Psittacosaurus houi, a longer snouted psittacosaurid from the Lower Cretaceous Lujiatun Unit of Yixian Formation, China, with the synonymy of the unresolved genus *Hongshanosaurus* revisited (#94217)

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Psittacosaurus houi, a longer snouted psittacosaurid from the Lower Cretaceous Lujiatun Unit of Yixian Formation, China, with the synonymy of the unresolved genus *Hongshanosaurus* revisited

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The taxonomic validities of some genera and species within Psittacosauridae have been disputed, including that of *Hongshanosaurus houi* which has been synonymized with *Psittacosaurus lujiatunensis* previously. To assess the validity of the former genus and species and elucidate the taxonomy and diversity of the family Psittacosauridae, we describe a nearly complete psittacosaurid skull (ZMNH M12414) with an aid of computed-tomography techniques. The specimen comes from the Lujiatun Unit of the Lower Cretaceous Yixian Formation, Liaoning, northeastern China, the locality that has also produced *P. major*, *P. lujiatunensis* and *H. houi*. ZMNH M12414 exhibits many features present in the adult ~~paratype~~ skull of *Hongshanosaurus houi* (-IVPP V12617), indicating they are assignable to the same species within Psittacosauridae. Large proportional length of the snout in ZMNH M12414, IVPP V12617, and *P. amitabha*~~, which~~ is subject to ~~the~~ ontogenetic change, ~~indicates~~ that the genus *Hongshanosaurus* is a junior synonym of *Psittacosaurus*. On the other hand, ZMNH M12414, together with IVPP V12617, exhibits a set of features that are not observed in any other species of *Psittacosaurus* including *P. lujiatunensis*, leading to an establishment of *P. houi*. The phylogenetic analysis supports the validity of *P. houi* where ZMNH M12414 and IVPP V12617 forms an independent clade within *Psittacosaurus*. The computed-tomography techniques employed in the present study facilitated re-assessment of the taxonomy and morphological diversity of *Psittacosaurus*, and its application is encouraged ~~to~~ previously described dinosaur taxa whose validities are in question. The detailed evaluation of ontogenetic, intra-specific, and inter-specific variations are crucial to understand the true taxonomy and diversity of *Psittacosaurus*.

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Abstract

The taxonomic validities of some genera and species within Psittacosauridae have been disputed, including that of *Hongshanosaurus houi* which has been synonymized with *Psittacosaurus lujiatunensis* previously. To assess the validity of the former genus and species and elucidate the taxonomy and diversity of the family Psittacosauridae, we describe a nearly complete psittacosaurid skull (ZMNH M12414) with an aid of computed-tomography techniques. The specimen comes from the Lujiatun Unit of the Lower Cretaceous Yixian Formation, Liaoning, northeastern China, the locality that has also produced *P. major*, *P. lujiatunensis* and *H. houi*. ZMNH M12414 exhibits many features present in the adult paratype skull of *Hongshanosaurus houi* (IVPP V12617), indicating they are assignable to the same species within Psittacosauridae. Large proportional length of the snout in ZMNH M12414, IVPP V12617, and *P. amitabha*, which is subject to the ontogenetic change, indicates that the genus *Hongshanosaurus* is a junior synonym of *Psittacosaurus*. On the other hand, ZMNH M12414, together with IVPP V12617, exhibits a set of features that are not observed in any other species of *Psittacosaurus* including *P. lujiatunensis*, leading to an establishment of *P. houi*. The phylogenetic analysis supports the validity of *P. houi* where ZMNH M12414 and IVPP V12617 forms an independent clade within *Psittacosaurus*. The computed-tomography techniques employed in the present study facilitated re-assessment of the taxonomy and morphological diversity of *Psittacosaurus*, and its application is encouraged to previously described dinosaur taxa whose validities are in question. The detailed evaluation of ontogenetic, intra-specific, and inter-specific variations are crucial to understand the true taxonomy and diversity of *Psittacosaurus*.

Introduction

Psittacosauridae represents a family of the ceratopsian dinosaurs with bipedal posture and characteristic upper and lower jaws to form a parrot-beak-like rostrum (Osborn, 1923). In the Lower Cretaceous of eastern Asia, numerous individuals of psittacosaurids have been reported from the Barremian to Albian of China and Mongolia (Sereno, 2010). The genus *Psittacosaurus* is one of the possible two genera that consists of the family Psittacosauridae, and the most species-rich genus within Dinosauria. So far, 15 species have been described within the genus, although a comparative study by Sereno (2010) re-assigns them into nine species (*P. mongoliensis*, *P. neimongoliensis*, *P. sinensis*, *P. sibiricus*, *P. lujiatunensis*, *P. major*, *P. meileyingensis*, *P. xinjiangensis* and *P. gobiensis*). More recently, Napoli et al. (2019) adds *P. amitabha* as a new species, and the total number of *Psittacosaurus* species remains debated.

Another genus that hypothetically constitutes the family Psittacosauridae is *Hongshanosaurus*, which is distinguished from *Psittacosaurus* by oval-shaped external naris and orbit, and a longer

rostrum. Within the genus is a single species *H. houi* described based upon a juvenile holotypic skull (IVPP V12507) and an adult ~~paratype~~, skull (IVPP V12617) (You, Xu and Wang., 2003; You and Xu, 2005). On the other hand, lack of definitive morphological differences between these genera have led to an argument that *Hongshanosaurus* may be a junior synonym of *Psittacosaurus*. For example, Sereno (2010) argues that the longer rostrum in *Hongshanosaurus* may come from the postmortem deformation and synonymizes *H. houi* with *Psittacosaurus lujiatunensis*. In addition, Hedrick and Dodson (2013) supports the synonymy of *H. houi* with *P. lujiatunensis* based on the three-dimensional geometric morphometric analyses in which *H. houi* forms a morphological cluster with *P. lujiautnensis* and *P. major*. It is noted, however, that Napoli et al. (2019) criticizes Hedrick and Dodson (2013) in that the study fails to take the intraspecific and ontogenetic variations into account. Nonetheless, the series of arguments advocate that the synonymy of *Hongshanosaurus* with *Psittacosaurus* as well as the validity of *H. houi* deserves further assessment.

In this study, we describe a well-preserved skull (ZMNH M12414) of Psittacosauridae with a long snout like *H. houi* to test the purported validity of *Hongshanosaurus* and address the Psittacosaurid taxonomy based on morphological comparisons and phylogenetic analyses. While the synonymy of *Hongshanosaurus* with *Psittacosaurus* is supported, the present analyses suggests that *Psittacosaurus* (~~*Hongshanosaurus*~~) *houi* is a valid species and can be distinguished from *P. lujiatunensis* or any other species of *Psittacosaurus*. The present study sorts out the continuously debated taxonomy of Psittacosauridae and provides a better understanding of the taxonomy and morphological diversity of the notably specious genus *Psittacosaurus*.

Abbreviations—AMNH = American Museum of Natural History, New York, U.S.A.; CAGS-IG = Chinese Academy of Geological Sciences, Institute of Geology, Beijing, China; FPDM = Fukui Prefectural Dinosaur Museum, Fukui, Japan;~~;~~ IGM = Mongolian Institute for Geology, Ulaanbaatar, Mongolia; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LH = Long Hao Institute for Stratigraphic Palaeontology, Inner Mongolia Autonomous Region, China; ZMNH = Zhejiang Museum of Natural History, Zhejiang, China.

Materials & Methods

Specimen and locality

ZMNH M12414 is preserved in three dimensions and represented by a nearly complete skull and mandible. The specimen is stored at ZMNH. The ~~caudal~~ surface of the skull is covered by sandstone matrix. The specimen was collected from the Lower Cretaceous Lujiatun Unit, which is the lowermost unit of the Yixian Formation, Jehol Group, cropping out near the village of Lujiatun, Beipiao, Western Liaoning, northeastern China. The unit consists of sandstones, grey siltstones, pink tuffaceous sandstones and tuffaceous siltstones, resulting from extensive volcanic activities and multiple flood events (Rogers et al., 2015). Volcanic rocks and interbedded fossil-bearing lake sediments of the unit have yielded 40Ar/39Ar date of 125.7±2.6 Ma (Barremian, Zhu et al., 2007). The species of Psittacosauridae previously reported from the unit include *P. lujiatunensis* (Zhou et al., 2006), *P. major* (Sereno et al., 2007; You, Tanoue and Dodson, 2008), and *H. houi* (You, Xu and Wang, 2003; You and Xu, 2005).

Reconstruction of the skull by computed tomography

Skull and mandible~~s~~ (ZMNH M12414: Fig.1A, B and C) were analyzed with a high-resolution X-ray computed tomography (CT) technique (NIKON XTH 320; Nikon, Tokyo, Japan) at College of Civil Engineering and Architecture, Zhejiang University, Hangzhou, Zhejiang, China. Tomographic images were obtained under a voltage of 300 kV, current of 280μA, interslice spacing of 0.08 mm and image size of 1,920× 1,507 pixels. The parameter resulted in a voxel size of 1.00 mm along the z-axis and 0.11 mm in the x- and y-axes. The resulting CT images were segmented and the three-dimensional model of the specimen rendered in Amira ver. 2019.4 (Thermo Fisher SCIENTIFIC, Tokyo, Japan).

Observations and measurements

Observations and measurements of ZMNH M12414 were performed on the rendered three-dimensional model (Fig. 1D, E and F). For comparative purposes, measurements on previously described psittacosaurid specimens were either taken from the descriptions of original literatures or from the figures within literatures if descriptive information is not available in the texts. Definitions of the preorbital length and the skull length followed Sereno (2010) (Fig. 2).

Phylogenetic analysis

To assess the phylogenetic positions within Psittacosauridae, ZMNH M12414 and IVPP V12617 (adult ~~paratype~~ skull of "*H. houi*") were added to the data matrix of Napoli et al. (2019)

and analyzed with T.N.T. (Version 1.5; Goloboff, Farris and Nixon, 2015). ZMNH M12414 was scored based on the rendered three-dimensional model, while IVPP V12617 was scored based on the previously published literatures (You and Xu, 2005; Taylor et al. 2017; Bullar et al. 2019; Landi et al. 2021).

Results

Systematic palaeontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1888
Ceratopsia Marsh, 1890
Psittacosauridae Osborn, 1923
Psittacosaurus Osborn, 1923
Psittacosaurus houi (You, Xu, and Wang, 2003)
Figures 1-11
Hongshanosaurus houi You, Xu, and Wang, 2003 (original description)
Psittacosaurus lujiatunensis (You, Xu, and Wang, 2003): Sereno, 2010 (synonymized)
Psittacosaurus houi (You, Xu, and Wang, 2003): Ishikawa, Zheng, Imai, Shibata, Kawabe, and Jin, 2023 (new combination)

Holotype—IVPP V12704, a nearly complete juvenile skull with lower jaws.

Referred Specimens—IVPP V12617, a complete adult skull with lower jaws; ZMNH M12414, a complete subadult skull with lower jaws.

Locality and horizon—Lujiatun, Liaoning, People's Republic of China; Lujiatun Unit, Yixian Formation, upper Barremian, Early Cretaceous (Zhou et al., 2006).

Diagnosis—*Psittacosaurus houi* is distinguished from other *Psittacosaurs* by the following combination of characters: (1) preorbital length about a half of the skull length; (2) anterior margin of the rostral and nasal sloped posterodorsally; (3) dorsoventrally elongated laterotemporal fenestra oriented at an angle of about 45 degrees in lateral view; (4) the ventral margin of premaxilla raised above maxillary tooth row; (5) large surface area of the jugals exposed in dorsal view; (6) the anterior ramus of the squamosal short, with the tip of the process in contact with the center of the supratemporal bar; (7) the supraoccipital subtriangular and widest at its ventral margin.

Description and comparisons

ZMNH M12414 measures a length of 160 mm from the tip of the snout to the back of the quadrate, a maximum width of 195 mm across the jugal horns and a maximum height of 120 mm. The cranial sutures are nearly obliterated, suggesting this specimen is nearly at its somatic maturity. In dorsal view, the skull is wider than long, as in *P. sinensis* and *P. lujiatunensis*. Notably, the skull features a relatively long snout. The proportion of the preorbital length against the skull length is approximately 53 %, being similar to those in IVPP V12716 and *P. amitabha*, 52 % and 46 % respectively and unlike other known *Psittacosaurus* species which exhibit less than 40 % of the proportion (Sereno, 2010).

Rostrum—In anterior view, the rostral bone is subtriangular with broad ventral margin, and extends above the premaxilla anteriorly (Fig. 3C). In lateral view, it is triangular, having nearly vertical sutural contact with premaxilla. Because the ~~distal~~ ends of the nasals are not fully preserved, the articulation between rostral and nasal is obscured. As in *P. amitabha* and IVPP V12617, the anterior margin of the rostral and nasal slopes posterodorsally in lateral view. In dorsal view, the rostral tip is rounded, and neither pointed nor strongly bowed ventrally (Fig. 4B).

Premaxilla—Both premaxillae are preserved, and make up most of the lateral surfaces of the snout. The premaxilla contacts the rostral anteriorly, the nasal and prefrontal dorsally, and lacrimal and maxilla posteriorly as in other species except for *P. sinensis*, in which the premaxilla also meets jugal posteriorly. Unlike in other *Psittacosaurs* species, the sutural contact between prefrontal and premaxilla is relatively narrow. A similar character is also found in IVPP V12617, although the contact is even narrower (You and Xu, 2005).

The dorsal portions of both premaxillae are partially missing. The posterior expansion of the posterolateral process of the premaxilla excludes the maxilla from the external nares, which are bounded solely by the nasals and premaxillae, as in all other *Psittacosaurus* species. The lateral surface is smooth and slightly depressed below the external naris, but becomes roughed with grooves and pits near its buccal margin, which is particularly apparent on the right premaxilla (Fig. 5B). A well-developed crest extends anterodorsally along the premaxillary-maxillary suture and a conspicuous groove crosses this suture horizontally just below the distal end of the premaxillary-maxillary ridge, as in *P. meileyingensis* and *P. lujiatunensis*. In lateral view, position of the ventral margin of the premaxilla is raised above maxillary tooth row, as in IVPP V12617. While similar features are present in *P. mongoliensis* and *P. major*, the distance between the ventral margin of the premaxilla to the maxillary tooth row is greater in ZMNH M12414 and IVPP V12617.

Maxilla—Both maxillae are preserved. In lateral view, the maxilla is subtriangular and contacts the jugal posteriorly, the premaxilla anteriorly and the lacrimal dorsally as in most other *Psittacosaurus* species. The dorsal part of the maxilla is tall, trapeziform and nearly positioned

anteroventral to the ventral border of the orbit as in *P. meileyingensis*, *P. neimongoliensis*, *P. lujiatunensis*, *P. major* and IVPP V12617, but differing from the lower, triangular maxilla in other psittacosaurids. As in *P. lujiatunensis*, *P. mongoliensis*, *P. amitabha* and *P. gobiensis*, sub-triangular maxillary fossa (Fig. 6A, B) is present on the lateral surface with a horizontal eminence lies along its buccal margin. The fossa is anteroposteriorly longer than dorsoventrally deep. Sereno (2010) describes the neurovascular foramina that open within, or on the rim of, the maxillary fossa and the anterolateral maxillary foramen located near or along the suture with the premaxilla in *Psittacosaurus*. The presence of these features are not confirmed in ZMNH M12414. Like most *Psittacosaurs*, posterior to the maxillary fossa, the maxillary protuberance is found on the posterior end of the rim of the cheek emargination near the maxilla-jugal suture as mentioned in Sereno (2010). In dorsal view, the anterior end of the tooth row is wide as in *P. amitabha* and *P. lujiatunensis*.

Lacrimal—Both lacrimal are preserved with the right one being better in its condition (Fig. 3B). As in other *Psittacosaurs* species, the lacrimal forms the anterior margin of the orbit and it is bounded by the premaxilla anteriorly, the prefrontal dorsally and the jugal ventrally with a relatively small trapezoid shape. It contributes to a small part of the anteroventral border of the orbit. Unlike IVPP V12617, the lacrimal foramen is located at the boundary between the lacrimal and the jugal, and it is unclear whether the feature is identical to the lacrimal foramen located along the margin of the orbit in other *Psittacosaurus* (Fig. 3B). This may be due to the detachment of the surface of the lacrimal, causing the lacrimal foramen to appear in a more ventrally.

Nasal—Both nasals are preserved (Fig. 3A, B). In dorsal view, it is a long bone, flanking its counterpart while running posterodorsally up the midline at its narrowest part where it contacts the rostral bone ventrally and expands slightly caudally, reaching the maximum width where it meets the prefrontal. Unlike *P. lujiatunensis*, at its narrowest part, the main body of the nasal is about as wide as the prefrontal. It terminates caudally with the frontal above the orbit.

Frontal—Both frontals are preserved. The frontal is flat and forms a broad central element of the skull roof, constituting the posterodorsal rim of the orbit (Fig. 4B). In dorsal view, both frontals are fused into a single unit along the midline and the interfrontal suture cannot be observed. The frontal contacts the nasal anteriorly, the prefrontal laterally, postorbital posterolaterally and parietal ~~caudally~~. The postorbital-frontal suture is absent in the right frontal; nevertheless, it is apparent in the left frontal and roughly L-shaped in dorsal view (Fig. 4B).

Prefrontal—Both prefrontals are preserved. It is narrow and meets the premaxillae and lacrimals ventrally, forming the anterodorsal corner of the orbit in left lateral view (Fig. 3A). In dorsal view, the prefrontal contacts the nasal medially and frontal posteriorly (Fig. 4B). The maximum

width of the prefrontal is nearly as wide as that of the nasal as commonly seen in the other *Psittacosaurus* species except for *P. lujiatunensis*, in which the nasal is wider than the prefrontal.

Parietal—Both parietals are preserved. The parietals form the ~~caudal~~most element of the central skull roof and fuse along the midline to form a low sagittal crest, as in other *Psittacosaurs* (Fig. 7). The parietal contacts the frontal and postorbital anteriorly, the laterosphenoid anteroventrally, the squamosal laterally and the supraoccipital ventrally. In dorsal view, the parietal frill has a horizontal posterior margin as in *P. meileyingensis* and IVPP V12617, while other species have a remarkable incised margin at the midline of the posterior end of parietals (Fig. 7). In *P. meileyingensis*, the lateral process of the parietal shows a distinctive slope angled posterodorsally (Sereno et al., 1988) whereas the parietal broadly contacts the squamosal in IVPP V12617 and ZMNH M12414.

Postorbital—Both postorbitals are preserved. The postorbital ~~forms~~ a three-pronged element ~~that contributes to~~ the skull roof process, the temporal bar and the jugal bar that separates the orbit from the infratemporal fenestra (Fig. 3A, B). The left preorbital is present in its original position, whereas the right postorbital is broken at the center of its triradiate bone and disarticulated from the squamosal (Fig. 8A, B). The jugal bar is thick and relatively long, compared with that of other *Psittacosaurus* species, overlapping the jugal and to form most of the ~~caudal~~ border of the orbit. The distal tip of left jugal bar is missing (Fig. 8A). The jugal bar is expanded as in *P. lujiatunensis* and *P. meileyingensis*, differing from the narrow tip in the other *Psittacosaurs* species. The squamosal process of the postorbital overlaps the postorbital process of the squamosal and forms the entire dorsal border of the infratemporal fenestra in lateral view. The skull roof process is the shortest compared to the temporal and jugal bars, as in most other *Psittacosaurus* species. The process extends along the margin of the orbit, contributing to form the posterodorsal rim of the orbit as in *P. meileyingensis* but others and IVPP V12617.

Squamosal—Both squamosals are preserved. They are nearly complete, except missing an anterior process on the right and posterior process on the left (Fig. 3A, B). The squamosal forms a tetraradiate bone as in other *Psittacosaurus* species and is located at the upper posterolateral corner of the skull. Anteriorly, it contacts the postorbital with which it forms a bar separating the upper and lower temporal fenestrae. The anterior ramus is short, while differing from others where the ramus reaches the anterior border of the supratemporal fenestra. While the short anterior ramus is also seen in *P. lujiatunensis* and *P. neimongoliensis*, it is even shorter, terminating almost at the middle of the supratemporal bar in IVPP V12617 and ZMNH M12414. The ventral ramus of both ZMNH M12414 and IVPP V12617 is relatively short and does not contact the quadratojugal as in *P. lujiatunensis*. The medial ramus juts medially to meet the parietal, with which it forms the posterior margin of the supratemporal fenestra. Further ventrally, the horizontal contact of the posterior process of the squamosal and the paroccipital process is ambiguous.

Jugal—Both jugals are present. The jugal forms a large element, consisting of infraorbital, infratemporal and dorsal rami, and the jugal horn (Fig. 3A, B). A gentle ridge runs posterolaterally from the tip of the dorsal ramus to the end of the jugal horn, dividing the lateral aspect of the jugal into anterior and posterior surfaces. As in *P. mongoliensis* and *P. lujiatunensis*, the anterior surface is much larger than the posterior one. Additionally, ZMNH M12414 exhibits relatively larger anterior proportion of the jugal than IVPP V12704 (holotype). The infraorbital ramus of the jugal is deeper dorsoventrally than the infratemporal ramus, leaving the ventral margin of the orbit slightly higher than the ventral margin of the infratemporal fenestra. The anterior surface of the jugal is smooth and flat as in *P. lujiatunensis*. The dorsal ramus of the jugal is overlapped by the ventral ramus of the postorbital, forming the bar between the orbit and infratemporal fenestra. The infraorbital ramus contributes to the ventral margin of the orbit and anteriorly contacts the lacrimal and maxilla. The infratemporal ramus bifurcates posteriorly as in other species of *Psittacosaurus* (although this feature is only seen in the right jugal in ZMNH M12414). A large posterodorsal process overlaps the quadratojugal, but never reaches the quadrate. In dorsal view, the surface area of the jugal is very large (Fig. 4B) and this feature is only found in ZMNH M12414 and IVPP V12617 among *Psittacosaurus*. The stout jugal horn protrudes laterally, forming the well-developed horn that is sub-triangular in dorsal view. The ventral surface of this horn is flat and level with ~~maxillary tooth row~~.

Quadratojugal—Both quadratojugals are preserved. In lateral view, the quadratojugal is divided into two parts by the contact between the jugal and quadrate. The posterior margin of the ventral part does not overlap the quadrate as in *P. lujiatunensis* (Fig. 3A, B). As in IVPP V12617 and ~~the~~ most other *Psittacosaurus* but unlike *P. lujiatunensis*, the dorsal process of the quadratojugal does not contact the ventral process of the squamosal, ~~not~~ contributing to the posterior rim of the infratemporal fenestra. In *P. meileyingensis*, *P. lujiatunensis* and *P. sinensis*, the ventral part supports a rugose prominence, while this surface is smooth in ZMNH M12414 and IVPP V12617. The ventral part of the quadratojugal extends forward to the level of the posterior margin of the infratemporal fenestra as in *P. sinensis*, *P. neimongoliensis P. mongoliensis*, *P. meileyingensis* and *P. lujiatunensis* (Zhou et al., 2006).

Quadrate—Both quadrates are preserved. As in other *Psittacosaurs*, the shaft is rotated anterolaterally and the condyle expands transversely into a broad articular surface (Fig. 3A, B and Fig. 4A). The shaft is slightly arched along its posterior margin as in *P. mongoliensis*, *P. neimongoliensis* and IVPP V12617, while unlike the strongly concave condition in *P. sinensis*, *P. meileyingensis* and *P. lujiatunensis*. The quadrate shaft and postorbital jugal bar are oriented at an angle of about 45 degrees in lateral view, a feature only seen in ZMNH M12414 and IVPP V12617. Dorsal to the condyle, the quadrate is not exposed in lateral view just posterior to the quadratojugal-quadrate suture, as in *P. mongoliensis*. The broad, thin pterygoid wing of the quadrate is typical in its development and completes the medial wall of the infratemporal fossa

as far anteriorly as the postorbital bar. The pterygoid wing of the quadrate and its complement on the pterygoid form a curtain that obscures the ventral portions of the braincase in lateral view, including most of the cranial nerve foramina.

Palatal bones—The palate is well exposed in ventral view (Fig. 4C). The maxilla, rostral and premaxilla forms a gentle vault and the central foramen is bordered by the same three elements. Long fused vomers are present along the midline and form a long and narrow bar in the roof of the buccal cavity. The internal naris opens to the anterior edge of maxillary tooth row in contrast to that of other species.

The pterygoid, vomer and palatine are fused and present as a complex (Fig. 4C). The pterygoid is in contact with the maxilla anteriorly and with the quadrate and basisphenoid posteriorly. The pterygoid comprises the ~~caudal~~ half of the palate and ventral processes of the mandibular rami. The pterygoid mandibular ramus is one of the diagnostic characters of the genus *Psittacosaurs*, where the ventral tip is elongated to form the mandibular process (Sereno, 2010). In ZMNH M12414, the mandibular process is short and mediolaterally broad, which can be seen from the lateral and ventral views (Fig. 3A, B and Fig. 4C). The vomer is rod-shaped, contacting the premaxilla posteriorly. Y-shaped quadrate ramus is thin and broadly meet the pterygoid ramus of the quadrate posterolaterally. Both ectopterygoid and parasphenoid are not ~~visible~~ due to ~~the~~ fusion.

Braincase—In ~~caudal~~ view, the foramen magnum is bordered by supraoccipital dorsally, the exoccipitals laterally and the basioccipital ventrally (Fig. 9). Whereas the shape of the supraoccipital of other *Psittacosaurus* species is diamond-shaped, the supraoccipital is dorsoventrally deep, sub-triangular in shape in ZMNH M12414 and IVPP V12617. It contributes only to the mid-portion of the dorsal border of the foramen magnum and is covered by parietal dorsally. The exooccipital and opisthotic are fused to form the parooccipital process, extending posterolaterally. The trigeminal foramen (CN V) is visible on both sides of laterosphenoids. It measures about 5 mm in a diameter and the trigeminal ganglion is housed in the trigeminal fossa. The exoccipitals borders the foramen magnum laterally, in which the distal ends of parocippital processes are missing. The basioccipital borders the foramen magnum ventrally and a well-preserved occipital condyle is directed ~~caudally~~ and slightly downward. The basal tubera have a subcircular and subvertical posterior surface, with a round, rough ventral margin that is slightly ventral to the occipital condyle.

Mandible—The mandible is composed of the following elements: predentary, left and right dentaries, left and right surangulars, left and right angulars, left and right splenials, left and right coronoids, left and right prearticulars and left and right articulars (Fig. 10A, B and C). In lateral view, the mandible is dorsoventrally deep and strongly bowed dorsally along its ventral margin, with predentary and angular forming the anterior and posterior ends of the arc respectively (Fig. 10A). The mandible is relatively deep as in *P. sinensis* and IVPP V12617 and in contrast to the

shallower mandible in *P. lujiatunensis*. The anterior margin of the predentary is ~~round and~~ U-shaped in ventral view (Fig. 11A). The ventral border of the dentary is sinuous and possesses a prominent dentary flange at its posteroventral corner, as in *P. major*, although this feature is ~~present only in~~ the right lateral surface (Fig. 10A). The presence of external mandibular fenestra is unclear. The angular is well exposed laterally with a sheet-like process that covers around the ventral margin of the mandible. In medial view, the angular is covered by the splenial anteriorly and the prearticular dorsally (Fig. 10B and Fig. 11B). The surangular forms the posterodorsal portion of the lower jaw in lateral view. It contacts the dentary anteriorly and forms the caudal half of the coronoid process. Unlike IVPP V12617, the position of coronoid process is close to main axis of dentary and posterior to the tooth row as in *P. major* (CAGS-ID-VG-004). The surangular extends posteroventrally to the end of the lower jaw, covering the angular underneath. The articular is mediolaterally broad, but dorsoventrally thin where it articulates with the robust quadrate.

Phylogenetic analysis

A phylogenetic analysis was conducted in T.N.T. (Version 1.5; Goloboff, Farris and Nixon, 2015), using a character matrix from Napoli et al. (2019) with in total of 380 characters and 78 taxa. The present study differs from the previous analysis (Napoli et al., 2019) in excluding two composite specimens (*P. mongoliensis* and *P. lujiatunensis*) and adding ZMNH M12414 and IVPP V12617. The analysis was conducted with maximum trees set to 99,999 and zero-length branches collapsed, using a heuristic search with 1,000 tree bisection and reconnection (TBR) replicates and holding 100 trees per replication. Bremer supports were then calculated.

The analysis produced 6,672 most parsimonious trees (MPTs) of 1,288 steps, with a consistency index (CI) of 0.332 and retention index (RI) of 0.700 (Fig. 12). In the strict consensus topology, *P. houi* (ZMNH M12414 and IVPP V12617) was recovered as a species more derived than *P. lujiatunensis*, *P. gobiensis*, *P. amitabha* and *P. mongoliensis*. Additionally, ZMNH M12414 and IVPP V12617 form an independent clade separate from the clade that includes *P. lujiatunensis* (Fig. 13).

Discussion

It should be noted that in the following discussion, reference to IVPP V12507, a holotypic specimen of *Psittacosaurus* (previously *Hongshanosaurus*) *houi*, is avoided. This is because the specimen represents a juvenile, which makes it difficult to directly compare it to other *Psittacosaurus* species that have been described based on mature specimens. For this reason, the present discussion is made mainly on ZMNH M12414 and IVPP V12617 to taxonomically compare and contrast *P. houi* against other *Psittacosaurus* species.

Are ZMNH M12414 and IVPP V12617 assignable to the same species?

Sereno (2010) suggests that the presence of the lacrimal foramen is one of the diagnostic characters for the genus *Psittacosaurus*. On the other hand, You and Xu (2005) notes that IVPP V12617 has no openings or canals in the lacrimal. A foramen is found in the lacrimal of ZMNH M12414, and its position is slightly offset from the typical lacrimal foramina described previously in the species of *Psittacosaurus* (see description), leaving its identify a little ambiguous. Nevertheless, Napoli et al. (2019) suggests that the presence or absence of the lacrimal foramen, a pathway innervating up to the rostrum, varies and may simply be an artefact created by the detachment of thin lacrimal bone fragments. These observations indicate that the presence or absence of the lacrimal foramen may be a preservational artefact and should not be considered an apomorphy. Therefore, while the true presence or absence of a lacrimal foramen in ZMNH M12414 and IVPP V12617 remains unclear, such observation does not lead to a conclusion that these specimens belong to separate species.

Other morphological features of ZMNH M12414 that are absent in IVPP V12617 include a skull roof process of the postorbital forming the posterodorsal rim of the orbit, and mandible coronoid process positioned close to the main axis of the dentary. Still, these specimens share multiple characters that suggest they belong to the same species. For example, ZMNH M12414 and IVPP V12617 have narrower prefrontal and premaxilla contacts than other *Psittacosaurus*. In addition, the parietal shape is parallel to the frill in dorsal view, and the ventral ramus of the squamosal is not in contact with the dorsal process of the quadratojugal. Furthermore, the absence of rugosity in the quadratojugal and the dorsoventrally deep mandibles are shared between the specimens. Considering a greater number of similarities than differences between the specimens, as well as the present phylogenetic hypothesis that finds them within their own clade and the shared locality within the Lujiatun Unit of the Yixian Formation, it is concluded that ZMNH M12414 and IVPP V12617 are assignable to the same species ~~of~~ Psittacosauridae.

Is *Hongshanosaurus* a junior synonym of *Psittacosaurus*?

The synonymy of the genus "*Hongshanosaurus*" with *Psittacosaurus* has been raised in previous studies (Sereno, 2010; Hedrick and Dodson, 2013). While the present study supports this synonymy, it does so on the basis of observations different from those made in the previous studies.

The genus "*Hongshanosaurs*" is originally diagnosed by its large proportion of preorbital length (> 40 %), the elliptical orbit, external naris and laterotemporal fenestra oriented postero-dorsally (You and Xu 2005). Sereno (2010) defines the short preorbital length (= 40 % or less, measured from the anterior end of the rostrum to the anterior margin of the orbit) as a diagnostic feature of *Psittacosaurus*. Sereno (2010) further argues that the greater proportion of the preorbital length, as well as other diagnostic features found in IVPP V12617 (~~paratype~~ specimen of *H. houi*) may come from the postmortem deformation of the skull proportions, concluding that the *Hongshanosaurus* is a junior synonym of *Psittacosaurus*. In addition, Hedrick and Dodson (2013) performs three-dimensional geometric morphometric analyses and supports the conclusion of Sereno (2010) based on the observation that "*Hongshanosaurus*" forms a morphological cluster with *P. lujiautnensis* and *P. major*. The same study posits that *Hongshanosaurus* exhibits a larger proportion of preorbital length due to the displaced vomer and dorsoventral compressive deformation. Following these studies, more recent analyses on

Psittacosauridae regard IVPP V12617 as a species of *Psittacosaurus* (*P. lujiatunensis* in particular) (Erickson et al. 2009; Zhao et al. 2013; Han et al. 2016; Taylor et al. 2017; Han et al. 2018; Bullar et al. 2019; Zhao et al. 2019; Landi et al. 2021). While the present study concurs with the previous hypothesis that "*Hongshanosaurus*" is to be synonymized with *Psittacosaurus*, its reasoning needs to be revisited.

A recently described psittacosaurid *P. amitabha* exhibits the preorbital length proportion apparently larger than 40 % without significant deformation (Napoli et al. 2019). The same study also criticizes the methodology in Hedrick and Dodson (2013) in that it does not take the intraspecific variation into account, and it includes both adults and juveniles in the same data set, possibly leaving the synonymy of "*Hongshanosaurus*" with *Psittacosaurus* inconclusive. It is also notable, as demonstrated by Sereno (2010), that the proportion of preorbital lengths ontogenetically increases (30 to 40 %), which is consistent with the juvenile-to-adult variation in *P. lujiatunensis* (Fig. 14). Therefore, a species of *Psittacosaurus* could exhibit the preorbital length proportion > 40 % and this proportion is likely subject to the ontogenetic change.

According to Hedrick and Dodson (2013), the vomer of IVPP V12617 is restored with a plaster, suggesting that the specimen has undergone dorsoventral crushing, whereas ZMNH M12414 possesses a complete set of fused vomers, indicating negligible (if any) deformation. Thus, unlike IVPP V12617, in which the postmortem deformation is in doubt, the preserved preorbital length proportion in ZMNH M12414 is original and > 40 %. Furthermore, ZMNH M12414 and IVPP V12617 are considered as matured skulls based on partial fusion of the skull elements and their sizes, indicating that the preorbital length proportion only increases and would have never gone less than 40 % through further maturity; this feature is also present in the holotypic specimen of *P. amitabha* (Napoli et al. 2019). Because more than one examples of mature psittacosaurid specimens have been found to exhibit the preorbital length proportion > 40 % and that this proportion is subject to the ontogenetic change, it is recommended the feature be excluded from the diagnostic characters of any psittacosaurid genera. This would leave the unique features of "*Hongshanosaurus*" as the following, the elliptical orbit, external naris and laterotemporal fenestra oriented postero-dorsally. On the other hand, other numerous features are shared between ZMNH M12414 and IVPP V12617 and previously described *Psittacosaurus* species. Therefore, this study concludes that "*Hongshanosaurus*" is a junior synonym of *Psittacosaurus*, and part of the unique features originally coined for the former genus are herein partly adapted as those for *P. houi*.

Is *P. houi* a separate species from *P. lujiatunensis*?

Sereno (2010) and Hedrick and Dodson (2013) have synonymized *Psittacosaurus* (*Hongshanosaurus*) *houi* with *P. lujiatunensis*, a psittacosaurid also known from the Lujiatun Unit of the Yixian Formation. Here, we present a series of evidence that leads to a conclusion that *P. houi* is distinguished from *P. lujiatunensis*. As noted, ZMNH M12414 retains a complete set of fused vomers, indicating minor (if any) postmortem deformation of the cranium. Based on ZMNH M12414 and IVPP V12617, *P. houi* lacks the diagnostic features exhibited in the holotypic skull of *P. lujiatunensis* (ZMNH M8137), which include short prefrontal width less than 50% of that of the nasal, quadratojugal and squamosal contact along anterior margin of quadrate shaft, and jugal and quadrate contact situated posteroventral to the laterotemporal fenestra (Sereno 2010).

Additionally, the following features seen in *P. houi* are absent in *P. lujiatunensis*: the long

rostrum formed by the prefrontal, ~~nasal sloping anteroventrally~~, the narrow prefrontal-premaxilla contact, the parallel caudal margin of the parietal, the quadrate shaft slightly arched along its posterior margin, ~~subtriangular-shaped supraoccipital~~ and ~~dorsoventrally deep mandible~~. The conclusion that *P. houi* is separate from *P. lujiatunensis* is further supported by the present phylogenetic analysis, where *P. lujiatunensis* does not form a clade with *P. houi* and is placed relatively far from it (Fig. 13).

Conclusions

Psittacosaurus is the most specious genus among Dinosauria, comprising to date ~~12~~ species described widely from Russia, Mongolia and China. The validity of these species and taxonomic diversity within the genus have received much attention to understand the role of this herbivorous dinosaur in the ecosystem of Asia during the Early Cretaceous.

In the present study, a new specimen of a psittacosaurid skull, ZMNH M12414, is described, leading to a taxonomic re-assessment of the previously coined species "*Hongshanosaurus*" *houi*. Anatomical observations and phylogenetic analyses including ZMNH M12414 and other previously described "*Hongshanosaurus*" specimens suggest the following; (1) a large preorbital region previously coined as a diagnostic feature of *Psittacosaurus* should be disregarded, (2) "*Hongshanosaurus*" is to be synonymized with *Psittacosaurus* as previously suggested (Sereno, 2010), and (3) *Psittacosaurus houi* is a valid species, being distinguished from *P. lujiatunensis* (*contra* Sereno, 2010).

The present study demonstrates the importance of the CT techniques to revisit the anatomy and taxonomy of previously described dinosaur taxon. As the genus *Psittacosaurus* remains the most species-rich dinosaur genera that has over 100 years of research history (Osborn, 1923), its taxonomy and morphological diversity should be re-assessed through detailed evaluation of ontogenetic, intra-specific, and inter-specific variations to understand these fascinating small herbivorous dinosaurs that flourished in the Early Cretaceous of Asia.

Acknowledgements

Yoichi Azuma (Fukui Prefectural University) and Yoshikazu Noda (Fukui Prefectural Dinosaur Museum) provided AI with constructive comments and support during the specimen observation. Authors are also grateful to Kazunori Miyata, Toru Sekiya, and Yuta Tsukiji (Fukui Prefectural Dinosaur Museum), to Hiroshi Nishi, Soki Hattori, Yasuyo Deyama, Shota Obuse, Naoto Horiguchi, Rina Sakagami, Mizuho Sano, Kanae Jinnouchi, Yuya Asakura, Kazuki Harigai (Fukui Prefectural University), and to Nozomu Oyama (Museum National d'Histoire Naturelle) for their constructive comments.

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Figure 1

Figure 1: Photographs and three-dimensional rendering of ZMNH M12414.

A-C, photographs in left lateral (A), dorsal (B), and caudal (C) views; D-F, three-dimensional rendering in left lateral (D), dorsal (E), and caudal (F) views. Scale bar equals 50 mm.

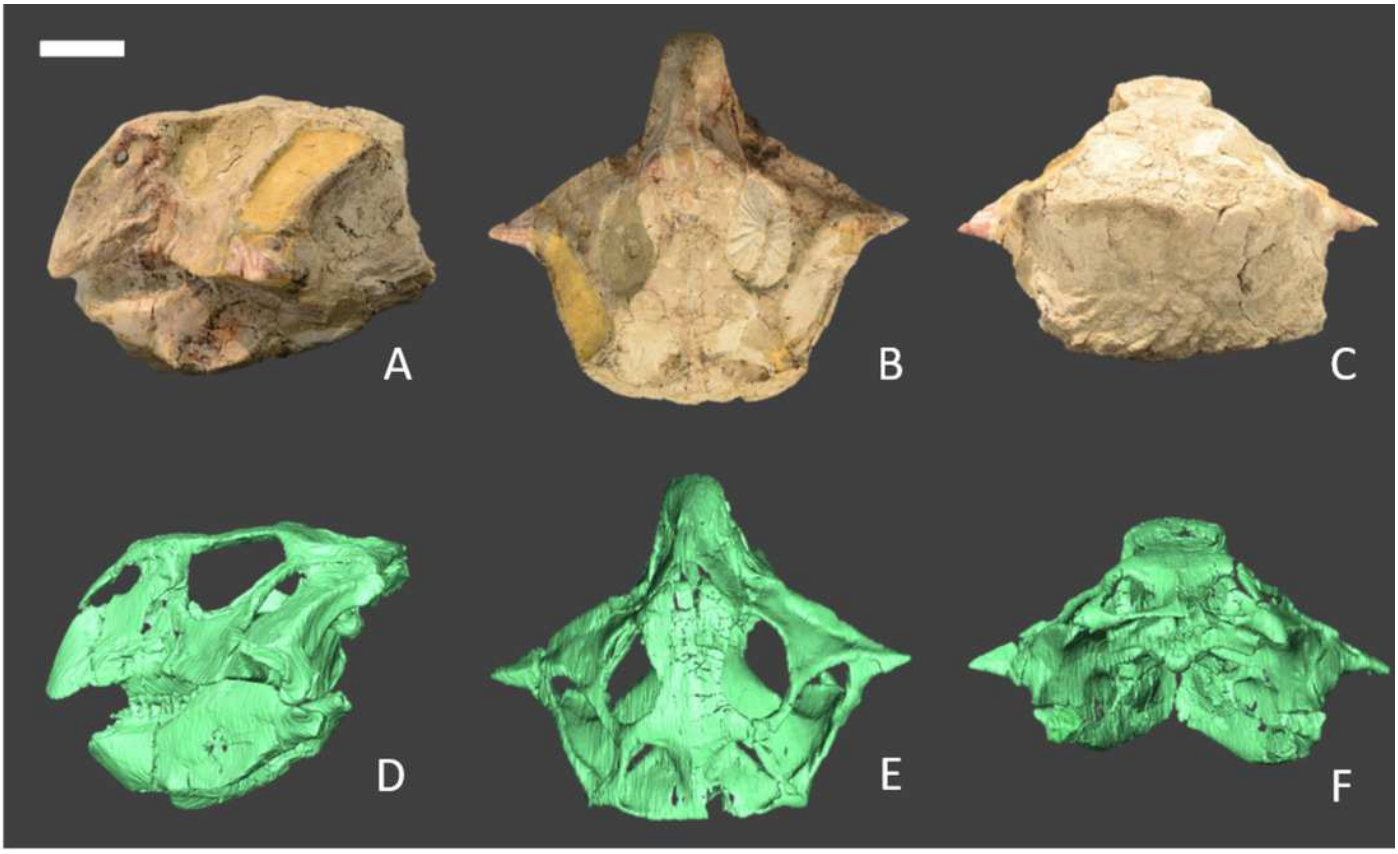

Figure 2

Figure 2: Measurements of the cranium.

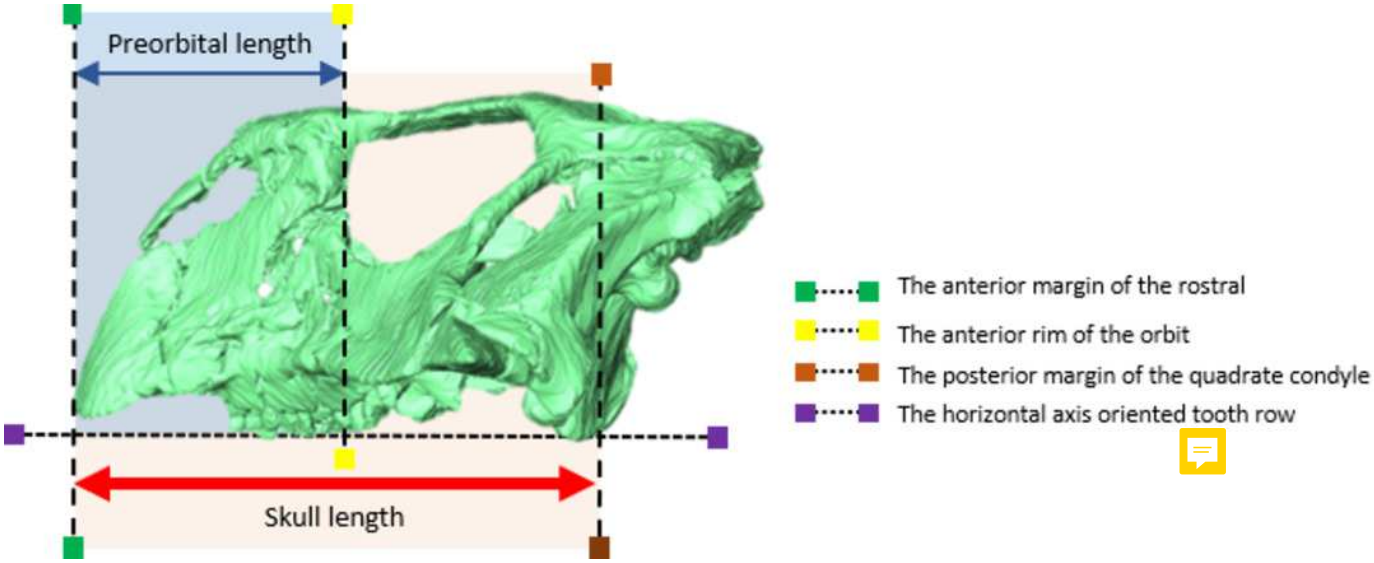

Figure 3

Figure 3: Three dimensionally rendered cranium of ZMNH M12414 with individual skull elements colored.

ZMNH M12414 in right lateral (A), left lateral (B), and anterior (C) views. Abbreviations: r, rostral; pm, premaxilla; n, nasal; prf, prefrontal; l, lacrimal; lf, lacrimal foramen; f, frontal; po, postorbital; popr, parooccipital process; p, parietal; bs, basisphenoid; sq, squamosal; q, quadrate; qj, quadratojugal; j, jugal; m, maxilla; ls, laterosphenoid. Scale bar equals 50 mm.

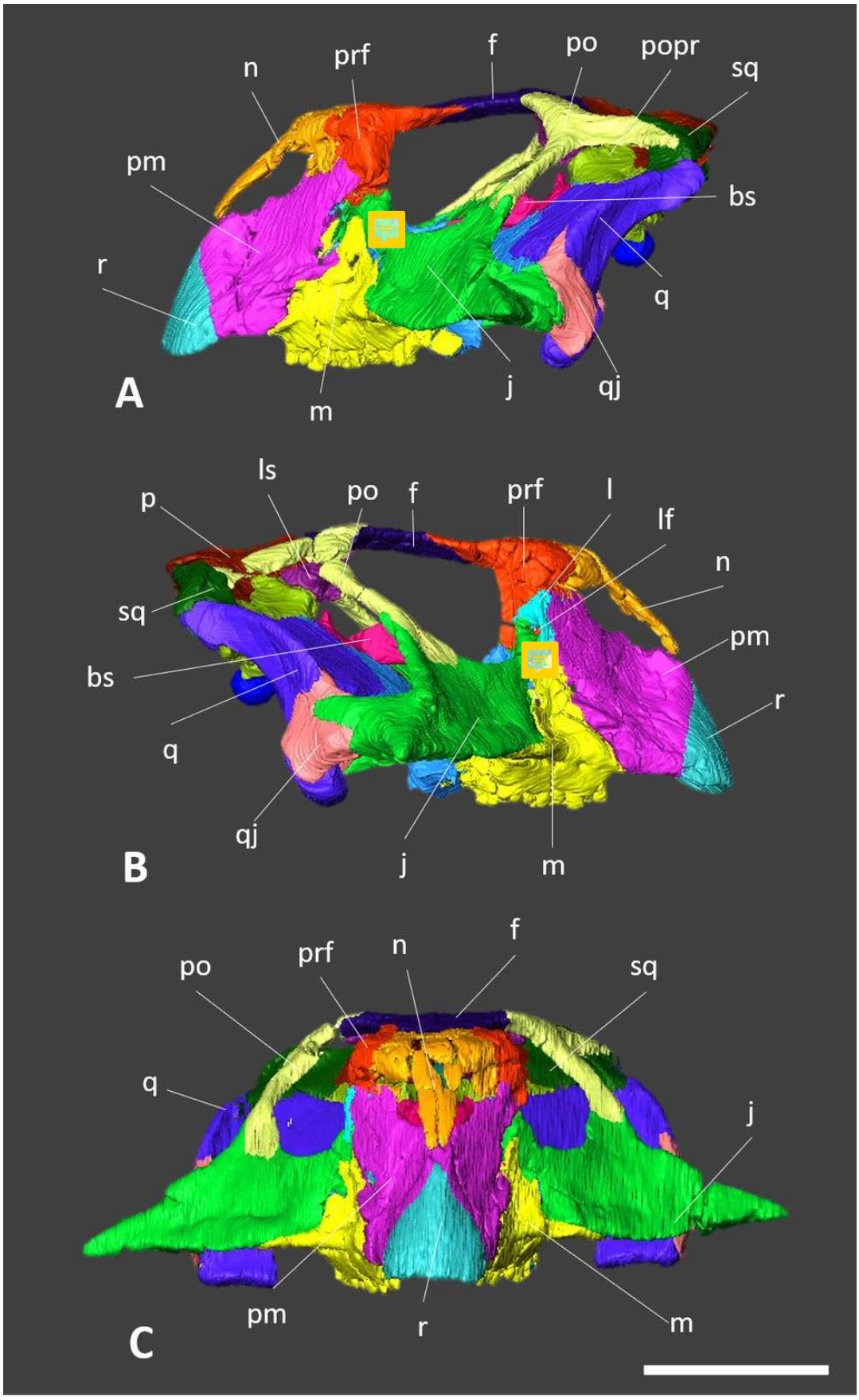
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Figure 4

Figure 4: Three dimensionally rendered cranium of ZMNH M12414 with individual skull elements colored.

ZMNH M12414 in caudal (A), dorsal (B), and ventral (C) views. Abbreviations: r, rostral; pm, premaxilla; prf, prefrontal; n, nasal; f, frontal; popr, parooccipital process; p, parietal; sq, squamosal; q, quadrate; qj, quadratojugal; p, parietal; j, jugal; m, maxilla; pt, pterygoid; bt, basal tubera; oc, occipital condyle; bs, basisphenoid; so, supraoccipital; v, vomer, Scale bar equals 50 mm.

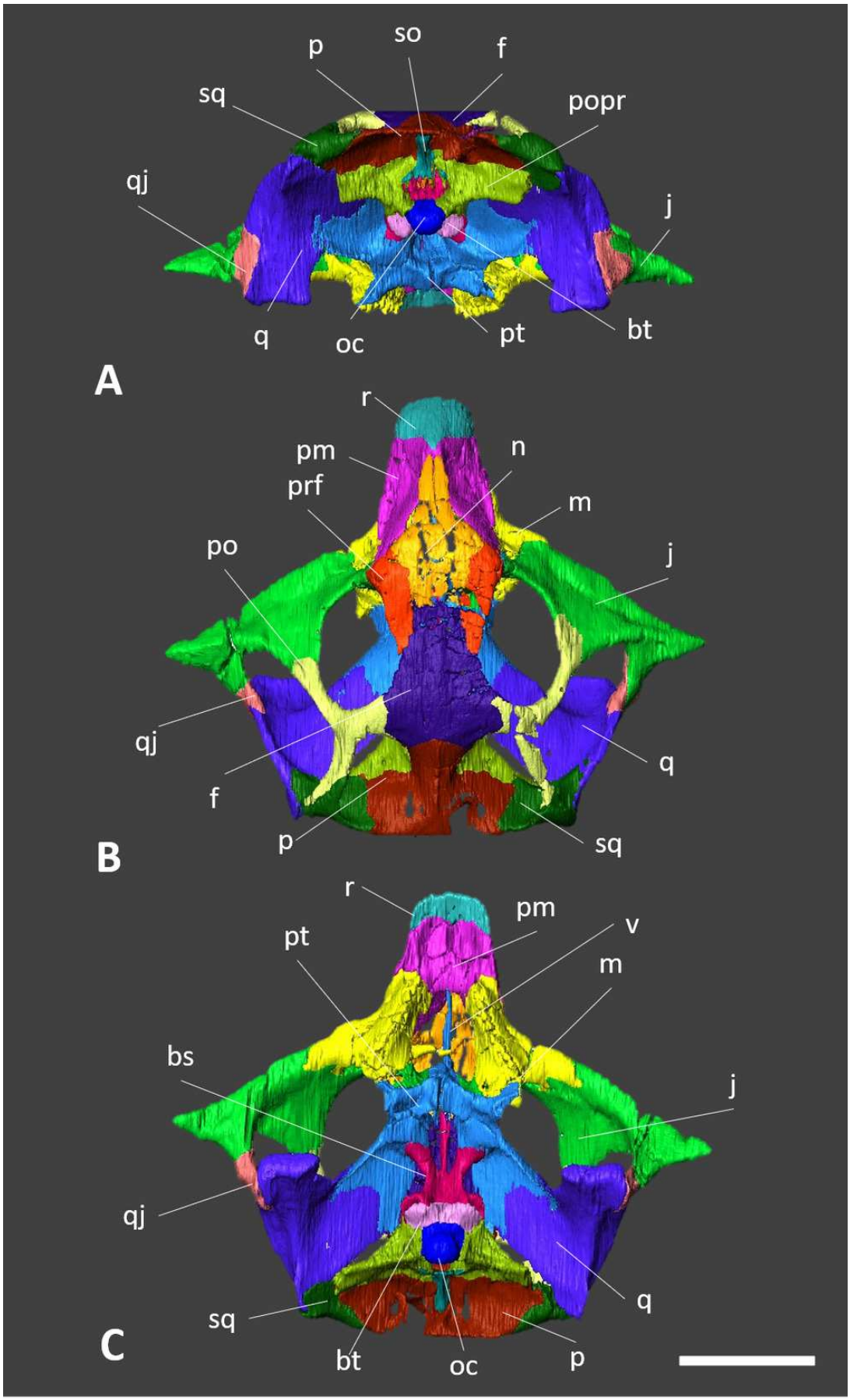
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Figure 5

Figure 5: Three dimensionally rendered rostrals and premaxillae of ZMNH M12414.

A, left rostral and premaxilla in left lateral view; B, right rostral and premaxilla right lateral view. White dotted lines indicate the missing part of the premaxillae. Abbreviations: n, nasal; r, rostral; pm, premaxilla; m, maxilla; dc, a developed crest; g, a groove, Scale bar equals 30 mm.

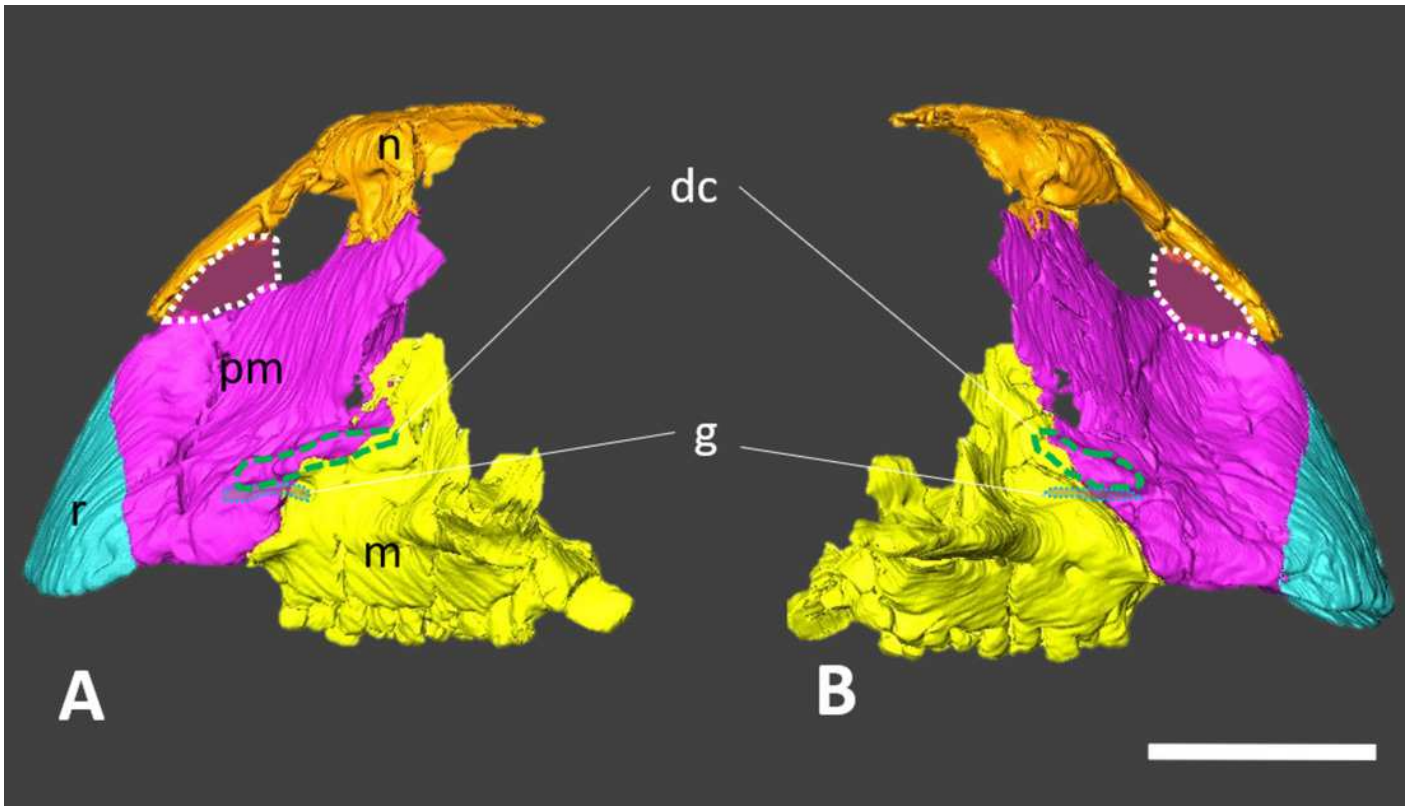

Figure 6

Figure 6: Three dimensionally rendered maxillae of ZMNH M12414.

A, left maxilla in left lateral view; B, right maxilla in right lateral view. Abbreviations: mfo, maxillary fossa. Scale bar equals 30 mm.

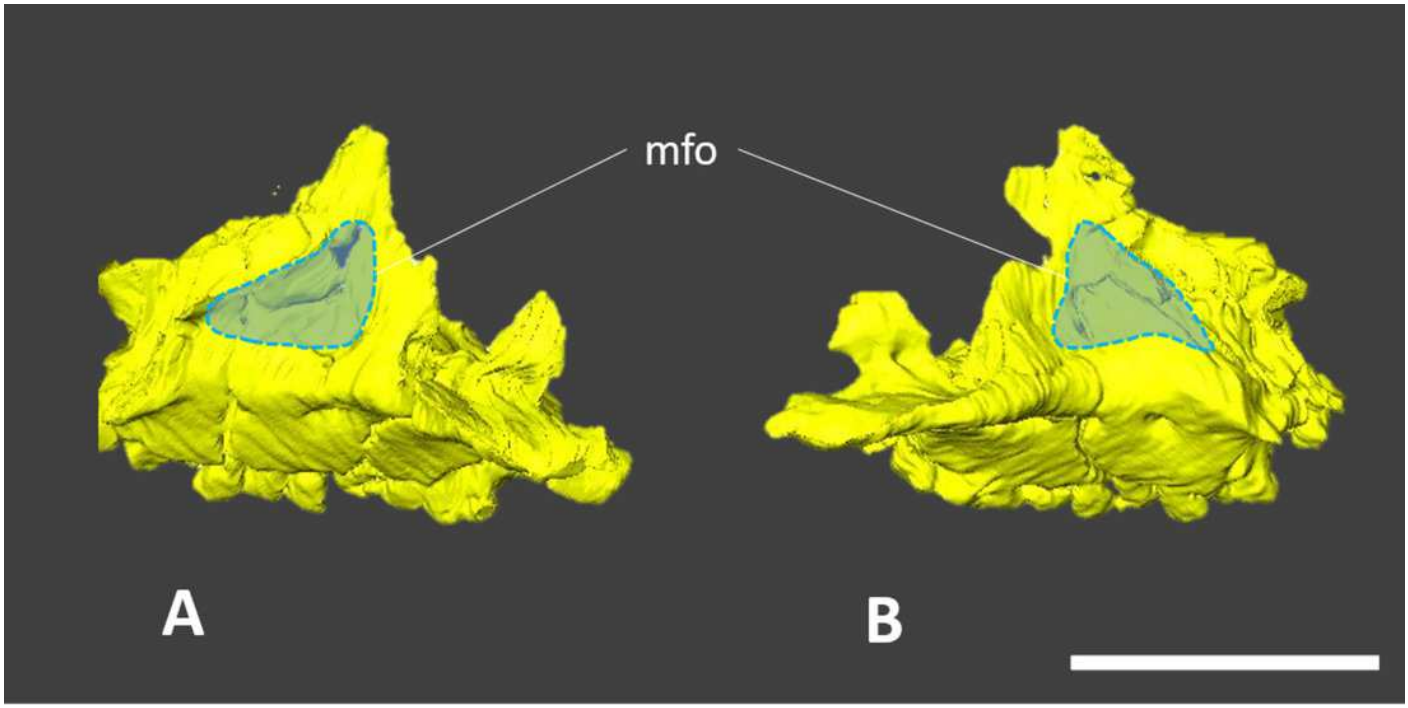

Figure 7

Figure 7: Three dimensionally rendered parietals of ZMNH M12414 in Dorsal view.

Yellow dotted line indicates the position of sagittal crest and white dotted line represents a horizontal posterior margin of parietal (i.e. posterior margin of the frill). Abbreviations: sgc, sagittal crest. Scale bar equals 30 mm.

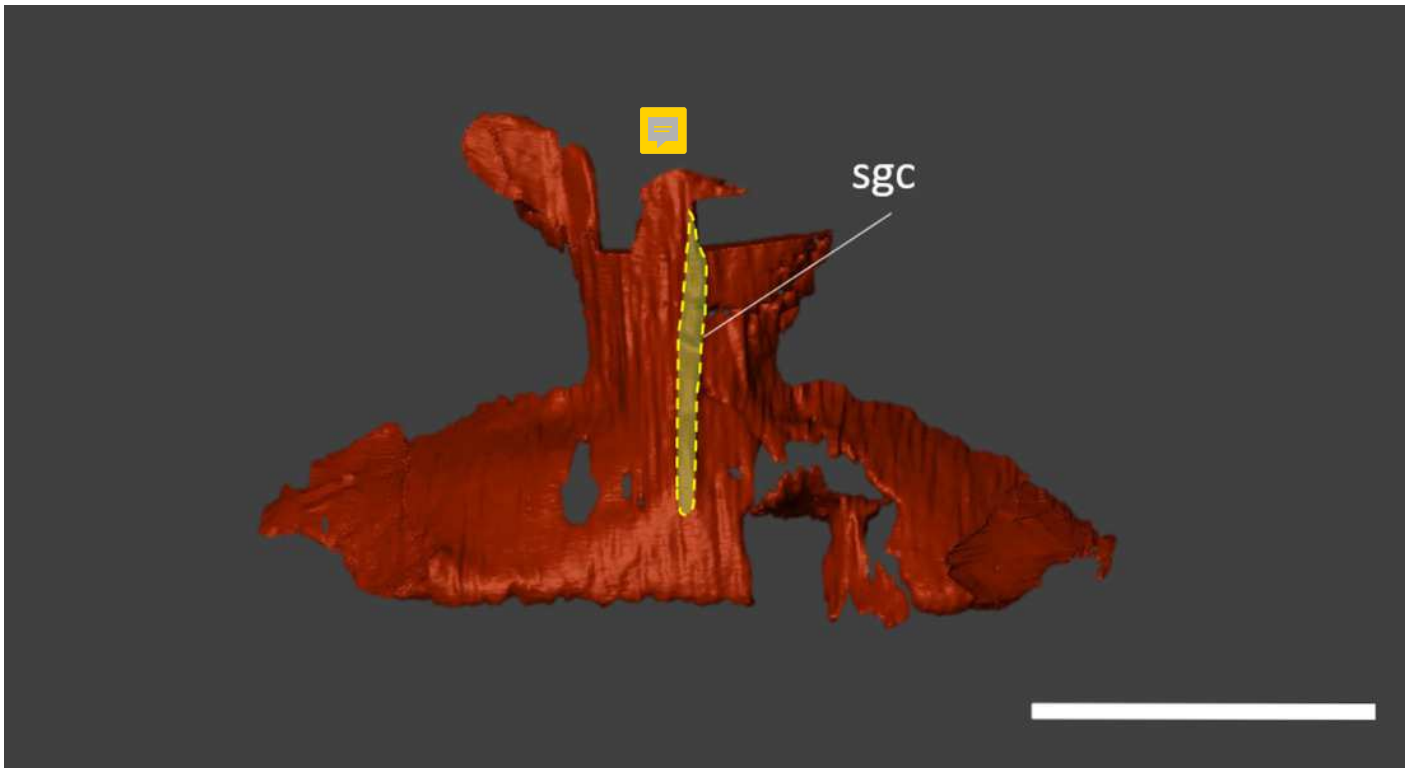

Figure 8

Figure 8: Three dimensionally rendered ~~parietals~~ of ZMNH M12414.

A, left postorbital in left lateral view; B, right postorbital in right lateral view. White dotted line indicates the missing part. Abbreviations: srp, roof process; tb, temporal bar; jb, jugal bar. Scale bar equals 30 mm.

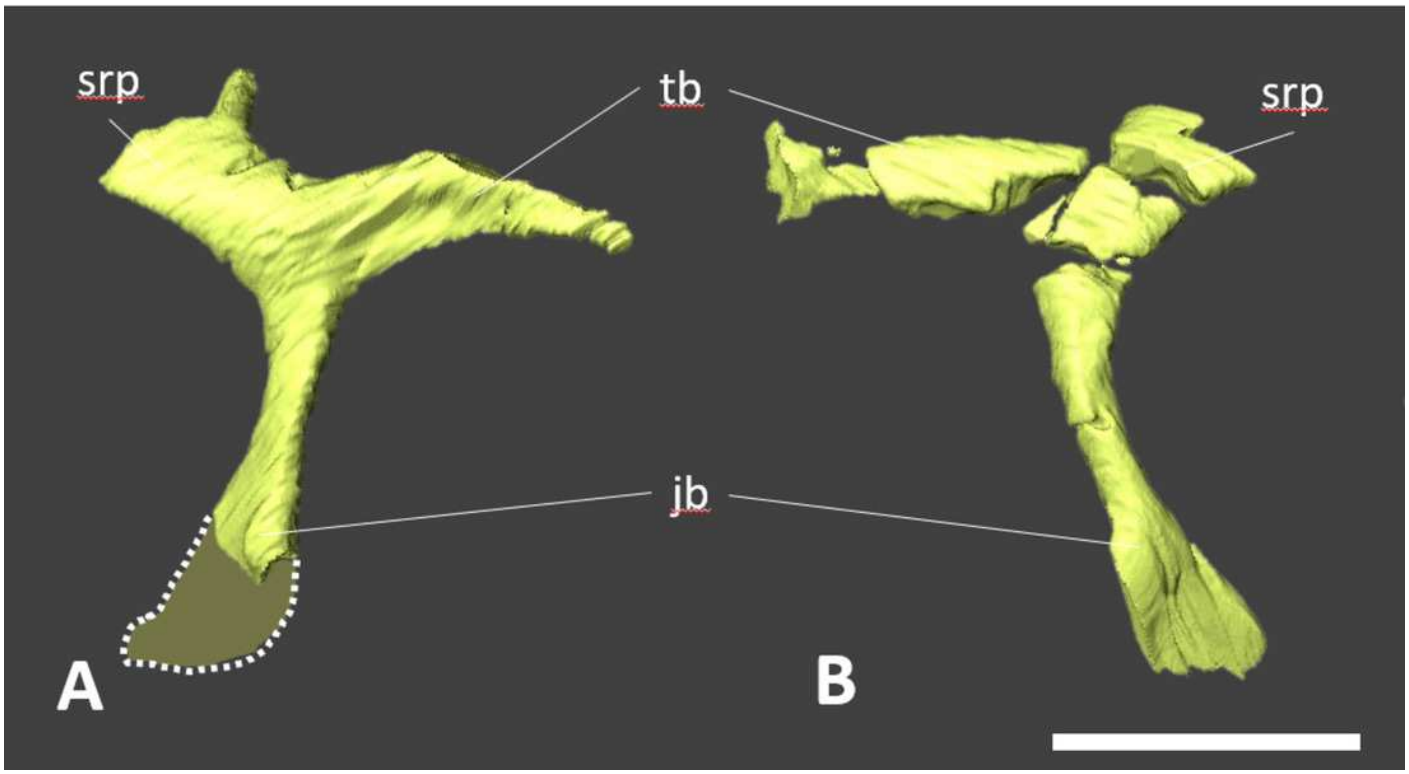

Figure 9

Figure 9: Three dimensionally rendered braincase of ZMNH M12414 in caudal view.

Abbreviations: so, supra occipital; p, parietal; popr, paroccipital process; oc, occipital condyle; bt, basal tubera. Scale bar equals 30 mm.

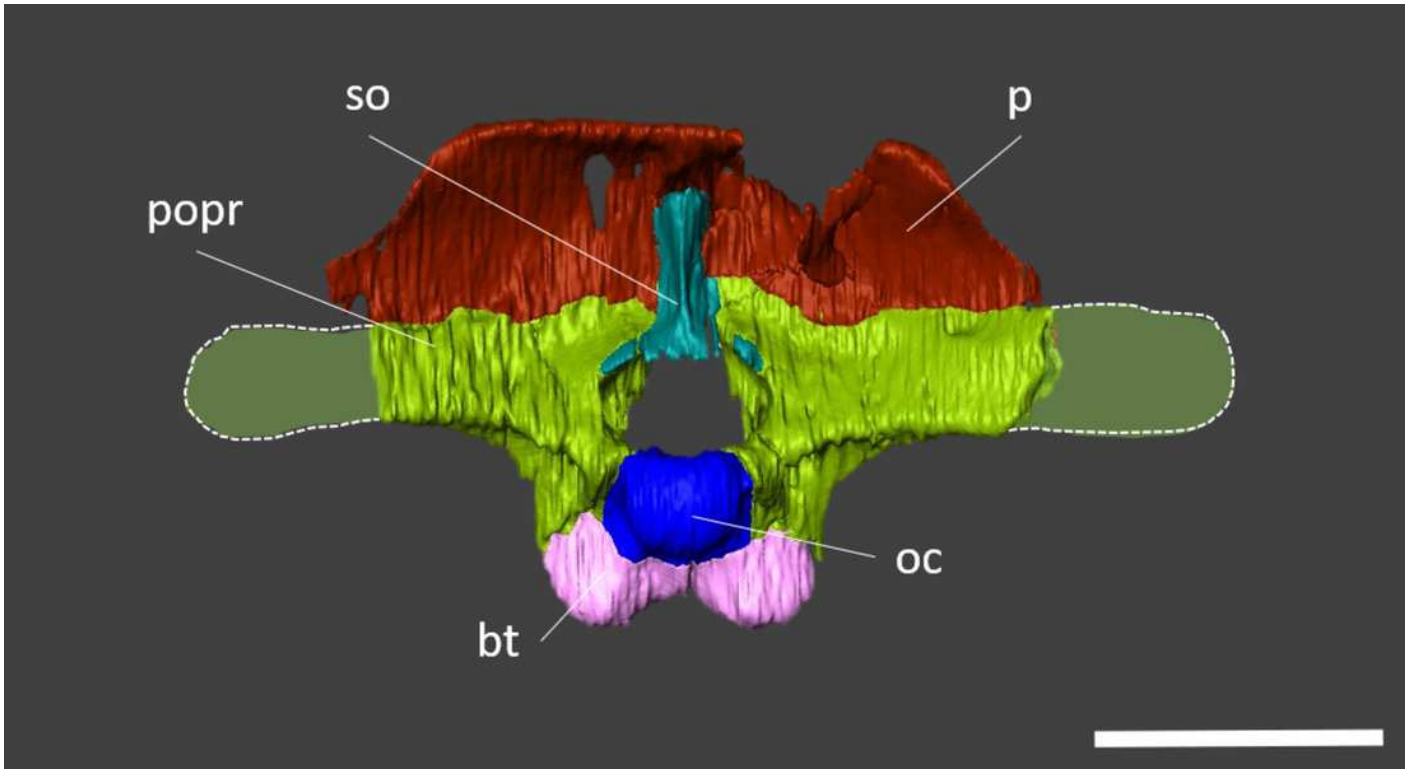

Figure 10

Figure 10: Three dimensionally rendered mandible of ZMNH M12414.

A, right lateral view; B, right medial view; C, dorsal view. Abbreviations: prd, predentary; d, dentary; sa, surangular; a, angular; c, coronoid; spl, splenial; ar, articular; pra, prearticular Scale bar equals 50 mm.

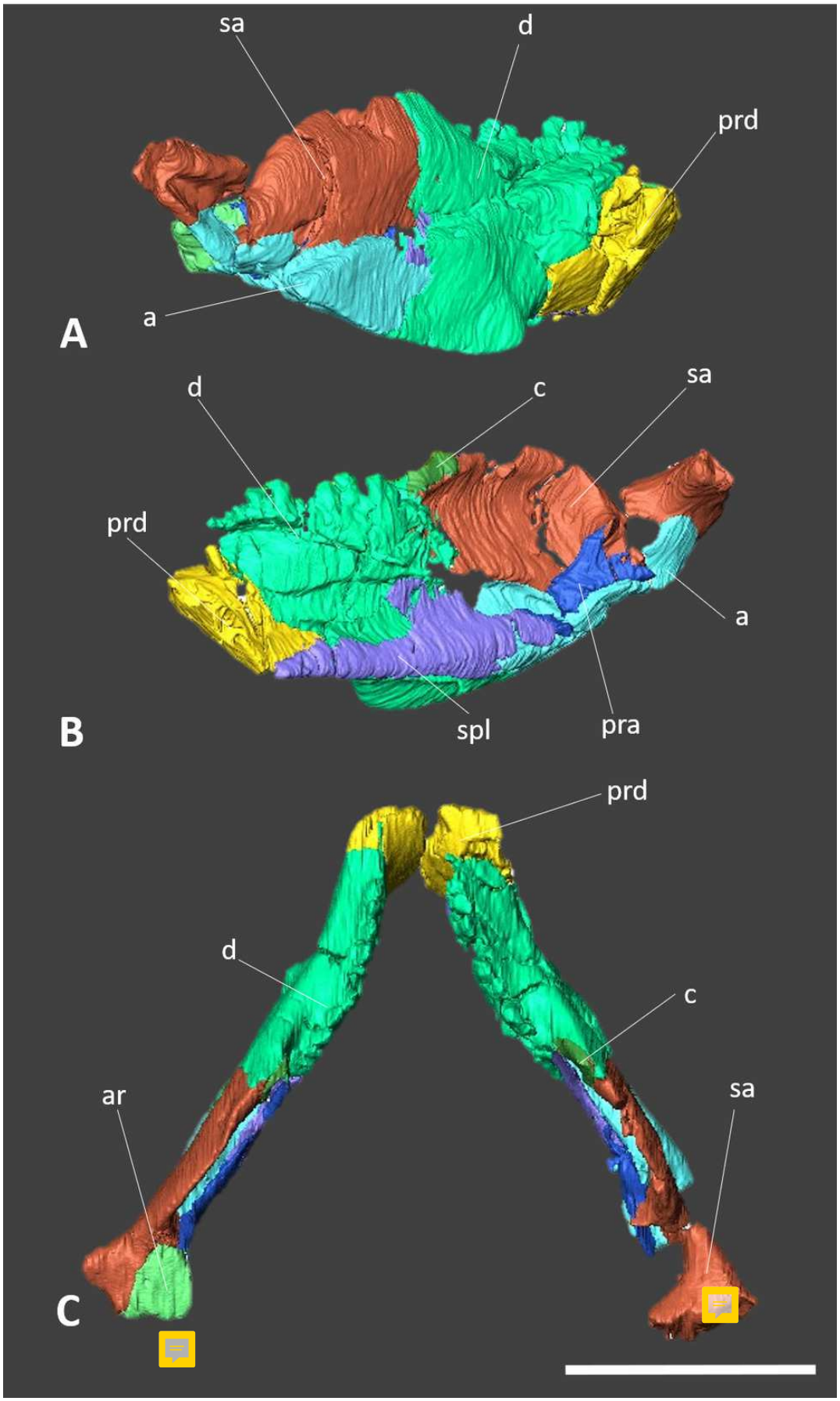
sa
d
prd
a
A
d
c
sa
prd
a
spl
pra
B
prd
d
c
ar
sa
C

Figure 11

Figure 11: Three dimensionally rendered mandible of ZMNH M12414.

A, ventral view; B, caudal view. Abbreviations: prd, predentary; d, dentary; sa, surangular; a, angular; c, coronoid; spl, splenial; ar, articular; pra, prearticular. Scale bar equals 50 mm.

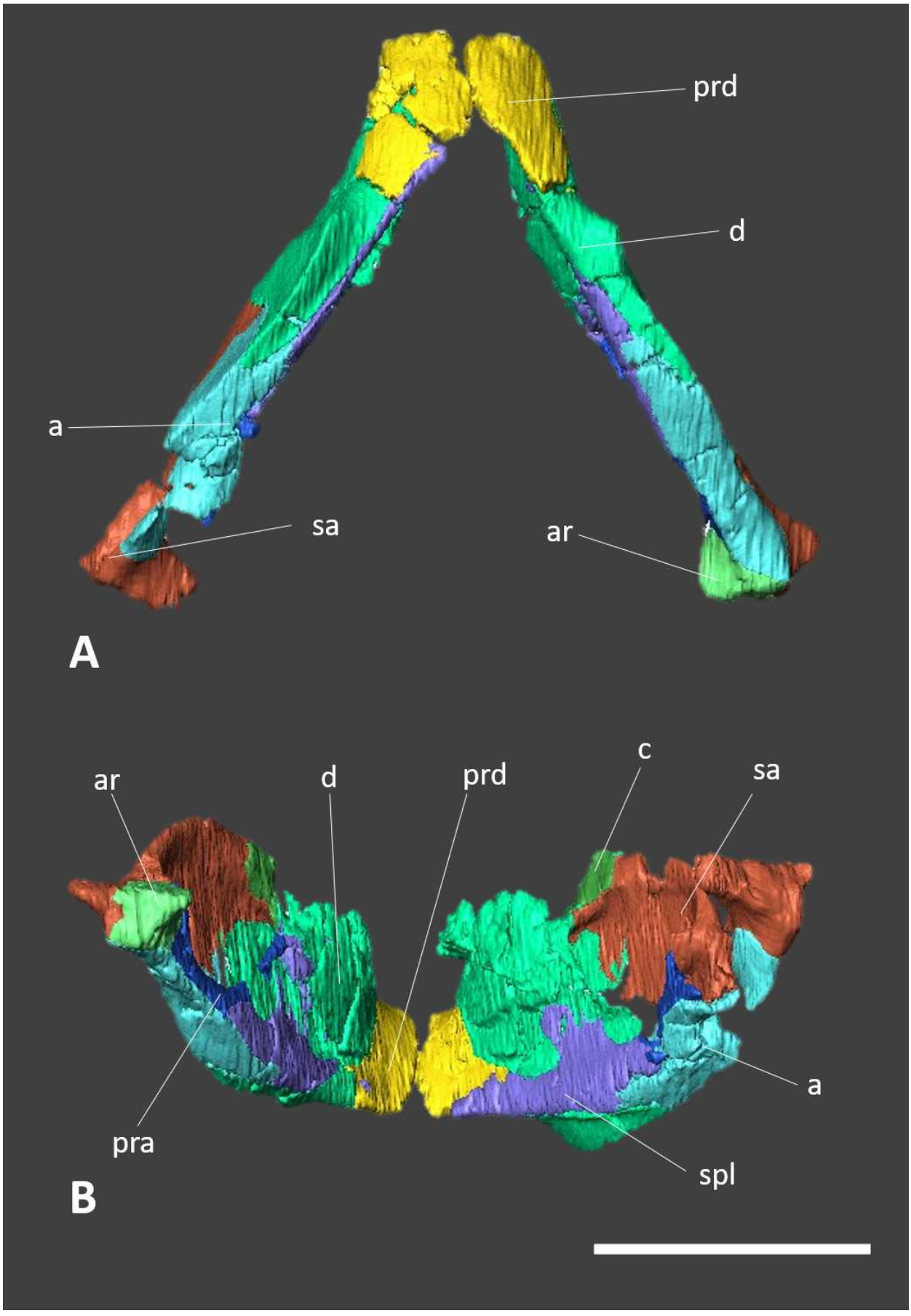
prd
d
a
sa
ar
A
ar
d
prd
c
sa
a
pra
spl
B

Figure 12

Figure 12: Strict consensus of 6,672 most parsimonious trees (MPTs) based on a data matrix of ~~77~~ taxa and 380 characters.

A value beneath each nodes indicates Bremer support (Bremer support = 1 if not shown).

Abbreviations: He, Heterodontosauridae; Th, Thyreophora; Pachy, Pachycephalosauria; Psi, *Psittacosaurus*.

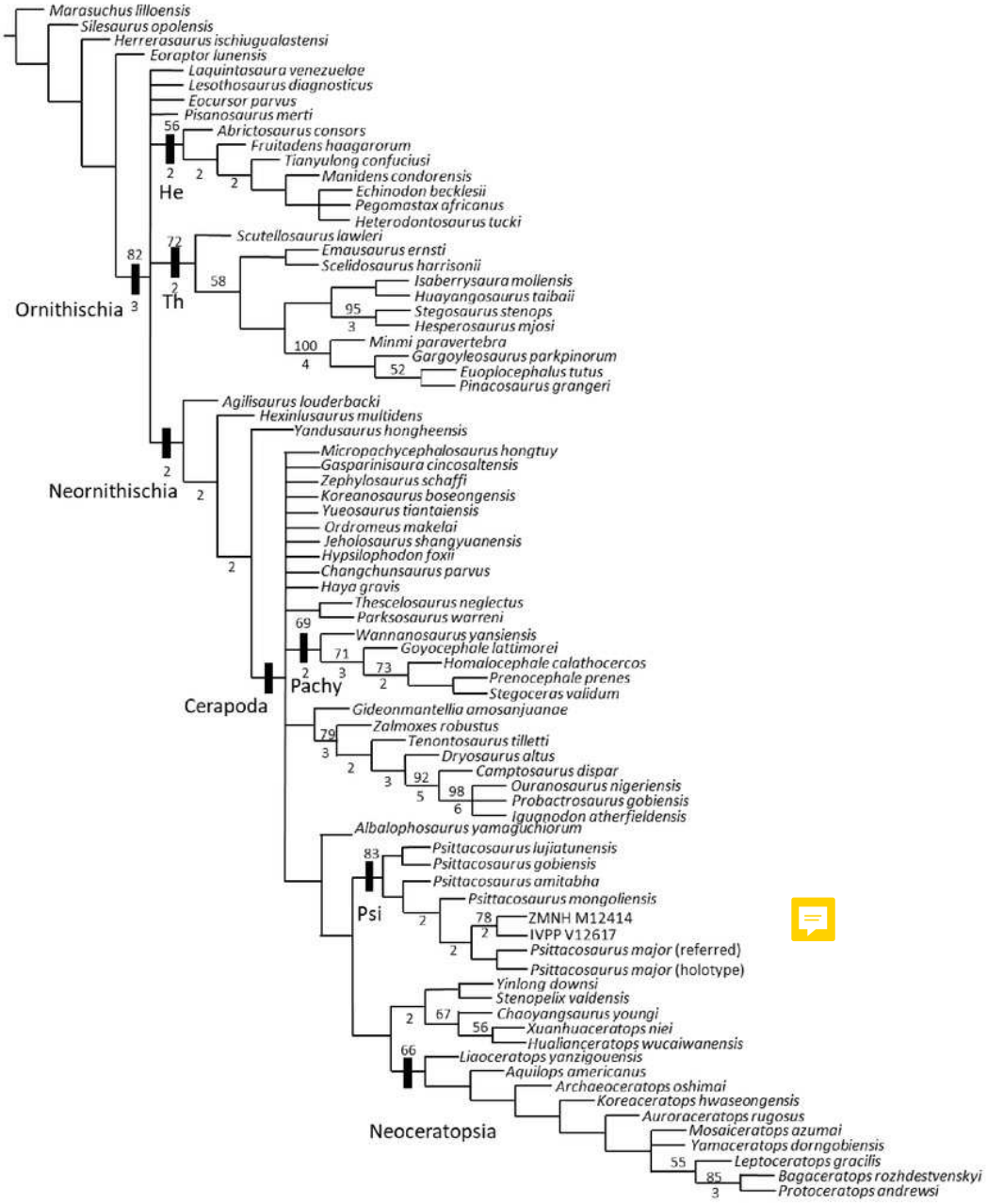
Marasuchus lilloensis
Silesaurus opolensis
Herrerasaurus ischigualastensi
Eoraptor lunensis
Laquintasaura venezuelae
Lesothosaurus diagnosticus
Eocursor parvus
Pisanosaurus merti
Abrictosaurus consors
Fruitadens haagarorum
Tianyulong confuciusi
Manidens condorensis
Echinodon becklesii
Pegomastax africanus
Heterodontosaurus tucki
He
Scutellosaurus lawleri
Emausaurus ernsti
Scelidosaurus harrisonii
Isaberrysaura moliensis
Huayangosaurus taibaii
Stegosaurus stenops
Hesperosaurus mjosi
Minmi paravertebra
Gargoyleosaurus parkpinorum
Euoplocephalus tutus
Pinacosaurus grangeri
Th
Ornithischia
Agilisaurus louderbacki
Hexinlusaurus multidens
Yandusaurus hongheensis
Micropachycephalosaurus hongtuy
Gasparinisaura cincosaltensis
Zephylosaurus schaffi
Koreanosaurus boseongensis
Yueosaurus tiantaiensis
Ordromeus makelai
Jeholosaurus shangyuanensis
Hypsilophodon foxii
Changchunsaurus parvus
Haya gravis
Thescelosaurus neglectus
Parksosaurus warreni
Wannanosaurus yansiensis
Goyocephale lattimorei
Homalocephale calathocercos
Prenocephale prenes
Stegoceras validum
Pachy
Neornithischia
Cerapoda
Gideonmantellia amosanjuanae
Zalmoxes robustus
Tenontosaurus tilletti
Dryosaurus altus
Camptosaurus dispar
Ouranosaurus nigeriensis
Probactrosaurus gobiensis
Iguanodon atherfieldensis
Albalophosaurus yamaguchiorum
Psittacosaurus lujiatunensis
Psittacosaurus gobiensis
Psittacosaurus amitabha
Psittacosaurus mongoliensis
ZMNH M12414
IVPP V12617
Psittacosaurus major (referred)
Psittacosaurus major (holotype)
Psi
Yinlong downsi
Stenopelix valdensis
Chaoyangsaurus youngi
Xuanhuaceratops niei
Hualiancératops wucaiwanensis
Liaoceratops yanzigouensis
Aquilops americanus
Archaeoceratops oshimai
Koreaceratops hwaseongensis
Auroraceratops rugosus
Mosaiceratops azumai
Yamaceratops dorngobiensis
Leptoceratops gracilis
Bagaceratops rozhdestvenskyi
Protoceratops andrewsi
Neoceratopsia

Figure 13

Figure 13: Phylogenetic hypothesis for *Psittacosaurus*.

Note that ZMNH M12414 forms a clade with IVPP V12617 but not with *P. lujiatunensis*.

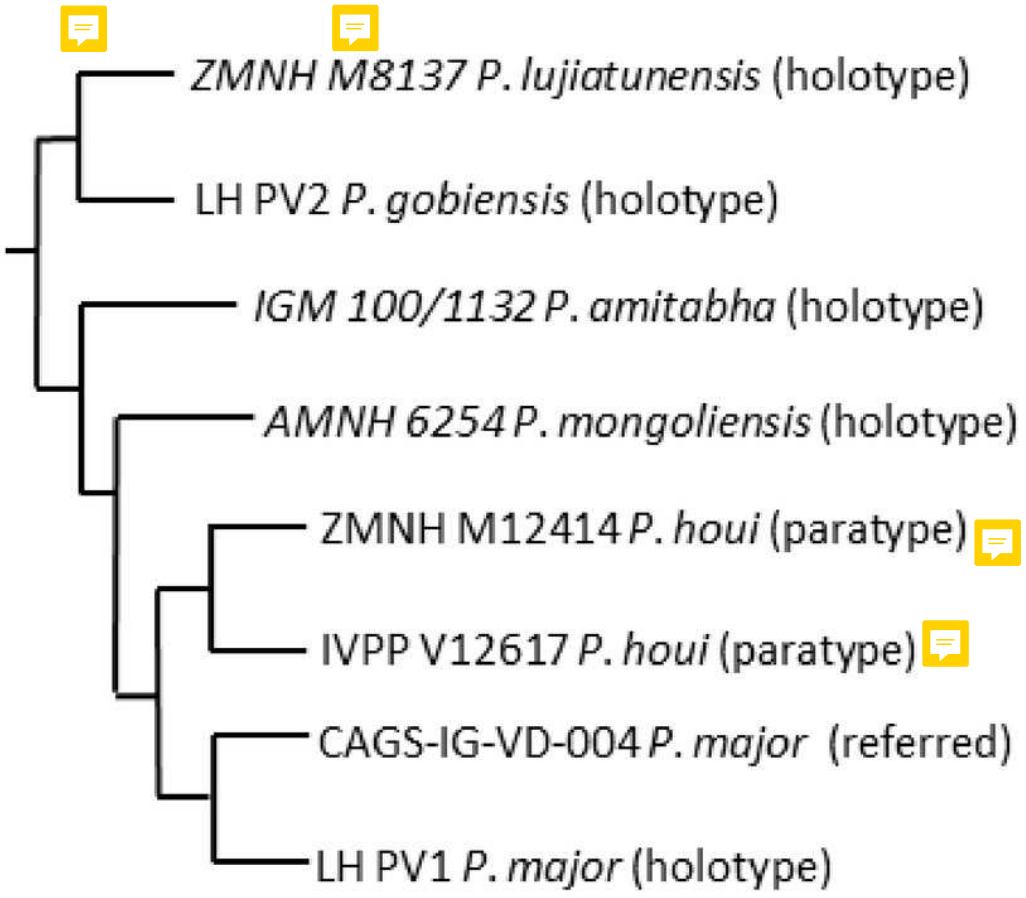
ZMNH M8137 P. lujiatunensis (holotype)
LH PV2 P. gobiensis (holotype)
IGM 100/1132 P. amitabha (holotype)
AMNH 6254 P. mongoliensis (holotype)
ZMNH M12414 P. houi (paratype)
IVPP V12617 P. houi (paratype)
CAGS-IG-VD-004 P. major (referred)
LH PV1 P. major (holotype)

Figure 14

Figure 14: Allometric relationship of preorbital regions among *P. lujiatunensis*.

A, hatchling (ZMNH M12430); B, juvenile (IVPP V22647), C, adult (ZMNH M8137). Scale bar equals 1 cm in A and B, and 5 cm in C. Scores indicate the proportions of the preorbital length to the skull length. Blue and Green arrows represent preorbital length and skull length, respectively.

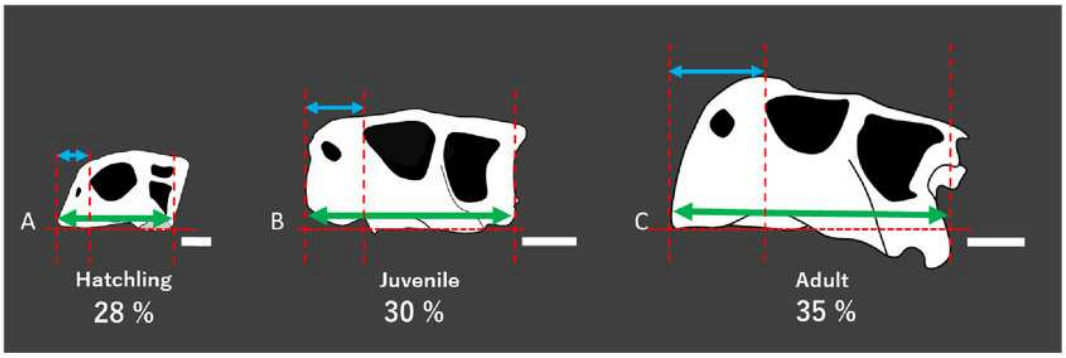
A
Hatchling
28 %
B
Juvenile
30 %
C
Adult
35 %

Table 1(on next page)

Table 1: Diagnostic characters of previously described *Psittacosaurus* species compared with the respective characters in ZMNH M12414.

All ~~the~~ characters are based on Sereno (2010), except for *P*. *gobiensis* (Sereno et al., 2010) and *P*. *amitabha* (Napoli et al., 2019). ✓, present in ZMNH M12414; -, not present in ZMNH M12414; ?, undetermined.

1

Species	Characters	ZMNH M12414
P. lujiatunensis	prefrontal width less than 50% that of the nasal	-
	quadratojugal-squamosal contact along anterior margin of quadrate shaft,	-
	jugal-quadrate contact posteroventral to the laterotemporal fenestra	-
P. major	maximum width across nasals and interorbital frontal width subequal to maximum width of the rostral	-
	tall subtriangular laterotemporal fenestra with anteroposterior width of the ventral margin approximately 25% of dorsoventral height	-
	anterior ramus of jugal convex	-
	elongate basipterygoid processes subequal in length to the body of the basisphenoid as measured from the notch between the processes to the basal tubera	-
	hypertrophied dentary flange with anterior corner approximately 30% of the depth of the dentary ramus andwith only a short gap to the predentary	-
	seven sacral vertebrae	?
P. meileyingensis	preorbital length only approximately 30% of skull length	-
	subtriangular orbit with acute ventral corner	-
	rugose quadratojugal eminence	-
P. mongoliensis	a raised lip on the orbital margin of the prefrontal	-
	transverse expansion of the distal end of the ischial blade to approximately twice its width at mid-shaft	?
P. neimongoliensis	posterior end of the nasal contacting its opposite in the midline (not separated by the frontal)	-
	frontal interorbital width approximately 30% of frontal length	-
	postorbital extending along the margin of the orbit (rather than inset from the margin by the frontal in dorsal view)	✓
P. sibiricus	laterotemporal fenestra subequal in maximum height and anteroposterior length	-
	postorbital ventral process with subvertical orientation set at an angle of approximately 95°to the posterior process	-
	postorbital with small dorsal horn	-
	enlarged palpebral subequal in transverse width to the adjacent skull roof	-
	palpebral posterior margin nearly straight and angled anterolaterally	?
	predentary dorsoventrally compressed with a wedge-shaped profile with external margins set at approximately 30°	-
	angular with arcuate ventral extension of the dentary flange	-
	angular process projecting laterally at posterior end of the ventral flange of the mandible	-
	14 dorsal vertebrae	?
P. sinensis	pendant rostrum that positions the ventral edge of the rostral bone below the level of the maxillary tooth row	✓
	anteroventral processes of the nasal separated in the midline by a narrow gap	-
	short lower jaw that positions the anterior margin of the predentary in opposition to the premaxilla rather than the rostral	-
	posteriorly flaring skull roof with postorbital-squamosal bars diverging at an angle of approximately 30°	✓
	absence of the maxillary fossa	-
	absence of the maxillary protuberance	-
	vertically elongate horn on the postorbital bar split between jugal and postorbital	-
	frontal participation in the supratemporal fossa	-
	ectopterygoid far removed from postpalatine foramen by broad maxilla-pterygoid contact	-
	internal mandibular fenestra reduced to a foramen	?
	absence of ossified tendons	?
	prepubic and postpubic processes transversely broad throughout their length (transversely wider than dorsoventrally tall)	?
	prepubic process projecting anteriorly as far as the preacetabular process of the ilium	?
P. gobiensis	pyramidal horn on the postorbital bar composed almost entirely of the postorbital	-
	postorbital–jugal fossa	-
	minimum width of the postorbital bar approximately 50 per cent the width of the base of the process	-
	retroarticular process deflected posteromedially at an angle of 408 from the axis of the mandible	-
	thin and restricted enamel on medial and lateral aspects of the maxillary and dentary crowns, respectively	?
P. amitabha	a relatively longer snout than Psittacosaurus mongoliensis, with a less steeply inclined anterior rostronasal margin	✓
	a cranium dorsally convex rather than flat	-
	a subtemporal length less than 40% of total skull length	?
	5 premaxillary foramina arranged in an arc	-
	posterior lamina of the maxilla cupped around the toothrow	-
	an antorbital fossa as long as tall	✓
	a palpebral with a well-developed posterior tonguelike process	?

2

Table 2(on next page)

Table 2: Diagnostic characters of the genus *Psittacosaurus* compared with the respective characters in ZMNH M12414.

All ~~the~~ characters are based on Sereno (2010) except the presence or absence of lacrimal foramen (see text). ✓, present in ZMNH M12414; -, not present in ZMNH M12414; ?, undetermined.

1

Characters	ZMNH M12414	*Psittacosaurus*
preorbital length less than 40% of skull length	-	✓
external naris with ventral margin dorsal to that of the orbit	✓	✓
nasal internarial process extending ventral to external naris	✓	✓
rostral-nasal contact present	✓	✓
premaxilla dorsolateral process maximum width subequal to dorsoventral orbital diameter	✓	✓
premaxilla-prefrontal contact present	✓	✓
premaxilla-jugal approximation or contact present	✓	✓
maxillary fossa	✓	✓
maxillary protuberance	✓	✓
fenestra of the lacrimal canal	?	?
antorbital fenestra and fossa absent	✓	✓
postorbital posterior process extends along the entire supratemporal bar	✓	✓
end of squamosal anterior process situated on the dorsal aspect of the postorbital	✓	✓
pterygoid with neomorphic palatal lamina forming the basal plate	✓	✓
pterygoid with hypertrophied mandibular ramus	✓	✓
medial quadrate condyle planar	✓	✓
laterally divergent palpebral with transverse posterior margin	?	✓
predentary with very short, tongue-shaped ventral processes	✓	✓
predentary with semicircular anterior margin	✓	✓
dentary with ventral ridge or flange	✓	✓
articular with planar surface for quadrate condyles	✓	✓
dentary teeth with bulbous cone-shaped primary ridge with secondary ridging	?	✓

2

3