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)

First revision

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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 validity 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 in 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 , which has also produced *Psittacosaurus major*, *P. lujiatunensis* and *H. houi*. ZMNH M12414 exhibits a series of unique features that are also present in the adult referred skull of *H. houi* (IVPP V12617), indicating that both specimens are attributable to the same species within Psittacosauridae. Large proportional length of the snout used to diagnose *H. houi* cannot be used for taxonomic distinction of *Psittacosaurus*, because this character is also found in *Psittacosaurus amitabha*, supporting that the genus *Hongshanosaurus* is a junior synonym of *Psittacosaurus.* On the other hand, ZMNH M12414 ~~(~~and IVPP V12617~~)~~ exhibit~~s~~ a set of features that are not observed in any other species of *Psittacosaurus* including *P*. *lujiatunensis*. Because of these features, the specimen in question better fits as its own species within *Psittacosaurus*: *P*. *houi*. A phylogenetic analysis supports the validity of *P*. *houi* where the specimens form an independent species 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 for previously described dinosaur taxa whose validities are in question. By utilizing such techniques, the

detailed evaluation of ontogenetic, intraspecific, and interspecific variations will be crucial to understand the true taxonomy and diversity of *Psittacosaurus* in future studies.

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Abstract

The taxonomic validity 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 in 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, which has also produced *Psittacosaurus major*, *P. lujiatunensis* and *H. houi*. ZMNH M12414 exhibits a series of unique features that are also present in the adult referred skull of *H. houi* (IVPP V12617), indicating that both specimens are attributable to the same species within Psittacosauridae. Large proportional length of the snout used to diagnose *H. houi* cannot be used for taxonomic distinction of *Psittacosaurus*, because this character is also found in *Psittacosaurus amitabha*, supporting that the genus *Hongshanosaurus* is a junior synonym of *Psittacosaurus.* On the other hand, ZMNH M12414 (and IVPP V12617) exhibits a set of features that are not observed in any other species of *Psittacosaurus* including *P. lujiatunensis*. Because of these features, the specimen in question better fits as its own species within *Psittacosaurus*: *P. houi*. A phylogenetic analysis supports the validity of *P. houi* where the specimens form an independent species 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 for previously described dinosaur taxa whose validities are in question. By utilizing such techniques, the detailed evaluation of ontogenetic, intraspecific, and interspecific variations will be crucial to understand the true taxonomy and diversity of *Psittacosaurus* in future studies.

Introduction

Psittacosauridae represents a family of basal ceratopsian dinosaurs with a bipedal posture and characteristic upper and lower jaws that form a beak-like rostrum similar to that of a parrot's (Osborn, 1923). In the Lower Cretaceous, hundreds to thousands of psittacosaurid specimens have been reported from the Barremian to Albian of China, Mongolia and Russia (Sereno, 2010; Sereno, ~~Xijin and Lin~~, 2010; Napoli et al., 2019; Podlesnov et al., 2023). The genus *Psittacosaurus* is one of the possible two genera that consists of the family Psittacosauridae, and the most species-rich genus within Dinosauria (Sereno, 2010).

In past, multiple species of *Psittacosaurus* were recognized, and their validities have been continuously tested. Along with the description of the type species, *Psittacosaurus mongoliensis* (AMNH 6254), Osborn (1923) described a specimen from the Ondai Sayr locality (AMNH 6253) and assigned it to a new genus and species *Protiguanodon mongoliense*. In a study that followed, these two genera were placed within a single new family Psittacosauridae based on the overall similarity (Osborn, 1924). Additionally, two new species, *P. osborni* and *P. tingi*, were coined following the series of Osborn's studies (Young, 1931). In Young (1958), another new species, *P. sinensis*, was described, which was followed by still another species, *P. youngi* (Zhao, 1962). In the 1980s, three additional species were described, *P. guyangensis*, *P. xinjiangensis*, and *P. meileyingensis* (Cheng, 1983; Sereno and ~~Shichin~~, 1988; Sereno et al., 1988). Subsequently, eight new species were added to the genus by the end of 2010 (Russell and Zhao, 1996; Averianov et al., 2006; Zhou et al., 2006; Sereno et al., 2007; Sereno, ~~Xijin and Lin~~, 2010), bringing the total number of potential species of *Psittacosaurus* to 16 (Sereno, 2010). On the other hand, a comparative study by Sereno (2010) recognized nine valid species, namely *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) added *P. amitabha* as a new species, with the total number of *Psittacosaurus* species still being debated.

Another genus that constitutes the family Psittacosauridae is *Hongshanosaurus*, which contains a single species *Hongshanosaurus houi*. The species was described based on a juvenile skull (IVPP V12507, holotype) and an adult skull (IVPP V12617, referred specimen) (You, Xu and Wang., 2003; You and Xu, 2005). *Hongshanosaurus* was distinguished from *Psittacosaurus* by oval-shaped external naris and orbit, and a longer rostrum (You and Xu, 2005). However, a lack of definitive morphological differences between *Hongshanosaurus* and *Psittacosaurus* has led to multiple proposals that the former may be a junior synonym of the latter. For example, Sereno (2010) argued that the longer rostrum in *Hongshanosaurus* might come from the taphonomic deformation and synonymize~~s~~ *H. houi* with *P. lujiatunensis*. Additionally, Hedrick and Dodson (2013) supported the synonymy of *H. houi* with *P. lujiatunensis* based on a three-dimensional geometric morphometric analysis in which *H. houi* formed a morphological cluster with *P. lujiautnensis* and *P. major*. The study further tested the validity of diagnosis of *P. lujiatunensis*, *P. major*, and *H. houi*, respectively, using 25 specimens of these psittacosaurids. The results showed that most of the diagnostic characters were intraspecifically and taphonomically variable, thus invalidating their diagnosis. However, Napoli et al. (2019) criticized Hedrick and Dodson (2013) for failing to account for ontogenetic and taphonomic variation, as well as intraspecific variation found in modern animals, in their geometric morphometric analysis, and argued that *P. lujiatunensis* and *P. major* were separate species because they did not form a sister clade in the phylogenetic analysis. While this result possibly suggested that *H. houi* is distinct from *P. lujiatunensis*, as in *P. major*, *H. houi* was not included as an operational taxonomic unit (OTU) in Napoli et al. (2019).

In this study, we describe a well-preserved adult skull (ZMNH M12414) of a psittacosaurid with a long snout resembling that of *Hongshanosaurus houi*. We test the purported validity of this genus *Hongshanosaurus* and address current *Psittacosaurus* taxonomy based on the morphology and the phylogenetic analysis. The application of computed tomography (CT) techniques has allowed the non-destructive rendering of individual skull elements, including those that are difficult to observe in articulated specimens (such as endocranial elements), and helped us to describe each of them. This leads to a revision of diagnostic characters based on the less deformed and articulated specimen and allows us to address the taxonomy and specific diversity within Psitacosauridae. While the synonymy of *Hongshanosaurus* with *Psittacosaurus* is supported, our study recognizes *Psittacosaurus* (formerly *Hongshanosaurus*) *houi* as a valid species that can be distinguished from all other *Psittacosaurus* species including the coeval *Psittacosaurus lujiatunensis*.

Institutional 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; KOKM – Kuzbass State Museum of Local Lore, Kemerovo, Russia; LH – Long Hao Institute for Stratigraphic Palaeontology, Inner Mongolia Autonomous Region, China; PM TGU – Paleontological Museum, Tomsk State University, Tomsk, Russia; ZMNH – Zhejiang Museum of Natural History, Zhejiang, China.

Materials & Methods

Specimen and locality

ZMNH M12414 is represented by a nearly complete skull including a mandible in articulation. The posterior surface of the skull is obscured by sandstone matrix (Fig. 1A, E). The specimen was collected from the Lower Cretaceous Lujiatun Unit cropping out near the village of Lujiatun, Beipiao, Western Liaoning, in northeastern China. Unfortunately, the specimen was delivered to ZMNH by a local villager without detailed information about the locality and horizon. The specimen was assigned to *Psittacosaurus* when it was deposited at ZMNH, but no formal descriptions and species assignments were made prior to the present study.

The Lujiatun Unit is overlain by the Lower Lava Unit and comprises the lowermost part of the Yixian Formation, Jehol Group in northeastern China. The Lujiatun Unit in Lujiatun village has been extensively studied in Rogers et al. (2015) through logging, which is summarized as follows. Sedimentologically, the Lujiatun Unit generally consists of tuffaceous siltstones, grey siltstones, and a variegated sequence of sandstones from the bottom to the top. The deposition of these sedimentary horizons is interpreted as a result of a series of sheet flood following the remobilization of pyroclastic material onto the floodplain. The sheet flood resulted in quick burials and fine preservation of dinosaur remains in the Lujiatun Unit.

Volcanic tuff from the Lujiatun Unit cropping out in the Jin-Yang Basin have yielded U-Pb chemical abrasion-isotope dilution-isotope ratio mass spectrometry of 125.719 ± 0.025 Ma (Barremian, Zhong et al., 2021). The psittacosaurid species previously reported from the unit include *Psittacosaurus lujiatunensis* (Zhou et al., 2006), *P. major* (Sereno et al., 2007; You, Tanoue and Dodson, 2008), and *Hongshanosaurus houi* (You, Xu and Wang, 2003; You and Xu, 2005).

Reconstruction of the skull using computed tomography techniques

The skull of ZMNH M12414 was scanned with a high-resolution X-ray CT (NIKON XTH 320; Nikon, Tokyo, Japan) at the College of Civil Engineering and Architecture, Zhejiang University, Hangzhou, Zhejiang, China. Tomographic images were obtained using a voltage of 300 kV, a current of 280 µA, an interslice spacing of 0.08 mm and image size of 1,920 × 1,507 pixels. These parameters 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 tomographic images (DICOM files) were segmented, and the three-dimensional computer model of the specimen was rendered using 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 computer model (Fig. 1B, D and F) with Amira ver. 2019.4 (Thermo Fisher SCIENTIFIC, Tokyo, Japan). For comparative purposes, measurements on previously described psittacosaurid specimens were taken from the texts and figures in previously published literature (Table S1). Following Sereno (2010), the preorbital length was measured from the anterior margin of the rostral to the anterior margin of the orbit, and the skull length was measured from the anterior margin of the rostral to the posterior margin of the quadrate condyle. In addition, the basal skull length was measured from the anterior margin of the rostral to the posterior margin of the occipital condyle, following Bullar et al. (2019) (Fig. 2).

Phylogenetic analysis

To assess the phylogenetic relationships among species of the genus *Psittacosaurus*, *Psittac~~so~~aurus houi*, *P. sinensis* and *P. sibiricus* were added to the character-taxon matrix of Napoli et al. (2019), which is based on the original matrix in Han et al. (2018). *Psittacosaurus houi* was scored based on the rendered three-dimensional computer model of ZMNH M12414 (Figs. 3−5, S1−32) and the descriptions of IVPP V12617 in the previously published literature (You and Xu, 2005; Tanoue, You and Dodson, 2009; Taylor et al., 2017; Bullar et al., 2019; Landi et al., 2021; Han et al., 2018). *Psittacosaurus sinensis* was scored based on published literature for the holotype IVPP V738 (Young, 1958; Sereno, 1990; Tanoue, You and Dodson, 2009; Sereno, 2010) and a referred specimen BNHM BPV149 (Chao, 1962; Sereno, 2010). *Psittacosaurus sibiricus* was scored based on published literature for the holotype PMTGU 16/4−20 (Averianov et al., 2006) and referred specimens KOKM 22985/2 (Podlesnov et al., 2023) and PM TGU 16/0−15, 20, 30–39, 16/1−11, 51, 136, 137, 166, 167, 175, 176, 179, 200, 201–203, 209, 216, 223, 228, 258, 271, 274, 276, 281, 283 and 284 (Averianov et al., 2006).

The character-taxon matrix in Napoli et al. (2019) was further modified in the following perspectives. We chose to set the OTUs of *P. mongoliensis* and *lujiatunensis* species based on the holotype specimens. This was because it was possible that "*Psittacosaurus mongoliensis* composite" and "*Psittacosaurus lujiatunensis* composite" in the previous studies included the specimens belonging to different species. For *P. major*, LH PV1 and CAGS-IG-VD-004 were integrated into a single OTU. While character 103, the distinctive indentation on the midline of the posterior edge of the parietals, was scored as absent (1) in *P. amitabha* and *P. major* in Napoli et al. (2019), they were scored as present (0) in the present study as it is apparent in the dorsal views (You, Tanoue and Dodson, 2008; Napoli et al., 2019). For character 238, the option indicating the presence of 14 dorsal vertebrae was added between the primitive (12–13 vertebrae) and the first derived (15 vertebrae) states defined by Han et al. (2018) so that *P. sibiricus* with 14 dorsal vertebrae (Averianov et al., 2006) can be scored.

Following the previous studies (Han et al., 2018; Napoli et al., 2019), the matrix was analyzed using T.N.T. version 1.5 (Goloboff, Farris and Nixon, 2015), treating all characters as equally weighted and the following characters as ordered (additive): 2, 23, 31, 40, 126, 164, 196, 203, 204, 222, 227, 238, 243, 247, 268, 292, 296, 302, 306, 320, 361. The analysis was performed with the default settings except for the following: maximum number of trees in memory equal to 99,999. The traditional search was chosen to find the most parsimonious trees (MPTs) with the tree bisection-reconnection (TBR) algorithm, where 1000 replicates of random stepwise addition and 100 trees held at each step. Then, a second TBR search was performed using the MPTs obtained in the previous procedure where branches were collapsed if the minimal branch length was zero. The strict consensus tree was generated based on the MPTs found after the second TBR search. Bootstrap and Bremer support values were calculated as support indices.

Results

Systematic paleontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1888
Ceratopsia Marsh, 1890
Psittacosauridae Osborn, 1923
Psittacosaurus Osborn, 1923
Psittacosaurus houi You, Xu, and Wang, 2003
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, Hattori, Shibata, Kawabe, and Jin, 2024 (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 adult skull with lower jaws.

Locality and horizon—Lujiatun, Liaoning, People’s Republic of China; Lujiatun Unit, Yixian Formation, upper Barremian, Early Cretaceous (Zhong et al., 2021).

Diagnosis— *Psittacosaurus houi* is distinguished from other *Psittacosaurus* species by the following combination of characters: (1) ~~long preorbital region reaching about one half of the skull length;~~ (2) posterodorsally sloped anterior margin formed by the rostrals and nasals; (3) narrow prefrontal-premaxilla contact; (4) posterodorsally-elongated laterotemporal fenestra oriented at an angle of about 45 degrees in lateral view; (5) higher ventral margin of the premaxilla raised above the maxillary tooth row; (6) large amount of surface area of the jugal exposed in dorsal view; (7) subtriangular supraoccipital widest at its ventral margin; (8) the posterior margin of the parietal nearly linear perpendicular to the sagittal crest with no indentation on the midline.

Description and comparisons

ZMNH M12414 measures 123 mm long in the skull length, 196 mm wide in the width from the lateral-most extents of jugal horns, and 125 mm tall in the height from the ventral-most dentary flange to the dorsal-most skull roof (Table S2).

The skull is divided into 32 elements by suture lines observable in the CT data (Fig. S33). The skull exhibits damages in some elements including premaxillae, the right prefrontal, postorbital, squamosal, parietal, angular, surangular and the left maxilla/jugal contact and dentary. Although slight deformations in the right supratemporal fenestra and mandibular condyle seem to be present, it does not appear to affect intraspecific morphological comparisons (see Discussion).

Histological evidence suggests that IVPP V12617, the other referred specimen of *Psittacosaurus houi*, is fully mature and at least 10 years old at the time of death (Zhao et al., 2013). Because the basal skull length of ZMNH M12414 is 139.1 mm long and almost equivalent to that of IVPP V12617 (143.7 mm long; Bullar et al., 2019), the former can also be regarded as mature. This interpretation about the full maturity ZMNH M12414 is also supported by the cranial sutures that are nearly obliterated in some parts.

In dorsal view, the skull is wider than long, as in *Psittacosaurus sinensis* and *P. lujiatunensis* (ZMNH M8137) (Fig. 3E). Notably, the skull exhibits a relatively large proportion for the preorbital length from the anterior-most extent of the rostral bone to the anterior-most orbital margin, against the total skull length (preorbital length proportion, PLP). The PLP against the total skull length is approximately 50%, being similar to 52% of IVPP V12617 and 46% of *P. amitabha*, and unlike those of other known *Psittacosaurus* species which exhibit less than 40% (Sereno, 2010).

Rostral—In anterior view, the rostral is subtriangular with a broad ventral margin, and the nasal process extends dorsally (Fig. S1C). The rostral is also triangular in lateral view, having a nearly vertical sutural contact with the premaxilla (Fig. S1A, B). Because the anterior-most ends of the nasals are not fully preserved, the articulation between the rostral and nasal is obscured (Fig. 3A–C). As in *Psittacosaurus mongoliensis*, *P. sinensis*, *P. amitabha* and IVPP V12617, the anterior margin formed by the rostral and nasal slopes posterodorsally in lateral view (Fig. 3A, B). The anterior-most extent of the rostral is rounded in dorsal and ventral views (Fig. S1E, F), and neither pointed nor strongly bowed ventrally in lateral view (Fig. S1A, B).

Premaxilla—Both premaxillae are preserved, and make up most of the lateral surfaces of the snout (Fig. 3A, B). The premaxilla contacts the rostral anteriorly, the nasal and prefrontal dorsally, and the lacrimal and maxilla posteriorly as in other species except for *Psittacosaurus sinensis*, in which the premaxilla also meets the jugal posteriorly (Fig. S2). Unlike in other *Psittacosaurus* species, the sutural contact between prefrontal and premaxilla is relatively narrow in lateral view (Fig. 3A, B). A similar character is also found in IVPP V12617, although the contact is even narrower (You and Xu, 2005).

The anterodorsal portions of both premaxillae are partially missing (Fig. S2A–D). 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 of the premaxilla is smooth and slightly depressed below the external naris, but has multiple grooves and pits near its buccal margin, which is particularly evident on the right premaxilla (Fig. S2B) probably due to the erosion of the left premaxilla. 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 (Fig. S2A, B), as in *Psittacosaurus meileyingensis* and *P. lujiatunensis* (ZMNH M8137). In lateral view, the position of the ventral margin of the premaxilla is raised above maxillary tooth row (Fig. 3A, B), as in IVPP V12617. While similar features are present in *P. sinensis*, *P. mongoliensis* and *P. major*, the distance from the posterior end of the ventral margin of the premaxilla to the maxillary tooth row is the widest in ZMNH M12414 and IVPP V12617.

Maxilla—Both maxillae are preserved (Fig. S3). 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. There are nine alveoli for each maxilla, with seven on the left and nine on the right are occupied by the erupted teeth (Fig. S3C–F). The position of the external naris is located above the anterior part of the maxilla as in *P. major*, *P. meileyingensis*, *P. sinensis* (Fig. 3A, B). The dorsal part of the maxilla is tall, trapeziform and reaches to the level with the ventral border of the orbit (Fig. 3A, B) as in *Psittacosaurus meileyingensis*, *P. neimongoliensis*, *P. lujiatunensis* (ZMNH M8137), *P. major* and IVPP V12617, but differing from the lower, triangular maxilla in all others. As in *P. lujiatunensis* (ZMNH M8137), *P. mongoliensis*, *P. amitabha* and *P. gobiensis*, a sub-triangular maxillary fossa (Fig. S3A, B) is present on the lateral surface with a horizontal eminence located along its ventral margin. The fossa is anteroposteriorly longer than dorsoventrally deep and positioned anterior to the orbit as in *P. amitabha* and *P. major*. 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 is not confirmed in ZMNH M12414 due to limited resolution of CT images. Like most *Psittacosaurus* species, a maxillary protuberance is found posterior to the maxillary fossa at the posterior margin near the maxilla-jugal suture (Fig. S3A, B). In ventral view, the distance between the anterior ends of the tooth row is wide, as the ratio of the width across the anterior ends to that across the posterior ends is greater than 45% (Fig. 3F), as in *P. amitabha* and *P. lujiatunensis* (ZMNH M8137).

Lacrimal—Both lacrimals are preserved with the right one being better preserved (Fig. S4). As in other *Psittacosaurus* 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 smaller trapezoid shape than other *Psittacosaurus* (Fig. 3A, B). It contributes to a small part of the anteroventral border of the orbit. The lacrimal foramen is located at the boundary between the lacrimal and the jugal (Fig. 3B, S4B), whereas the foramen is located along the orbital margin in other *Psittacosaurus* species (Zhao, 1962; Sereno et al., 1988; Sereno, 1990; Russell and Zhao, 1996; Zhou et al., 2006; Sereno et al., 2007; Sereno, ~~Xijin and Lin,~~ 2010; Sereno, 2010). This may be due to the partial breakage of the lateral surface of the right lacrimal, causing the lacrimal foramen to appear in a more anteroventral position. A right lacrimal canal continuous with the foramen can be seen in the CT image (Fig. S34), supporting the identification of the lacrimal foramen.

Nasal— Both nasals are preserved (Fig. S5). In dorsal view, the nasal is a long bone that flanks its counterpart in the anterior half including the rostroventral process, where it contacts the rostral bone ventrally (Fig. S5E, F). The posterior part of the internasal suture is unclear (Fig. S5E, F). The posterior part of the nasal expands laterally, reaching its maximum width where it meets the prefrontal. At its narrowest part, the main body of the nasal is about as wide as the prefrontal and it terminates posteriorly in contact with the frontals above the orbit as in other *Psittacosaurus* species (Fig. 3E).

Frontal—Both frontals are preserved (Fig. S6). The frontals are flat and forms a broad central element of the skull roof, constituting the posterodorsal rim of the orbit (Fig. 3E). In dorsal view, both frontals are fused into a single unit along the midline as the interfrontal suture cannot be observed (Fig. S6E, F). The frontals contact the nasals anteriorly, the prefrontals laterally, the postorbitals posterolaterally and the parietals posteriorly. The ventral surface of the frontals has distinct depressions for the olfactory bulbs anteriorly and for the cerebral hemispheres posteriorly (Fig. S6F).

Prefrontal—Both prefrontals are preserved (Fig. S7). They are narrow and meets the premaxillae and lacrimals ventrally, forming the anterodorsal corner of the orbit in left lateral view (Fig. 3A, B). In dorsal view, the prefrontal contacts the nasal anteromedially and the frontal posteriorly (Fig. 3E). The maximum width of the prefrontal is nearly as wide as that of the nasal (Fig. 3E) as commonly seen in the other *Psittacosaurus* species.

Parietal—Both parietals are preserved (Fig. S8). The parietals form the posterior-most element of the central skull roof and fuse along the midline to form a low sagittal crest, as in other *Psittacosaurus* (Fig. S8A, B and E). The parietal contacts the frontal and the postorbital anteriorly, the laterosphenoid anteroventrally, the squamosal laterally and the supraoccipital ventrally. In dorsal view, the posterior margin of the parietal is almost linear and runs perpendicular to the sagittal crest (Fig. S8E) as in IVPP V12617 and in *Psittacosaurus meileyingensis*, while other species have a distinct incised margin at the middle of the posterior end of parietals. 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 (Fig. 3E).

Postorbital—Both postorbitals are preserved (Fig. S9). The postorbital is a three-pronged element ~~that~~ ~~comprising~~ of the skull roof bar, the temporal bar and the jugal bar that separates the orbit from the infratemporal fenestra (Fig. S9A–D). The left ~~pre~~orbital is present in its original position, whereas the right postorbital is broken at the center of its triradiate bone and the temporal bar is disarticulated from the squamosal (Fig. S9B, D). This results in a slight deformation of the right supratemporal fenestra. The jugal bar is thick and relatively long, compared with that of other *Psittacosaurus* species, overlapping the jugal and to form most of the posterior border of the orbit (Fig. 3A, B). The distal-most extent of the left jugal bar is missing (Fig. S9A, B, I and K). The jugal bar is expanded anteroventrally (Fig. S9A–D) as in *Psittacosaurus lujiatunensis* (ZMNH M8137) and *P. meileyingensis*, differing from the narrow tip in the other *Psittacosaurus* species. The squamosal bar of the postorbital overlaps the postorbital bar of the squamosal and forms the entire dorsal border of the infratemporal fenestra in lateral view (Fig. 3A). The skull roof bar is shorter than the temporal and jugal bars (Fig. S9A–D), as in most other *Psittacosaurus* species. In lateral view, the skull roof bar extends along the margin of the orbit, contributing to form the posterodorsal rim of the orbit as in the other *Psittacosaurus* species (Fig. 3A, B).

Squamosal— Both squamosals are preserved (Fig. S10). They are nearly complete except for the missing anterior ramus on the right squamosal (Fig. S10B, D, F, H, J and L). The squamosal is a tetraradiate bone as in other *Psittacosaurus* species and is located at the upper posterolateral corner of the skull. Anteriorly, the squamosal contacts the postorbital to form a bar separating the upper and lower temporal fenestrae. In dorsal view, the anterior ramus is short as in *Psittacosaurus lujiatunensis* and *P. major* (Fig. 3E), while differing from most other *Psittacosaurus* species. The anterior ramus of the right squamosal is missing due to a local damage (Fig. S10B, H), as well as the clacked postorbital, causing deformation of the right supratemporal fenestra. The ventral ramus is relatively short and does not contact the quadratojugal (Fig. 3A–C). Although Hedrick and Dodson (2013) argues that the ventral ramus of the squamosal and the dorsal ramus of the quadratojugal are almost always broken in *P. lujiatunensis*, *P. major* and *Hongshanosaurus houi* (=*Psittacosaurus houi*, IVPP V12617), our CT images and rendered model show no evidence of such damages. The medial ramus projects medially to meet the parietal, with which it forms the posterior margin of the supratemporal fenestra (Fig. 3E, S10G, H). Further ventrally, the ventromedial ramus of the squamosal contacts the exoccipital (Fig. S10I, J).

Jugal—Both jugals are present (Fig. S11). The jugal is large and consists of infraorbital, infratemporal and dorsal rami, and the jugal horn (Fig. 3A, B). The antero~~laterall~~y curved infraorbital ramus, the dorsal ramus, and the posterolaterally sloped infratemporal ramus are plate-shaped. The ventral surface of the jugal is flat (Fig. S11E, F). A gentle ridge runs posterolaterally from the apex of the dorsal process to the lateral end of the jugal horn, dividing the lateral aspect of the jugal into anterior and posterior surfaces. In lateral view, the area of the anterior surface is much larger than that of the posterior surface as in *Psittacosaurus major*, which is thought to be due to the shorter infratemporal bar than in other *Psittacosaurus* (Fig. S11A, B). 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 (Fig. S11A−D). The anterior surface of the jugal is smooth and flat as in *P. lujiatunensis* (ZMNH M8137). The dorsal process of the jugal is overlapped by the ventral ramus of the postorbital, forming the bar between the orbit and infratemporal fenestra (Fig. S11A, B). The infraorbital ramus forms the ventral margin of the orbit and anteriorly contacts the lacrimal and the maxilla (Fig. 3A, B). The infratemporal ramus bifurcates posteriorly as in other species of *Psittacosaurus*, although this feature is not seen in the incomplete left jugal (Fig. S11D, L). The dorsal part of the bifurcated infratemporal ramus is large and overlaps the quadratojugal, but never reaches the quadrate (Fig. 3B). The infratemporal ramus forms the anteroventral and ventral margins of the infratemporal fenestra, without expanding posterodorsally to form the posteroventral margin as in most other *Psittacosaurus* species (Fig. 3A, B). In dorsal view, the surface area of the jugal is very large (Fig. 3E), 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 sagittal section of the horn is also sub-triangular. The ventral surface of this horn is flat and lies more dorsal than the level of the maxillary tooth row (Fig. 3A, B, S11E, F).

Quadratojugal— Both quadratojugals are preserved but the left one is partly missing (Fig. S12). The quadratojugal is subtriangular in lateral view (Fig. S12B) and mediolaterally flattened in posterior view (Fig. S12L). The posterior margin of the quadratojugal extensively overlaps the quadrate, while the quadrate condyle is exposed in lateral view as in *Psittacosaurus lujiatunensis* (ZMNH M8137) and *P. gobiensis* (Fig. 3A−C, E). As in most other species of *Psittacosaurus*, the dorsal process of the quadratojugal does not contact the ventral process of the squamosal, only slightly contributing to the posterior rim of the infratemporal fenestra (Fig. 3A–C, E). In *P. meileyingensis*, *P. lujiatunensis* (PKUP V1054), *P. sinensis*, IVPP V12617, the quadratojugal prominence is present in the ventral part, whereas only a weak eminence (bump) is observed in the right quadratojugal of ZMNH M12414 (Fig. S12B, F). The ventral part of the quadratojugal extends anteriorly to the level of the posterior margin of the infratemporal fenestra (Fig. 3A, B) as in *P. sinensis*, *P. neimongoliensis P. mongoliensis*, *P. meileyingensis* and *P. lujiatunensis* (ZMNH M8137) (Zhou et al., 2006).

Quadrate— Both quadrates are preserved (Fig. S13). As in other *Psittacosaurus*, the quadrate shaft is oriented anterolaterally in dorsal view (Fig. 3E, S13G, H) and the condyles expands transversely to form a broad articular surface in ventral view (Fig. 3F, S13E, F). The shaft is slightly arched along its posterior margin (Fig. S13A, B) as in *Psittacosaurus mongoliensis*, *P. sinensis* (IVPP V738), *P. neimongoliensis* and IVPP V12617, but unlike the strongly concave condition of *P. sinensis* (BNHM BPV149), *P. meileyingensis* and *P. lujiatunensis* (ZMNH M8137). The quadrate shaft is oriented at an angle of approximately 45 degrees in lateral view, as is the postorbital jugal bar (Fig. 3A, B), a feature only seen in ZMNH M12414 and IVPP V12617. Dorsal to the condyles, the quadrate is not exposed in lateral view just posterior to the quadratojugal-quadrate suture (Fig. 3A, B), as in *P. mongoliensis*, *P. sinensis* and *P. meileyingensis* (also in *P. major* and *P. lujiatunensis* to a lesser degree). The pterygoid wing developed as a typically broad and thin bone and completes the medial wall of the infratemporal fossa as far anterior as the postorbital bar (Fig. S13G–L). This medial wall obscures the ventral portions of the braincase in lateral view (Fig. 3A, B), including most of the cranial nerve foramina.

Palate—The palate consists of premaxillae, maxillae, vomers, palatines, pterygoid and ectopterygoid (Fig. 3F, S2, S3 and S14–17). The short secondary palate is formed by the palatal processes of premaxillae and maxillae and well-exposed anteriorly in ventral view (Fig. 3F). The choanae (internal nostrils) are bordered anteriorly and laterally by the maxillae, medially by the vomers, posteriorly by palatines and posteromedially by the pterygoids (Fig. 3F). In ZMNH M12414, the choanae are fully exposed in ventral view as large elliptical openings into the oral cavity, which is one of the major differences in palate between psittacosaurids and basal neoceratopsians (Dodson, You and Tanoue, 2010). Anterior to the internal naris, the rostral ~~bones~~, maxillae and premaxillae forms a gentle vault (arched cavity), and the incisive foramen is bounded by the same three elements. The internal naris extends anteriorly to the level of the anterior edge of maxillary tooth row (Fig. 3F) as in other species of *Psittacosaurus*.

Palatine— Both palatines are well preserved in ZMNH M12414 (Fig. S15). The palatine contacts with the maxilla and the jugal laterally, the pterygoid posteriorly and the vomer medially. In some *Psittacosaurus* species, the palatine does not extend dorsally enough to contact the vomers, which are instead embraced by the pterygoids (Dodson, You and Tanoue, 2010; Podlesnov et al., 2023), while the palatine contacts with the vomer in ZMNH M12414 (Fig. S15). However, it should be noted that the exact point of contact is not discernible. Whether this is due to CT image resolution or fused and obscured sutures cannot be determined.

Vomer— The long, fused vomer is an unpaired bone located along the midline of the skull, contacting the maxillae anteriorly and the pterygoids posteriorly and forming the medial margins of the choanae (Fig. 3F). The bone consists of a plate-like posterior vertical part and a rod-like, slightly arched vomerine bar (Fig. S14A, B). The anterior end of the vomer does not contribute to the formation of the secondary palate but lies dorsally, in a subnarial position (Figs. 3F, S14). This feature is one of the major differences in palate between psittacosaurids and basal neoceratopsians (Dodson, you and Tanoue, 2010). The vomer is in contact with the palatine laterally, and the pterygoid posteriorly (Fig. S14C, D).

Pterygoid—Both pterygoids are preserved and a well-developed pterygoid is triradiate, with a posterolaterally directed quadrate ramus, a posteroventrally directed mandibular ramus and an anterodorsally extending palatal ramus (Fig. S16). The quadrate ramus is Y-shaped and the largest part of the pterygoid. The quadrate ramus is thin and broadly meets the pterygoid ramus of the quadrate and the prootic posterolaterally (Fig. S16A–D). On the medial side, there is a large cup-like facet for the basipterygoid process of the basisphenoid, which is adjacent to the dorsal margin of the quadrate ramus (Fig. S16G, H). The pterygoid forms the posterior half of the palate. The mandibular ramus is one of the diagnostic characters of the genus *Psittacosaurus*, where the ventral-most extent 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. S16A–D). The mandibular ramus is in contact with the maxilla anterolaterally (Fig. S16A–B). The palatal ramus is larger than the mandibular ramus and in contact with the vomers and the palatine anteriorly (Fig. S16A, B). As in other *Psittacosaurus*, the anterior end of the pterygoid (Fig. S16E, F) forms a very short median joint between the left and right pterygoids, which is located very anteriorly, at approximately the midpoint of the skull (Fig. 3F). This feature is noted as one of the major differences in palate between psittacosaurids and basal neoceratopsians (Dodson, You and Tanoue, 2010).

Ectopterygoid— Both ectopterygoids are well preserved in ZMNH M12414 (Fig. S17). The outline of the ectopterygoid is a tall triangle in dorsal and ventral view, and it contacts with the jugal anterolaterally and the maxilla ventrally (Fig. S17G–L). The ectopterygoid is separated from the palatine by the maxilla as in *Psittacosaurus sinensis* and *P. neimongoliensis* (Sereno, 1987; Russell and Zhao, 1996), while the bone meets the palatine in *P. lujiatunensis* and *P. mongoliensis* (Zhou et al., 2006). The maxillary articular surface is flat (Fig. S17E, F), while the dorsal surface forms a gentle ridge (Fig. S17C, D).

Braincase—The braincase of ZMNH M12414 includes a supraoccipital, partly missing exoccipitals, basioccipitals, ~~exoccipitals~~, opisthotics, laterosphenoids, a basisphenoid and prootics (Fig. 4). In posterior view, the foramen magnum is about 18.3 mm long in diameter, bordered by the supraoccipital dorsally, the exoccipitals laterally and the basioccipital ventrally (Fig. 4D). The supraoccipital is dorsoventrally deep and subtriangular in posterior view (Fig. S18) unlike the diamond-shaped ones in other *Psittacosaurus* species. Similarly, IVPP V12617~~,~~ seems to have a tall subtriangular-shaped supraoccipital (You and Xu, 2005; Bullar et al., 2019), although Bullar et al. (2019) notes that the fused and obscured sutures between the supraoccipital and the parietal or the exoccipital make the exact location of the contact difficult to determine. Because the supraoccipital of ZMNH M12414 is undeformed and there is no evidence of breakage, we conclude that this character is an autapomorphy of ZMNH M12414 and IVPP V12617. The supraoccipital contributes only to the middle portion of the dorsal border of the foramen magnum and is covered dorsally by the parietals. The exoccipitals borders the foramen magnum laterally. The exooccipital and opisthotic are fused to form the parooccipital process, which extends posterolaterally but lacks the distal end (Fig. S19). As in other *Psittacosaurus*, the ~~basioccipital~~ present~~s~~ as paired processes projecting ventrally to the occipital condyle (Fig. S20). The basioccipital borders the foramen magnum ventrally (Fig. 4D) and forms the occipital condyle that is directed posteriorly and slightly ventrally as in other *Psittacosaurus* species (Fig. S21). The condyle is about 12.5 mm ~~long~~ in diameter with ~~having~~ a smooth hemisphere. The basioccipital fuses with the basisphenoid anteroventrally and exoccipital-opisthotic dorsolaterally. The latter suture is almost completely fused and is difficult to discern. There are no foramen or fossa along the midline between the basal tubera and the occipital condyle (Fig. 4F), ~~as~~ in *Psittacosaurus amitabha* and *P. lujiatunensis* (ZMNH M8137). The laterosphenoid contacts the prootic posteroventrally and the frontal anterodorsally as in other *Psittacosaurus* species (Fig. S22). The trigeminal foramen (CN V) is 5 mm in diameter and bounded by the laterosphenoid, the prootic and the basisphenoid, which is visible on both lateral sides of the bones (Fig. 4A–C). The basisphenoid is well preserved and in contact with the prootic dorsally, the pterygoid anteriorly and the basioccipital posteriorly (Fig. S23). In Hedrick and Dodson (2013), a disconnection between the braincase and the palate was shown ~~to be responsible~~ for the dorsoventral compressive deformation, however the connection is completely preserved in ZMNH M12414 (Fig. S23). The basal tubera have a subcircular and subvertical posterior surface, with a round, rough ventral margin that is located slightly ventral to the occipital condyle (Fig. 4D, F, S23A, B, F). The basipterygoid processes are elongated to reach 14.4 mm in length, which is subequal to the length of the basisphenoid body measured from the notch between the processes to the basal tubera (13.5 mm), as in *P. major* (Sereno et al., 2007; Sereno, 2010). Both prootics are preserved, although their boundaries to the exoccipital and basisphenoid are obscured (Fig. S24). The prootic forms the lateral wall of the braincase and appears to have a contact with the laterosphenoid dorsally, the parietal posterodorsally, the pterygoid ventrally and the exoccipital posteriorly. The shape of the prootic is sub-rectangular in lateral view (Fig. S24A, B).

Mandible— The mandible is composed of the following elements: a 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. 5, S25–32). In lateral view, the mandible is strongly curved dorsally along its ventral margin, with the predentary and angulars forming the anterior and posterior ends of the arc, respectively (Fig. 5A, B). The mandible is dorsoventrally deep relative to the anteroposterior length as in *Psittacosaurus lujiatunensis* (ZMNH M8137), *P. major* and IVPP V12617. Posteriorly, the articular and surangular form the retroarticular process as in other *Psittacosaurus* species (Fig. 5A–D). The height of the retroarticular process is approximately at the same level as the dentary tooth row (Fig. 5C) as in IVPP V12617 and *P. neimongoliensis*. In contrast to other *Psittacosaurus* species, the retroarticular process is reduced so that the mandibles appear dorsoventrally deep in lateral view (Fig. 5A–D). The anterior margin of the predentary is U-shaped in dorsal and ventral views (Fig. 5G, H, S25E, F). There are nine alveoli in the dentary, which are fully occupied by the erupted teeth on the left, while only six alveoli are occupied on the right (Fig. S26A–D, G and H). The ventral border of the dentary is strongly curved and possesses a prominent dentary flange at its posteroventral corner, as in *P. major*. Although this feature is particularly evident in the right dentary, the left dentary flange is poorly preserved (Fig. S26A, B). The presence of external mandibular fenestra is unclear. The surangular forms the posterodorsal portion of the lower jaw in lateral view (Fig. 5A, B), and contacts the dentary anteriorly with forming the posterior half of the coronoid process (Fig. S27). The surangular extends posteroventrally to the end of the mandible, covering the angular underneath. The posterior portions of the right surangular and angular are broken (Fig. 5B, D), and the right mandibular condyle is somewhat deformed. In addition, the deformation is indicated by the asymmetry between the left and right mandibular condyles in posterior view (Fig. 5F). The obliteration of the sutural boundaries between the right surangular and articular, which resulted in the incomplete restoration of these bones (Figs. S27, S28) in the CT images, may be due to these damages. The articular is mediolaterally broad, but dorsoventrally thin where it articulates with the robust quadrate (Fig. S28). The angular is well-exposed laterally with a sheet-like process that covers around the ventral margin of the mandible (Fig. S29). In medial view, the angular is covered by the splenial anteriorly and the prearticular dorsally (Fig. 5C, D). The splenial is a thin plate-like bone on the medial side of the mandible, covering the dentary anteriorly and the angular posteriorly, and contacting the prearticular posterodorsally and coronoid dorsally (Fig. S30). Both coronoids are preserved but the left one shows the better preservation (Fig. S31). Unlike IVPP V12617, the position of the coronoid process is on the main axis of the dentary in dorsal view and posterior to the tooth row in lateral view as in *P. major* (CAGS-ID-VG-004) and *P. sibiricus* (Podlesnov et al., 2023). The prearticular is more complete on the left side, while the right side is missing the anterior process (Fig. S32A, B).

Phylogenetic analysis

The analysis yielded 16,001 MPTs with a length of 1,323 steps, a consistency index (CI) of 0.318 and a retention index (RI) of 0.679 (Fig. 6). In the strict consensus topology, *Psittacosaurus houi* is recovered as the most derived species of *Psittacosaurus* together with *P. major* (Fig. 7). In addition, *P. houi* is found within a clade comprising the genus *Psittacosaurus*.

According to the strict consensus topology of the present analysis, the monophyly of *Psittacosaurus* is supported by 14 unambiguous synapomorphies and *Psittacosaurus houi* presents 13 of them:

10(1) posterolateral process of the premaxilla in contact with lacrimal, interfering with maxilla-nasal contact (convergent with some heterodontosaurids, *Jeholosaurus*, some iguanodontians and some neoceratopsians);
11(1) premaxilla-lacrimal contact wide, and almost the entire anterior edge of the lacrimal contacting the premaxilla (convergent with some heterodontosaurids, *Jeholosaurus*, some iguanodontians and some neoceratopsians);
17(1) premaxilla-prefontal contact present (convergent with *Heterodontosaurus*, some iguanodontians and *Liaoceratops*);

19(2) premaxilla fully edentulous;
23(2) ventral border of external nares located significantly above that of the infratemporal fenestra (convergent with *Herrerasaurus* and *Eoraptor*);
24(1) dorsoventral depth of snout at external nares large and about or more than 60% relative to that of orbital region (convergent with *Herrerasaurus*, *Huayangosaurus*, *Chaoyangsaurus* and some neoceratopsians);
26(0) deep elliptical fossa along sutural line of nasals absent (convergent with *Silesaurus*, *Eoraptor*, *Herrerasaurus*, *Lesothosaurus*, *Hypsilophodon*, some thyreophorans, *Thescelosaurus*, *Parksosaurus*, some pachycephalosaurians, some iguanodontians and some neoceratopsians).
28(1) location of anterior end of nasal (internarial bar) far anterior to external naris (convergent with *Mosaiceratops*).
32(0) external antorbital fenestra absent (convergent with *Herrerasaurus*, some thyreophorans and some iguanodontians);
73(1) jugal process of postorbital extending to ventral margin of orbit (convergent with *Mosaiceratops*);
88(1) anterior margin above quadrate wing transversely expanded, rounded and thickened (convergent with *Hualianceratops*);
156(0) anterior end of the predentary rounded in dorsal view (convergent with *Chaoyangsaurus*, some iguanodontians, *Pinacosaurus* and some thyreophorans);
173(1) minimum height greater than 50% of total length of dentary in lateral view (convergent with *Goyocephale*, *Hualianceratops* and some neoceratopsians).

Psittacosaurus houi also presents three unambiguous synapomorphies for *Psittacosaurus* diverging later than *P. sinensis*:

56(1) jugal ridge divides the lateral surface of into two (convergent with *P. mongoliensis*, *P. major*, *P. gobiensis*, *P. lujiatunensis*, *P. sibiricus* and some neoceratopsians);
164(1) first dentary tooth separated from predentary by short diastema (convergent with *Echinodon*, *Chaungchunsaurus*, *Haya*, *Thescelosaurus*, *Parksosaurus*, some iguanodontians, some thyreophorans, *P. mongoliensis*, *P. major*, *P. gobiensis*, *P. sibiricus* and some neoceratopsians);
184(1) surangular length more than 50% of mandibular length (convergent with *P. mongoliensis*, *P. gobiensis*, *P. lujiatunensis*, *P. sibiricus* and some chaoyangsaurids).

Psittacosaurus houi also presents three unambiguous synapomorphies for *Psittacosaurus* diverging later than *P. sibiricus*:

33(1) antorbital fossa present (convergent with *P. amitabha*, *P. mongoliensis*, *P. major*, *P. gobiensis* and *P. lujiatunensis*);
84(1) lateral ramus of quadrate absent (convergent with some thyreophorans, *P. amitabha*, *P. major*, *P. gobiensis* and *P. lujiatunensis*);
139(1) pterygoid-maxilla contact at posterior end of tooth row present (convergent with *P. amitabha*, *P. mongoliensis*, *P. major*, *P. gobiensis*, *P. lujiatunensis* and some neoceratopsians).

Psittacosaurus houi also presents two unambiguous synapomorphies for *Psittacosaurus* diverging later than *P. lujiatunensis* and *P. gobiensis*:

102(1) anteroventral corner of infratemporal fenestra forms an acute angle (convergent with *Silesaurus*, *Eoraptor*, some heterodonsaurids, *Agilisaurus*, *Haya*, *Changchunsaurus*, *Hypsilophodon*, *Jeholosaurus*, *Orodromeus*, *Parksosaurus*, *Zephyrosaurus*, *Thescelosaurus*, *Gasparinisaura*, some pachycephalosaurians, some iguanodontians, *P. amitabha* and *P. mongoliensis*);
126(0) ratio of maximum occipital width to maximum occipital height > 1.1 (convergent with some thyreophorans, *Ouranosaurus, P. amitabha* and *P. mongoliensis*);

Psittacosaurus houi also presents three unambiguous synapomorphies for *Psittacosaurus* diverging later than *P. amitabha*:

12(2) ventral (oral) margin of premaxilla raised above maxillary tooth row (convergent with *P. mongoliensis*, *P. major*, *P. sinensis* and some neoceratopsians);
61(1) infratemporal process of jugal strongly arched laterally (convergent with *P. mongoliensis*, *P. major*, some chaoyangsaurids and *Mosaiceratops*);
82(1) quadratojugal facing posterolaterally (convergent with some thyreophorans, *P. mongoliensis*, *P. gobiensis* and some neoceratopsians).

Psittacosaurus houi also presents four unambiguous synapomorphies for *Psittacosaurus* diverging later than *P. mongoliensis*:

37(2) ventral margin of antorbital fossa poorly delineated (convergent with *P. major*);
93(0) medial quadrate condyle subequal to lateral condyle in size (convergent with *Agilisaurus*, *Haya*, *Changchunsaurus*, *Hypsilophodon*, *Jeholosaurus*, *Zephyrosaurus*, *Parksosaurus*, some pachycephalosaurians, some iguanodontians, *P. major*, *P. gobiensis*, *P. sinensis* and *Hualianceratops*);
94(1) frontal involved in supratemporal fenestra (convergent with some *Herrerasaurus*, *Heterodontosaurus*, *Lesothosaurus*, some thyreophorans, *Ouranosaurus*, *P. major*, *P. sinensis*, *Yinlong*, and some neoceratopsians);
167(1) anterior end of dentary tooth row (and edentulous anterior portion) downturned in lateral view (convergent with *Pegomastax*, some thyreophorans, some iguanodontians, *P. major*, *P. gobiensis* and *P. sibiricus*).

Psittacosaurus houi exhibits five diagnostic features. Among them, one diagnostic feature is autapomorphic within *Psittacosaurus*:

125(2) supraoccipital subtriangular and widest near its ventral margin (convergent with *Herrerasaurus*, *Thescelosaurus* and some iguanodontians).

Remaining four diagnostic features of *Psittacosaurus houi* are homoplastic within *Psittacosaurus*.

2(0) preorbital skull length relative to basal skull length more than 50% (convergent with *Eoraptor*, *Herrerasaurus*, some thyreophorans, *Thescelosaurus*, *Parksosaurus*, *Prenocephale*, some iguanodontians and *P. amitabha*);

96(1) arched smooth depression on posterior edge of frontal (convergent with *Heterodontosaurus*, *P. sinensis*, some chaoyangsaurids and some neoceratopsians);
129(0) contribution of basioccipital to basal tubera restricted, not extending ventrally, and basisphenoid contribution to the tubera seen in posterior view (convergent with *Lesothosaurus*, some pachycephalosaurians, *P. lujiatunensis*, *P. sibiricus*, *P. sinensis* and *Yinlong*);
160(1) ventral process of predentary bifurcated (convergent with *Haya*, *Changchunsaurus*, *Hypsilophodon*, *Thescelosaurus*, some iguanodontians, *P. lujiatunensis*, some chaoyangsaurids and some neoceratopsians).

For more details on unambiguous synapomorphies on all nodes of the strict consensus tree, see Fig. S35 and appendix.

Discussion

It should be noted that the following discussion avoids reference to IVPP V12507, a holotype specimen of *Psittacosaurus* (formerly *Hongshanosaurus*) *houi* because the specimen represents a juvenile, making it difficult to directly compare the specimen to other *Psittacosaurus* species that have been described based on mature specimens. For this reason, the following discussion focuses on ZMNH M12414 and IVPP V12617 to taxonomically compare *P. houi* with other *Psittacosaurus* species.

Notes on deformations in ZMNH M12414

ZMNH M12414 shows some deformations in the right supratemporal fenestra, which is distorted ventrally (Fig. 3D) ~~due to~~ the missing right anterior ramus of the squamosal (Fig. S10B, H) and the broken central portion and the incomplete temporal bar of the right postorbital (Fig. S9B, D). In addition, the right angular and surangular are damaged (Fig. 5B), and the left and right mandibular condyles are deformed and tilted (Fig. 5F). Here, we demonstrate that these post-depositional deformations are minimal to address taxonomic questions based on the diagnostic characters of *Psittacosaurus houi* raised in this study.

Psittacosaurus houi is distinguished from other *Psittacosaurus* species by the combination of eight diagnostic characters:

(1) preorbital length about one half of skull length

This character is valid only if the dorsoventral compressive deformation is minimal as suggested by the previous studies (Sereno, 2010; Hedrick and Dodson, 2013). The following lines of evidence falsifies major dorsoventral compressive deformation affecting the proportion of the preorbital length against the skull length (PLP). To begin with, the bones comprising the preorbital region of ZMNH M12414 (rostral, premaxilla, prefrontal, lacrimal, maxilla and jugal) are generally well-preserved on both sides (Fig. 3A, B). The right lateral surface shows a better preservation than the left one with only some breakages in the premaxilla and lacrimal, and there is no displacement of each bone. Similarly, there is no displacement of the bones that contribute to the skull length (rostral, premaxilla, maxilla, jugal, pterygoid, ectopterygoid, vomer, palatine, quadratojugal and quadrate; Fig. 3A, B and F). In addition, the connection between the braincase and the palate is completely preserved in ZMNH M12414 (Fig. S14), where the broken process in IVPP V12617 (referred specimen of *Psittacosaurus houi*) is raised as evidence of the dorsoventral compression (Hedrick and Dodson, 2013).

(2) anterior margin of rostral and nasal sloped posterodorsally

As noted earlier, the right preorbital region is minimally damaged and less affected by dorsoventral compressive deformation. The bones comprising the anterior margin of the preorbital region (nasal, rostral, prefrontal and premaxilla) have a partial breakage in premaxilla, but without displacement of each element.

(3) prefrontal-premaxilla contact narrow

The contact between the prefrontal and premaxilla exists on both lateral sides of the skull (Fig. 3A, B), whereas the left lacrimal is damaged. The bones surrounding this contact (lacrimal, nasal and maxilla) also shows no signs of displacement, particularly on the right side.

(4) laterotemporal fenestra dorsoventrally elongated and oriented at an angle of about 45 degrees in lateral view

As noted earlier, the cranium is minimally affected by the dorsoventral compressive deformation. The left laterotemporal fenestra shows a better preservation than the right one, as the shape of the right supratemporal fenestra is affected by the breakage of the postorbital and squamosal (Fig. 3). In posterior view, only the right supratemporal fenestra is distorted (Fig. 3D), suggesting that this deformation was localized. On the left side, the bones comprising the laterotemporal fenestra (postorbital, squamosal, quadrate, quadratojugal and jugal) is well preserved, with only the ventral-most extent of the postorbital missing, but without any displacement between each bone (Fig. 3A).

(5) ventral margin of premaxilla raised above maxillary tooth row

If this feature is more likely due to post-depositional deformation, it probably results from the bilateral compression, or localized deformation and dorsal displacement of the ventral margin of the premaxilla. However, both jugal horns extend straight outward on each side, suggesting that there was less compressive deformation bilaterally (Fig. 3E). In addition, there is no significant misalignment in the articulations between the right premaxilla and maxilla and the surrounding bones (rostral, lacrimal, nasal, prefrontal and jugal; Fig. 3B).

(6) large amount of surface area of jugal exposed in dorsal view

As noted earlier, the cranium is minimally affected by the dorsoventral compressive deformation. The jugal articulates with several bones (lacrimal, maxilla, quadratojugal, palatine, ectopterygoid and postorbital), and there is no displacement of their articulations. The jugal horns (especially on the well-preserved right one) extend straight outward on both sides, suggesting that there was less bilaterally compressive deformation.

(7) supraoccipital subtriangular and widest at its ventral margin

The supraoccipital of *Psittacosaurus*, except for *Psittacosaurus houi*, is diamond-shaped. If the subtriangular shape of the supraoccipital of *P. houi* results from the deformation of the originally diamond-shaped supraoccipital, it should have been due to significant bilateral compression. However, the lack of misalignment of the adjacent bones (parietals and exoccipitals) and the preservation of both jugal horns suggest that the compressive deformation was insufficient to affect the shape of the supraoccipital.

(8) posterior margin of parietal nearly linear and perpendicular to sagittal crest with no indentation on midline

Except for Psittacosaurus *houi* and *P. meileyingensis*, there is a distinctive indentation on the midline of the posterior margin of parietals in *Psittacosaurus*. However, for this "indentation" to be formed by post-depositional deformation, only the center of the posterior margin would have to be locally deformed, which is inconceivable. Moreover, the presence or absence of the indentation among *Psittacosaurus* species in different conditions is clearly distinguished in the literature.

Notes on phylogenetic analysis

In our phylogenetic analysis, *Psittacosaurus houi* was recovered as the latest-diverging *Psittacosaurus* species along with *P. major*. Although *P. mongoliensis* has often been assigned to the basal species in previous studies focusing on the intraspecific relationships (Sereno, 1987; Russell and Zhao, 1996; Xu, 1997; Averianov et al., 2006; You et al., 2008; Sereno, 2010), it was recovered as a derived taxon next to the node of *P. major* and *P. houi*, in which the phylogenetic position of *P. mongoliensis* and *P. major* is consistent with Napoli et al. (2019).

Compared to Napoli et al. (2019), the addition of *Psittacosaurus houi*, *P. sinensis* and *P. sibiricus* results in a slight change in their phylogenetic relationships. For example, the present analysis finds *P. sinensis* as the most basal taxon, followed by *P. sibiricus*. Additionally, *P. lujiatunensis* and *P. gobiensis* form a sister group of the clade comprising *P. amitabha* and other later diverging species. This result contrasts with the one in Napoli et al. (2019) where *P. amitabha* is the most basal species of *Psittacosaurus*. This could be attributed to the morphological similarity between *P. houi* and *P. amitabha*, and their shared characters (2, 9, 21, 30, 102 and 114).

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

While we interpret that ZMNH M12414 and IVPP V12617 are assignable to *Psittacosaurus houi*, these specimens exhibit few morphological differences: presence/absence of the lacrimal foramen and the reduced retroarticular and coronoid processes of the mandible. Here, we address these apparent differences and present lines of evidence that these specimens belong to the same species.

Sereno (2010) suggests that the presence of the lacrimal foramen is one of the diagnostic characters for the genus *Psittacosaurus*. You and Xu (2005) notes that IVPP V12617 has no openings or canals in the lacrimal. Although the lacrimal foramen found in the right lacrimal of ZMNH M12414 is slightly offset from the typical position described previously in *Psittacosaurus*, the coronal slices of the CT images show that the lacrimal canal is connected to this foramen (Fig. S34), supporting this identification. The distinct position of the lacrimal foramen in ZMNH M12414 is caused by a postmortem damage on the right lacrimal. On the other hand, there is no lacrimal foramen in IVPP V12617 (You and Xu, 2005), and whether this is an intraspecific variation or the post-depositional deformation needs to be determined through identification of the lacrimal canals with CT techniques.

Other morphological features of ZMNH M12414 that are absent in IVPP V12617 include reduced retroarticular and coronoid processes of the mandible positioned close to the main axis of the dentary. In ZMNH M12414, the right mandible is partially damaged with a misalignment between the surangular and angular. On the left side, however, the bones comprising the retroarticular processes (surangular, angular and articular) and the coronoid process (coronoid, surangular and dentary) are almost completely preserved, and no misalignment between the bones can be seen, suggesting that the effect of the deformation is small. Thus, future studies may clarify whether this morphological difference between ZMNH M12414 and IVPP V12617 are due to the post-depositional deformation or intraspecific variation (Fig. 5A, C and G).

Still, these specimens share multiple characters unique to them among *Psittacosaurus* species, and suggest that they belong to the same species. For example, ZMNH M12414 and IVPP V12617 share (1) a long preorbital length, which is about one half of the skull length, and (2) the dorsoventrally elongated laterotemporal fenestra, which is oriented at an angle of about 45 degrees in lateral view. In addition, (3) the narrow prefrontal-premaxilla contact, (4) the ventral margin of the premaxilla raised above the maxillary tooth row, (5) the large surface area of the jugals exposed in dorsal view, and (6) the subtriangular supraoccipital, which is widest at its ventral margin. Furthermore, (7) the anterior margin of the rostral and nasal sloped posterodorsally (as in *Psittacosaurus amitabha*), (8) the posterior margin of the parietal nearly linear perpendicular to the sagittal crest with no indentation on the midline (as in *P. meileyingensis*), and (9) the height of the retroarticular process approximately at the level of the dentary tooth row (as in *P. neimongoliensis*) are shared between the two specimens. Considering a greater number of similarities than differences between the specimens, it is concluded that ZMNH M12414 and IVPP V12617 are assignable to the same species, namely *Psittacosaurus houi.*

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

The synonymy of the genus "*Hongshanosaurus*" with *Psittacosaurus* has been proposed in previous studies (Sereno, 2010; Hedrick and Dodson, 2013). The present study supports this hypothesis based on the observation that the most apparent difference between these two genera, the magnitude of the PLP, is no longer supported.

The genus "*Hongshanosaurus*" is originally diagnosed by the PLP nearly equal to 50%, the elliptical shape of the orbit and external naris, and the posterodorsally-elongated laterotemporal fenestra (You and Xu, 2005). Sereno (2010) coins the PLP lower than 40% as a diagnostic feature of *Psittacosaurus*. Sereno (2010) further argues that, for "*Hongshanosaurus*", the diagnostic features listed above comes from the post-depositional deformation of the skull, concluding that "*Hongshanosaurus"* is a junior synonym of *Psittacosaurus*. In support of Sereno (2010), Hedrick and Dodson (2013) performs the three-dimensional geometric morphometric analyses and finds that "*Hongshanosaurus*" forms a morphological cluster with *Psittacosaurus lujiautnensis* and *P. major*. The same study also posits that "*Hongshanosaurus*" appears to have a large PLP due to the dorsoventral compressive deformation. Following these studies, more recent analyses on the family Psittacosauridae have regarded 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; Sakagami et al., 2023; ~~Logan~~ et al., 2024).

These studies regard "*Hongshanosaurus*" as a junior synonym of *Psittacosaurus* based on the interpretation that all purported "*Hongshanosaurus*" specimens in fact have the PLP < 40 %, and *Psittacosaurus* among basal ceratopsians is diagnosed by the PLP < 40%. However, a recent description of the psittacosaurid *Psittacosaurus amitabha* demonstrates that the PLP of the taxon is larger than 40% without significant post-depositional deformation of the skull (Napoli et al., 2019), suggesting that the PLP < 40 % may not be diagnostic to the genus *Psittacosaurus*.

ZMNH M12414 in the present study provides additional evidence that the PLP can exceed 40 % in *Psittacosaurus*.

According to Hedrick and Dodson (2013), the connection between the braincase and the palate are reconstructed by plaster in IVPP V12617 (referred specimen of "*Hongshanosaurus houi"*), suggesting that the specimen has undergone dorsoventral post-depositional compression, leading to the conclusion that the PLP exceeding 40% is not the original feature of "*H. houi*". On the other hand, ZMNH M12414 possesses a complete connection between the braincase and the palate, shows no misalignment in the bones comprising preorbital region and skull length, indicating that the deformation had little effect on the PLP. Thus, unlike IVPP V12617, the PLP in ZMNH M12414 is likely original and exceeds 40%. Furthermore, ZMNH M12414 and IVPP V12617 likely represent fully mature skulls based on the histological evidence for IVPP V12617 (Zhao et al., 2013) and their sizes, suggesting that the PLP would not undergo significant changes with further ontogeny. Together with *Psittacosaurus amitabha*, because more than one example of mature psittacosaurid specimens exhibits the PLP exceeding 40%, this feature cannot be used as a criterion to diagnose "*Hongshanosaurus*" nor *Psittacosaurus*. This observation would leave two features to distinguish "*Hongshanosaurus*" from *Psittacosaurus*: the elliptical shape of the orbit and external naris, and the posterodorsally-oriented laterotemporal fenestra, although these may be affected by post-depositional deformation (Sereno, 2010; Hedrick and Dodson, 2013). Numerous features are shared between ZMNH M12414 and IVPP V12617, and the genus *Psittacosaurus* by Sereno (2010) (See Table 1). Additionally, our phylogenetic analysis placed the OTU comprising ZMNH M12414 and IVPP V12617 deep within the *Psittacosaurus* clade. For these reasons, we argue that there is insufficient evidence to support the genus "*Hongshanosaurus*" and suggest that it ~~to~~ be synonymized with *Psittacosaurus*.

Is *P. houi* a separate species from other *Psittacosaurus* species?

To establish *Psittacosaurus houi* as a distinct species within the genus *Psittacosaurus*, the presence or absence of diagnostic characters of all 10 valid species defined in previous studies should be confirmed (Sereno, 2010; Sereno, ~~Xijin and Lin~~, 2010; Napoli et al., 2019). However, following Hedrick and Dodson (2013), the diagnostic characters of the Lujiatun psittacosaurids, *Psittacosaurus lujiatunensis* and *P. major*, are considered invalid and therefore not used in this comparison. Instead, we have listed and compared characters among *P. houi*, *P. lujiatunensis* and *P. major* recognized in the present study (Table 2).

The validity of *P. houi* is supported by nine characters commonly found in ZMNH M12414 and IVPP V12617 but absent in *P. major* and *P. lujiatunensis*, species with which "*Hongshanosaurus houi*" were previously synonymized. Furthermore, although several diagnostic characters of other *Psittacosaurus* species are also present in *P. houi*, the discordance of their combination with any other *Psittacosaurus* species supports the distinctiveness of *P. houi* (Table 3). The conclusion that *P. houi* is separate from *P. lujiatunensis* is further supported by the present phylogenetic analysis, where they do not form a sister clade to each other (Fig. 7). Napoli et al. (2019) argues that *P. lujiatunensis* and *P. major* are separate species, citing their failure to form a sister group as the basis. The present phylogenetic analysis also does not support the sister relationship between *P. lujiatunensis* and *P. major*.

Conclusions

In the present study, a new specimen of a psittacosaurid skull, ZMNH M12414, was described, leading to a taxonomic reevaluation of the previously coined species "*Hongshanosaurus*" *houi*. Anatomical observations and phylogenetic analyses involving ZMNH M12414 and other previously described "*Hongshanosaurus*" specimens suggest the following: (1) ZMNH M12414 exhibits the features most consistent with those found in the previously described psittacosaurid "*Hongshanosaurus houi*", (2) "*Hongshanosaurus*" is to be synonymized with *Psittacosaurus*, and (3) *Psittacosaurus houi* is a valid species. *Psittacosaurus* is known from numerous specimens from many localities, but its diversity remains controversial. The recognition of *Psittacosaurus houi* supports the highly diverse nature of the genus. The present study leaves some questions for future work regarding the taxonomy and morphological characters of the genus, such as intraspecific variations and ontogeny. Revisiting other previously described species of *Psittacosaurus* based on additional specimens is necessary, and disputed anatomical questions may be addressed through CT analyses as demonstrated in the present work.

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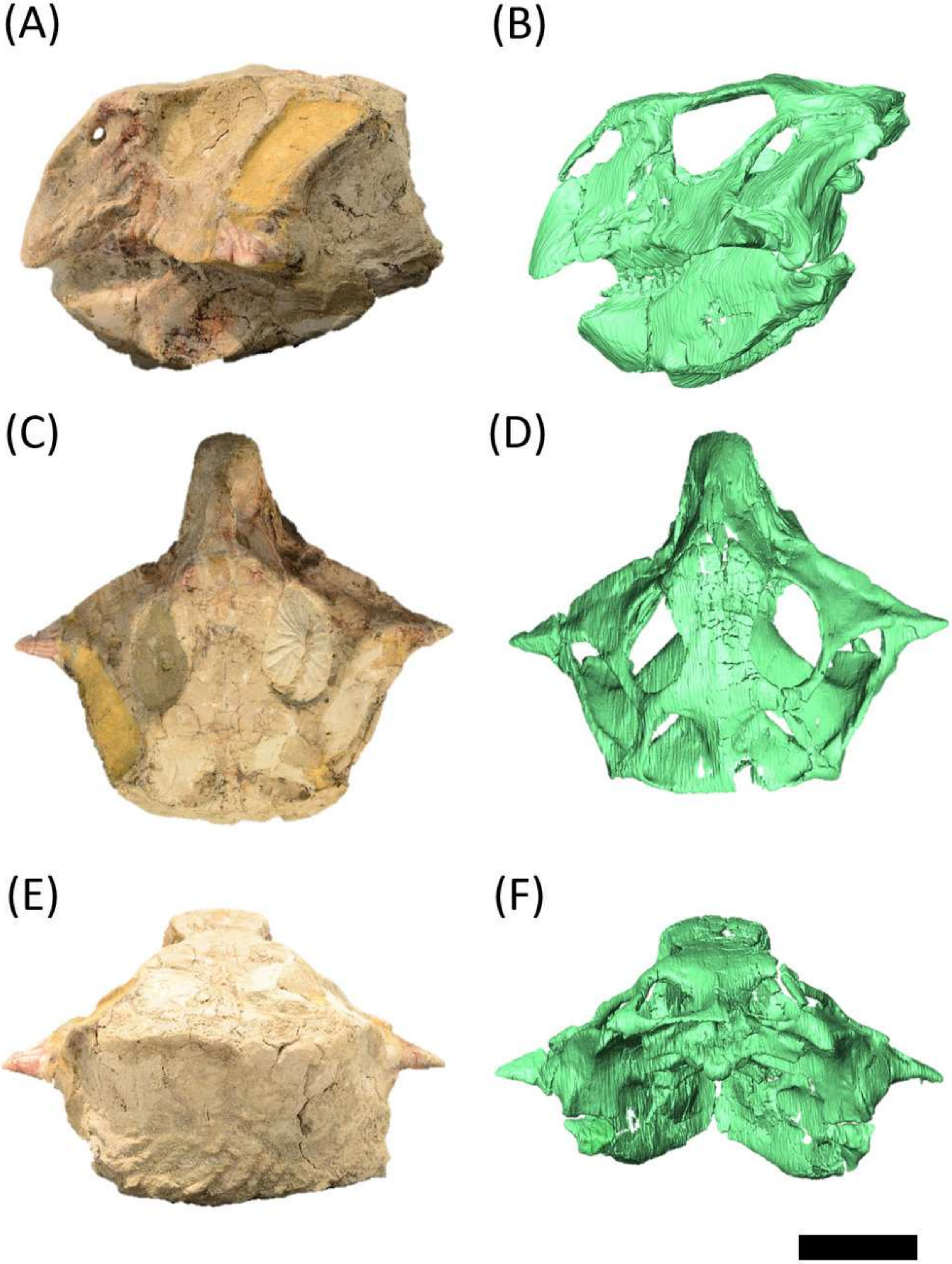
Figure 1

Photographs and three-dimensional rendering of *P. houi* (ZMNH M12414).

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


(A)
(B)
(C)
(D)
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(F)

Figure 2

Measurements of the cranium following Sereno (2010).

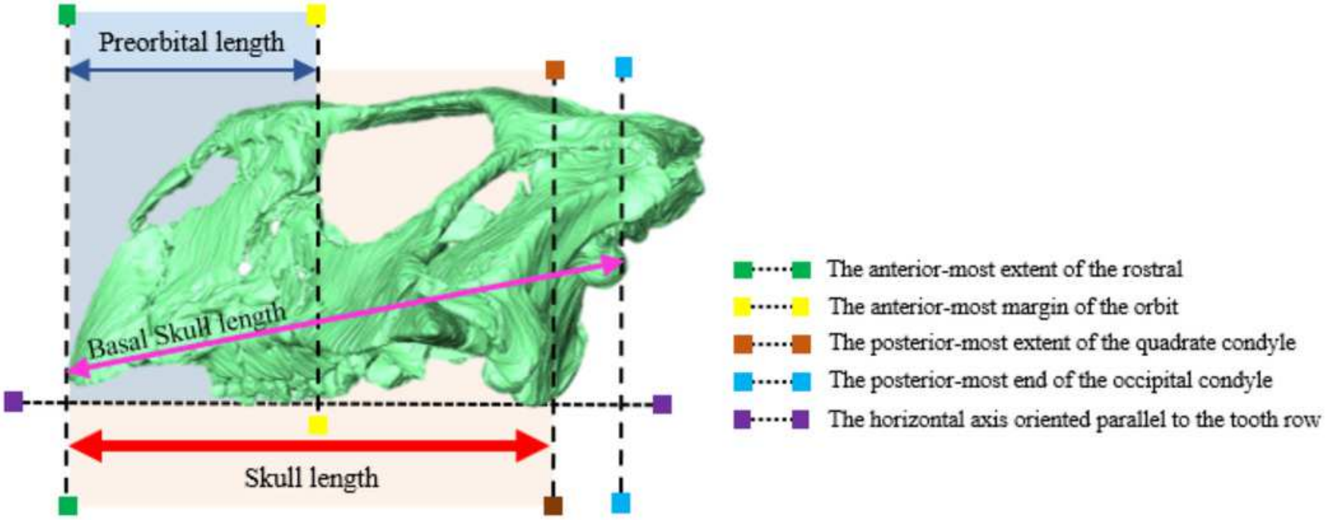
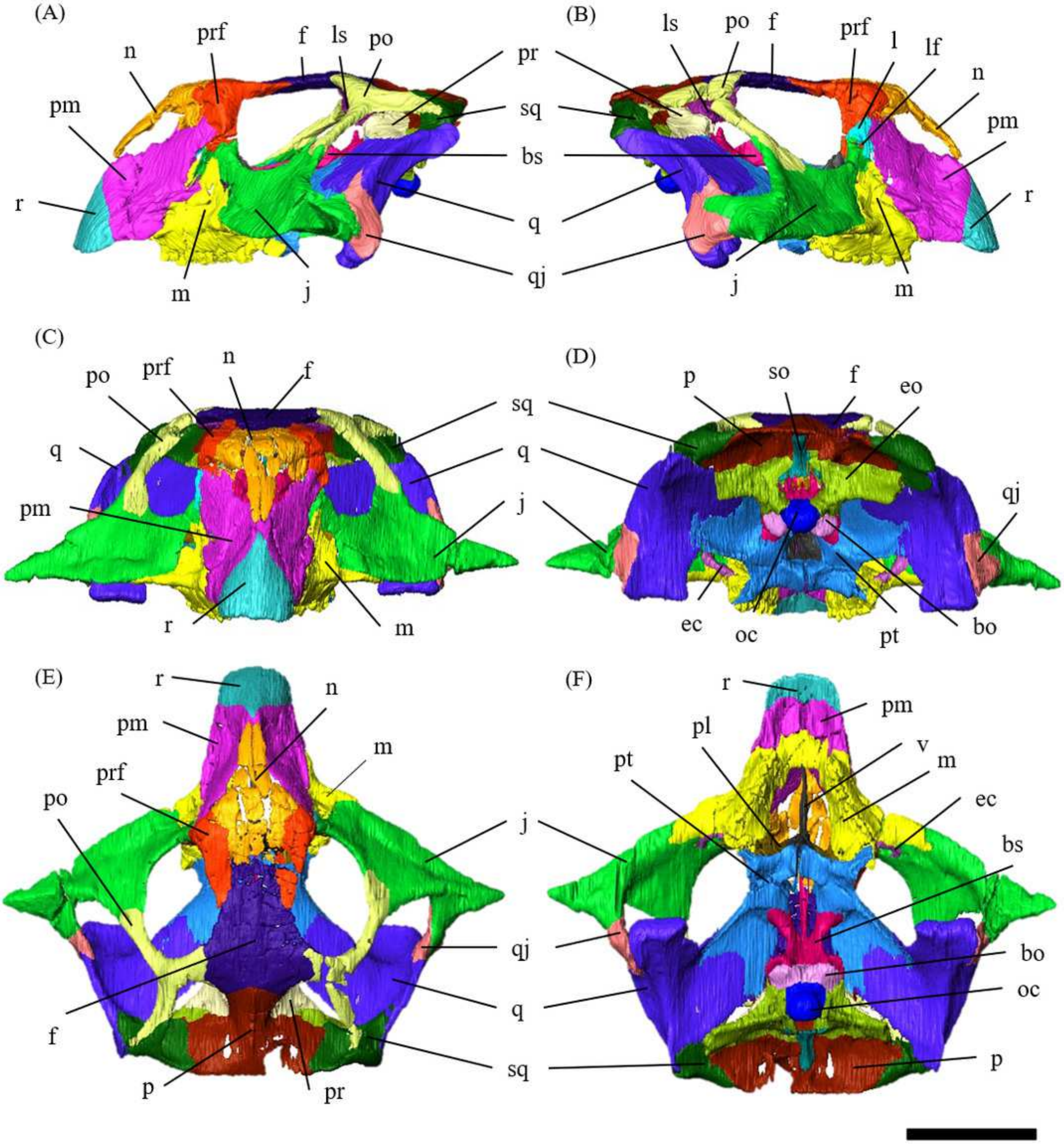


Figure 3

Segmented cranium of *P. houi* (ZMNH M12414) in left lateral (A), right lateral (B), anterior (C), posterior (D), dorsal (E) and ventral (F) views.

Abbreviations: bo, basioccipital; bs, basisphenoid; ec, ectopterygoid; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; lf, lacrimal foramen; ls, laterosphenoid; m, maxilla; n, nasal; oc, occipital condyle; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; pr, prootic; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; r, rostral; so, supraoccipital; sq, squamosal; v, vomer. Scale bar equals 50 mm.


(A)
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f
ls
po
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m
j
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sq
bs
q
qj
(B)
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po
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prf
l
lf
n
pm
r
j
m
(C)
po
prf
n
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q
pm
r
m
(D)
p
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f
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q
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oc
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(E)
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(F)
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bo
oc
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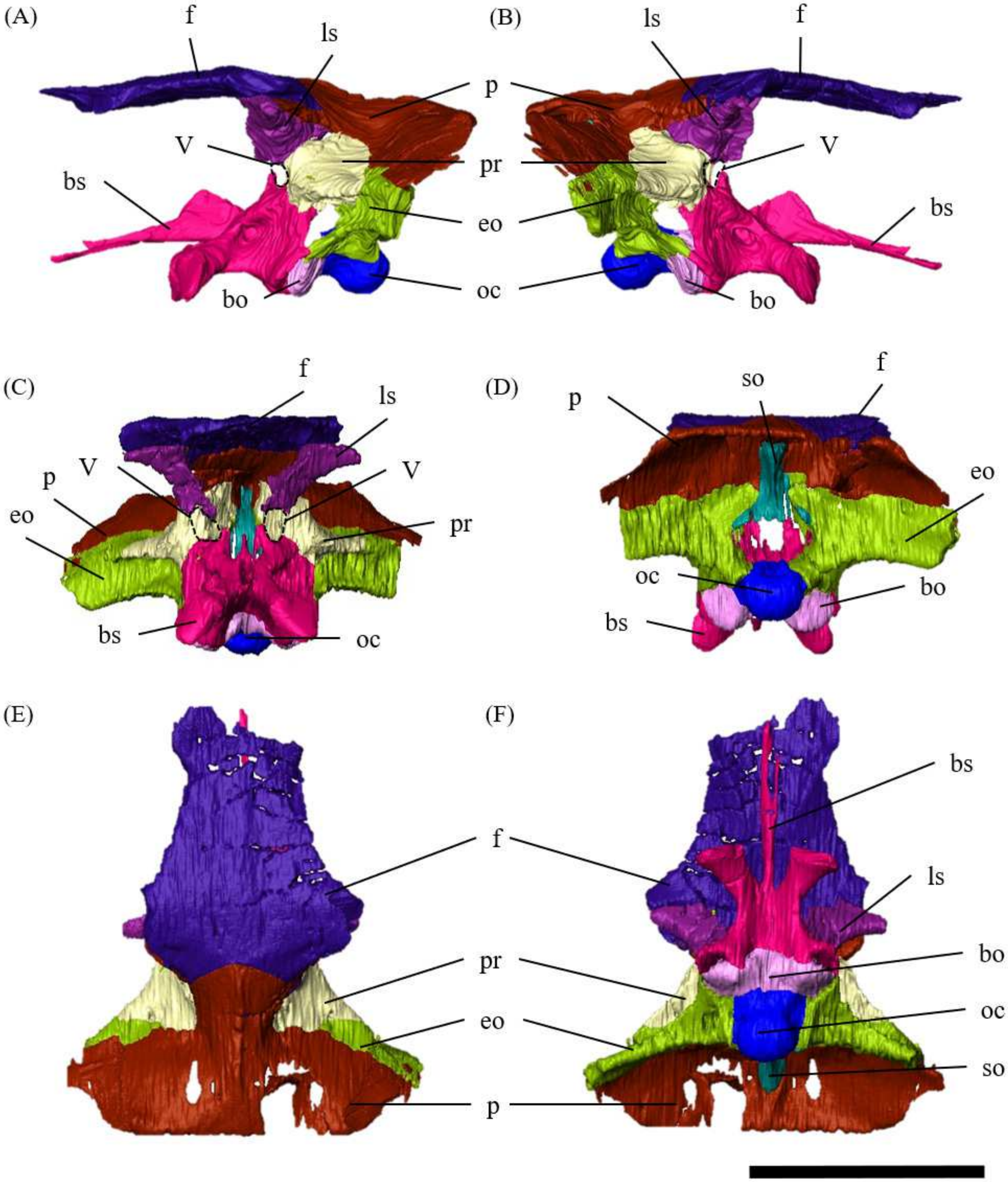
Figure 4

Braincase of *P. houi* (ZMNH M12414) in left lateral (A), right lateral (B), anterior (C), posterior (D), dorsal (E) and ventral (F) views.

Abbreviations: bo, basioccipital; bs, basisphenoid; eo, exoccipital; f, frontal; ls, laterosphenoid; oc, occipital condyle; p, parietal; so, supraoccipital; V, trigeminal foramen. Scale bar equals 50 mm.


(A)
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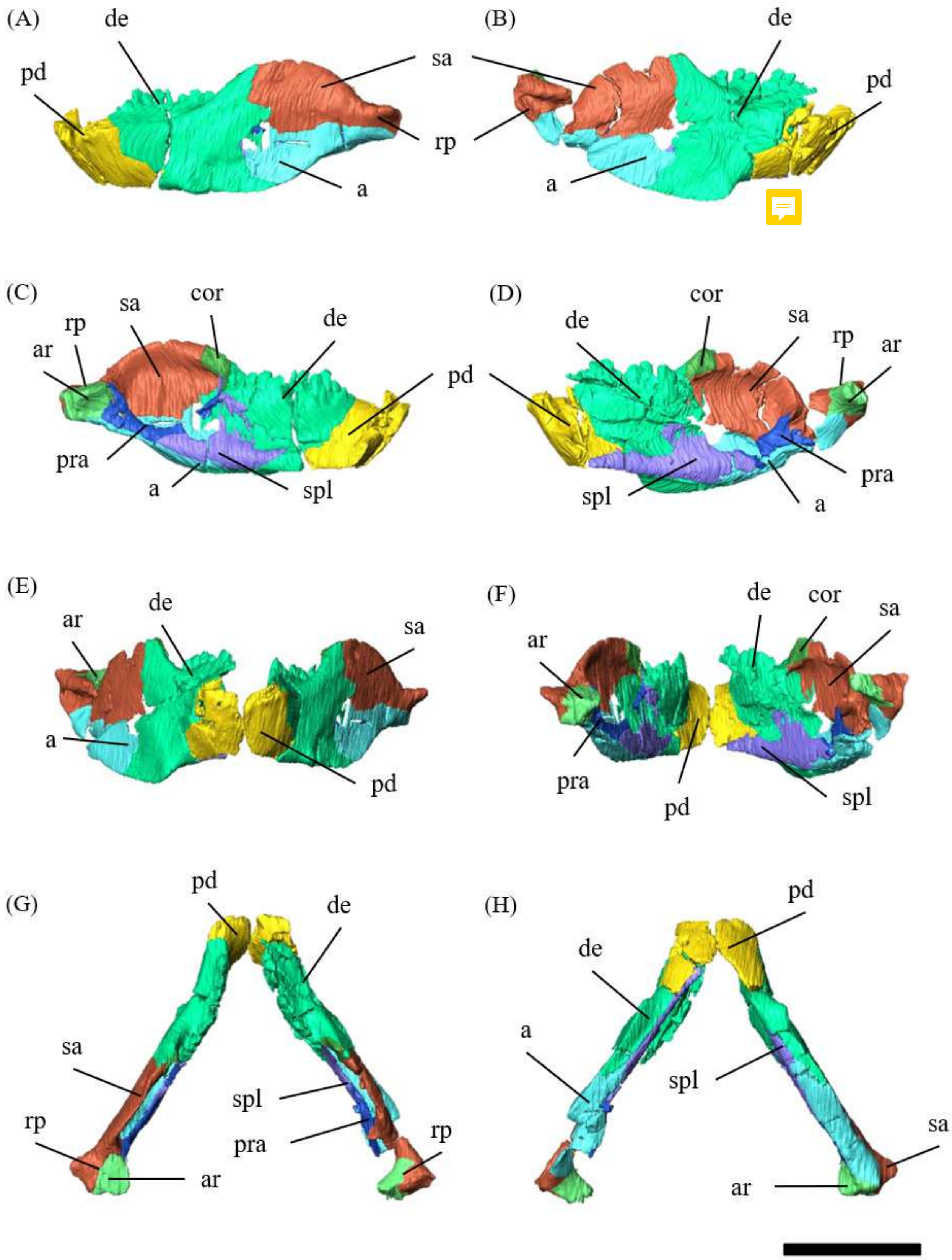
bo
(C)
f
ls
V
p
V
eo
pr
bs
oc
(D)
so
f
p
eo
oc
bo
bs
(E)
(F)
bs
f
ls
pr
bo
eo
oc
so
p

Figure 5

Mandibles of *P. houi* (ZMNH M12414) with individual lower jaw elements colored in left lateral (A), right lateral (B), left medial (C), right medial (D), anterior (E), posterior (F), dorsal (G) and ventral (H) views.

Abbreviations: a, angular; ar, articular; cor, coronoid; de, dentary; pd, predentary; pra, prearticular; sa, surangular; spl, splenial. Scale bar equals 50 mm.


(A)
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pd
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rp
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(B)
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(C)
cor
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rp
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pra
a
spl
(D)
cor
de
sa
rp
ar
pd
pra
spl
a
(E)
ar
de
sa
a
pd
(F)
de
cor
sa
ar
pra
pd
spl
(G)
pd
de
sa
spl
rp
pra
rp
ar
(H)
pd
de
a
spl
sa
ar

Figure 6

Strict consensus of 16,001 most parsimonious trees (MPTs) based on the dataset of 78 taxa and 380 characters.

Values above and beneath each node indicate bootstrap and Bremer support, respectively (bootstrap values under 50 and Bremer support values equal 1 are not shown). Abbreviations: He, Heterodontosauridae ; Th, Thyreophora ; Pachy, Pachycephalosauria ; Iguan, Iguanodontia; Psi, *Psittacosaurus*; Ch, Chaoyangsauridae .

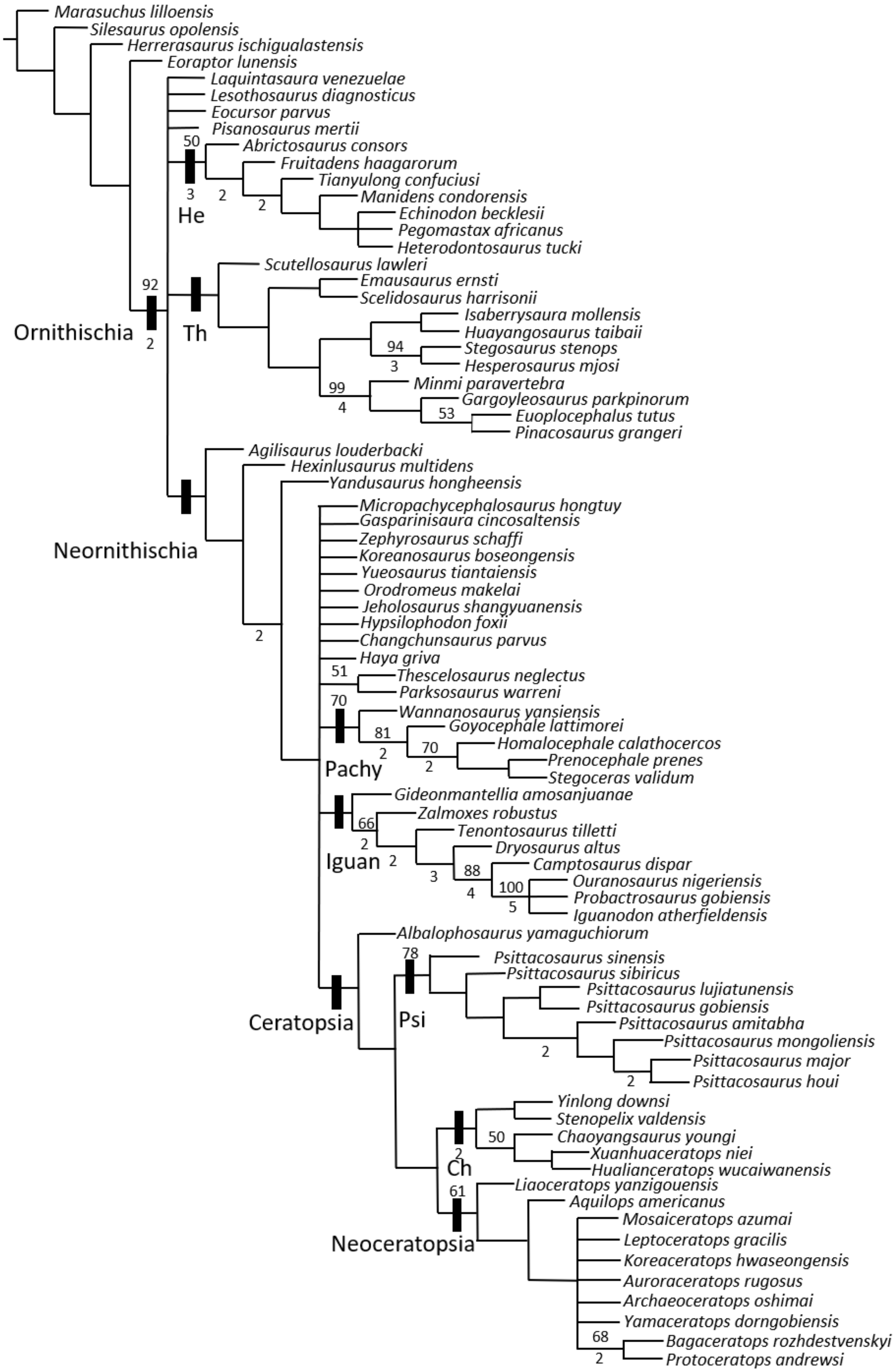
Marasuchus lilloensis
Silesaurus opolensis
Herrerasaurus ischigualastensis
Eoraptor lunensis
Laquintasaura venezuelae
Lesothosaurus diagnosticus
Eocursor parvus
Pisanosaurus mertii
50
Abrictosaurus consors
Fruitadens haagarorum
Tianyulong confuciusi
Manidens condorensis
Echinodon becklesii
Pegomastax africanus
Heterodontosaurus tucki
3
2
2
He
Scutellosaurus lawleri
Emausaurus ernsti
Scelidosaurus harrisonii
Isaberrysaura mollensis
Huayangosaurus taibaii
94
3
Stegosaurus stenops
Hesperosaurus mjosi
99
4
Minmi paravertebra
Gargoyleosaurus parkpinorum
53
Euoplocephalus tutus
Pinacosaurus grangeri
92
2
Ornithischia
Th
Agilisaurus louderbacki
Hexinlusaurus multidens
Yandusaurus hongheensis
Neornithischia
2
Micropachycephalosaurus hongtuy
Gasparinisaura cincosaltensis
Zephyrosaurus schaffi
Koreanosaurus boseongensis
Yueosaurus tiantaiensis
Orodromeus makelai
Jeholosaurus shangyuanensis
Hypsilophodon foxii
Changchunsaurus parvus
Haya griva
51
Thescelosaurus neglectus
Parksosaurus warreni
70
Wannanosaurus yansiensis
81
2
Goyocephale lattimorei
70
2
Homalocephale calathocercos
Prenocephale prenes
Stegoceras validum
Pachy
Gideonmantellia amosanjuanae
66
2
Zalmoxes robustus
Tenontosaurus tilletti
2
Dryosaurus altus
3
88
4
Camptosaurus dispar
100
5
Ouranosaurus nigeriensis
Probactrosaurus gobiensis
Iguanodon atherfieldensis
Iguan
Albalophosaurus yamaguchiorum
78
Psittacosaurus sinensis
Psittacosaurus sibiricus
Psittacosaurus lujiatunensis
Psittacosaurus gobiensis
Psittacosaurus amitabha
2
Psittacosaurus mongoliensis
Psittacosaurus major
2
Psittacosaurus houi
Ceratopsia
Psi
Yinlong downsi
Stenopelix valdensis
50
Chaoyangsaurus youngi
Xuanhuaceratops niei
Hualianceratops wucaiwanensis
2
Ch
61
Liaoceratops yanzigouensis
Aquilops americanus
Mosaiceratops azumai
Leptoceratops gracilis
Koreaceratops hwaseongensis
Auroraceratops rugosus
Archaeoceratops oshimai
Yamaceratops dorngobiensis
68
2
Bagaceratops rozhdestvenskyi
Protoceratops andrewsi
Neoceratopsia

Figure 7

Phylogenetic relationships and fossil occurrences with reference to the geological time scale for *Psittacosaurus* species.

Each occurrence is based on Zhong et al. (2021) for *P. houi*, *P.* major and *P. lujiatunensis*, Napoli et al., (2019) for *P. amitabha*, and Sereno (2010) for *P. sinensis*, *P. sibiricus*, *P. gobiensis* and *P. mongoliensis*.

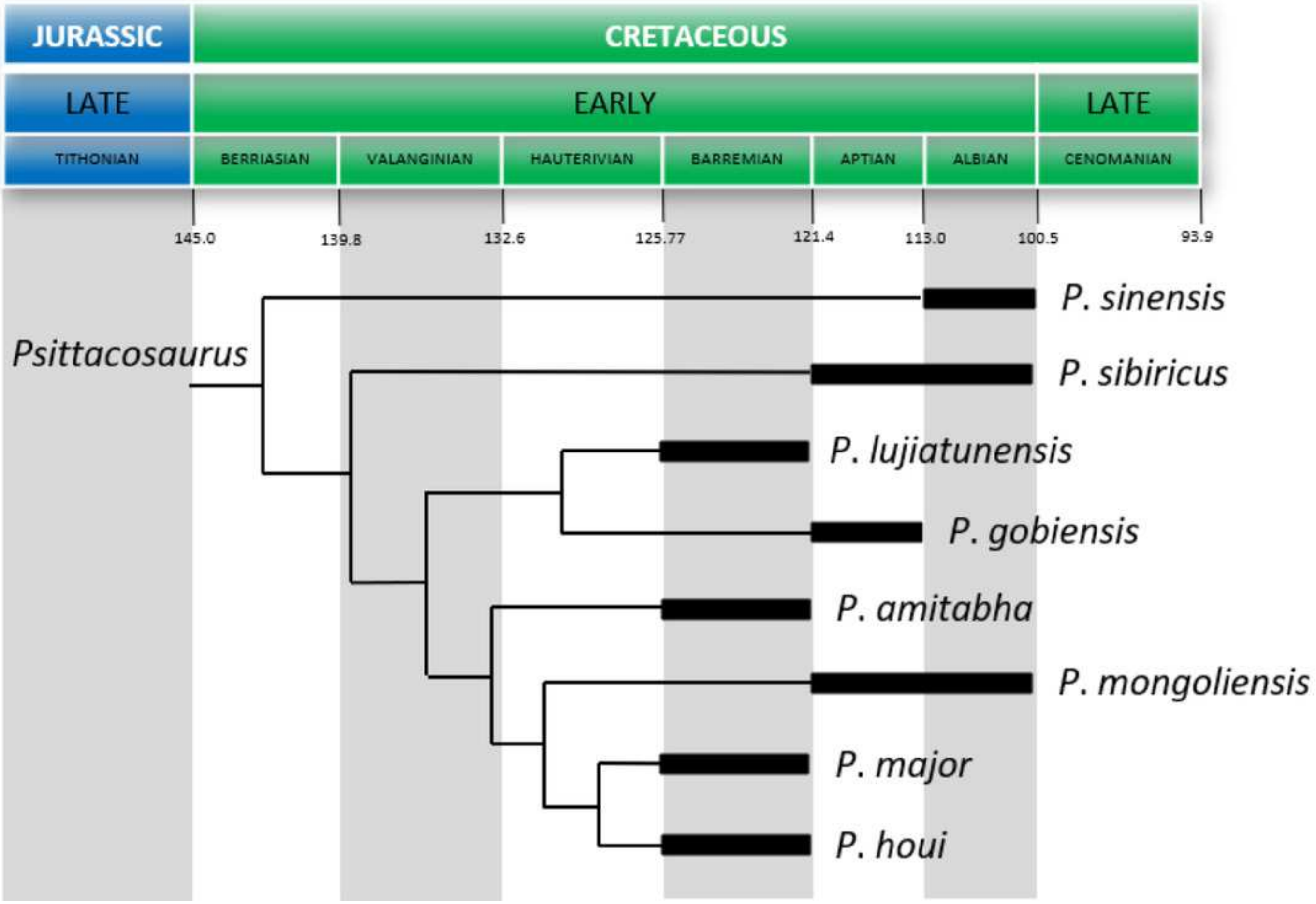

Table 1(on next page)

Diagnostic characters of the genus *Psittacosaurus* compared with the respective characters in *Psittacosaurus houi* (ZMNH M12414 and IVPP V12617).

All characters are based on Sereno (2010) except the presence or absence of the lacrimal canal fenestra, which is considered as a taphonomic artifact by Napoli et al. (2019) (see text). ✓, present; -, not present; ?, undetermined.

Characters	***Psittacosaurus***	***P. houi***	
		ZMNH M12414	**IVPP V12617**
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	✓	✓	✓
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	✓	?	✓

Table 2(on next page)

Characters compared between *Psittacosaurus houi* (ZMNH M12414 and IVPP V12617) and *P. lujiatunensis* and *P. major*.

✓, present; -, not present.

Characters	Citation	*P. houi*		*P. lujiatunensis*	*P. major*
		ZMNH M12414	**IVPP V12617**		
long preorbital region reaching about one half of the skull length	in this study	✓	✓	-	-
posterodorsally sloped anterior margin formed by the rostrals and nasals	in this study	✓	✓	-	-
narrow prefrontal-premaxilla contact	in this study	✓	✓	-	-
posterodorsally-elongated laterotemporal fenestra oriented at an angle of about 45 degrees in lateral view	in this study	✓	✓	-	-
higher ventral margin of the premaxilla raised above the maxillary tooth row	in this study	✓	✓	-	-
large surface area of the jugal exposed in dorsal view	in this study	✓	✓	-	-
subtriangular supraoccipital widest at its ventral margin	in this study	✓	✓	-	-
posterior margin of the parietal nearly linear perpendicular to the sagittal crest with no indentation on the midline	in this study	✓	✓	-	-
height of the retroarticular process approximately at the same level as the dentary tooth row	in this study	✓	✓	-	-
proportion of the width across the anterior margins to that across the posterior margins of the maxillary tooth rows more than 45% in ventral view	Han et al., 2018	✓	✓	✓	-
triangular, or subtriangular, shape of the maxillary fossa	Han et al., 2018	✓	✓	✓	-
infratemporal ramus of the jugal forming the anteroventral margin of the infratemporal fenestra, without expanding dorsally to form a part of the posterior margin	Han et al., 2018	✓	✓	✓	-

elongate basipterygoid processes subequal in length to the body of the basisphenoid as measured from the notch between the processes to the basal tubera	Sereno, 2010; Hedrick and Dodson, 2013	✓	✓	-	✓
external naris lying above the maxilla	Han et al., 2018	✓	✓	-	✓
position of the maxillary fossa lying anterior to the orbit	Han et al., 2018	✓	✓	-	✓
strongly curved ventral margin of the dentary	Han et al., 2018	✓	✓	-	✓

1

Table 3(on next page)

Diagnostic characters of previously described *Psittacosaurus* species compared with the respective characters in *P*. *houi* (ZMNH M12414 and IVPP V12617).

All characters are based on Sereno (2010), except for *P*. *gobiensis* (Sereno et al., 2010) and *P*. *amitabha* (Napoli et al., 2019). *P*. *lujiatunensis* and *P*. *major* were excluded because the referred characters was shown to be invalid (Hedrick and Dodson, 2013). ✓, present in ZMNH M12414; -, not present in ZMNH M12414; ?, undetermined.

Species	**Characters**	***P. houi***	
		ZMNH M12414	**IVPP V12617**
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. xinjiangensis	hook-shaped palpebral with V-shaped posterior margin	?	?
	dentary teeth with as many 21 denticles in the posterior center of the tooth row	?	-
	ossified tendons extending into mid-caudal vertebrae	?	?
	narrow iliac postacetabular process with height at midlength less than 25% of the length of the process	?	?
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 40 degrees 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	?	?