

= Psittacosaurus =

Psittacosaurus (/ ˈsɪtəˈkɒsɔːrəs / SIT @-@ ? @-@ k? @-@ SOR @-@ ?s ; " parrot lizard ") is a genus of extinct ceratopsian dinosaur from the Early Cretaceous of what is now Asia , existing between 123 @.@ 2 and 100 million years ago . It is notable for being the most species @-@ rich dinosaur genus . Up to 11 species are known , from across Mongolia , Siberia , China , and possibly Thailand . The species of *Psittacosaurus* were obligate bipeds at adulthood , with a high skull and a robust beak . One individual was found preserved with long filaments on the tail , similar to those of *Tianyulong* , and scales across the rest of the animal . *Psittacosaurus* probably had complex behaviours , based on the proportions and relative size of the brain . It may have been active for short periods of time during the day and night , and had well @-@ developed senses of smell and vision .

Psittacosaurus was one of the earliest ceratopsians , but closer to *Triceratops* than *Yinlong* . Once in its own family , *Psittacosauridae* , with other genera like *Hongshanosaurus* , it is now considered to be senior synonym of the latter and an early offshoot of the branch that led to more derived forms . The genera closely related to *Psittacosaurus* are all from Asia , with the exception of *Aquilops* , from North America . The first species was either *P. lujiatunensis* or closely related , and it may have given rise to later forms of *Psittacosaurus* .

Psittacosaurus is one of the most completely known dinosaur genera . Fossils of hundreds of individuals have been collected so far , including many complete skeletons . Most age classes are represented , from hatchling through to adult , which has allowed several detailed studies of *Psittacosaurus* growth rates and reproductive biology . The abundance of this dinosaur in the fossil record has led to the labelling of Lower Cretaceous sediments of east Asia the *Psittacosaurus* biochron .

= = Description = =

The species of *Psittacosaurus* vary in size and specific features of the skull and skeleton , but share the same overall body shape . The best @-@ known ? *P. mongoliensis* ? can reach 2 metres (6 @.@ 5 ft) in length . The maximum adult body weight was most likely over 20 kilogrammes (44 lb) in *P. mongoliensis* . Several species approach *P. mongoliensis* in size (*P. lujiatunensis* , *P. neimongoliensis* , *P. xinjiangensis*) , while others are somewhat smaller (*P. sinensis* , *P. meileyingensis*) . The smallest known species , *P. ordosensis* , is 30 % smaller than *P. mongoliensis* . The largest are *P. lujiatunensis* and *P. sibiricus* , although neither is significantly larger than *P. mongoliensis* . *Psittacosaurus* postcranial skeletons are more typical of a ' generic ' bipedal ornithischian . There are only four digits on the manus (' hand ') , as opposed to the five found in most other ornithischians (including all other ceratopsians) , while the four @-@ toed hindfoot is very similar to many other small ornithischians .

The skull of *Psittacosaurus* is highly modified compared to other ornithischian dinosaurs of its time . Extremely tall in height and short in length , the skull has an almost round profile in some species . The portion in front of the orbit (eye socket) is only 40 % of total skull length , shorter than any other known ornithischian . The lower jaws of psittacosaurids are characterised by a bulbous vertical ridge down the centre of each tooth . Both upper and lower jaws sport a pronounced beak , formed from the rostral and predentary bones , respectively . The bony core of the beak may have been sheathed in keratin to provide a sharp cutting surface for cropping plant material . As the generic name suggests , the short skull and beak superficially resemble those of modern parrots . *Psittacosaurus* skulls share several adaptations with more derived ceratopsians , such as the unique rostral bone at the tip of the upper jaw , and the flared jugal (cheek) bones . There is still no sign of the bony neck frill or prominent facial horns which would develop in later ceratopsians . Bony horns protrude from the skull of *P. sibiricus* , but these are thought to be an example of convergent evolution .

= = = Species characteristics = = =

Skulls of *P. mongoliensis* are flat on top , especially over the back of the skull , with a triangular depression , the antorbital fossa , on the outside surface of the maxilla (an upper jaw bone) . A flange is present on the lower edge of the dentary (the tooth @-@ bearing bone of the lower jaw) , although it is not as prominent as in *P. meileyingensis* or *P. major* (= *P. lujiatunensis*) . *P. mongoliensis* is among the largest known species . The skull of the type specimen , which is probably a juvenile , is 15 @.@ 2 centimetres (6 in) long , and the associated femur is 16 @.@ 2 centimetres (6 @.@ 4 in) in length . Other specimens are larger , with the largest documented femur measuring about 21 centimetres (8 @.@ 25 in) long .

P. sinensis is readily distinguished from all other species by numerous features of the skull . Adult skulls are smaller than those of *P. mongoliensis* and have less teeth . Uniquely , the premaxillary bone contacts the jugal (cheek) bone on the outside of the skull . The jugals flare out sideways , forming ' horns ' proportionally wider than in any other known *Psittacosaurus* species except *P. sibiricus* and *P. lujiatunensis* . Because of the flared cheeks , the skull is actually wider than it is long . A smaller ' horn ' is present behind the eye , at the contact of the jugal and postorbital bones , a feature also seen in *P. sibiricus* . The mandible (lower jaw) lacks the hollow opening , or fenestra , seen in other species , and the entire lower jaw is bowed outwards , giving the animal the appearance of an underbite . The skull of an adult *P. sinensis* can reach 11 @.@ 5 centimeters (4 @.@ 5 in) in length .

P. sibiricus is the largest known species of *Psittacosaurus* . The skull of the type specimen is 20 @.@ 7 centimetres long (8 @.@ 25 in) , and the femur is 22 @.@ 3 cm (8 @.@ 75 in) in length . It is also distinguished by its neck frill , which is longer than any other species , at 15 to 18 % of skull length . A very striking feature of *P. sibiricus* is the number of ' horns ' around the eyes , with three prominences on each postorbital , and one in front of each eye , on the palpebral bones . Similar horns found on the postorbital of *P. sinensis* are not as pronounced but may be homologous . The jugal has extremely prominent ' horns ' and may contact the premaxilla , both features also seen in the possibly related *P. sinensis* . There is a flange on the dentary of the lower jaw , similar to *P. mongoliensis* , *P. meileyingensis* , and *P. sattayarakhi* . It can be told apart from the other species of *Psittacosaurus* by a combination of 32 anatomical features , including six that are unique to the species . Most of these are skull details , but one unusual feature is the presence of 23 vertebrae between the skull and pelvis , unlike the 21 or 22 in the other species where the vertebrae are known .

P. xinjiangensis is distinguished by a prominent jugal ' horn ' that is flattened on the front end , as well as some features of the teeth . The ilium , one of the three bones of the pelvis , also bears a characteristically long bony process behind the acetabulum (hip socket) . An adult femur has a published length of about 16 centimetres (6 @.@ 3 in) . *P. meileyingensis* has the shortest snout and neck frill of any species , making the skull nearly circular in profile . The orbit (eye socket) is roughly triangular , and there is a prominent flange on the lower edge of the dentary , a feature also seen in specimens of *P. lujiatunensis* , and to a lesser degree in *P. mongoliensis* , *P. sattayarakhi* , and *P. sibiricus* . The complete type skull , probably adult , is 13 @.@ 7 centimetres (5 @.@ 5 in) long . The dentary of *P. sattayarakhi* has a flange similar to that found in *P. mongoliensis* , *P. sibiricus* , *P. lujiatunensis* and *P. meileyingensis* , although it is less pronounced than in those species . The material appears to be roughly the same size as *P. sinensis* . The frontal bone of *P. neimongoliensis* is distinctly narrow compared to that of other species , resulting in a narrower skull overall . The ischium bone of the pelvis is also longer than the femur , which differs from other species in which these bones are known . The type specimen has a skull length of 13 @.@ 2 centimetres (5 @.@ 2 in) and a femoral length of 13 centimetres (5 @.@ 1 in) , but is not fully grown . An adult *P. neimongoliensis* was probably smaller than *P. mongoliensis* , with a proportionately longer skull and tail . *P. ordosensis* can be distinguished by numerous features of the jugals , which have very prominent ' horns ' . It is also the smallest known species . One adult skull measures only 9 @.@ 5 centimeters (3 @.@ 75 in) in length .

The type skull of *P. lujiatunensis* measures 19 cm (7 @.@ 5 in) in length , while the largest known skull is 20 @.@ 5 centimetres (8 in) long , so this species was similar in size to *P. mongoliensis*

and *P. sibiricus* . There is a fossa in front of the eye , as in *P. mongoliensis* . The jugal bones flare outwards widely , making the skull wider than it is long , as seen in *P. sinensis* . Widely flared jugals are also found in *P. sibiricus* . Overall , this species is thought to exhibit several primitive characteristics compared to other species of *Psittacosaurus* , which is consistent with its greater geological age . *P. gobiensis* was small @-@ bodied (1 metre (3 @.@ 3 ft) long) and differs from other species of *Psittacosaurus* by " significant , but structurally minor , details . " These include the presence of a pyramidal horn on the postorbital , a depression on the postorbital @-@ jugal contact , and enamel thickness . *P. mongoliensis* was a contemporary .

= = = Integument = = =

The integument , or body covering , of *Psittacosaurus* is known from a Chinese specimen , which most likely comes from the Yixian Formation of Liaoning Province , China . The specimen , which is not yet assigned to any particular species , was illegally exported from China , in violation of Chinese law , but was purchased by a German museum . It was described while awaiting repatriation .

Most of the body was covered in scales . Larger scales were arranged in irregular patterns , with numerous smaller scales occupying the spaces between them , similarly to skin impressions known from other ceratopsians , such as *Chasmosaurus* . A series of what appear to be hollow , tubular bristle @-@ like structures , approximately 16 centimetres (6 @.@ 4 in) long , were also preserved , arranged in a row down the dorsal (upper) surface of the tail . These were confirmed by the authors , as well as an independent scientist , to not represent plant material . The bristle @-@ like integumentary structures extend into the skin nearly to the vertebrae , and were likely circular or tubular before being preserved . Under ultraviolet light , they gave off the same fluorescence as scales , providing the possibility they were keratinized . As the authors of the study said , " At present , there is no convincing evidence which shows these structures to be homologous to the structurally different integumentary filaments of theropod dinosaurs " , however , they stated that all other feathery integument from the Yixian Formation is indeed feathers .

In 2008 , another study was published describing the integument and dermis of *Psittacosaurus* sp . , from two different specimens . The skin remains could be observed by a natural cross @-@ section to compare them to modern animals , showing that dinosaurian dermal layers evolved in parallel to those in many other large vertebrates . The collagen tissue fibres in *Psittacosaurus* are complex , virtually identical to all other vertebrates in structure but having an exceptional thickness of about forty layers . As the sections of dermis were collected from the abdomen , where the scales were eroded , the tissue may have assisted with the musculature of the stomach and intestines and offered protection against predators .

= = Paleobiology = =

The brain of *P. lujiatunensis* is well known ; a study on the anatomy and functionality of three specimens was published in 2007 . Until the study , it was generally thought the brain of *Psittacosaurus* would have been similar to other ceratopsians with low Encephalisation Quotients . Russell and Zhao (1996) believed " the small brain size of psittacosaur implies a very restrictive behavioural repertoire relative to that of modern mammals of similar body size " . However , the 2007 study dispelled this theory when it found the brain to be more advanced . There is generally negative allometry for brain size with development in vertebrates , but this was shown not to be true in *Psittacosaurus* . The EQ score for *P. lujiatunensis* is 0 @.@ 31 , significantly higher than genera such as *Triceratops* . A higher EQ correlates with more complex behaviour , and various dinosaurs have high EQs , similar to birds , which range from 0 @.@ 36 to 2 @.@ 98 . Thus , *Psittacosaurus* behaviour could have been as complex as that in *Tyrannosaurus* , whose EQ ranges from 0 @.@ 30 to 0 @.@ 38 . Behaviours influenced by high EQs include nest @-@ building , parental care , and bird @-@ like sleeping , some of which have been shown to be present in *Psittacosaurus* .

The senses of *Psittacosaurus* can be inferred from the endocast . Large olfactory bulbs are present

, indicating the genus had an acute sense of smell . The size of these bulbs are comparable to large predatory theropods , although they likely evolved to avoid predators instead of to seek out prey . The sclerotic rings in reptiles directly show the size of the eyeball . The rings are not well preserved in Psittacosaurus , with one individual preserving them likely contracted postmortem , but if they are similar to those of Protoceratops , Psittacosaurus would have had large eyes and acute vision . The curvature of the semicircular canals is related to the agility of reptiles , and the large curved canals in Psittacosaurus show that the genus was much more agile than later ceratopsians . Comparisons between the scleral rings of Psittacosaurus and modern birds and reptiles suggest that it may have been cathemeral , active throughout the day and for short intervals at night .

Ford and Martin (2010) proposed that Psittacosaurus was semi @-@ aquatic , swimming with its tail like a crocodile , and paddling and kicking . They based their interpretation on evidence including : the lacustrine (lake) depositional setting of many specimens ; the position of the nostrils and eyes ; interpretations of the motions of the arms and legs ; tails with long chevrons (and with the bristles on the tail interpreted as possibly skin @-@ covered , forming a fin) , providing a propulsive surface ; and the presence of gastroliths , interpreted as ballast . They further suggested that some species of Psittacosaurus were more terrestrial than others .

= = = Diet = = =

Psittacosaurus had self @-@ sharpening teeth that would have been useful for cropping and slicing tough plant material . Unlike later ceratopsians , they did not have teeth suitable for grinding or chewing their food . Instead , they used gastroliths ? stones swallowed to wear down food as it passed through the digestive system . Sometimes numbering more than fifty , these stones are occasionally found in the abdominal cavities of psittacosaurus , and may have been stored in a gizzard , as in modern birds .

Unlike many other dinosaurs , psittacosaurus had akinetic skulls : that is to say , the upper and lower jaws each behaved as a single unit , without internal joints . The only joint was the jaw joint itself , and psittacosaurus could slide their lower jaws forward and backward on the joint , permitting a shearing action . Unlike most ceratopsians , their beaks did not form curved tips , but were instead rounded and flattened . If the jaws were aligned , the beaks could be used to crop objects , but if the lower jaw was retracted so that the lower beak was inside the upper beak , the jaws may have served a nutcracking function . A nut- or seed @-@ rich diet would also match well with the gastroliths often seen in well @-@ preserved psittacosaur skeletons .

= = = Limb function = = =

Studies by Phil Senter in 2007 conducted on *P. neimongoliensis* and *P. mongoliensis* concluded that the forelimbs of these taxa (and likely those of other Psittacosaurus species) were too short (only about 58 % as long as the hindlimbs) to reach the ground , and their range of motion indicates they could neither be pronated nor generate propulsive force for locomotion , suggesting that Psittacosaurus was entirely bipedal . The forelimbs were also too short to be used in digging or bringing food to the mouth , and Senter suggested that if Psittacosaurus needed to dig depressions in the ground it may have used its hindlimbs instead . The forelimbs could be used for two @-@ handed grasping of objects or scratching the body , but due to their extremely limited flexibility and reach , they could have only been used to grasp objects very close to the belly or sides of the animal and could have scratched only the belly , flank and knees . Even though the hands could not reach the mouth , Psittacosaurus could have still used them to carry nesting material or food to a desired location .

However , Psittacosaurus may not have been entirely bipedal for its entire lifespan . Taking sections from the limb bones of 16 specimens of Psittacosaurus , ranging in age from less than a year old to ten @-@ year old adults , Qi Zhao from the University of Bristol found that Psittacosaurus was probably secondarily bipedal . The infants ' front limbs grew at faster rates than the hind limbs at between birth and three years of age . At the age of between four and six years , arm growth slowed

and leg growth accelerated as the animal became mature . At this stage , Psittacosaurus would switch to a bipedal stance . These findings further reveal that the ancestor of Psittacosaurus was likely quadrupedal and eventually gained the ability to become bipedal as it evolved , with the young retaining the quadrupedal gait of the ancestor in question . These findings also lead to the hypothesis that many such dinosaur families may have evolved along this path at some point in their evolution .

== Growth rate ==

Several juvenile Psittacosaurus have been found . The smallest is a *P. mongoliensis* hatchling conserved in the American Museum of Natural History (AMNH) , which is only 11 to 13 centimetres (4 ? 5 inches) long , with a skull 2 @. @ 8 centimetres (1 in) in length . Another hatchling skull at the AMNH is only 4 @. @ 6 centimetres (1 @. @ 8 inches) long . Both specimens are from Mongolia . Juveniles discovered in the Yixian Formation are approximately the same age as the larger AMNH specimen .

A histological examination of *P. mongoliensis* has determined the growth rate of these animals . The smallest specimens in the study were estimated at three years old and less than 1 kilogramme (2 @. @ 2 lb) , while the largest were nine years old and weighed almost 20 kilogrammes (44 lb) . This indicates relatively rapid growth compared to most reptiles and marsupial mammals , but slower than modern birds and placental mammals . An age determination study performed on the fossilized remains of *P. mongoliensis* by using growth ring counts suggest that the longevity of the basal ceratopsian was 10 to 11 years .

== Gregarious juveniles ==

The find of a herd of six Psittacosaurus individuals killed and buried by a volcanic mudflow indicates the presence of at least two age groups from two distinct clutches gathered together . This find has been taken as evidence for group fidelity and gregariousness extending beyond the nest ; the earliest such evidence for any ceratopsian . Even very young psittacosaur teeth appear worn , indicating they chewed their own food and may have been precocial . Another juvenile @-@ only cluster shows that specimens of different ages grouped together . These juveniles may have associated together as a close knit , mixed @-@ age herd either for protection , to enhance their foraging , or as putative helpers at the parental nest . There is no evidence for parental care .

In 2004 , a specimen found in the Yixian Formation was claimed as evidence for parental care in dinosaurs . The specimen DNHM D2156 consists of 34 articulated juvenile Psittacosaurus skeletons , closely associated with the skull of an adult . The juveniles , all approximately the same age , are intertwined in a group underneath the adult , although all 34 skulls are positioned above the mass of bodies , as they would have been in life . This suggests that the animals were alive at the time of burial , which must have been extremely rapid , perhaps due to the collapse of a burrow . However , a 2013 paper pointed out that the adult specimen did not belong with the nest , its skull having no sedimentary connection to the main slab where the juveniles occurred , but had been glued onto it . This artificial association led to the inference that the skull belonged to an individual , possibly a " mother " , that was providing parental care for the 34 juveniles ? a claim that is unfounded . Furthermore , the adult was also shown to be six years old , whereas histological studies have shown *P. mongoliensis* was unable to breed until it reached ten years of age . It is also unlikely that a single female would have so many offspring at one time .

A 2014 analysis of the same specimen concluded that the proximity of the six @-@ year @-@ old specimen to the post @-@ hatchlings may indicate post @-@ hatchling cooperation , making the six @-@ year @-@ old specimen a possible caretaker . Such behaviour is also found in cooperative breeding modern birds .

== Pathology ==

Out of the hundreds of known *Psittacosaurus* specimens , only one has been described to possess any sort of pathology . The specimen in question , consisting of a complete adult skeleton and tentatively assigned to *P. mongoliensis* , was found in the lower beds of the Yixian Formation . There is no sign of a bone fracture , but very clear signs of an infection can be seen near the midpoint of the right fibula . The bone exhibits a large round pit , evidence of necrosis due to a lack of blood supply to the region . The pit is surrounded by a massive amount of swelling along the lower third of the bone . This large amount of bone deposited around the injury indicates that the animal survived for quite a while despite the injury and subsequent infection . As psittacosaurids were bipedal animals , a similar injury to a weight bearing bone in the leg would most likely have been fatal . Unlike the femur and tibia , the fibula is not a weight @-@ bearing bone , so this animal would still have been able to walk to some extent . The source of the injury remains unknown .

= = = Predation = = =

Another fossil from the Yixian Formation provides direct evidence of *Psittacosaurus* as a prey animal . One skeleton of *Repenomamus robustus* , a large triconodont mammal , is preserved with the remains of a juvenile *Psittacosaurus* in its abdominal cavity . Several of the juvenile 's bones are still articulated , indicating that the carnivorous mammal swallowed its prey in large chunks . This specimen is notable in that it is the first known example of Mesozoic mammals preying on live dinosaurs . Heavy predation on juvenile *Psittacosaurus* may have resulted in R @-@ selection , the production of more numerous offspring to counteract this loss .

= = Paleoecology = =

Psittacosaurus is known from hundreds of individual specimens , of which over 75 have been assigned to the type species , *P. mongoliensis* . All *Psittacosaurus* fossils discovered so far have been found in Early Cretaceous sediments in Asia , from southern Siberia to northern China , and possibly as far south as Thailand . The most common age of geologic formations bearing *Psittacosaurus* fossils is from the late Barremian through Albian stages of the Early Cretaceous , or approximately 123 to 100 mya (million years ago) . Many terrestrial sedimentary formations of this age in Mongolia and northern China have produced fossils of *Psittacosaurus* , leading to the definition of this time period in the region as the *Psittacosaurus* biochron .

The earliest known species is *P. lujiatunensis* , found in the lowest beds of the Yixian Formation . Over 200 specimens attributed to this genus have been recovered from these and other beds of the Yixian , the age of which is the subject of much debate . Although many early studies using radiometric dating put the Yixian in the Jurassic Period , tens of millions of years outside of the expected temporal range of *Psittacosaurus* , most recent work dates it to the Early Cretaceous . Using argon @-@ argon dating , a team of Chinese scientists dated the lowest beds in the formation to about 128 mya , and the highest to approximately 122 mya . A more recent Chinese study , using uranium @-@ lead dating , suggests that the lower beds are younger , approximately 123 @.@ 2 mya , while agreeing with an age of 122 mya for the upper beds .

= = History of discovery = =

Psittacosaurus was first described as a genus in 1923 , by Henry Fairfield Osborn . He named the type species *P. mongoliensis* , for the location of its discovery in Mongolia , placing it in the new family Psittacosauridae . Remains of this dinosaur were first discovered the year before , on the third American Museum of Natural History expedition to the Gobi Desert of Mongolia , when one of the expedition 's drivers found the type specimen (AMNH 6254) , which preserves a nearly complete skull , as well as a post cranial skeleton lacking sections of the limbs . This same expedition turned up the remains of many other famous Mongolian dinosaurs , including Protoceratops , Oviraptor , and Velociraptor . Many later expeditions by various combinations of Mongolian , Russian , Chinese , American , Polish , Japanese , and Canadian paleontologists also recovered specimens from

throughout Mongolia and northern China . In these areas , *Psittacosaurus mongoliensis* fossils are found in most sedimentary strata dating to the Aptian to Albian stages of the Early Cretaceous Period , or approximately 125 to 100 Ma (million years ago) . Fossil remains of over 75 individuals have been recovered , including nearly 20 complete skeletons with skulls . Individuals of all ages are known , from hatchlings less than 13 centimetres (5 in) long , to very old adults reaching nearly 2 metres (6 @.@ 5 ft) in length .

When describing *Psittacosaurus mongoliensis* in 1923 , Osborn also gave the name *Protiguanodon mongoliense* to another skeleton found nearby , believing it to represent an ancestor of the ornithomimid *Iguanodon* , in the new subfamily *Protiguanodontinae* . *Protiguanodon mongoliense* , AMNH 6523 , measured 1 @.@ 35 m (4 @.@ 4 ft) long , and was known from much of the skeleton , although at the time of description the neck vertebrae were still covered by matrix . Osborn diagnosed his taxa on the basis of features of the teeth and snout . However , modern taxonomists find these features insignificant , instead placing *Protiguanodon mongoliense* within *Psittacosaurus mongoliensis* . When the skeleton was prepared further , it became clear that it was nearly identical to *Psittacosaurus mongoliensis* . In 1958 , Chinese paleontologist Yang Zhongjian (better known as C. C. Young) renamed the skeleton *Psittacosaurus protiguanodonensis* . Today the specimen is generally referred to as the species *Psittacosaurus mongoliensis* and the names *Protiguanodon mongoliense* and *Psittacosaurus protiguanodonensis* are considered junior synonyms of the name *Psittacosaurus mongoliensis* , which was coined first .

In 1931 , C. C. Young named a new species of *Psittacosaurus* for a partial skull discovered in Inner Mongolia , China . The skull was named *P. osborni* after Henry Fairfield Osborn . The validity of this species is now considered equivocal . Sereno (1990) considered it a synonym of *P. mongoliensis* , which is found in nearby strata of the same age . You and Dodson (2004) listed it as valid in a table , but not in their text . In a 2010 review , Sereno again regarded *P. osborni* as a synonym of *P. mongoliensis* , but noted it was tentative because of the presence of multiple valid psittacosaur species in Inner Mongolia . Young also described the species *P. tingi* in the same 1931 report which contained *P. osborni* . It is based on several skull fragments . He later synonymised the two species under the name *P. osborni* . You and Dodson (2004) followed this in a table , but Sereno regarded both species as synonyms of *P. mongoliensis* ; a table in the latter reported *P. tingi* as a *nomen dubium* , however . The front half of a skull from Guyang County in Inner Mongolia was described as *Psittacosaurus guyangensis* in 1983 . Disarticulated postcranial remains representing multiple individuals were found at the same locality and were assigned to the species . While it differs from the type specimen of *P. mongoliensis* , it falls within the range of individual variation seen in other specimens of that species and is no longer recognised as a valid species . You and Dodson (2004) included *P. guyangensis* in a table of valid taxa , but did not include it as such in their text .

= = = Assigned species = = =

Seventeen species have been referred to the genus *Psittacosaurus* , although only nine to eleven are considered valid today . This is the highest number of valid species currently assigned to any single dinosaur genus (not including birds) . In contrast , most other dinosaur genera are monospecific , containing only a single known species . The difference is most likely due to artifacts of the fossilisation process . While *Psittacosaurus* is known from hundreds of fossil specimens , most other dinosaur species are known from far fewer , and many are represented by only a single specimen . With a very high sample size , the diversity of *Psittacosaurus* can be analysed more completely than that of most dinosaur genera , resulting in the recognition of more species . Most extant animal genera are represented by multiple species , suggesting that this may have been the case for extinct dinosaur genera as well , although most of these species may not have been preserved . In addition , most dinosaurs are known solely from bones and can only be evaluated from a morphological standpoint , whereas extant species often have very similar skeletal morphology but differ in other ways which would not normally be preserved in the fossil record , such as behaviour , or colouration . Therefore , actual species diversity may be much higher than currently recognised in this and other dinosaur genera . As some species are known only from skull

material , species of *Psittacosaurus* are primarily distinguished by features of the skull and teeth . Several species can be recognised by features of the pelvis as well .

In the 1950s , a new Chinese species of *Psittacosaurus* was found in the Aptian @-@ Albian Qingshan Formation of Shandong Province , southeast of Beijing . C. C. Young called it *P. sinensis* to differentiate it from *P. mongoliensis* , which had originally been found in Mongolia . Fossils of more than twenty individuals have since been recovered , including several complete skulls and skeletons , making this the most well @-@ known species after *P. mongoliensis* . Chinese paleontologist Zhao Xijin named a new species after his mentor , C. C. Young , in 1962 . However , the type specimen of *P. youngi* (a partial skeleton and skull) was discovered in the same rocks as *P. sinensis* and appears to be very similar , so *P. youngi* is generally considered a junior synonym of that better @-@ known species . As with *P. guyangensis* and *P. osborni* , You and Dodson (2004) listed it as valid in a table , but not in their text .

In 1988 , Zhao and American paleontologist Paul Sereno described *P. xinjiangensis* , named after the Xinjiang Autonomous Region in which it was discovered . Several individuals of different ages were discovered in the early 1970s by Chinese paleontologists and described by Sereno and Zhao , although the holotype and most complete skeleton belonged to a juvenile . An adult skeleton was later discovered at a different locality in Xinjiang . These specimens come from the upper part of the Tugulu Group , which is regarded as Aptian @-@ Albian in age . A second species described in 1988 by Sereno and Zhao , along with two Chinese colleagues , was *P. meileyingensis* from the Jiufotang Formation , near the town of Meileyingzi , Liaoning Province , northeastern China . This species is known from four fossil skulls , one associated with some skeletal material , found in 1973 by Chinese scientists . The age of the Jiufotang in Liaoning is unknown , but in the neighbouring province of Inner Mongolia , it has been dated to about 110 Ma , in the Albian stage of the Early Cretaceous .

French paleontologist Eric Buffetaut and a Thai colleague , Varavudh Suteethorn , described a partial upper and lower jaw from the Aptian @-@ Albian Khok Kruat Formation of Thailand in 1992 , giving it the name *Psittacosaurus sattayarak* . In 2000 , Sereno questioned the validity of this species , citing its eroded and fragmentary nature , and noted an absence of features characteristic of the genus *Psittacosaurus* . However , in 2002 the original authors published new images of the fossil which seem to show teeth in the lower jaw that exhibit the bulbous vertical ridge characteristic of psittacosaurids . Other authors have also defended its validity , while some continue to regard it as dubious . Sereno (2010) proposed that the best assignment for the type material may be *Ceratopsia incertae sedis* .

Two new species of *Psittacosaurus* were described by Canadian Dale Russell and Zhao in 1996 . The first was named *P. neimongoliensis* , after the Mandarin Chinese name for Inner Mongolia . It is based on a nearly complete fossil skeleton , including most of the skull , found in the Early Cretaceous Ejinhor Formation with seven other individuals . Russell and Zhao also named *P. ordosensis* in 1996 , after the Ordos prefecture of the Inner Mongolia Autonomous Region . The type specimen is a nearly complete skeleton , including part of the skull . However , only the skull , lower jaw , and foot have been described . Three other specimens were referred to this species but remain undescribed . Like *P. neimongoliensis* , this species was discovered in the Eijnhor Formation . Sereno (2010) found the species as described to be indistinguishable from *P. sinensis* , another small species , but suggested that additional study of *P. ordosensis* might reveal diagnostic features . He provisionally designated *P. ordosensis* a nomen dubium .

Xu Xing , another Chinese paleontologist , named a new species of *Psittacosaurus* in 1997 , based on a complete skull with associated vertebrae and a forelimb . This material was recovered in Gansu Province , near the border with Inner Mongolia . This species is named *P. mazongshanensis* after the nearby mountain called Mazongshan (Horse Mane Mountain) and has been described in a preliminary manner . Unfortunately , the skull was damaged while in the care of the Chinese Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) , and several fragments have been lost , including all of the teeth . The remains were found in the Lower Xinminbao Formation , which have not been precisely dated , although there is some evidence that they were deposited in the late Barremian through Aptian stages . Sereno suggested in 2000 that *P. mazongshanensis* was a

nomen dubium , with no unique features that separate it from any other species of *Psittacosaurus* . However , more recent authors have noted that it can be distinguished by its proportionally long snout compared to other species of *Psittacosaurus* , as well as a prominent bony protuberance , pointing outwards and downwards , on the maxilla of the upper jaw . The maxillary protuberance is also now missing . Other features originally used to distinguish the species have been recognised as the results of the deformation of the skull after fossilisation . Sereno (2010) remained unconvinced of its validity .

Beginning in the 1950s , Russian paleontologists began excavating *Psittacosaurus* remains at a locality near the village of Shestakovo in the oblast of Kemerovo in Siberia . Two other nearby localities were explored in the 1990s , one of which produced several complete skeletons . This species was named *P. sibiricus* in 2000 in a scientific paper written by five Russian paleontologists , but credit for the name is officially given to two of those authors , Alexei Voronkevich and Alexander Averianov . The remains were not completely described until 2006 . Two nearly complete , articulated skeletons and a variety of disarticulated material from other individuals of all ages are known from the Ilek Formation of Siberia , which ranges from the Aptian to Albian stages of the Early Cretaceous .

P. lujiatunensis , named in 2006 by Chinese paleontologist Zhou Chang @-@ Fu and three Chinese colleagues , is one of the oldest known species , based on four skulls from the lower beds of Yixian Formation , near the village of Lujiatun . While this bed has been dated differently by different authors , from 128 Ma in the Barremian stage , to 125 Ma in the earliest Aptian , revised dating methods have shown them to be about 123 million years old . *P. lujiatunensis* was contemporaneous with another psittacosaurid species , *Hongshanosaurus houi* , which was found in the same beds . It is potentially synonymous with *H. houi* ; Sereno (2010) , who proposed that *Hongshanosaurus* is a synonym of *Psittacosaurus* , opted to leave *P. lujiatunensis* and *H. houi* separate species due to the inadequacies of the latter 's type specimen . One nearly complete skeleton of *P. lujiatunensis* from the same lower beds of the Yixian Formation had previously been classified in its own species , *Psittacosaurus major* , named for the large size of its skull by Sereno , Zhao and two colleagues in 2007 . You and colleagues described an additional specimen and concurred that it was distinct from *P. lujiatunensis* . *P. major* was originally characterised by a proportionately large skull , which was 39 % of the length of its torso , compared to 30 % in *P. mongoliensis* , and other features . However , a 2013 study utilising morphometric analysis showed that the supposed differences between *P. lujiatunensis* and *P. major* were due to differences in preservation and crushing . The study concluded that both represented a single species .

A third species of Lujiatun psittacosaur , the first to be named , was described as *Hongshanosaurus houi* in 2003 . The generic name *Hongshanosaurus* was derived from the Mandarin Chinese words ? (hóng : " red ") and ? (sh?n : " hill ") , as well as the Greek word *sauros* (" lizard ") . This name refers to the ancient Hongshan culture of northeastern China , who lived in the same general area in which the fossil skull of *Hongshanosaurus* was found . The type and only named species , *H. houi* , honours Hou Lianhai , a professor at the IVPP in Beijing , who curated the specimen . Genus and species were both named by Chinese paleontologists You Hailu , Xu Xing , and Wang Xiaolin in 2003 . Sereno (2010) regarded its distinct proportions as due to crushing and compression of the *Hongshanosaurus* skulls . He regarded *Hongshanosaurus* as a junior synonym of *Psittacosaurus* , and potentially the same as *P. lujiatunensis* . He did not synonymise the two species because of difficulties with the holotype skull of *H. houi* , instead considering new combination *P. houi* a nomen dubium within *Psittacosaurus* . Sereno 's hypothesis was supported by a morphometric study in 2013 , which found *P. houi* and *P. lujiatunensis* to be synonymous . While *P. houi* is the oldest available name , the researchers argued that because the type specimen of *P. lujiatunensis* was better preserved , the correct name for this species should be *P. lujiatunensis* rather than *P. houi* , which would normally have priority .

P. gobiensis is named for the region it was found in 2001 , and first described by Sereno , Zhao and Lin in 2010 . It is known from a skull and partial articulated skeleton with gastroliths . Many other specimens either cannot be determined to belong to any particular species , or have not yet been assigned to one . These specimens are generally all referred to as *Psittacosaurus* sp . , although it

is not assumed that they belong to the same species . More than 200 specimens of *Psittacosaurus* have been found in the Yixian Formation , which is famous for its fossils of feathered dinosaurs . The vast majority of these have not been assigned to any published species , although many are very well preserved and some have already been partially described . Nearly 100 *Psittacosaurus* skeletons were excavated in Mongolia during the summers of 2005 and 2006 by a team led by Mongolian paleontologist Bolortsetseg Minjin and American Jack Horner from the Museum of the Rockies in Montana . Although only *P. mongoliensis* has been described from Mongolia so far , these specimens are still in preparation and have not yet been assigned to a species .

= = Classification = =

Psittacosaurus is the type genus of the family *Psittacosauridae* , which was also named by Osborn in 1923 . *Psittacosaurids* were basal to almost all known ceratopsians except *Yinlong* and perhaps the *Chaoyangsauridae* . While *Psittacosauridae* was an early branch of the ceratopsian family tree , *Psittacosaurus* itself was probably not directly ancestral to any other groups of ceratopsians . All other ceratopsians retained the fifth digit of the hand , a plesiomorphy or primitive trait , whereas all species of *Psittacosaurus* had only four digits on the hand . In addition , the antorbital fenestra , an opening in the skull between the eye socket and nostril , was lost during the evolution of *Psittacosauridae* , but is still found in most other ceratopsians and in fact most other archosaurs . It is considered highly unlikely that the fifth digit or antorbital fenestra would evolve a second time .

In 2014 , the describers of a new taxon of basal ceratopsian published a phylogenetic analysis encompassing *Psittacosaurus* . The below cladogram is from their analysis , placing the genus as one of the most primitive ceratopsians . The authors (Farke et al .) noted that all taxa outside of *Leptoceratopsidae* and *Coronosauria* with the exception of their genus *Aquilops* are from Asia , meaning the group likely originated there .

Although many species of *Psittacosaurus* have been named , their relationships to each other have not yet been fully explored and no scientific consensus exists on the subject . Several phylogenetic analyses have been published , with the most detailed being those by Alexander Averianov and colleagues in 2006 , Hai @-@ Lu You and colleagues in 2008 , and Paul Sereno in 2010 . The middle one is shown below .

In 2005 , Zhou and colleagues suggested that *P. lujiatunensis* is basal to all other species . This would be consistent with its earlier appearance in the fossil record .