presence in extant lizards as opposed to the orbital glands in sea turtles and the oral glands in extant crocodiles and snakes [28].

1.10 Lacrimal

The lacrimal has not previously been described in dolichosaurids and is only generally known in mosasaurids from brief descriptions of the element for a few taxa (e.g., [16, 29]; but see also [30] for misidentification of the ectopterygoid as the lacrimal in *Mosasaurus*). Most early diverging mosasaurian specimens, even when articulated, are crushed with the antorbital series only visible in lateral view. The right lacrimal has been reported in *Aigialosaurus dalmaticus* (BSP 1902II501) where the poor preservation of the element was noted and described as "small and oblong, roughly half the length of the prefrontals and wider posteriorly than anteriorly" [29] and also indicated "contributes to the anterior orbital margin and appears to have a lengthy contact with the jugal" [29]. That specimen is badly crushed and nothing can be said of the medial contact of the lacrimal with the prefrontal or palatine. The lacrimal region of *Opetiosaurus bucchichi* is better preserved (Supplementary Figure 7.S4h), and described by Dutchak and Caldwell [31] as "... small and triangular, with the base of the triangle forming a contact with both the jugal and the maxilla. It contributes slightly to the anterior rim of the orbit, as in both varanids and mosasaurs... " and "The lacrimal process of the palatine, a fragment of which is preserved along the anterior rim of the orbit, extends to contact the lacrimal posteriorly" [31]. Caldwell's [9] description of *Coniasaurus gracilodens* provided details of a small element purported to be the septomaxilla (but referred to as the prefrontal in the caption to his figure 9). It is in fact the lacrimal as shown by comparison with HRCT reconstruction of that element in *Tethysaurus* (Fig. 7.3) and is described below. This is the first lacrimal reported in a dolichosaurid.

The lacrimal in *C. gracilodens* is subtriangular in lateral view and approximately three times as long as tall (Fig. 7.2n–r). In lateral view, demarcation of the maxilla articulation is clearly visible as an anterodorsal trending ridge of bone separating the recessed sutural surface which underlies the maxilla and the exposed portion, broadening from its posterior terminus anterodorsally and terminating on the posterior half of the dorsal margin. The exposed part of the lacrimal in *Opetiosaurus* is nearly identical (Supplementary Figure 7.S4h). In medial view, the posterior two-thirds of the dorsal area projects medially and is rugose and would have articulated with the prefrontal (Fig. 7.2o, q). The dorsomedial process forms an arch roofing the lacrimal foramen. The medial surface ventral to the dorsal prefrontal articulation is concave forming the lateral wall of the lacrimal foramen (Fig. 7.2o, p). The medially rugose posteroventral margin projects medially and would have articulated with the prefrontal forming the relatively large, single lacrimal foramen (Fig. 7.2p) in contrast with *Tethysaurus* which possesses two foramina (Fig. 7.3g–i). The dorsal contact with the prefrontal is anterior to the ventral contact, yielding an anteriorly inclined lacrimal foramen. Ventrally, the lacrimal bears a hook-shaped sulcus, with a long longitudinal anterior part and a shorter anteromedial part posteriorly. The medial wall of the longitudinal ventral sulcus receives the dorsal lamina of the maxilla. The posteromedial part would likely have overlain the infraorbital process of the palatine and the area lateral to the ventral sulcus would have overlain the jugal as in *Tethysaurus* (Fig. 7.3g–i) and *Clidastes* (Supplementary Figure 7.S3d).

The lacrimal in *Tethysaurus* (SMU 75486) preserves the articulation with adjacent bones (Fig. 7.3g-i). It is similar in overall morphology to that in *C. gracilodens* as described above, except the dorsal articulation with the prefrontal is more dorsoventrally extensive, yielding a relatively small ventral lacrimal foramen, and a second smaller foramen just dorsal to that one. The anterior portion underlying the maxilla is relatively smaller, and also bears a posterolateral boss in a similar position to that in *Varanus,* also present in other mosasaurids [23] (Fig. 7.3g–i; Supplementary Figure 7.S4d–g).

1.11 Ectopterygoid

In mosasaurids the ectopterygoid process (lateral process) of the pterygoid is relatively elongate and emerges from the main body of the pterygoid at a high angle in most mosasaurid taxa. The ectopterygoid process terminates laterally near the posteroventral jugal, anterolaterally meeting the ectopterygoid in a relatively loose contact in most taxa. Additionally, the lightly built ectopterygoid in most mosasaurids is approximately L-shaped and dorsoventrally thin (e.g., Supplementary Figure 7.S4j), and articulates laterally with the horizontal ramus of the jugal much of its length, only loosely contacting the maxilla in some taxa. This morphology stands in stark contrast to the robust rod-like ectopterygoid in snakes and most varanoids. Although the ectopterygoid and palatines do not contact in snakes and mosasaurs [32], it is due to fundamentally different configurations. In snakes, loss of contact is associated with the elongate suborbital projection of the maxilla terminating in a typical relationship with the ectopterygoid, but well posterior to the palatine-maxillary articulation. In mosasaurs, the two elements are in close proximity but have lost contact in association with the unique and substantially reduced ectopterygoid. This is well illustrated in *Tethysaurus* (Fig. 7.3g–i) in which the anterior ramus of the ectopterygoid articulates with the medial jugal for much of its length and clasps only a small portion of the medial part of the maxilla but is separated from the palatine. The ectopterygoid is unknown in dolichosaurids with the exception of *Judeasaurus* [33]. An ectopterygoid facet on the posterior end of the left maxilla of the holotype of *Coniasaurus crassidens* (BMB-007155) has been previously reported [34]; however, reexamination of that specimen shows the posterior maxilla is broken, transecting the posterior part of the alveolus of a tooth position, and thus no evidence of an ectopterygoid contact can be confirmed.

1.12 Parietal downgrowth

Lee [17] considered the lateral descending margins of the parietal in derived mosasaurs homologous to the condition in snakes. Rieppel and Zaher [35] compared the braincases of *Varanus*, *Platecarpus*, and snakes, showing the morphology of the mosasaur did not significantly deviate from that of *Varanus*. However, the condition of the parietal and its relationship with the braincase in early diverging mosasaurids shows an even more plesiomorphic condition addressed below.

In *Varanus*, the bony enclosure of the posterolateral braincase is incomplete, forming a small fenestra bounded by the parietal, prootic, and supraoccipital

(Supplementary Figure 7.S5a). The lower Turonian *Tethysaurus* retains the *Varanus* condition, possessing a small posterolateral fenestra (Fig 7.4a, b). There is no downgrowth of the lateral margin of the parietal, and the braincase underlies the posterior parietal table to a greater extent than in *Varanus.* The supraoccipital anterodorsal contact with the parietal is expansive and sutural. The parietal in the middle Turonian *Russellosaurus,* another stem plioplatecarpine, is similar to *Tethysaurus* with no ventral descending lateral margins (Supplementary Figure 7.S5b). The alar process of the prootic is only loosely in contact with the parietal margin [8] and the supraoccipital loosely contacts the parietal. In later diverging plioplatecarpine mosasaurids, the braincase is more robust and rostrocaudally compact, almost entirely underlying the parietal table, and the parietal does form descending processes that contact the prootic and supraoccipital. In halisaurines such as *Phosphorosaurus ponpetelegans* [13], the posterolateral fenestra is closed by the supraoccipital and prootic, and moderate downgrowth of the lateral parietal margins articulate with the distal part of the relatively short alar process of the prootic (Fig 7.4c, d). However, the downgrowth of the parietal descending processes is no greater than in adult *Varanus niloticus* (Supplementary Figure 7.S5a). The condition in mosasaurines such as *Clidastes* (Fig. 7.4e) is derived with significant downgrowth of the parietal lateral margin articulating with the dorsal part of the extremely short alar processes of the prootic. The downgrowth also articulates posteriorly with the tall supraoccipital. This morphology is further developed in later diverging mosasaurine mosasaurids like *Prognathodon saturator* (Fig. 7.4f) [36]. Vertical expansion of the parietal facilitates increased area for muscle attachment, and together with the combination of sutural contacts with the anteriorly shifted braincase, forms a pillar-like structure, well suited to resist the likely increased bite forces in these large mosasaurs.

In dolichosaurids the braincase and its relationship with surrounding bones is poorly known. All known specimens of *Pontosaurus* are preserved on carbonate slabs (Supplementary Figure 7.S1b–e), and do not show many details of the parietal descending processes or their relationship with the prootic or other elements of the braincase. *Pontosaurus kornhuberi* (MSNM-V3662) is crushed and sheared to the right, but preserves the parietal lateral margins and the left prootic. There is slight downgrowth of descending processes similar to the state in *Phosphorosaurus ponpetelegans*, but given the crushing in MSNM V3662 it is not clear if any fenestration was present between the dorsal margins of the prootic and supraoccipital and parietal. Development of the descending process of the parietal is comparable in *Pontosaurus lesinensis* [3], again similar to the state in *P. ponpetelegans,* but no relationship with the other braincase elements could be assessed. A fragment of the anterior part of the parietal is preserved in *Coniasaurus gracilodens* [9] and shows no evidence of anterior downgrowth, and consistent with the frontal (Fig 7.1f) which possesses relatively poorly developed descending processes, unlike snakes and varanoids. An anterior portion of a North American *Coniasaurus* parietal (DMNH-1601) preserves a moderate lateral descending process [15], similar to that in *Pontosaurus*. It is broken posteriorly but the anterior part is well preserved and shows no evidence of anterior development of descending processes nor enclosure of the anterior braincase. In summary, downgrowth of the parietal forming flanges that suture with the ventral braincase elements is seen only in relatively derived mosasaurids. In no case can it be demonstrated that the parietal and its relationship with the braincase in mosasaurians is comparable to the snake condition.

1.13 Squamosal and Supratemporal

The relationships of the supratemporal to the parietal and squamosal in mosasaurians are diverse in later diverging mosasaurids but in dolichosaurids, "aigialosaurids" and halisaurines, though not completely exposed in most specimens, appear to retain a typicalvaranoid condition. Caldwell [9] described a bone preserved with *Coniasaurus gracilodens* under the heading of "Unknown bone ?squamosal?", but referred to as the surangular in his figure caption. Digital reconstruction from HRCT confirms it is the squamosal and similar to that of other dolichosaurids but appears to be a bit more robust. It is briefly described and figured here (Supplementary Figure 7.S5c–f). The element is well preserved but missing its anterior terminus. In dorsal view, there is a deep broad groove to accommodate a rod-like, posteriorly tapering, ramus of the postorbitofrontal terminating just prior to a posteromedial expansion of the squamosal, which ultimately forms the supratemporal articulation. In dorsal view, the posterolateral margin curves medially, converging with the posterior part of the supratemporal articulation. In lateral view, anteriorly the dorsal margin is gently curved adjacent to the postorbitofrontal articulation, but then slopes posteroventrally dividing the posterolateral face, with the dorsal division adjacent to the supratemporal articulation sloping dorsolaterally and the ventral division facing ventrolaterally. In medial view, the supratemporal articulation is an elongate tear-drop shape, broad part posterior, and bears a flat contact. In ventral view, there is a posterior rugose area, about half the length of the supratemporal contact, that likely represents the quadrate contact.

In *Judeasaurus*, most of the supratemporal is missing, but the preserved portion is still in articulation with the parietal, received by posterolateral facets of the elongate parietal rami [33]. The process appears to be subconical and loosely articulated with the parietal, the joint described as synovial by Haber and Polcyn [33]. The squamosal in *Judeasaurus* is preserved and its contact with the supratemporal is a simple flat surface. In halisaurines, the relationship of the supratemporal and parietal rami is nearly identical to that in *Varanus* (Fig. 7.4k–m), with a flat blade-like process of the supratemporal lying in a shallow flat-bottomed receiving part on the posterolateral ramus. A new parietal specimen of *Dallasaurus* (SMU-76529) exhibits morphology similar to *Judeasaurus,* possessing a laterally directed and deeply incised facet for the supratemporal on the posterolateral ramus. *Tethysaurus* and *Russellosaurus* show more complex supratemporal-parietal contact. The supratemporal is wider and its contact with the parietal comprised of a medial part and dorsal part of the distal parietal ramus. The supratemporal-squamosal contact develops an interdigitating non-rotational contact, and thus further arresting the rotation of the braincase in the metakinetic axis. Later diverging mosasaurids possess a variety of morphologies in the contacts of the supratemporal with the parietal and the squamosal, regressed and simplified in some clades and increasingly complex in others.

1.14 Braincase

Most dolichosaurid fossils are crushed or do not preserve the braincase. However, new HRCT data reveals details of the braincase of *Dolichosaurus longicollis* which are briefly described here. The specimen was redescribed by Caldwell [37]; the element identified as the parietal is instead the basioccipital and small fragments of the otooccipitals and possibly the prootic in articulation but crushed. (Fig. 7.4; Supplementary Figure 7.S6). Though badly damaged, portions of both otooccipitals are present. The left preserves only the ventral portion in articulation with the basioccipital, and the right one preserves the more dorsal parts and is separated from the basioccipital, though a small broken fragment remains in articulation with the right sphenooccipital tubercle.

The basioccipital is roughly hexagonal in dorsal view and the medullary surface shallowly concave. Anteriorly, the articulation for the parabasisphenoid is formed by a relatively narrow, flat central part bounded posterolaterally by facets covering the anteroventral surfaces of the sphenooccipital tubercles. The tubercles diverge ventrolaterally at about 45°. The basioccipital contribution to the occipital condyle is about one-third and the exoccipitals would each have contributed about one-third. Anterior to the condyle, a short weakly constricted neck is present, anterior to which the bone expands anterolaterally, its lateral margin forming the crista tuberalis. In posterior view, the crista tuberalis rises posterolaterally as in *Varanus*. A small hole is present near the broken dorsal margin of the preserved portion on the left which may be the jugular foramen; however, the area is poorly preserved and this feature may merely be damage. The foramen thought to be for the accessory nerve (fig. 7 in [37]) is present on the lateral face of the opisthotic; however, no other mosasaurian examined presents a foramen in that position and its homology remains unclear. Though damaged, the distal part of the elongate paroccipital is expanded, its lateral surface shallowly dished. The posterior ramus of the prootic is relatively short, exposing a long portion of the paroccipital laterally. Taken together, this is reminiscent of the condition in mosasaurs; however, the damage leaves this point inconclusive. The more distal parts of the left otooccipital are badly crushed and expose broken surfaces, that Caldwell [37] interpreted as the basioccipital. The anterior part may be a portion of the parabasisphenoid and the canal that Caldwell [37] interpreted for the basilar artery is likely the right Vidian canal. Though poorly preserved, in all respects which it can be assessed, the braincase of *Dolichosaurus* retains typical varanoid morphology.

1.15 Quadrate

The long posteroventrally curved suprastapedial process (SSP) in mosasaurs does not fully participate in the support of the element (e.g., Supplementary Figure 7.S5b) in contrast to the condition seen in stem snakes like *Najash* and *Dinilysia*, and some crown snakes such as *Cylindrophis* wherein the entire dorsomedial surface of the quadrate is in contact with the supratemporal. We consider the condition in snakes as independently derived as a structural imperative. Mosasaurs share with *Varanus* a similar quadrate-suspensorium relationship in which only the distal part of the suprastapedial process of the quadrate participates in the dorsal articulation of the element (compare Supplementary Figure 7.S5a, b). Given the structural differences, there are likely other drivers selecting for an elongate suprastapedial in mosasaurians, possibly related to hearing. Mosasaurians retain a typical lizard-like arrangement of the middle ear, and share with *Lanthanotus* an enlarged lateral part of the extracolumella, filling the external aperture of the quadrate [38]; however, in mosasaurians the cartilage is calcified and the internal process set within a well-defined fossa. An enlarged disk-like extracolumella and similar quadrate shape is present in the turtle *Trachemys*, and those features were recently interpreted as optimizations for underwater hearing [39]. Furthermore, the mosasaurian quadrate was compared to that of turtles [40], concluding both the acoustic isolation provided by quadrate shape and the nature of the tympanic disk provide similar functional adaptations for underwater hearing.

1.16 Mandibular symphysis and orientation of Meckel's groove

Morphology of the symphysial area in mosasaurs that would have been available to Cope [41] and those examined by Lee [17] are highly modified compared to *Varanus,* leading those workers to interpret that morphology as possessing the condition seen in snakes. Most recently, Paparella et al. [42] included "mobile anterior tips of dentary smoothly rounded and without distinct symphysial area ..." in their diagnosis of Pythonomorpha. The anterior medial dentaries of mosasaurids do superficially resemble those of snakes in that Meckel's groove lies in a more medial position and the anterior profile is somewhat blunt. However, the contention that mosasaurs do not have a "distinct symphysial area" is incorrect as we will show below.

The anteromedial dentaries of most dolichosaurids are not exposed or are too poorly preserved to assess details of their morphology. Although Paparella et al. [42] scored this character in *Pontosaurus lesinensis* for the derived condition, examination of that specimen reveals generally poor preservation and plastic deformation (Supplementary Figure 7.S8a, b). Only the left dentary is exposed in medial view and it is slightly shorter than the right and its anterior terminus a different shape suggesting the anterior most part of the dentary may be damaged and/or still partially embedded in the matrix. Thus, scoring of that character for *Pontosaurus lesinensis* is questionable. This opinion is reinforced by comparison with a well-preserved, three-dimensional specimen of *Coniasaurus* that possesses a symphysial area identical to that of *Varanus* (Fig. 7.6h, i). This morphology is also present in *Opetiosaurus* though the anterior portion is hidden in that specimen (Fig. 7.6j; Supplementary Figure 7.S8g).

A trend toward a more medial orientation of Meckel's groove in mosasaurids does appear to have altered the symphysial area, reducing the dorsal symphysial area and increasing the ventral part. Examination of well-preserved specimens reveals extensive ligamentous attachment sites (Supplementary Figure 7.S8c–f) dorsal and ventral to the Meckel's groove. Additionally, later diverging mosasaurid specimens that are preserved three-dimensionally or with little displacement, show elongate contact of the ventral margins of the anterior dentaries (Supplementary Figure 7.S8h, i) consistent with ligamentous attachment area (Supplementary Figure 7.S8c–f). Histological data [43] allows some inference of soft-tissue organization based on *Varanus* in which the attachment tissues between the opposing surfaces of the anteromedial dentaries is comprised of loose connective tissues dorsally, parallel fibers ventrally, and the majority being fibrocartilage. Ventral to Meckel's groove it is predominantly woven fibrous tissues with loose connective tissues in the ventralmost part. Adjacent to the woven fibrous tissues is Sharpey fibre bone. This may provide an explanation for the distinct bone surface textures seen in the dorsal and ventral parts of the mosasaurid symphyses and it is likely that evidence of dense Sharpey fibre bone will be found in this region (Supplementary Figure 7.S8e, f). Diversity of morphology of the mandibular symphyses of lizards has only been briefly addressed in the literature [43–45] and additional work is needed to characterize the attachment areas in mosasaurians. Nonetheless, it is clear from the examples presented here that well-preserved dolichosaur and mosasaurid specimens do not show the snake condition.

Orientation of Meckel's groove has also been included in diagnoses of Pythonomopha; "Meckelian groove confined to medial surface of lower jaw" was reported by Lee [17] and Lee and Caldwell [46], but was later modified to "Anterior end of Meckel's canal on medial surface of dentary" [3, 4, 42, 47]. As we have shown in the discussion of the symphysis above, *Coniasaurus* and *Opetiosaurus* possess the *Varanus* condition (Fig. 7.6h–j) and derived mosasaurids independently acquired a more medial orientation. Furthermore, since the anterior Meckel's groove is within the symphysial area even in early diverging mosasaurians, it must be more or less medially oriented, as can be observed in extant forms like *Varanus* [43].

1.17 Dentary margin

Paparella et al. [42] presented as a pythonomorph synapomorphy the questionable character of a "straight dentary margin". The dorsal dentary margin in *Pontosaurus kornhuberi* is largely hidden and substantial crushing is obvious in the specimen (Supplementary Figure 7.S1b). The same is true for *P. lesinensis* (Supplementary Figure 7.S8a, b) which also has substantial crushing, plastic deformation and damaged bone surfaces, making this assessment tenuous. The exposed portion of the dentary in *Tetrapodophis* does appear to be straight, but this specimen is badly crushed too. Notwithstanding the effects of taphonomy, the shape of the dentary is influenced by prey preference and feeding style, and those may even change during ontogeny of a single species (e.g., *Varanus niloticus*) with dramatic changes in the tooth morphology and the curvature of the jaw. Examination of three-dimensionally preserved specimens of *Coniasaurus*, where crushing is minimal or absent, reveals curvature of the dorsal margin (Supplementary Figure 7.S9a–c). This is also the case in *Judeasaurus* and *Haasiasaurus* (Supplementary Figure 7.S9d, e). *Opetiosaurus* appears to be straight; however, it is unclear if this is real or an artifact of crushing. The taxa sampled in the phylogenetic analysis of Paparella et al. [42] do exhibit a relatively straight dorsal margin; however, among derived mosasaurids there is taxonomic variation in the curvature of the dentary. In the genus *Prognathodon* a number of species and especially robust forms like *P. saturator* and *P. overtoni* exhibit notable curvature of the dentary [13, 36].

1.18 Intramandibular joint

The intramandibular joint in snakes was described in detail by Rieppel and Zaher [27] and compared with the condition in derived mosasaurs and varanoid lizards finding substantial differences. Here we present new HRCT-derived data from two dolichosaurids.

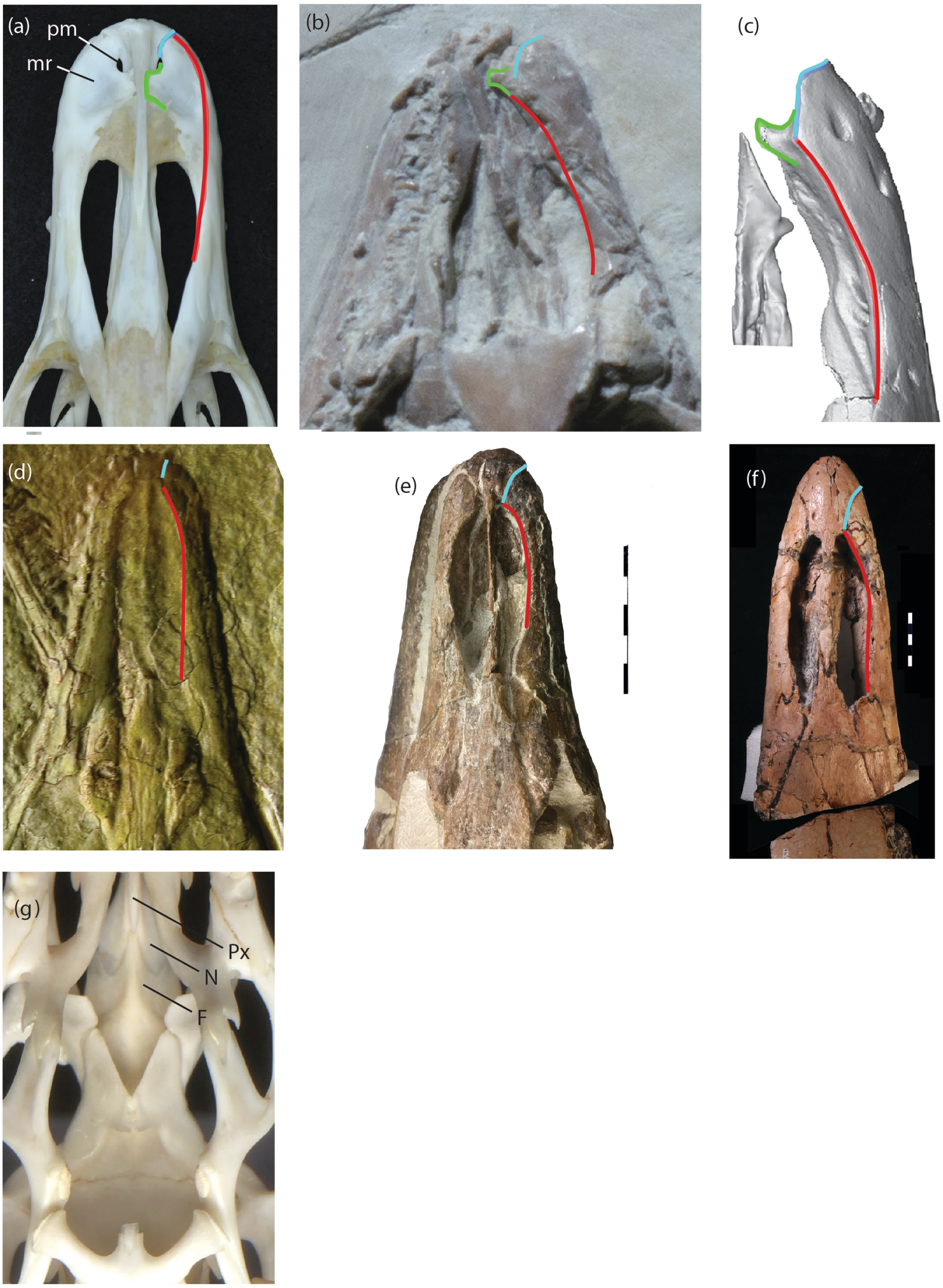
The mandibles of *Coniasaurus crassidens* and *Dolichosaurus longicollis* (Fig.7.5; Supplementary Figure 7.S10) are preserved in three-dimensions with minor crushing although both are broken and incomplete. The left mandible in *C. crassidens* (NHRI-R-342 1) is the only one preserving articulation of all of the constituent bones of the intramandibular region. Compared to *Varanus*, the mandible in *C. crassidens* is similar to the condition in 'aigialosaurs' in reduction of the medial ventral processes of the coronoid, reduction of the posterodorsal process of the splenial (rendering a minimally abutting contact with coronoid), a relatively straight posterior margin of the dentary in lateral view, and possession of a typical mosasaurian angular-splenial contact. *Coniasaurus crassidens* is more similar to the condition in *Varanus* in greater overlap of the dentary-splenial complex with the post-dentary bones, the posterodorsal dentary tucks under the anteromedial coronoid within a cleft, the splenial is ventrally oriented anteriorly, and the subdental shelf is ventrally bowed with no upgrowth of a medial ridge.

In *Coniasaurus and Dolichosaurus,* the angular receives the articular from above in a U-shaped contact (Fig. 7.5b cross-sections 1 and 2) posterior to the angular foramen. Anterior to the foramen, the articular narrows and crosses the angular-splenial junction as a laterally compressed blade-like projection, inserting between the lateral and medial dorsal lamina of the splenial, and extending anteriorly to between the 3rd and 4th posterior tooth position (Fig. 7.5b cross-section 8). Thus, as concluded by Gauthier [48] and Rieppel and Zaher [49] the articular provides the primary support for the dentary via the splenial.

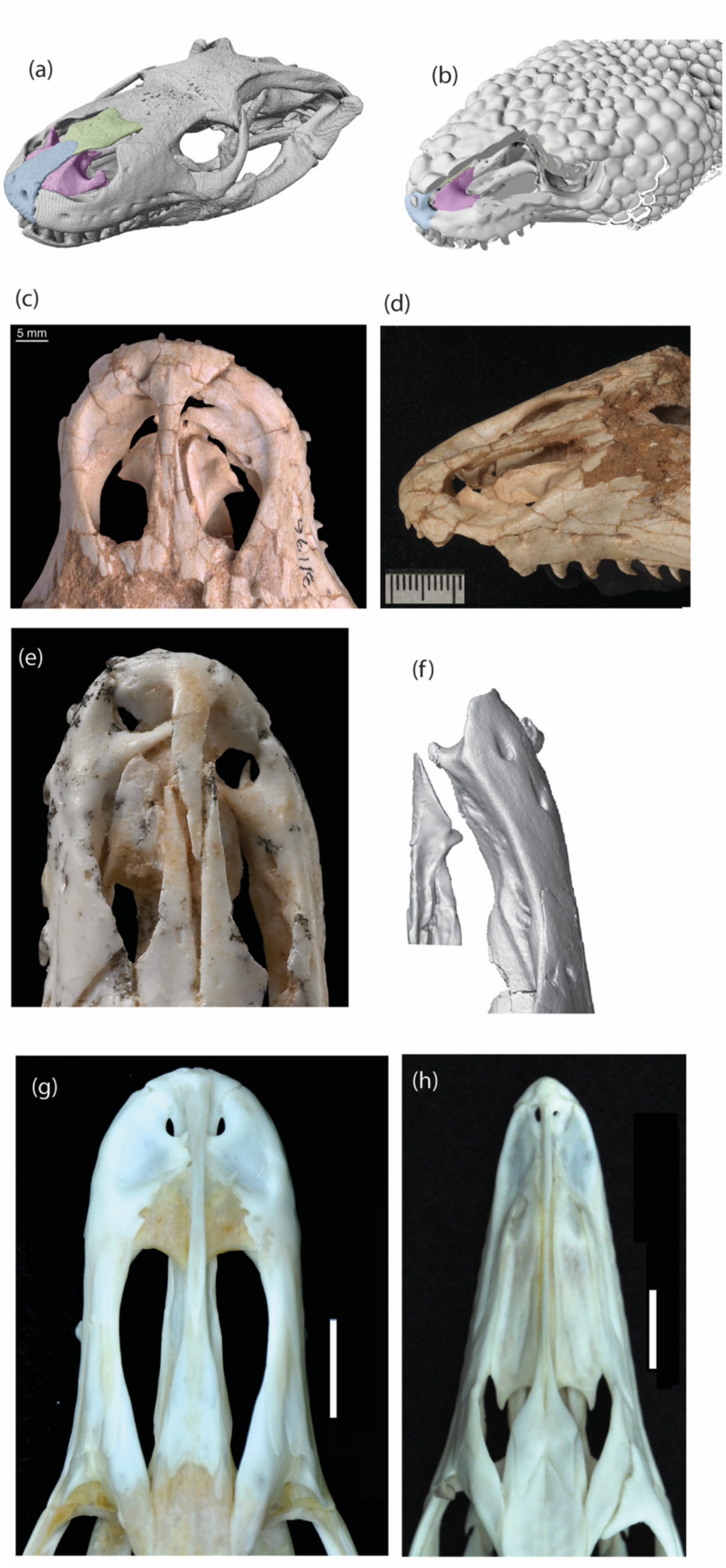
The coronoid in both *Coniasaurus* and *Dolichosaurus* straddles the surangular in an inverted U-shaped contact with broad lateral exposure (7.5c, d, g, k; Supplementary Figure 7.S10). In *Coniasaurus*, although broken on its anterolateral side, the coronoid bears a median cleft embracing the posterior dentary as in *Varanus* (Supplementary Figure 7.S10l). The condition in *Opetiosaurus* and *Haasiasaurus* is equivocal, but in many derived mosasaurids the coronoid retains an anterior cleft (absent in snakes) in close proximity to the posterior dentary.

2. Supplementary Figures

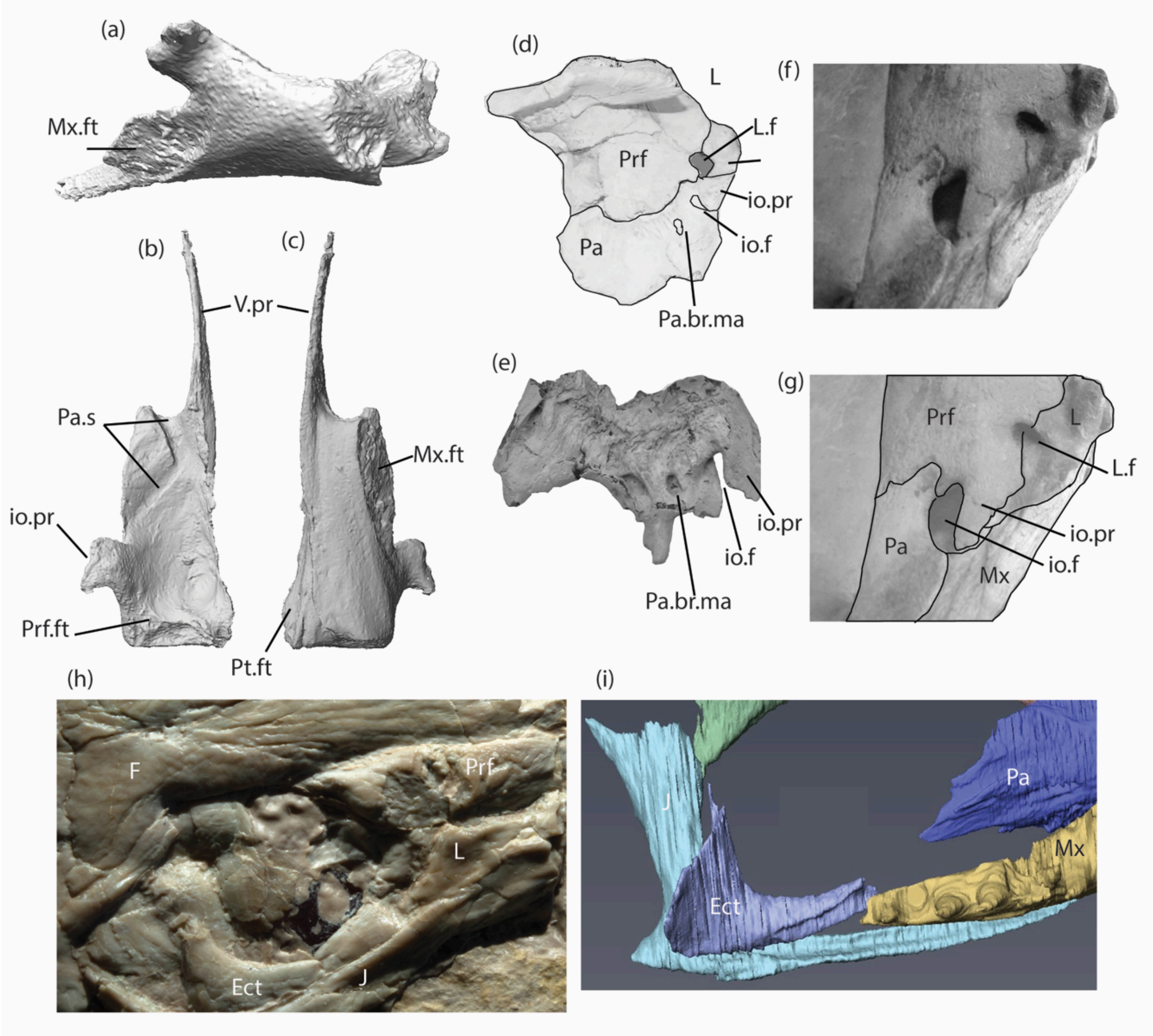
Supplementary Figure 7.S1 Taxonomic nomenclature and overview of select specimens – (a) Simplified cladogram of mosasaurian relationships. *Pontosaurus kornhuberi* (MSNM V3662) in (b) dorsal view; *Pontosaurus lesinensis* (GBA 1873/4/2) in dorsal view (c) embedded in resin, and (d) cast taken prior to embedding; *Adriosaurus suessi* (NHMUK R2867) in (e) dorsal view. *Opetiosaurus buchichii* (GBA-1901-002-0005) main block in (f) dorsal view and (g) detail of snout region, and (h) palatal view of natural mold (GBA-1901-002-0001- counterpart).



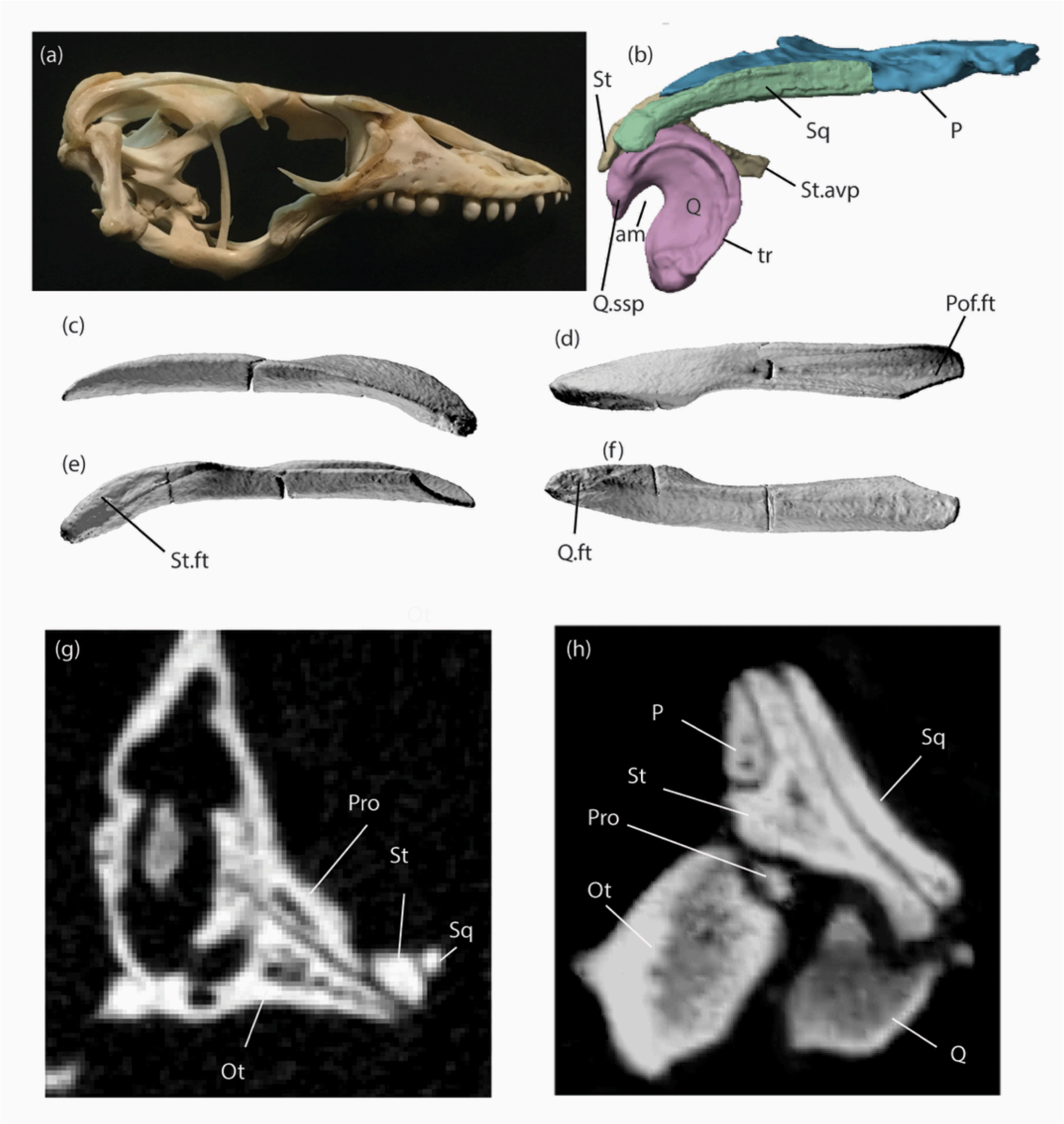
Supplementary Figure 7.S2 Narial retraction – The dorsal view of the snout in (a) *Varanus salvadorii;* (b) *Pontosaurus kornhuberi*; (c) *Coniasaurus gracilodens;* (d) *Opetiosaurus buchichi;*(e) *Tethysaurus nopcsai;* (f)*Yaguarasaurus columbianus. Ventral view of (g) Varanus rudicollis.* Dorsal margin of maxilla indicated by the red line, the anteromedial process by the green line and the premaxilla-maxilla suture by the blue line. Anatomical abbreviations: F, frontal; mr, maxillary recess; N, nasal; pm, premaxillary fenestra; Px, premaxilla.



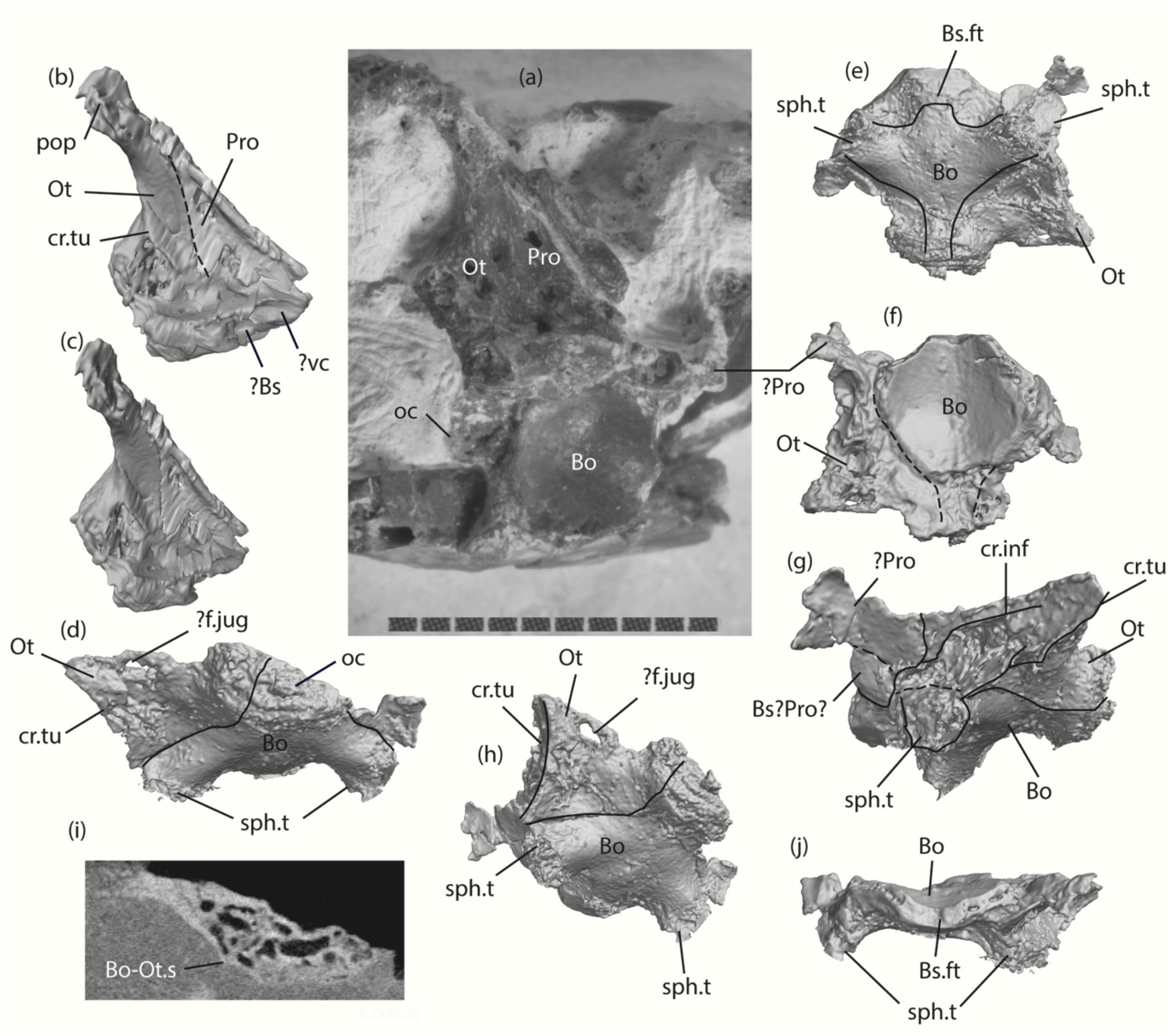
Supplementary Figure 7.S3 Variation in the morphology of the septomaxilla – The septomaxilla and associated structures in (a) *Lanthanotus*, (b) *Heloderma*, (c, d) *Estesia*, (e) *Ovoo*, (f) *Coniasaurus gracilodens*, (g) *Varanus salvadorii*, and (h) *Varanus rudicollis.*



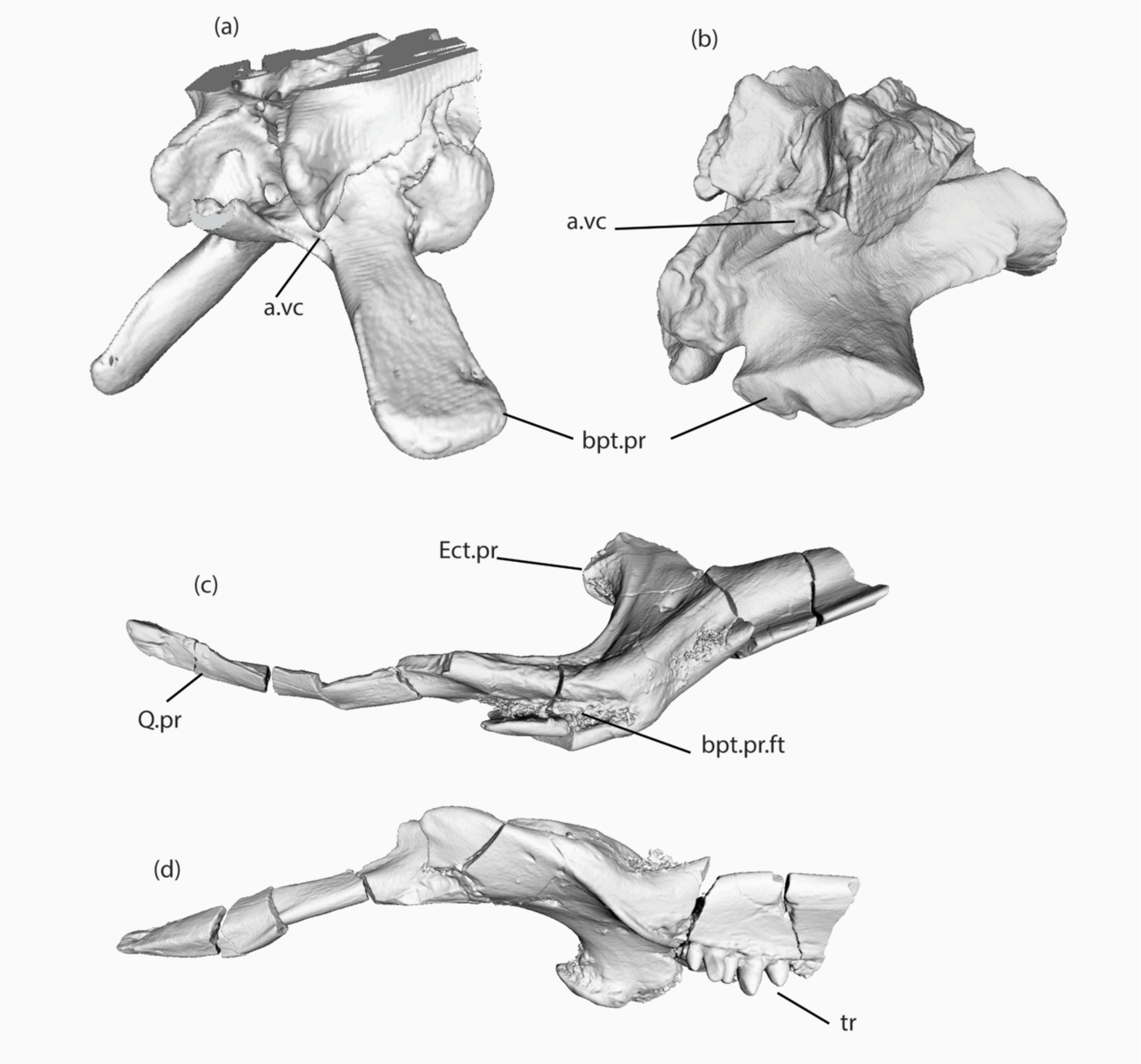
Supplementary Figure 7.S4 Palatine-infraorbital complex – Left palatine of *Phosphorosaurus ponpetelegans* (HMG-1528) in (a) posteroventrolateral oblique, (b) dorsal, and (c) ventral views. Re-articulated right prefrontal palatine and lacrimal of a well preserved *Clidastes* sp. (TMM 43208-1) in (d) posterior view. Partial left palatine (reversed) of *Clidastes* sp. (RMM 2479) in (e) posterior view. Articulated prefrontal palatine and lacrimal of *Mosasaurus* cf. *hoffmanni* (TLAM NH.HR.2009.032.0001) in (f) posterior view and (g) with annotation. Right orbital detail of *Opetiosaurus buchichii* (GBA-1901-002-0001 through GBA-1901-002-0005) in (h) dorsal view. *Tethysaurus nopcsai* (SMU-75486) in (i) ventromedial oblique view. Anatomical abbreviations: Ect, ectopterygoid; d.lf, dorsal lacrimal foramen; F, frontal; io.f, infraorbital foramen; io.pr, infraorbital process; J, jugal; L, lacrimal; L.f, lacrimal foramen; Mx, maxilla; Mx.ft, maxillary facet; N.ft,nasal facet; Pa, palatine; Pa.br.ma, foramen for the palatine branch of the maxillary artery; Pa.s, palatine dorsal sulci; Prf, prefrontal; Prf.ft, prefrontal facet; Pt.ft, pterygoid facet; Px, premaxilla; Sx, septomaxilla; V, vomer; v.lf, ventral lacrimal foramen; V.pr, vomer process.



Supplementary Figure 7.S5 Braincase, suspensorium and quadrates – *Varanus niloticus* in (a) right lateral view. (note moderate parietal downgrowth). *Russellosaurus coheni* posterior suspensorium and quadrate in (b) right lateral view. Note no parietal downgrowth. *Coniasaurus gracilodens* left squamosal in (c) lateral, (d) dorsal, (e) medial, and (f) ventral views. HRCT slices showing the close proximity of the prootic and supratemporal in (g) *Lanthanotus borneensis* (YPM6057; Digimorph) and (h) *Varanus salvator* (FMNH 35144; Digimorph). Anatomical abbreviations: am, auditory meatus; Ot, otooccipital; P, parietal; Pof.ft, postorbitofrontal facet; Pro, prootic; St, supratemporal; St.ft, suprastapedial facet; Sg, squamosal; St.avp, anteroventral process of supratemporal; Sq, squamosal; tr, tympanic rim; Q.ft, quadrate facet; Q, quadrate; Q.ssp, suprastapedial process of quadrate.

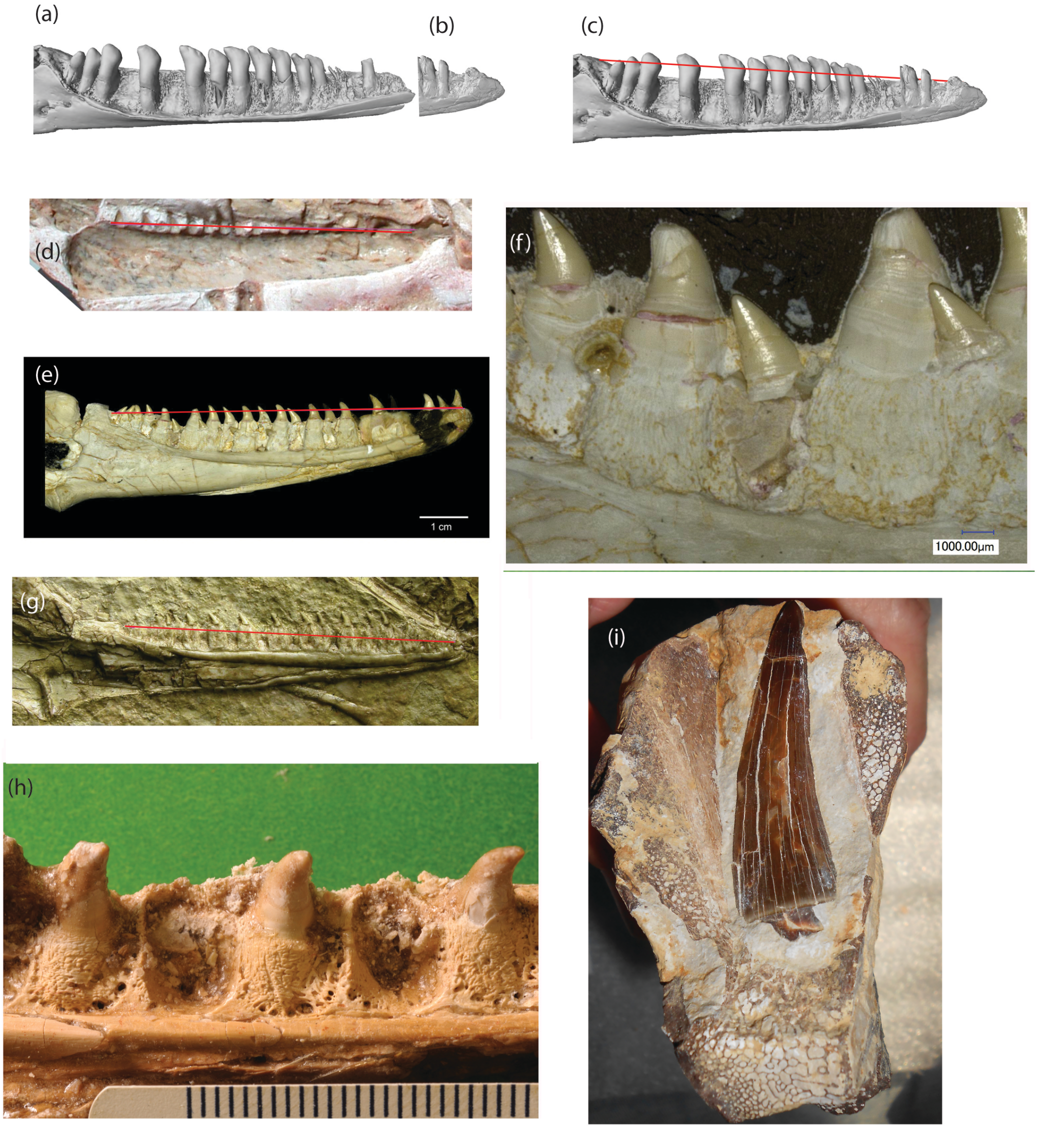


Supplementary Figure 7.S6 The braincase of *Dolichosaurus longicollis* – (a) braincase region in (b, c) fragmentary right otooccipital and prootic in posterolateral left views, (d) articulated left otooccipital and basioccipital in posterior view, (e) ventral, (f) dorsal, (g) anteroventrolateral oblique, (h) posteroventrolateral oblique, and (j) anterior views; (i) is a subset of a HRCT slice through left otooccipital and basioccipital to show suture. Anatomical abbreviations: a.vc, anterior opening of vidian canal; Bo, basioccipital; Bs, basisphenoid; bt.pr, basipterygoid process of basisphenoid; cr.tu, crista tuberalis; f.jug, jugular foramen; Ot, otooccipital; oc, occipital condyle; P, parietal; P.plp, posterolateral process of parietal; Pro, prootic; psr, parasphenoid rostrum; p.vc, posterior opening of vidian canal; Q.ft, quadrate facet; So, supraoccipital; sph.t, spheno-occipital tubercle; St, supratemporal; St.avp, supratemporal anterooventral process; St.ft, supratemporal facet; Sq, squamosal; vc, vidian canal.

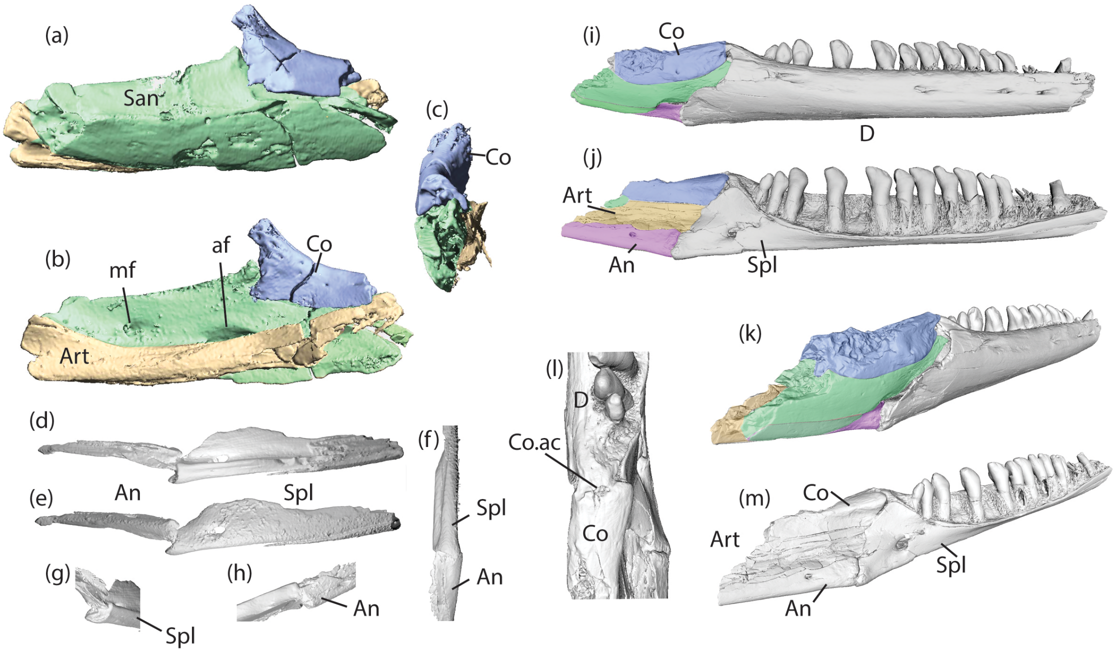


Supplementary Figure 7.S7 Basipterygoid and conjugate pterygoid articulation in mosasaurians – *Varanus komodoensis* (TNHC 95803-Digimorph) anterior ventral part of braincase in (a) anterolateral oblique view; *Clidastes propython* (YPM1368) parabasisphenoid in (b) anterolateral oblique view; *Coniasaurus* sp. (SMU 69018) left pterygoid in (c) dorsomedial and (d) ventromedial views to show articulation for basipterygoid process of basisphenoid. Anatomical abbreviations: a.vc, anterior opening of vidian canal; bpt.pr, basipterygoid process; bpt.pr.ft, facet for basipterygoid process of parabasisphenoid; Ect.pr, ectopterygoid process; tr, tooth row; Q.pr, quadrate process.

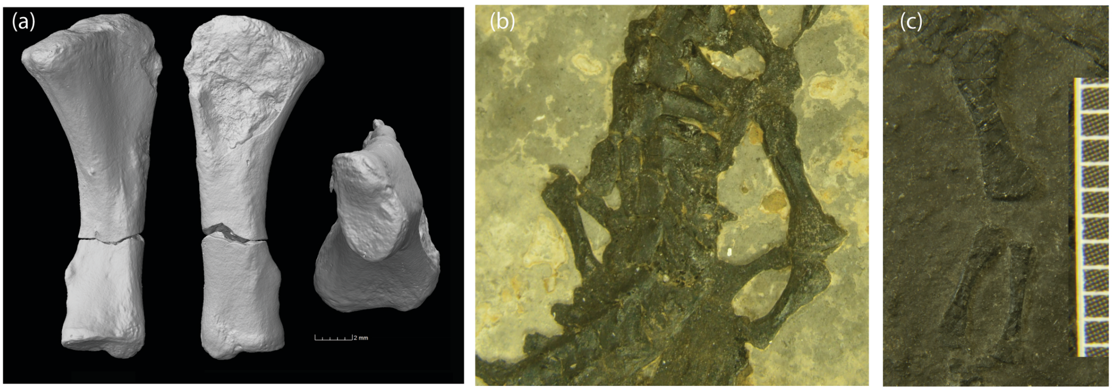
Supplementary Figure 7.S8 Mandibular symphyses – *Pontosaurus lesinensis* (GBA 1873/4/2) in (a) overview and (b) detail of left medial dentary; *Plesiolatecarpus planifrons* (SMU 76516) right dentary in (c) overview and (e) detail of symphysial region; *Globidens alabamensis* (SMU 76241) juvenile specimen, left dentary in (d) overview and (f) detail of symphysial region; *Opetiosaurus bucchichi* (GBA-1901-002-0005) showing (g) details of symphysis of right dentary; *Plotosaurus bennisoni* (UCMP 32778) in (h) ventral view and *Tylosaurus nepaeolicus* (SMU76546) in (i) ventral view, showing mandibular pose and anterior symphysial proximity.



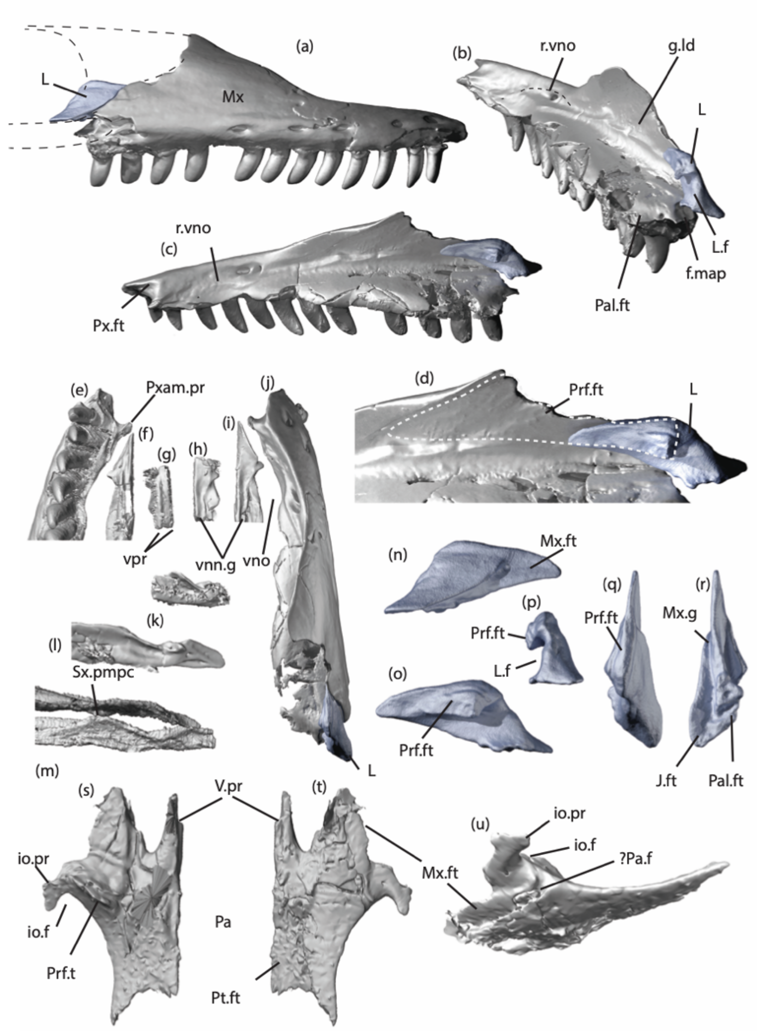
Supplementary Figure 7.S9 Dental morphology in mosasaurians – (a) *Coniasausaurus crassidens* (NHMUK R 3421) left partial mandible, (b) *Coniasaurus* sp. (SMU 69019) anterior part of left dentary, (c) Composite of (a) and (b), (d) *Judeasaurus tchernovi* (HUJI P4000), (e) *Haasiasaurus gittelmani* partial left mandible (HUJI EJ 693), (f) detail of the same, posterior tooth row, (g) *Opetiosaurus bucchichi* (GBA-1901-002-0005) partial left mandible (reversed), (h) *Tethysaurus nopcsai* (SMU), (i) *Mosasaurus cf. M. hoffmani* (ATU unnumbered specimen) right maxilla, fifth tooth position replacement tooth in crypt. Red line is to highlight dorsal dentary margin curvature.



Supplementary Figure 7.S10 Dolichosaurid partial mandibles – *Dolichosaurus longicollis* (NHMUK R49002) right partial mandible with rearticulated left coronoid in (a) right lateral, (b) medial (reversed), (c) anterior views. *Dolichosaurus longicollis* (NHMUK R49002) left angular and splenial in (d) lateral, (e) medial (reversed), (f) ventral, (g) left posterolateral oblique, (h) anteromedial and below oblique views. C*oniasaurus crassidens* (NHMUK R 3421) left mandible in (i) lateral (reversed), (j), medial, (k) posterolateral oblique (reversed), (l) dorsal detail of anterior coronoid and posterior dentary, and (m) posteromedial oblique views. Abbreviations: An, angular; af, adductor fossa; Art, articular; Co, coronoid; Co.ac, coronoid anterior cleft; D, dentary; mf, mandibular foramen; Mk.fs, Meckel's fossa; San, surangular; Spl, splenial; t, tooth.



Supplementary Figure 7.S11 Postcranial elements – Three-dimensionally preserved tibia in (a) *Coniasaurus* sp. (DMNH 1601) in flexar, palmer, and distal views; the pelvic region and rear limbs (b) *Adriosaurus suessi* (NHMUK R2867); and the rear limb of (c) *Acteosaurus tommasinii* (MCSNT 9960).



Supplementary Figure 7.S12 (colour version of Fig. 7.2) Snout region of *Conisaurus gracilodens* (NHMUK-R44141) and the palatine of *Dolichosaurus longicollis* (NHMUK-R49002). Right maxilla and rearticulated lacrimal in (a) lateral, (b) dorsal, posterolateral oblique, (c) medial, (d) medial, showing detail of maxilla-lacrimal contact, (e) ventral, and (j) dorsal views. Right vomer in (f) ventral, (i) dorsal, and (l) lateral views. Left vomer in (g) ventral, (h) dorsal, and (k) lateral views (k is reversed for comparison). Articulated anterior part of right vomer and septomaxilla of *Tethysaurus nopcsai* (SMU-75486) in (m) lateral view. Right lacrimal of *Coniasaurus gracilodens* in (n) lateral, (o) medial, (p) posterior, (q) dorsal, and (r) ventral views. *Dolichosaurus longicollis* palatine in (s) dorsal, (t) ventral, and (u) posteroventral oblique views. Abbreviations: Ec, ectopterygoid; F, frontal; f.map, maxillary artery posterior; f.maa, foramen maxillary artery anterior; g.Ld, groove for lacrimal duct; in.pr, incisive process; io.f, infraorbital foramen; io.pr, infraorbital process; J, jugal; L, lacrimal; L.f, lacrimal foramen; L.f.d, dorsal lacrimal foramen; L.f.v, ventral lacrimal foramen; Mx, maxilla; Mx.ft, maxillary facet; Mx.g, groove to receive dorsal margin of maxilla; N, nasal; N.ft, nasal facet; P, parietal; Pa, palatine; Pa.f, palatine foramen; Pa.vp.ft, palatine vomer process facet; Pt.ft, pterygoid facet; Px, premaxilla; Pxam.pr, anteromedial process of premaxilla; Px.ft, premaxillary facet; Prf.ft, prefrontal facet; r.vno, recess for vomernasal organ; Sx, septomaxilla; Sx.pmpc, septomaxilla posteromedial process of cupola; Sx.ft, septomaxilla facet; V.pr, vomer process; vno, vomeronasal opening; vno.r, recess for vomernasal organ; vnn.g, groove for vomeronasal nerve; vpr, ventral parallel ridges; Scale bar = 5mm.

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