A large crested theropod from the Jurassic of Xinjiang, People's Republic of China

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A skull and partial skeleton of a new genus and species, *Monolophosaurus jiangi* n.gen., n.sp., of large theropod has been recovered from the Middle Jurassic beds in the Junggar Basin of Xinjiang, China. The most striking characteristic is a crest, formed primarily by the nasal and lacrimal bones, on the midline of the skull. Several foramina connect the hollow interior of the crest with the antorbital fossa. The function of the crest is unknown, although it most likely was used for visual recognition by other members of the same species. It is difficult to make a precise taxonomic assignment in the absence of information on the appendicular skeleton, but it appears to be more closely related to *Allosaurus* than to other megalosaur grade theropods.

Un crâne et un squelette partiel d'un nouveau genre et espèce, *Monolophosaurus jiangi* n.gen., n.sp., d'un grand théropode, ont été recueillis dans les couches jurassiques du bassin de Junggar de Xinjiang, en Chine. Le trait le plus marquant est la présence d'une crête sur la ligne médiane du crâne qui formée principalement des os nasal et lacrymal. De nombreux foramina relient le creux intérieur de la crête au fosses antorbitales. La fonction de la crête est inconnue, quoique d'autres membres de la même espèce l'utilisaient vraisemblablement pour la reconnaissance visuelle. Le manque d'information sur le squelette appendiculaire ne permet pas une attribution taxonomique précise, mais il semble que son plus proche parent soit l'*Allosaurus*, plutôt qu'un autre membre de mégalosauridés du groupe des théropodes.

[Traduit par la rédaction]

在中国新疆准哥尔盆地发现了中侏罗世大型兽脚类的一具头骨和部分骨架,以此建立为新属新种江氏单嵴龙(Monolophosaurus jiangi)。它最显著的特点是鼻骨和泪骨在头骨中线处形成一嵴状突。中空的嵴状突与眼前凹之间有数个小孔连接。嵴状突的功能目前尚未可知,虽然它可能是同种群成员相互认识的标志。附肢骨骼的缺失给本属种的准确分类带来困难,但是它可能与 Allosaurus 的关系比与兽脚类中其它巨齿龙类(megalosaurs)更为密切。

[译文由杂志社提供]

Череп и фрагменты скелета нового рода и вида <u>Monolophosaurus jiangi</u>, крупного теропода, были обнаружены в среднеюрских пластах бассейна Джунгар (Ксиньянг, Китай). Наиболее яркой его особенностью является гребень, образованный преимущественно носовой и слезной костями, на срединной части черепа. Внутренняя полость гребня соединяется с антиорбитальным тоссером с помощью нескольких отверстий. Функция гребня неизвестна, хотя вероятнее всего он использовался для визуального опознания особей своего вида. В связи с отсутствием данных об аппендикулярном скелете трудно дать точную таксономическую оценку, но складывается впечатление, что данный вид более близок к <u>Allosaurus</u>, чем к прочим тераподам - мегалозаврам.

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Introduction

In 1981, the first author was working in the Jiangjunmiao region of the Junggar Basin with the Petroleum Stratigraphic Team of the Xinjiang Petroleum Bureau from Karamay. During the course of that project, a large theropod skeleton was

discovered and was subsequently excavated by a party from the Institute of Vertebrate Paleontology and Paleoanthropology in 1984. The theropod included a skull and partial skeleton that over the years has been referred to in the popular press as "Jiangjunmiaosaurus." The specimen was found in the upper 30 m of the Middle Jurassic Wucaiwan Formation (in the highest of three members). The skeleton includes the skull, all of the cervical, dorsal, and sacral vertebrae, the first six caudal vertebrae, cervical, dorsal, and sacral ribs, and all of the pelvic girdle. The skull and the atlas neuropophyses were found almost half a meter from the rest of the skeleton. The two sides of the skull were separate but associated. Some of the teeth had fallen out of their alveoli, but were found nearby. The posterior cervical and dorsal vertebrae were arched dorsally, as was the tail.

The Wucaiwan Formation is about 200 m thick and can be divided into three informal horizons (Zhao et al. 1987). The lowest horizon is yellow, pink, and green-grey. The second horizon has more cross-bedded sandstones and calcareous concretions, and more red and purple hues. There are many fossil logs preserved at this level, where fossilized bones of theropods, sauropods, crocodiles, and turtles tend to be disarticulated. The upper horizon has thicker units of reddish sandstones, a few of which show ripple marked surfaces. This upper unit tends to produce the best articulated specimens, including the new theropod, an unidentified small theropod, a sauropod, tritylodonts (Sun and Cui 1990), crocodiles, and complete turtles, as well as at least one species of freshwater clam. Fossilized tree trunks are relatively common and appear to be identifiable as the coniferous form genus Araucarioxylon (McKnight et al. 1990). It should be noted that the fossil wood from the "Shishu Formation" of McKnight et al. (1990) came from both the Wucaiwan and Shishugou formations.

The Wucaiwan Formation is limited to the eastern part of the Junggar Basin, but is probably equivalent to the Toutunhe Formation immediately to the west (north of Urumqi and Fukang). The Toutunhe has few vertebrate fossils and is characterized by its white sandstones. One specimen found in this formation appears to represent an ankylosaur. Both the underlying Badaowan Formation (Lower Jurassic) and the overlying Tugulu Group (Lower Cretaceous) have extensive distributions with lithological homogeneity throughout the Junggar Basin and beyond. For some reason, the Middle and Upper Jurassic formations are more localized.

Systematic palaeontology

Reptilia Linnaeus, 1758 Dinosauria Owen, 1842 Theropoda Marsh, 1881 *Monolophosaurus* n.gen.

Etymology

Monolophosaurus is a derivative of three Greek words that can be loosely translated as single (monos) crested (lophos) lizard (sauros), which refer to the single crest on the midline of the skull roof.

Diagnosis

Skull with midline crest (formed by the paired premaxillary, nasal, lacrimal, and frontal bones) extending from above external naris to a point between orbits. Long, low external naris, and anteroposteriorly elongate premaxilla. Antorbital sinuses in nasals confluent through openings in base of crest.

Monolophosaurus jiangi n.sp.

Etymology

Jiangjunmiao (translated as General Jiang's Temple) is the site of an abandoned desert inn in the Gurbantunggut (previous

transliteration is Kurban Tangut) Desert of the Junggar Basin of Xinjiang.

Diagnosis

Same as for genus (monospecific).

Holotype

IVPP 84019, complete skull and partial skeleton collected in 1984.

Age and locality

Collected from the Middle Jurassic Wucaiwan Formation 34 km northeast of Jiangjunmiao (44°30′N, 90°0′E) in the Jiangjunmiao Depression within the Junggar Basin, Xinjiang, People's Republic of China.

Description

Monolophosaurus is a medium-sized theropod with a skull that is 670 mm long (tip of snout to back of quadrate). The length of the mounted skeleton is 5.1 m, and the animal would have been about 1.7 m high at the hips (top of the ilium). The skull (Fig. 1) is easily distinguished from all other known theropod genera by a low, but prominent, medial crest extending from the bridge between the external nares back to a point between the orbits. Although the crest is asymmetrical, it is well formed and has a hollow interior connected to the antorbital fossae, clearly demonstrating that it is not a pathologic artifact. The skull is 205 mm high at the lacrimal, if the crest is not included, and 290 mm if it is included. This crest is pierced by several large foramina anterodorsal to the orbits and by a number of smaller foramina. The skull appears to be tall, long, and narrow, although the proportions are similar to the skulls of Allosaurus (Madsen 1976) and Yangchuanosaurus (Dong et al. 1983) if the elongate premaxilla and crest are ignored. The external naris is long (155 cm) and low (65 cm, 42% of the length), and comparable in shape to that of *Procer*atosaurus (Woodward 1910; Paul 1988) and Dilophosaurus (Welles 1984). Because of the elongation of the premaxilla and external naris, the antorbital length is relatively long (440 mm). As in Allosaurus, Ceratosaurus (Gilmore 1920), and other Jurassic theropods, the maxilla separates the premaxilla and nasal below the external naris. The antorbital fenestra is 160 mm long, only slightly longer than the external naris, but is almost double the height (120 mm). The antorbital opening is relatively small, making up only about a third of the antorbital length of the skull and a quarter of the length of the whole skull. It is part of an extensive antorbital fossa (Witmer 1987), the well-defined margins of which can be seen on the maxilla, jugal, lacrimal, and nasal (Fig. 1a). The nasal crest is pierced by two large and two small openings, through which the antorbital fossa is confluent with the pneumatic system on the other side of the skull. There is a single maxillary fenestra (height is 45 mm) anterior to the antorbital opening. As in other theropods (but not ceratosaurs), the maxillary fenestra is found in the anteroventral corner of the well-defined antorbital fossa. The maxillary fenestra opens into a maxillary sinus (Madsen 1976), which is open internally as in most theropods. In contrast with Yangchuanosaurus and Sinraptor (Currie and Zhao 1993), there are no additional foramina in the maxillary portion of the antorbital fossa. Posteroventrally, the antorbital fossa extends well back onto the lateral surfaces of the jugal and lacrimal. As in Sinraptor, Allosaurus, and tyrannosaurids, the pneumatic system opens into the interior of the jugal through a small foramen at the back of the pneumatic fossa.

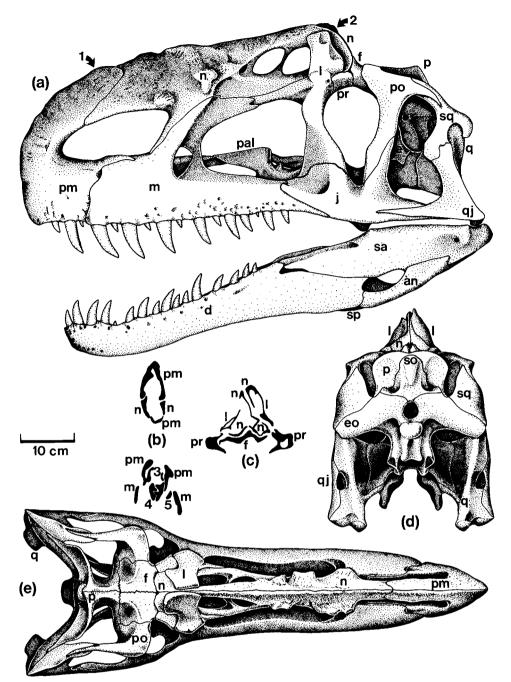


FIG. 1. Monolophosaurus jiangi, IVPP 84019. Skull in (a) left lateral, (d) occipital, and (e) dorsal aspects. Temporal region partially reconstructed from right side of the skull. (b) Cross section of snout showing hollow interior, drawn from CT scan. (c) Cross section of crest above orbit, drawn from CT scan. an, angular; d, dentary; e, epipterygoid; eo, exoccipital—opisthotic complex; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pal, palatine; pm, premaxilla; po, postorbital; pr, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sp, splenial; sq, squamosal. 1, position of vertical cross section of snout; 2, position of vertical cross section of crest; 3, slips of bone on either side of number are probably the anterior ends of the pterygoids; 4, anterodorsal processes of maxillae; 5, maxillary process of the right premaxilla.

A break revealed that the interior of the jugal is hollow.

The orbital opening is keyhole shaped, and the eye would have resided in the upper, circular portion (which has an anteroposterior diameter of 89 mm). The upper temporal fenestra is visible mostly in dorsal view (Fig. 1e). The lateral temporal opening is relatively large (height is 148 mm) and is divided into dorsal and ventral sections by anterior processes of the squamosal and quadratojugal.

The premaxilla is very distinctive. As in Sinraptor, Torvo-

saurus (Britt 1991), and Yangchuanosaurus, it has a deep ventral body. A thin, tapering process extends posteriorly from the ventral body to form the ventral margin of the external naris. It does not contact a thin process of the nasal that forms the posterior margin of the external naris. The subnarial foramen (Figs. 1a, 1b) passes between the premaxilla and maxilla as it does in most theropods. The nasal processes of the premaxillae are deeper along the midline than in other theropods and form the anterior portion of the crest. The internarial

region of the premaxillae enclose a hollow, pneumatic space that extends forward from the nasal portion of the crest (Fig. 1b). In lateral view (Fig. 1a), the nasal bifurcates to receive the posterior end of the premaxilla. On the midline (Fig. 1e), the nasals separate the posterior ends of the premaxillae as in other theropods. The nasal process of the premaxilla is oriented posterodorsally at a much lower angle (only 30°) than in most other theropods because of the elongation of the external naris. The premaxilla protrudes anteriorly more than 25 mm beyond the most anterior alveolus. Although only three teeth are visible in lateral view, there is a fourth alveolus, with a germ tooth, on the right side. Therefore, as in most Jurassic theropods, there were four premaxillary teeth. This contrasts with Ceratosaurus and Torvosaurus, which have only three teeth in each premaxilla, whereas Allosaurus usually has five (Gilmore 1920).

The maxilla has a long, tall anterior body ventral to the external naris. The elongation of the subnarial portion of the maxilla gives the outline of the bone a shape remarkably similar to that of BM(NH) R332, "Megalosaurus" hesperis (Waldman 1974). It differs from this specimen in that the medial wall of the maxillary sinus is pierced by a large opening (Fig. 1a). As previously noted, the maxilla of Monolophosaurus makes a limited contribution to the ventrolateral margin of the external naris, thereby separating the premaxilla and the nasal. The maxilla forms the boundary for the anterior half of the antorbital fenestra and completely surrounds the relatively large maxillary fenestra. There are 13 maxillary teeth. Computed tomography (CT) scans show that the maxilla had a welldeveloped anterodorsal process that contacted its equivalent on the midline (Fig. 1b) and would have also been in contact with the vomer and the maxillary process of the premaxilla.

Unlike most large, Jurassic theropods, the nasal is remarkable in that it is not flat dorsally, but is greatly thickened along the midline to form a crest. Even the nasals of Ceratosaurus are flattened posterior to the nasal horn (J. Madsen, personal communication, 1990), although those of abelisaurids are both convex and rugose dorsally (Bonaparte and Novas 1985; Bonaparte et al. 1990). In this specimen, the nasals have coossified, but the midline suture can still be traced. CT scans (Figs. 1b, 1c) reveal that the crest is hollow, presumably pneumatic. Air would have entered the nasal from the antorbital sinus through openings dorsal to the maxillary-nasal suture (Fig. 1a). The medial hollow extended anteriorly into the internarial process of the paired premaxillae (Fig. 1b). The nasals extensively overlap the frontals (Fig. 1c), and externally contact the frontals along the midline in a raised suture. The crest is relatively thin mediolaterally, and the surface of the bone is gnarly and asymmetrical (Fig. 1e). The outer surface of the nasal (excluding the sutures with other bones and the wall of the antorbital fossa) is very rugose. Above the external naris, the surface is ornamented with vertical striations, and above the anterodorsal margin of the antorbital fossa there are two or more knobs of bone on each side.

Dorsal growth of the nasal has permitted dorsal extension of the antorbital fossa. As in *Allosaurus* (Gilmore 1920; Lisak 1980), *Yangchuanosaurus* (Dong et al. 1978), and *Sinraptor* (Currie and Zhao 1993), the nasal portion of the wall of the antorbital fossa is penetrated by pneumatic foramina (the nasal foramina of Madsen 1976). Unlike those other genera, however, two of the openings are large fenestra that pass through the crest to open into the antorbital fossa on the opposite side of the skull. Extensions of these pierce the floor of the nasal

and may open ventrally in a "nasal sinus," as in *Allosaurus* (Lisak 1980). As previously mentioned, two smaller pneumatopores anterior to the large pair pass into the hollow interior of the crest.

The lacrimal is as amazing in its development as that of Dilophosaurus (Welles 1984). The antorbital and maxillary rami are similar to those of most large Jurassic theropods and merit no additional comment. However, the posterodorsal region, which in other theropods is usually a low mound of bone penetrated by one or more pneumatic openings, makes a significant contribution to the crest. The lacrimal has grown dorsally into a sheet of bone that covers the lateral surface of the crest (Fig. 1a), although most of it is separated from the nasal by a sinus (Fig. 1c). There are no pneumatopores evident in this vertical ramus, which forms the posterior margin of the upper recess of the antorbital fossa. The left lacrimal does not quite reach the dorsal margin of the crest. However, the dorsal extension of the right lacrimal is higher (Fig. 1e), and it is highly probable that in other individuals the lacrimals may actually have contacted each other dorsally.

The prefrontal forms the anterodorsal margin of the orbit. As in *Sinraptor*, *Allosaurus*, and more primitive theropods, a slip of the prefrontal extends ventrally along the medial surface of the antorbital process of the lacrimal. Dorsomedially, the prefrontal has been overgrown by the nasal crest.

In appearance, the jugal is closest to those of *Sinraptor* (Currie and Zhao 1993) and *Yangchuanosaurus* (Dong et al. 1978). Unlike *Allosaurus* (Madsen 1976) and *Ceratosaurus* (Gilmore 1920), the jugal separates the maxilla and lacrimal externally. This is presumably retention of the primitive state that is seen in *Coelophysis* (Colbert 1989), *Dilophosaurus* (Welles 1984), and even more primitive archosaurs like *Ornithosuchus* (Walker 1964), but has little taxonomic value as it also appears in such highly derived forms as *Carnotaurus* (Bonaparte et al. 1990) and *Tyrannosaurus* (Osborn 1912). The antorbital fossa extends onto the jugal. On the left side of the skull, a small, slitlike pneumatic foramen enters the body of the jugal.

The postorbital is conservative, contacting the jugal, frontal, parietal, laterosphenoid, and squamosal to form much of the postorbital and intertemporal bars. The anterolateral surface is only slightly rugose and has not developed into a pronounced boss or postorbital "horn." In contrast to *Sinraptor*, the intertemporal process of the postorbital is not covered by the squamosal.

Primitive theropods like *Dilophosaurus* (Welles 1984), *Coelophysis* (Colbert 1989), and *Syntarsus* (Raath 1990) have a low quadratojugal that does not contact the squamosal. In most other theropods, including *Monolophosaurus*, there is a long dorsal process of the quadratojugal that reaches the squamosal. The quadratojugal has limited exposure in occipital view, mostly lateral and ventrolateral to the quadratojugal foramen (Fig. 1d).

The squamosal is well preserved on the right side of the skull. As in other theropods, it is a complex bone with a socketlike articulation for the quadrate. The quadratojugal process is relatively long and protrudes into the lateral temporal fenestra in a manner characteristic of allosaurids and tyrannosaurids. This is considered to be significant for determining the relationship of this animal because there is no anterior protrusion into the lateral temporal fenestra of megalosaur grade theropods like *Sinraptor* (Currie and Zhao 1993).

The frontal makes up a small portion of the orbital rim at

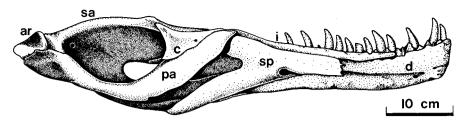


Fig. 2. Monolophosaurus jiangi, IVPP 84019. Medial view of left mandible. ar, articular; c, coronoid; d, dentary; i, intercoronoid (supradentary); pa, prearticular; sa, surangular; sp, splenial.

the medial end of a notch between the prefrontal and the postorbital (Figs. 1a, 1e), which is the same situation as most other large theropods, including Ceratosaurus (Gilmore 1920). The dorsal surface of the frontal is relatively flat, although the temporal musculature attaches to the dished out portion of the frontal within the upper temporal fenestra (Fig. 1e). The frontals are strongly sutured to each other and to the parietals. As in Sinraptor, the frontoparietal suture is strengthened by additional bone growth that bulges laterally into the upper temporal fenestra. Because of the crest, the anterior region of the frontal is modified. The dorsal surface of the frontal makes a minor contribution to the posterior margin of the crest in the form of an elevated process (Fig. 1a). These small paired frontal processes separate the nasals ventroposteriorly on the midline of the crest (Fig. 1e). Anterior to these processes, the frontals are overlapped by the nasal portion of the crest (Fig. 1c).

The fused parietals form a low, flat-topped crest between the supratemporal fenestra. This is similar to the situation in *Allosaurus* (Madsen 1976) and *Sinraptor*, but it would be inappropriate to refer to this as a sagittal crest, as it is in troodontids and tyrannosaurids. The nuchal (supraoccipital) crest is relatively low, but pronounced, and has a significant amount of exposure on the occiput (Fig. 1d). In occipital view, the parietal tapers ventrolaterally to meet the squamosal in a limited contact at the ventral end of a deep but relatively narrow notch spilling out from the upper temporal fenestra.

The supraoccipital had not fused to the exoccipital—opisthotic complex, but was indistinguishably fused to the epiotic. It forms part of the foramen magnum and thickens dorsally along the midline into a triangular supraoccipital wedge that extends almost to the top of the nuchal crest of the parietals. The lateral wings of the bone are separated from the dorsal process by a pair of conspicuous notches.

The exoccipital—opisthotic complex can be seen only in occipital aspect (Fig. 1d). The elongate paroccipital wings are directed laterally, ventrally, and posteriorly. The degree of ventral flexion is similar to that seen in most other theropods, and is not as pronounced as in *Allosaurus* (Madsen 1976).

The sutures between the basioccipital and the exoccipitals cannot be seen on the kidney-shaped occipital condyle, although the separation between the bones is discernable ventral to the condyle.

The basisphenoid forms part of the basal tubera and is invaded ventrally by a deep basisphenoidal recess that can be seen in occipital view (Fig. 1d).

Both lower jaws are well preserved. There are 17 teeth and alveoli preserved on the left side and 18 on the right. The symphysial surface of the dentary is not well defined, and the jaws were clearly able to move independently. As in *Yangchu-anosaurus*, *Allosaurus*, abelisaurids (Bonaparte et al. 1990),

and the tyrannosaurids (Bakker et al. 1988), there is a distinct intramandibular joint. The external mandibular fenestra is 67 mm × 25 mm high. Its boundaries are formed by the dentary, surangular and angular as in *Yangchuanosaurus* (Dong et al. 1983), *Carnotaurus* (Bonaparte et al. 1990), and *Coelophysis* (Colbert 1989), although it is a relatively smaller opening. In *Allosaurus*, the external mandibular foramen is further reduced in size and the dentary is excluded from the anterior margin.

The dentary is more than half the length of the jaw. It is shallow and relatively straight in dorsal view. The ventral margin is sinuous in lateral view (Fig. 1a), convex anteriorly, and concave posteriorly. The teeth are held in position by interdental plates (Fig. 2), which have not fused to each other. These, in turn, are covered medially by a bandlike supradentary at the margin of the jaw, as in *Allosaurus* (Lisak 1980), *Dromaeosaurus*, *Tarbosaurus*, *Tyrannosaurus*, and other toothed theropods. The bases of the interdental plates are still visible ventral to the supradentary, however, as are the tips of the germ teeth in many alveoli.

The splenial is a triangular, thin-walled plate of bone that is deeply notched posteriorly where it forms the anterior boundaries of the internal mandibular fenestra (Fig. 2). The posteroventral end is thin, but wraps around the ventral margins of the angular and dentary for a very limited lateral exposure (Fig. 1a). This is a plesiomorphic character of the Theropoda (Currie and Zhao 1993).

Molnar et al. (1990) suggest that the depth of the surangular at the intramandibular joint is a useful character for determining the relationships of theropod genera. In *Monolophosaurus*, the surangular is deep, as it is in *Allosaurus*, and in sharp contrast with *Yangchuanosaurus* and *Sinraptor*, which have lower surangulars above larger mandibular fenestra. Anterodorsally, *Monolophosaurus* has the well-defined tongue-in-groove articulation with the dentary (Fig. 1a) that is characteristic of most theropods. The diameter of the posterior surangular foramen is 5 mm.

As in most other theropods, the angular formed a sliding joint anteriorly with the splenial and dentary. Although the external mandibular fenestra is relatively small, there is no contact with the surangular anterior to the fenestra as there is in *Allosaurus* (Madsen 1976). Posteriorly, there is a ventral process (Fig. 1a) that extends along the jaw margin to the level of the articular. This is a derived character similar to the condition seen in *Allosaurus*.

The coronoid is exposed mostly on the medial surface of the jaw (Fig. 2), but its dorsal margin can also be seen in lateral aspect. It contacts the dorsomedial margin of the surangular and anteriorly is medially covered by the prearticular. Small breaks in the region of contact with the supradentary make it impossible to determine whether or not the coronoid and

TABLE 1. Vertebral measurements (mm) of type specimen of Monolophosaurus jiangi

Vertebra No.	Centrum length	Posterior width ^a	Mid. width ^b	Total height ^c	Neural spine			
					Height ^d	Length ^e	Width	Zyg. width ^g
2	61.8	34.5	22.9	162+	58e	_	_	
3	67.1	45.0	28.6	_	_	_	_	83.1
4	69.3	47.9	29 +	143	50e	53.2	10.9	88.3
5	70.6		27.5 +	134 +	_	39.5	10.2	91.8
6	69.6	59.0	29.5	122 +	_	33+	10.9	90.2
7	67.8	52.0	26.5	137 +	_	42+	12	82.1
8	72.3	58.4	30.4	147 +	52+	33.2	11.0	
9	68.4	62.0	30.7	150 +	_	30e	15.8	88.3
D1	67.3	55.8+	30.7	160 +	_	19.7	20.6	91.0
D2	60.0	60.0	31.9	155 +	_	23.3	25.4	90.5
D3	60.6	51.5	24.2	178		36.0	21.2	73.5
D4	60.9	53.8	24.0	178	91	28.4	13.3	70.9
D5	65.5	54.3	23.5	185	_	43.2	16.0	63.0
D6	70.0	57.2	24.7	187	_	65.2	14.8	55.0
D7	71.2	60.5	26.0	196	118	59.2	13.2	56.0
D8	74.0	61.0	28.1	195	_	59.2	12.6	61.3
D9	79.6	69.7	29.8	198		60.1	10.3	75.3
D10	79.5	72.2	32.0	202	. —	Path	Path 19	56.1
D11	78.8	74.8	35.0	210	_	Path	11.4	_
D12	80.9	84.2	38.5	212		53.0	12.1	47.5
D13	81.5	91.3	41.2	234	_	51.6	_	47.8
D14	79.8	93.1	42.6	211 +	_	_	_	56.4
S 1	82.8	65.2	41.3		_	*		_
S2	75.4	63.9	38.9	_		*		
S3	67.4	67.3	40.3	_		*		
S4	69.5	62.4	44.3	216	_	*		
S5	72.1	86.8	42.1	177 +	_	*	10.9	_
C1	78.0	82.5	44.3	177 +	_	49.0	10.8	29.2
C2	76.1	80.9	44.3	179+	_	50.2	8.9	31.0
C3	74.2	71.0	40.5	178+		55.8	9.5	28.0
C4	74.9	64.8	36.8	150+	_	58.0	11.3	31.4
C5	78.7		36.9			_	_	29.0
C6	78.5	51.8	31.2			_	_	_

Notes: *, the anteroposterior length of the 5 fused sacral neural spines is 33.8 cm. The pathology in dorsal vertebrae 10 and 11 is restricted to the neural spines, which appear to have been broken in life and fused together when they healed. C, caudal; D, dorsal; S, sacral; e, estimated; Path, Pathological; +, incomplete bone.

supradentary were a single bone.

The prearticular (Fig. 2) is similar in outline and sutures to those of other large theropods.

Only the left articular was recovered, and it is not well preserved. The retroarticular process was broken off, and the glenoid region was badly damaged.

There is no evidence of an antarticular, a neomorph known presently only in *Allosaurus* (Madsen 1976).

The 9 cervical, 14 dorsal, and 5 sacral vertebrae were preserved, along with the first 6 caudals (Table 1). In many cases, tips of the neural spines and transverse processes were damaged during collection and preparation. The neural arches are fused to their corresponding centra, although the sutures are still visible on many of the vertebrae. The sacral centra have coossified. These facts strongly suggest that IVPP 84019

was a relatively mature individual and that *Monolophosaurus* did not grow much longer than 5 m.

Monolophosaurus vertebrae are comparable with those of Allosaurus in most respects. Most significantly, the neural spines of the cervicals and anterior dorsals tend to be relatively low, anteroposteriorly short, and laterally thick. They are more gracile than the neural spines of Allosaurus, but this may be a size-related characteristic. The dorsal neural spines certainly do not resemble the tall, thin bladelike neural spines seen in Ceratosaurus (Madsen, personal communication, 1992), Piatnitzkysaurus (Bonaparte 1986), Sinraptor (Currie and Zhao 1993), Torvosaurus (Britt 1991), and other large Jurassic theropods. Where the anterior and posterior surface of the neural spines can be seen, there are usually scars for the interspinous ligaments. The hyposphene tends to be better

^aMaximum width of the posterior end of the centrum.

^bWidth of the waist of the centrum.

^cTotal height of vertebra including centrum and neural spine (measured at posterior end).

^dHeight of the neural spine measured from the top of the neural canal.

^{&#}x27;Anteroposterior length of the neural spine measured above the neural arch.

Width of the neural spine measured above the neural arch.

⁸Distance between the lateral margins of the articulating facets of the anterior zygapophyses.

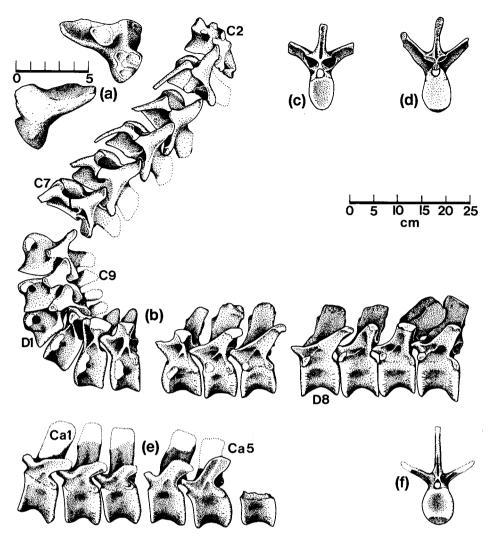


Fig. 3. Vertebrae of *Monolophosaurus jiangi*, IVPP 84019: (a) enlargement of left neurapophysis in lateral (lower left) and medial (upper right) views; (b) cervical vertebrae and ribs, and dorsal vertebrae in left lateral aspects; (c) posterior view of fourth dorsal vertebra; (d) seventh dorsal in posterior aspect; (e) first five caudal vertebrae in left lateral view, plus centrum of a more posterior caudal; (f) posterior view of third caudal. C2, C7, C9, cervical vertebrae; D1, D8, dorsal vertebrae; Ca1, Ca5, caudal vertebrae.

developed in *Monolophosaurus*, and unlike *Allosaurus* it is found in the caudal vertebrae at the base of the tail.

Both neuropophyses (Fig. 3a) were recovered with the skull. Unlike *Ceratosaurus*, they are not elongate L-shaped bones (Gilmore 1920), but are triangular like those of *Allosaurus* (Madsen 1976) and more advanced forms. The neural spine of the axis is a posterodorsally inclined, rodlike process that also compares more favorably in shape with *Allosaurus* than *Ceratosaurus*. The posterior zygapophyses of the cervicals are wide and are capped by relatively short epipophyses. The cervical vertebrae are opisthocoelous, as in most large theropods that are more derived than *Ceratosaurus*.

The largest central pleurocoel is found on the first dorsal vertebra posterodorsal to the parapophysis. The ventral surfaces of the second to fourth dorsal vertebrae bear distinctive keels, the most pronounced of which is on the third dorsal. Anteriorly, as in *Allosaurus*, the keel of the third bears a short hypapophysis. The distal end of the third dorsal diapophysis (Fig. 3b) has a larger capitular articulation than any other vertebrae, again like *Allosaurus*. The fourth and fifth dorsal vertebrae show greater separation between the transverse process

and the prezygapophysis than in *Allosaurus*. The neural spine of the sixth dorsal is anteroposteriorly long and closely resembles the seventh dorsal of *Allosaurus*. In contrast with *Sinraptor*, the posterior zygapophyses of *Monolophosaurus* and *Allosaurus* are only slightly lower than the junction of the diapophyses and the neural spines. The tenth and eleventh dorsal vertebrae bear evidence of an injury received by the animal when it was alive. The tenth neural spine, and possibly the eleventh, were broken (Fig. 3), but had enough time to reheal before the animal died. The tenth neural spine is distorted, has thick bony callosities, and has fused to the eleventh spine.

The centra of *Monolophosaurus* are taller than wide (Table 1), in contrast with *Allosaurus* where the centra are almost round in end view. This is in part related to the greater development of the rimlike margins of the allosaurid centra, which may be related to larger size.

As in most of the larger theropods, there are five coossified sacral vertebrae. In the terminology used by Welles (1984), there are two dorsosacrals, two true sacrals, and one caudo-sacral. Like *Dilophosaurus* and *Allosaurus*, the true sacrals share a wider contact than any other combination of two

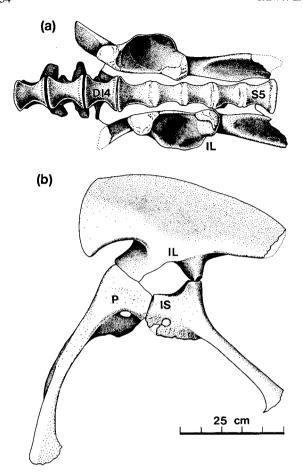


Fig. 4. Pelvic region of *Monolophosaurus jiangi*, IVPP 84019: (a) last three dorsal vertebrae, sacrum and ilia in ventral view; (b) left side of pelvic girdle in lateral aspect. D14, last dorsal vertebra; IL, ilium; IS, ischium; P, pubis; S5, last sacral vertebra.

sacrals, and this suture is level with the ischial peduncles of the ilia (Fig. 4a). The second sacral (first dorsosacral) has the narrowest central waist, and the fourth sacral (second true sacral) has the widest waist (Table 1). This is comparable with *Allosaurus*, and very different than *Ceratosaurus* (Gilmore 1920) and *Carnotaurus* (Bonaparte et al. 1990), in which all of the sacral centra have become narrow waisted and do not expand much at the intercentral contacts.

The caudal vertebrae have broad, flat transverse processes as in other theropods, but lack the distal expansion seen in *Allosaurus*. The ventral surface of each of the fourth to sixth caudal centra has a longitudinal depression that is not as deeply impressed as those of *Ceratosaurus* (Gilmore 1920, Pl. 22) nor as wide as the depression in *Allosaurus*.

Most of the cervical and dorsal ribs (Figs. 3, 5) were recovered with the specimen, although none of the cervicals are complete. There was an axial rib. The anterolateral processes associated with the tubercula of cervical ribs are relatively shorter than those of *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie and Zhao 1993). There is no remnant of the anterolateral process on the first dorsal rib (of the tenth presacral vertebra). The longest rib, presumably the fourth or fifth dorsal, has a relatively straight shaft that is 585 mm long (including the capitulum). The sacral ribs are covered by the ilia and cannot be seen.

Both ilia are well preserved, although the anterior margin

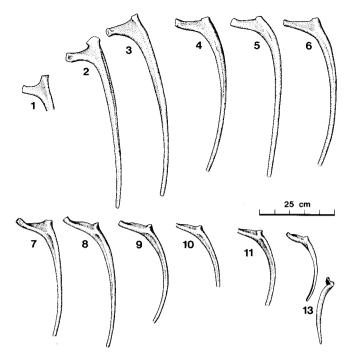


FIG. 5. Anterior views of dorsal ribs of *Monolophosaurus jiangi*, IVPP 84019. Numbers represent thoracic segments. Dorsal rib 13 is shown in both anterior and lateral views.

is missing on the right side. The ilium is 498 mm long and 278 mm high at the pubic peduncle. The maximum height of the anterior blade is 168 mm. The maximum length of the iliac portion of the acetabulum is 140 mm, and the ilium is 168 mm wide at the ventral margin of the supraacetabular shelf. The lateral surface of the iliac blade is finely sculptured with fine, vertical striations for attachment of the pelvic musculature. As in *Allosaurus* (Madsen 1976) and *Sinraptor* (Currie and Zhao 1993), the posterior margin of the ilium seems to have been squared off. The medial blade of the ilium arises from the base of the ischial peduncle and is oriented posterodorsally. As in other theropods it forms a wide trough (70 mm across) for the caudofemoralis brevis musculature. Compared with *Ceratosaurus*, the brevis shelf is relatively narrow as in *Allosaurus* and more advanced theropods (Fig. 4a).

The paired pubic bones are 495 mm in length. The rugose sutural surface for the ilium is 46 mm in length, the pubic portion of the acetabulum has a straight-line maximum length of 67 mm, and the ischiatic suture is 73 mm long. Distally, the pubis is only slightly expanded into a rudimentary pubic boot (Fig. 4b) 90 mm across. The minimum height of the shaft is 28.4 mm at mid-length, although the pubis is much wider here because of the shelf forming the medial symphysis with the other pubis. As in Ceratosaurus (Gilmore 1920), Carnotaurus (Bonaparte et al. 1990), Gasosaurus (Dong and Tang 1985), Piatnitzkysaurus (Bonaparte 1986), Torvosaurus (Galton and Jensen 1979), and Yangchuanosaurus (Dong et al. 1983), but in contrast with Allosaurus (Madsen 1976) and all other Upper Jurassic and Cretaceous theropods, there is a conspicuous obturator foramen proximally, which has a maximum anteroposterior diameter of 25 mm. And similar to Ceratosaurus. the ischial process is platelike and curves inward to contact the other pubis on the midline. The left pubis is broken midshaft, and the pubis is twisted ventroposteriorly. It is possible that this break occurred when the animal was alive, but the

unhealed nature of the break suggests that it was postmortem.

The ischia are 390 mm in length, with a minimum shaft diameter of 29.6 mm. The iliac peduncle is 70.5 mm along the suture, the acetabulum is 73 mm across, and the pubic process extends at least 25 mm beyond the ventral margin of the pubic suture. As in *Ceratosaurus*, there is no distinct obturator process, although there is a closed obturator foramen (Fig. 4b). The distal end is slightly expanded, and lateromedially flattened. The medial surface is covered by longitudinal striations marking the point of contact with the other ischium.

Discussion

The discovery of a crested species in the Middle Jurassic beds of central Asia reveals a new type of theropod cranial ornamentation. The medial crest of Monolophosaurus is formed by the paired premaxillary, nasal, lacrimal, and frontal bones, which form a hollow tube with contralateral pneumatic extensions from the antorbital fossae. Dilophosaurus, of the lower Jurassic Kayenta Formation of Arizona and the Lufeng Formation of Yunnan (China), has a characteristic pair of bladelike crests on top of the skull. Each of the two crests is composed of the nasal and lacrimal and is positioned on the lateral margin of the skull roof. Many other theropods, including Carnotaurus, Allosaurus, and tyrannosaurids, also have bilateral pairs of hornlike or crestlike structures, although they are never as powerfully developed as in Dilophosaurus. Ceratosaurus is one of the few theropods that shows a midline horn that may have been used for display, but it is not a crest and is confined to the front of the nasals. Woodward (1910), von Huene (1926), and Paul (1988a) have all assumed that a projection above the narial opening in Proceratosaurus represents the anteroproximal portion of a horn core. Although it rises abruptly from the nasal bar in contrast to the crest of Monolophosaurus, it is conceivable that Proceratosaurus has a midline crest rather than a nasal horn. Abelisaurid (Bonaparte et al. 1990) and tyrannosaurid nasals are dorsally convex in transverse section and have rugose surfaces that suggest the possible presence of epidermal excrescences. The crest of Monolophosaurus is autapomorphic and appears to have little potential for the determination of the relationships of this animal to other theropods.

Monolophosaurus is best referred to as a megalosaurid, although this name presently refers to an evolutionary grade of large theropods characteristic of Middle to Late Jurassic times. It is important to understand the plesiomorphic characters retained by *Monolophosaurus* before looking at possible synapomorphies with other genera. Like most theropods, there are four premaxillary teeth. An internasal suture is still visible, although the nasals are firmly sutured to each other. The prefrontal is a relatively large bone with an antorbital extension on the medial surface of the lacrimal. The paroccipital processes are not sharply downturned distally. The quadrate is intermediate between the relatively tall quadrate of Ceratosaurus and the low one of Allosaurus. In the mandible, the surangular does not contact the angular in front of the external mandibular fenestra, and there is no antarticular. The splenial has a limited exposure on the lateral surface of the jaw. Interdental plates are not fused to each other in the dentary, but cannot be seen clearly in the premaxilla or maxilla. Postcranially, there is a diapophysis on the axis. The pneumatic chambers within the centra of the cervicals and anterior dorsals are simple and are not subdivided by trabeculae. The pneumatic fossae of the neural arches are neither as elaborate nor as invasive, as those seen in *Sinraptor* (Currie and Zhao 1993) and *Torvosaurus* (Britt 1991). The hyposphene—hypantrum articulations are not restricted to the cervicals and anterior dorsals and are even found in the anterior caudals. The supraacetabular shelf of the ilium is broad. There is a pubic fenestra as in *Ceratosaurus* and *Yangchuanosaurus*, and the pubic boot is small. The paired pubes contact each other along most of their length. The obturator fenestra of the ischium is surrounded by bone as in *Yangchuanosaurus*, representing a stage between the primitive condition of *Dilophosaurus* and the advanced notchlike condition of *Sinraptor* and *Allosaurus*.

There are synapomorphies shared by allosaurids and megalosaurid-grade theropods like *Monolophosaurus*, *Sinraptor*, and *Yangchuanosaurus*. The position of the last maxillary tooth is anterior to the orbit. An accessory opening is conspicuous in lateral view anterior to the antorbital fenestra. The nasals are elongate and are invaded by pneumatic diverticula from the antorbital fossa. The jugal is pneumatized by the antorbital air sack. There is a deep basisphenoidal recess, bound posterolaterally by relatively short basal tubera. The axial neural spine is reduced from the condition seen in *Ceratosaurus*, *Dilophosaurus*, and other primitive theropods, and the lengths of cervical parapophyses are also shorter. The brevis shelf of the ilium is relatively narrow.

Some characters suggest that Monolophosaurus is more advanced than Sinraptor and Yangchuanosaurus, and may be more closely related to allosaurids. The premaxilla does not contact the nasal below the external naris. The length of the subtemporal bar is reduced from the primitive condition, and the lateral temporal fenestra is relatively small. There is an anterior process formed by the squamosal and quadratojugal that constricts the lateral temporal fenestra. Although the jugal is pneumatic, the pneumatopore is very small. In the lower jaw, the angular has a posterior extension that reaches the level of the articular. The epipophyses of the cervical vertebrae, and the neural spines of the dorsals are relatively short. The tenth presacral vertebra is, judging from its rib, a dorsal. Although nothing is known about the appendicular skeleton of Monolophosaurus, the known characters suggest this animal may be closer to allosaurids than any of the other wellunderstood megalosaurid grade theropods. Even so, there are many autapomorphies associated with the development of the crest in Monolophosaurus that clearly show it was not a suitable ancestral allosaurid.

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