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The Maastrichtian (Late Cretaceous) lambeosaurine dinosaur *Charonosaurus jiayinensis* from north-eastern China

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Abstract

Since the beginning of the 20th century, the Yuliangze Formation of the Jiayin locality, in north-eastern China, has yielded abundant dinosaur material. Palynological data suggest that the Yuliangze Formation is late Maastrichtian (Late Cretaceous) in age. About 90 percent of the bones recovered from this locality belong to the lambeosaurine (Hadrosauridae) dinosaur *Charonosaurus jiayinensis* GODEFROIT, ZAN & JIN, 2000. An osteological reconstruction of this dinosaur is proposed in the present paper. A phylogenetic analysis, based on 34 cranial, dental and postcranial characters, indicates that *Charonosaurus* is the sister-taxon of the Late Cretaceous North American genus *Parasaurolophus*. Comparisons of postcranial features indicate that *Charonosaurus jiayinensis* was probably less well-adapted for quadruped gait than was *Iguanodon bernissartensis*, but was probably a more efficient biped. It is suggested that the great development of the distal ischial foot in lambeosaurines, that served as attachment site for *M. rectus abdominis*, may be correlated to the hypertrophy of the nasal passage in these dinosaurs. If lambeosaurine dinosaurs dominated potential late Maastrichtian localities in eastern Asia, these dinosaurs are not represented anymore in synchronous Lancian localities from western North America, dominated either by ceratopsian or by titanosaurid dinosaurs.

Key-words: *Charonosaurus jiayinensis*, Lambeosaurinae, Late Cretaceous, north-eastern China, osteology, phylogeny.

Résumé

Depuis le début du vingtième siècle, la Formation de Yuliangze a livré de nombreux restes de dinosaures à Jiayin, en Chine du nord-est. Des données palynologiques suggèrent que la Formation de Yuliangze serait d'âge Maastrichtien supérieur (Crétacé supérieur). Environ 90 pour cent des ossements découverts appartiennent au dinosaure lambéosauriné (Hadrosauridae) *Charonosaurus jiayinensis* GODEFROIT, ZAN & JIN, 2000. Une reconstitution ostéologique de ce dinosaure est proposée dans cet article. Une analyse phylogénétique, basée sur 34 caractères crâniens, dentaires et postcrâniens, indique que *Charonosaurus* est le groupe-frère du genre *Parasaurolophus*, du Crétacé supérieur d'Amérique du Nord. Des comparaisons de certains caractères postcrâniens indiquent que *Charonosaurus jiayinensis* n'était pas aussi bien adapté à la station quadrupède qu'*Iguanodon bernissartensis*, mais était probablement un bipède plus efficace. L'important développement, chez les lambéosaurinés, de l'extrémité distale de l'ischium, qui servait de point d'attache pour le *M. rectus abdominis*, est peut être lié à l'hypertrophie du conduit nasal chez ces mêmes dinosaures. Si les lambéosaurinés étaient les dinosaures dominants dans les gisements d'âge maastrichtien supérieur présumé en Asie orientale, ces dinosaures ne sont plus représentés dans les gisements contemporains d'âge "lancien" en Amérique du Nord, dans lesquels les cératopsiens ou les titanosauridés sont dominants.

Mots-clefs: *Charonosaurus jiayinensis*, Lambeosaurinae, Crétacé supérieur, Chine du nord-est, ostéologie, phylogenie.

Historical review

The history of early discoveries of dinosaurs along the Amur river is related in detail by RIABININ (1925, 1930a). In 1902, the Russian Colonel Manakin obtained a few fossil bones from Kazakh fishermen; the bones came from the banks of the Amur River (called Heilonjang, meaning Black Dragon River by Chinese People). Manakin immediately believed that the fossils belonged to the famous Siberian mammoth and reported the discovery in the local journal "Priamourskie Vedomosti". He deposited the bones in the local Museum of Khabarovsk. This is the first dinosaur discovery to be mentioned from China.

Manakin's discovery aroused the attention of Russian geologists to the Amur area. In 1914, a large fragmentary bone was discovered in the Amur Valley by A.N. Krishtofovitsh, geologist at the Russian Geological Committee in St. Peterburg. On the returning to St. Peterburg (in the meantime renamed Petrograd), he showed the bone to his colleague A.N. Riabinin, who identified it as the proximal end of a dinosaurian tibia or fibula (RIABININ, 1914). During the winter of 1915-1916, W.P. Renngarten, also a geologist at the Russian Geological Committee, went to the Amur Region and studied a geological section opened in the "Belyie Kruchi" ("White Cliffs"), "... on the right shore of the Amur River, some distance downstream from the mouth of Ayan, between the villages Kasatkino and Sagibovo" (RIABININ, 1925, fig. 1). At the bottom of the cliff, he discovered dinosaur bones within a greenish conglomerate. The excavation spot is in fact located in the vicinity of Jiayin village (48°53'N, 130°27'E; Fig. 1), in Heilongjang Province, P.R. China.

Following these preliminary researches, the Russian Geological Committee undertook, during the summers of 1916 and 1917, two excavation campaigns, under the direction of preparator N.P. Stepanov, and unearthed several bonebeds in the greenish conglomerate along the right side of the Amur River. Before the October 1917 Revolution, all finds, including the incomplete skeleton of a hadrosaurian dinosaur, were transported to the Museum of the Geological Committee at Petrograd to be prepared and studied.

The hadrosaur skeleton was prepared by Stepanov

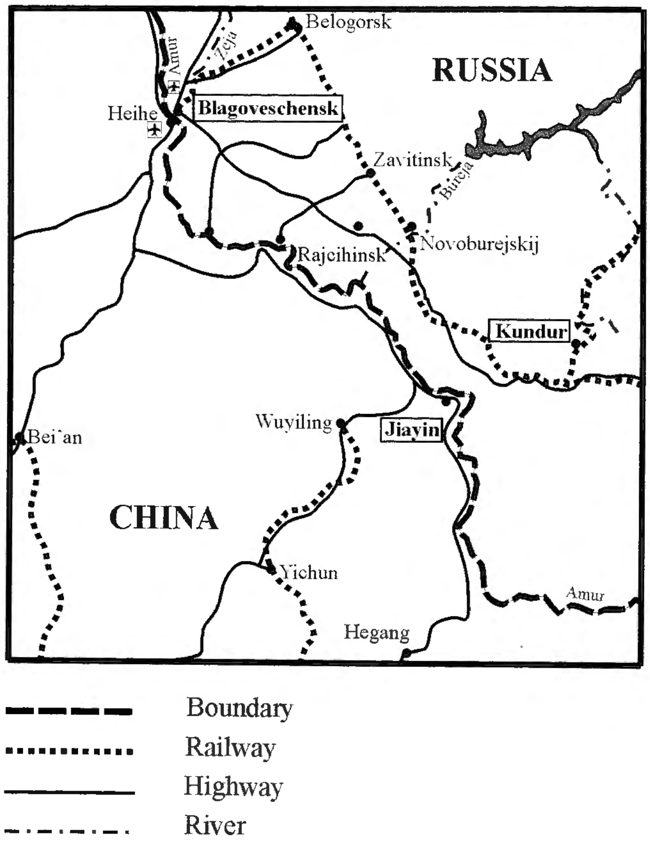


Fig. 1 — Geographic location of Late Cretaceous dinosaur localities in the Heilongjang Province (P.R. China) and the Amur Region (Russia). Scale: 1/5 267 000.

between 1918 and 1923 and mounted under the supervision of Riabinin in 1924. Riabinin (1925) gave a preliminary description of the skeleton, naming it *Trachodon amurense*. He subsequently described it in detail and attributed it to the new genus *Mandschurosaurus* (Riabinin, 1930a), regarded as a member of the subfamily Hadrosaurinae.

In another paper, Riabinin (1930b) described fragmentary turtle bones from the same locality as *Aspederetes planicostatus* nov. sp., isolated theropod teeth as *Albertosaurus periculosus* nov. sp. and the proximal end of hadrosaurian left ischium as *Saurolophus Krischtofovici* (sic) nov. sp. Because of the presence of the genera *Albertosaurus* and *Saurolophus*, he concluded that the age of the Belyie Kruchi fauna is similar to that of the Edmonton Formation in Canada. However, because of the very fragmentary state of preservation of the type-material, *Saurolophus kristofovici* is unanimously regarded as a *nomen dubium* (see e.g. Maryańska & Osmólska, 1981a; Weishampel & Horner, 1990). According to Molnar *et al.* (1990: 190), *Albertosaurus periculosus* might be a junior synonym of *Tarbosaurus bataar*. Nevertheless, the teeth illustrated by Riabinin (1930b, pl. 1, fig. 2) do not display any diagnostical character and must consequently be referred to as Carnosauria indet.

Rozhdestvensky (1957) was very sceptical about the validity of *Mandschurosaurus amurensis* because of the scarcity of the material and the absence of diagnostical skull element. Moreover, as admitted by Riabinin (1930a) himself, the type skeleton is probably reconstructed from several individuals. Young (1958) observed that "the specimen is so much restored for mounting that the real characters are mostly difficult to see". Brett-Surman (1979) regarded *Mandschurosaurus amurensis* as a *nomen dubium*, because "there is not one single landmark or major morphological feature on any of the elements". This opinion was subsequently followed by Maryańska & Osmólska (1981a) and Weishampel & Horner (1990) and is retained herein.

Between 1975 and 1979 the Heilongjang Provincial Museum (Harbin) undertook new excavations along the Chinese banks of the Amur River near Jiayin and discovered many new hadrosaur and carnosaur fossils. Two partial specimens identified as *Mandschurosaurus amurensis* were restored and exhibited in the Heilongjang Provincial Museum. Unfortunately, one of the restored skeletons was completely destroyed during a fire. The material collected during these excavations was briefly described by Yang *et al.* (1986) and Yang (1987). New material was also recovered from this area, in 1989, by the Changchun Geological College (currently named Changchun University of Sciences and Technology); one incomplete specimen, identified as *Mandschurosaurus amurensis*, was restored for exhibition in the geological Museum of this institution. In 1992, the Geological Museum of Heilongjang (Harbin) also started excavations along the Amur river, unearthing one large incomplete skeleton, displayed in this institution as "*Mandschurosaurus magnus*", and also isolated hadrosaur, carnosaur and turtle bones (Xing *et al.*, 1994).

Geological setting

In northern Heilongjang Province, Cretaceous formations are scattered along the banks of the Amur River. They lie above the Jurassic Jielihe Formation and are widely covered by Neogene and Quaternary sediments (Fig. 2). The Yongancun and Taipinglinchang Formations are usually regarded as Early Cretaceous in age. The Late Cretaceous Yuliangze Formation is restricted in Jiayin County to the "Belyie Kruchi": it consists of greyish-green sandstones, purple mudstones and light-coloured conglomerates. The dinosaur bones form large bonebeds extending over several tens of square meters. The disarticulated skeletons of numerous animals are completely mixed together, the apophyses and neural arches of the vertebrae are usually broken off and the long bones indicate a preferential direction: it is therefore clear that the carcasses of the dinosaurs accumulated in a fluvial environment, with relatively strong currents. The assemblages are near-monospecific, the lambeosaurine bones constituting more than 90% of the fauna, along with isolated theropod, possible hadrosaurine, crocodile and turtle bones. The abundance of resorbed theropod teeth indicate either that the hadrosaurs were killed by predators along the river or that their carcasses were eaten and dismembered by scavengers.

Dinosaurs have also been discovered along the northern Russian banks of the Amur River. Rozhdestvensky

(1957) first described a dinosaur-bearing layer at Blagoveschensk, about 300 km to the north-west to Belyie Kruchi; he regarded this locality as similar in structure and age to "Belyie Kruchi". Bolotsky & Kurzanov (1991) described the Lambeosaurinae *Amurosaurus riabinini*, discovered by the Amur Complex Integrated Institute of the Far East Branch of the Russian Academy of Sciences in the Tsagayan Formation along the Russian banks of the Amur River at Blagoveschensk. In 1991, Bolotsky discovered another dinosaur locality in the Tsagayan Formation at Kundur. The stratigraphic section revealed at Kundur is particularly interesting, because it is very thick and apparently continuous from the Campanian to the Danian (Markevich & Bugdaeva, 1997). The dinosaur bones lie in the middle part of the section: the palynocomplex observed at this level reveals a savannah-like landscape in hot-temperate climatic conditions. From a biostratigraphic point of view, this assemblage belongs to the *Wodehouseia spinata* - *Aquilapollenites subtilis* palynozone, recognised by Markevich (1994) in several regions of the Russian Far East. It has been suggested that this palynozone may be early Maastrichtian (Markevich, 1994) or middle Maastrichtian (Markevich & Bugdaeva, 1997) in age. However, the presence of *Wodehouseia spinata* rather suggests a late Maastrichtian age. Indeed, in North America, this species is regarded as a good biostratigraphic indicator for typical late Maastrichtian ("Lancian") formations, such as the Scollard Formation in Alberta (Srivastava, 1970), the Lance Formation in Wyoming (Leffingwell, 1970), the Hell Creek Formation in Montana and the Dakotas (Hotton, 1988), the Laramie, Arapahoe and lower part of the Denver Formations in Colorado (Newman, 1987). It has been demonstrated that, in North America, the iridium anomaly and the massive extinction event marking the K-T boundary occur within the *Wodehouseia spinata* palynozone (Sweet *et al.*, 1990). Of course, further palynological studies are needed to demonstrate that the *Wodehouseia spinata* - *Aquilapollenites subtilis* palynozone in eastern Asia and the *Wodehouseia spinata* palynozone in North America are really synchronous, but this is not the aim of the present paper. Markevich & Bugdaeva (1997) indicate that the Blagoveschensk fossil

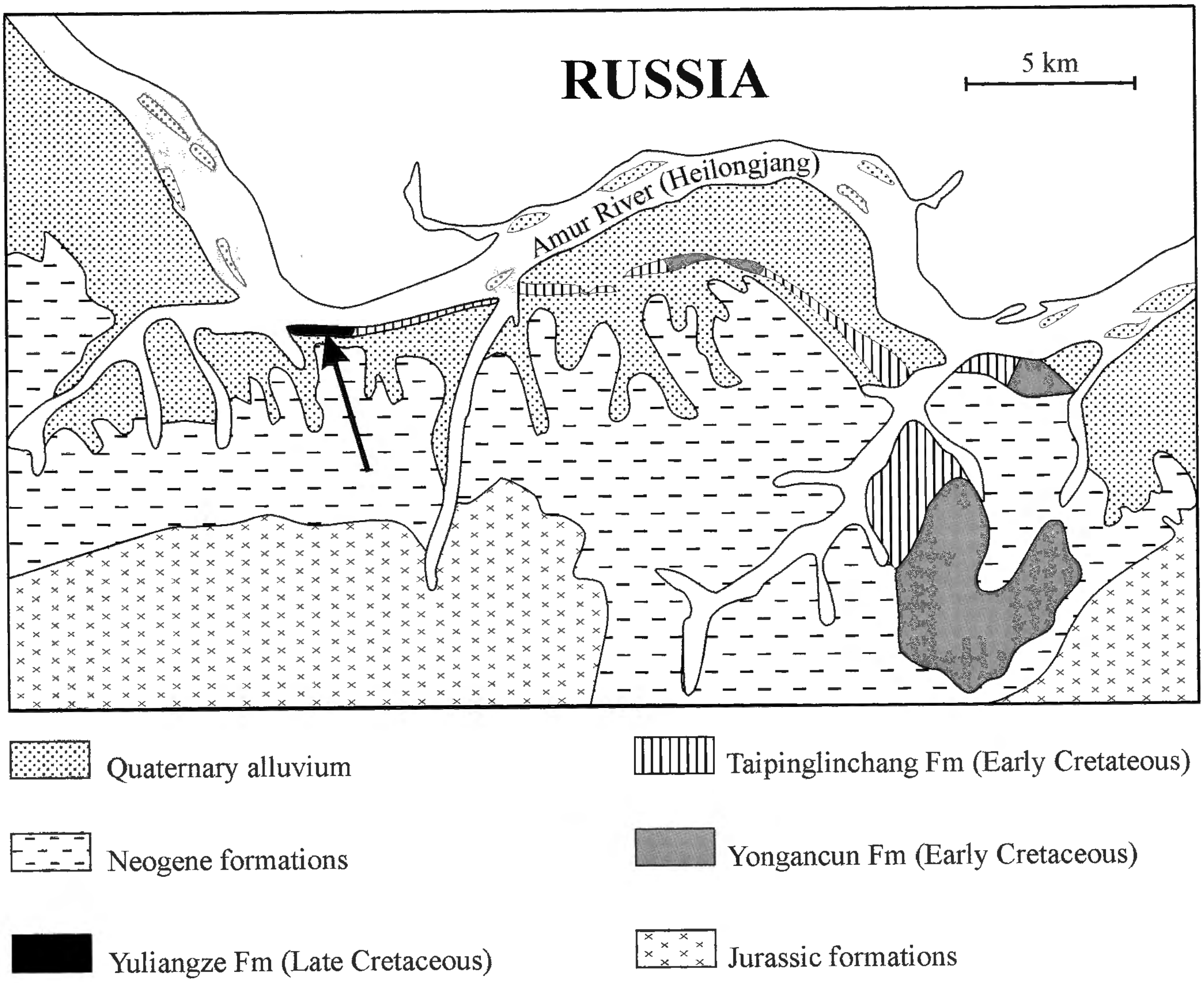


Fig. 2 — Simplified geological map of the Jiayin area (Heilongjang Province, P.R. China). The arrow indicates the position of the "Belyie Kruchi", *locus typicus* of *Charonosaurus jiayinensis*.

locality also belongs to the *Wodehouseia spinata* - *Aquilapollenites subtilis* palynozone. The same age is assigned to the strata that have yielded the type-specimen of *Nipponosaurus sachalinensis* NAGAO, 1936 in Sakhalin Island (MARKEVICH & BUGDAEVA, 1997).

No stratigraphic correlation has currently been established between the Chinese Yuliangze and the Russian Tsagayan Formations, but preliminary palynological investigations reveal the abundance of *Wodehouseia spinata* and *Aquilapollenites* sp. in sediments enclosing the bones from "Belyie Kruchi" (see also YANG, 1987). The bone-bearing beds in the Yuliangze Formation therefore belong to the same palynozone as the dinosaur localities in eastern Russia (Blagoveschensk, Kundur and Sakhalin Island). It is therefore Maastrichtian in age, maybe late Maastrichtian if palynological correlation with Lancian formations in North America can be confirmed.

Taxonomy

Preliminary remark - Since cladistic analysis was first applied to dinosaur systematics, a plethora of scenarios have been proposed attempting to resolve ornithopod phylogeny (see MILNER & NORMAN, 1984; NORMAN, 1984a, b, 1990; SERENO, 1984, 1986, 1991, 1998; COOPER, 1985; MARYAŃSKA & OSMÓLSKA, 1985; HORNER, 1988, 1990, 1992; NORMAN & WEISHAMPEL, 1990; WEISHAMPEL & HORNER, 1990; WEISHAMPEL *et al.*, 1993; FORSTER, 1997; GODEFROIT *et al.*, 1998; HEAD, 1998), leading to indescribable taxonomic confusion. Although we do not completely agree with the phylogeny of ornithopods proposed by SERENO (1998, fig. 5), we have decided, when possible, to follow the taxonomy developed by this author because it appears to be the most logical and supports modifications to the original scenario. The taxa used in the present paper are briefly explained below, using SERENO's (1998) definitions. Ornithopoda MARSH, 1881 include *Heterodontosaurus*, *Parasaurolophus*, their most common ancestor and all descendants; Euornithopoda SERENO, 1986 include all ornithopods closer to *Parasaurolophus* than to *Heterodontosaurus*; Iguanodontia DOLLO, 1888 include all Euornithopoda closer to *Parasaurolophus* than to *Hypsilophodon*; Ankylopollexia SERENO, 1986 include *Camptosaurus*, *Parasaurolophus*, their most common ancestor and descendants; Hadrosauriformes SERENO, 1986 include *Iguanodon*, *Parasaurolophus*, their most recent common ancestor and all descendants; Iguanodontidae COPE, 1869 include all hadrosauriforms closer to *Iguanodon* than to *Parasaurolophus*; Hadrosauroidea COPE, 1869 include all hadrosauriforms closer to *Parasaurolophus* than to *Iguanodon*; Hadrosauridae COPE, 1869 include *Saurolophus*, *Parasaurolophus*, their most common ancestor and all descendants; Hadrosaurinae COPE, 1869 include all hadrosaurids closer to *Saurolophus* than to *Parasaurolophus*; Lambeosaurinae PARKS, 1923 include all hadrosaurids closer to *Parasaurolophus* than to *Saurolophus*. We have not retained the Styracosterna SERENO, 1986 (all ankylopollexians closer to *Parasaurolophus* than to *Camptosaurus*). According to SERENO (1986, 1998), this taxon includes *Probactrosaurus* and the Hadrosauriformes. Recent discoveries in Inner Mongolia (GODEFROIT *et al.*, in prep.) indicate that *Probactrosaurus* must rather be regarded as a Hadrosauroidea taxon; therefore, Styracosterna is provisionally a synomym of Hadrosauriformes.

Abbreviations - CUST: Museum of Natural History, Jilin University, Changchun, P.R. China; GMH: Geological Museum of Heilongjang Province, Harbin, P.R. China.

Ornithopoda MARSH, 1881
Ankylopollexia SERENO, 1986
Hadrosauriformes SERENO, 1986
Hadrosauroidea COPE, 1869
Hadrosauridae COPE, 1869
Lambeosaurinae PARKS, 1923
Genus *Charonosaurus* GODEFROIT, ZAN & JIN, 2000

Diagnosis. See specific diagnosis (monospecific genus).

Type species. *Charonosaurus jiayinensis* GODEFROIT, ZAN & JIN, 2000.

Charonosaurus jiayinensis GODEFROIT, ZAN & JIN, 2000

? 1925	*Trachodon amurense* nov. sp. - RIABININ, p. 1, pl. 1 {*nomen dubium*}.
? 1930a	*Mandschurosaurus amurensis* nov. gen. nov. sp. - RIABININ, p. 15, figs. 3-4; pls.1-4 {*nomen dubium*}
1986	*Mandschurosaurus amurensis* - YANG, p. 2, pls.1-4.
1994	*Mandschurosaurus amurensis* RIABININ - XING *et al.*, p. 17.
* 2000	*Charonosaurus jiayinensis* n.g. n.sp. - GODEFROIT *et al.*, p. 877, fig. 2.

Holotype. CUST J-V1251-57, a partial skull.

Referred material. Collections CUST J-III and J-V; GMH Hlj-16, 77, 87, 101, 140, 143, 144, 178, 195, 196, 207, 278, A10, A12 and "magnus". We have also studied the fossils housed in the Heilongjang Provincial Museum, but the senior author did not receive the authorisation from the authorities of this institution to include their material in the present paper.

Locus typicus. "Belyie Kruchi", southern banks of Amur (Heilongjang) River, 8 km west of Jiayin village (Heilongjang Province, P.R. China; 48°53' N, 130°27'E; Figs. 1-2).

Stratum typicum. Yuliangze Formation, ?late Maastrichtian, Late Cretaceous.

Diagnosis. Dorsal surface of parietal regularly rounded, without sagittal crest; lateral side of squamosal nearly completely covered by caudal ramus of postorbital; paroccipital and postcotyloid processes very low, extending only to the mid-height of *foramen magnum*; alar process of basisphenoid very prominent and symmetrical;

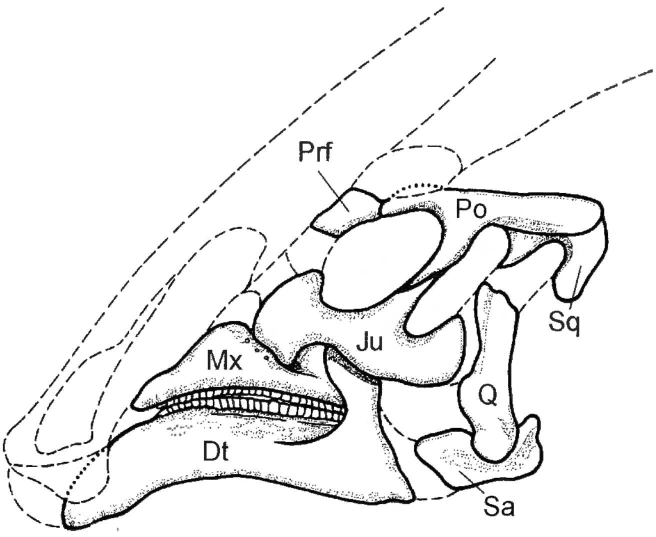


Fig. 3 — Reconstruction of the skull of *Charonosaurus jiayinensis*, from the Yuliangze Formation of Jiayin, in left lateral view. Dt , dentary; Ju, jugal; Mx, maxilla; Po, postorbital; Prf, prefrontal; Q, quadrate; Sa, surangular; Sq, squamosal.

caudal crest very developed on the humerus; forearm particularly elongated and slender: ratio "total length/maximal width of the proximal head" > 6.3 for the ulna and > 6.6 for the radius; preaceabular process of ilium very long: ilium length/preacetabular length > 2.1.

Description

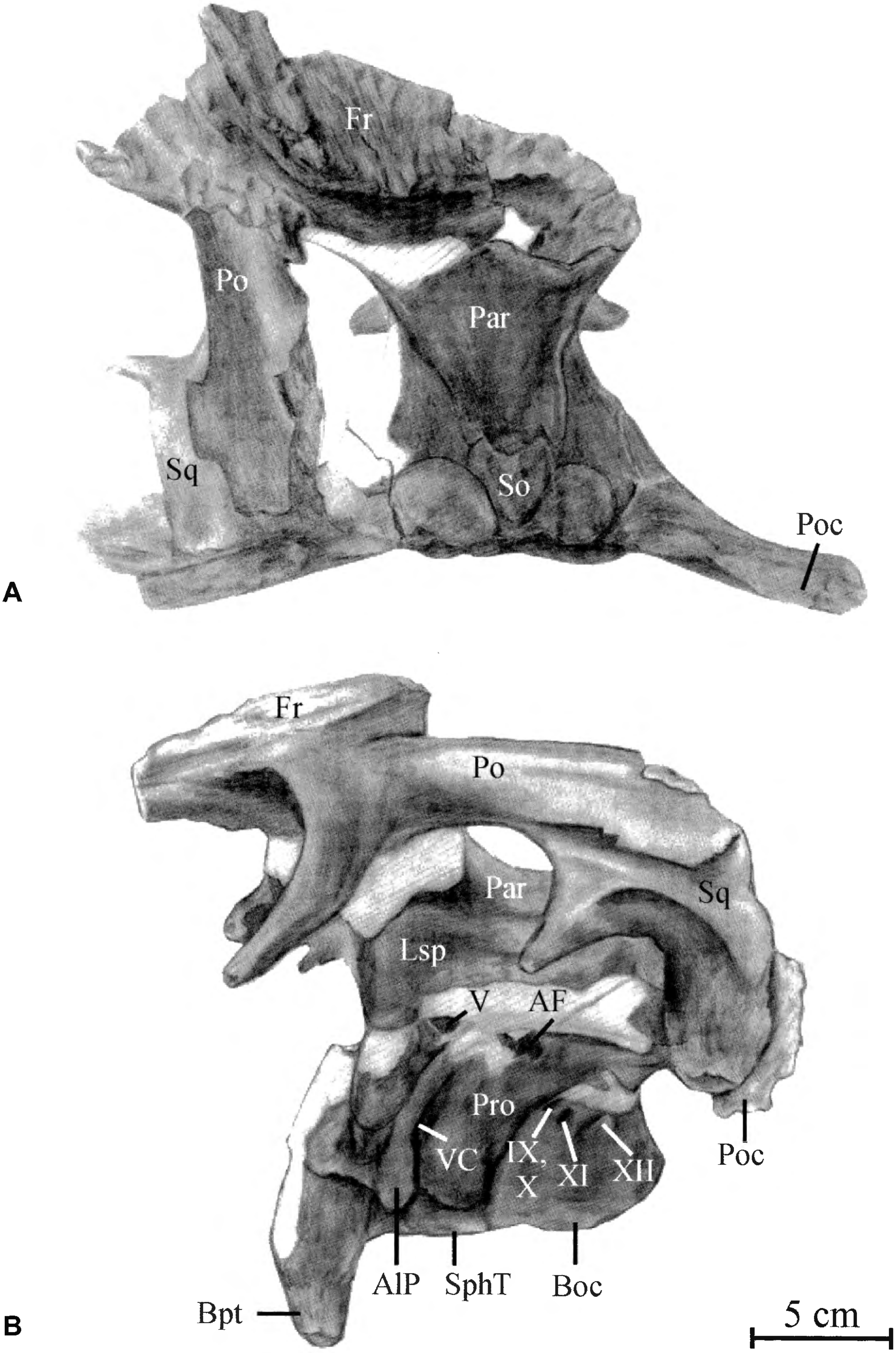
Although both juvenile and adult specimens are represented, the lambeosaurine sample from Jiayin is particularly homogeneous and there is to date no reason to consider that more than one lambeosaurine species coexisted in this limited area. For that reason, it has been decided to include all the studied lambeosaurine material from that locality into a single description.

Skull, mandible and dentition (Figs. 3-5; Pls. 1-2)

Basioccipital (CUST JV1251-57) - The basioccipital (**Boc**) forms the main portion of the occipital condyle. In caudal view, the condyle is particularly low and transversely broadened. It is incised by a relatively deep median vertical furrow. Its articular surface is perfectly vertical, perpendicular to the long axis of the braincase, and moderately rounded. Because of its important broadening, the median part of the dorsal side of the basioccipital participates in the floor of the *foramen magnum*. The rostral portion of the basioccipital slightly projects ventrolaterally to form the caudal half of not very prominent sphenooccipital tubercles (**SphT**). Between the occipital condyle and the sphenooccipital tubercles, the neck of the basioccipital is extremely short.

Basisphenoid (CUST JV1251-57) - The basisphenoid is completely fused with the basioccipital to form the rostral half of the sphenooccipital tubercles; a rather deep fossa opens between these tubercles. In front of the sphenooccipital processes, the basisphenoid forms a pair of long and robust basipterygoid processes (**Bpt**). They project both ventrally and laterally well below the level of the occipital condyle, forming an angle of about 45° with the horizontal axis of the skull. Above each basipterygoid process, the lateral side of the basisphenoid forms a large and particularly well-detached alar process (**AlP**); this process is nearly symmetrical in lateral view and formed by a large caudal process, extending caudolaterally to conceal partially the Vidian canal (**VC**), and a slightly smaller rostral process extending rostrolaterally over the basipterygoid process. Between the sphenooccipital tubercle and the alar process, the deep Vidian canal carried the internal carotid artery through the basisphenoid into the pituitary fossa.

Exoccipitals (CUST JV1251-57) - The exoccipital condyloids are very expanded rostro-caudally. They form the lateral wall of the *foramen magnum* and participate in the formation of the dorsolateral portion of the occipital condyle, where they form the cranio-vertebral joint with the atlas. They are well separated from each other along the mid-line of the floor of the *foramen magnum*. They are pierced by three foramina for transmission of cranial nerves. The caudal one enters the *foramen magnum* just within its external opening; according to Ostrom (1961), this foramen transmitted the caudal branch of the hypoglossal nerve (**c.n. XII**). More rostrally, the foramen for the spinal accessory nerve (**c.n. XI**) is by far the smallest of the three. The third foramen is very large and set more dorsally, for transmission of the vagus and glossopharyngeal nerves (**c.n. X** and **IX**, respectively). It is bordered by a big pillar, extending from the base of the paroccipital process to the rostroventral corner of the exoccipital condyloid, which probably marks the contact with the opisthotic. Above the *foramen magnum*, the medial borders of the exoccipitals reach each other and exclude the supraoccipital from this opening, as usual in Hadrosauriformes (see e.g. Godefroit *et al.*, 1998). Lambe (1920) and Lull & Wright (1942) suggested that the hadrosaurian paroccipital process is entirely formed by the opisthotic, as often observed in modern reptiles. Langston (1960, fig. 152) also showed that the opisthotic participates in the formation of the paroccipital process in the hadrosaurine *Lophorhothon atopus*. On the other hand the paroccipital process is clearly formed only by the exoccipital in the hadrosauroid *Bactrosaurus johnsoni* (Gilmore, 1933, fig. 23). Ostrom (1961) thought that it is in fact impossible to estimate the contribution of the exoccipital and opisthotic in this process, because, in Hadrosauridae, both bones are too intimately fused together. In *Charonosaurus jiayinensis*, the paroccipital processes (**Poc**) are very expanded laterally, but are not ventrally deflected as usual in hadrosaurids: their ventrolateral corner, which offered the site of origin for *M. depressor mandibulae* (see Ostrom, 1961, fig. 51), only reaches the middle of the height of the *foramen magnum*. Their caudal surface perfectly faces vertically. The dorsal border of the paroccipital process is concave at the level of the articular facet for the supraoccipital. Both the dorsal surface and the tip of the paroccipital process are very roughened, indicating the presence of a cartilage cap in life.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Supraoccipital (CUST JV1251-57; GMH HljA12) - The supraoccipital (**So**) is a stout pyramidal bone that extends rostrally and dorsally within the dorsal region of the occiput between exoccipitals, parietal, opisthotics and squamosals. Its concave caudoventral border articulates with the paired exoccipitals, so that it is completely excluded from the roof of the *foramen magnum*. Its dorsal surface is strongly sculptured: a very prominent median promontorium, for insertion of a powerful *ligamentum nuchae*, is bordered laterally and ventrally by two very depressed areas for insertion of *M. spinalis capitis* and of *M. rectis capitis posterior*. Laterally to these depressed areas, two very prominent knobs, lodging into the caudolateral depression of the parietal, form the caudolateral corner of the supraoccipital.

Opisthotic (CUST JV1251-57; GMH HljA12; GMH Hlj144) - The opisthotic is completely fused to the exoccipital and to the prootic so that the respective limits of these bones cannot be accurately discerned. The caudal portion of *crista otosphenoidale* forms a very prominent horizontal crest on the lateral surface of the opisthotic, extending into the rostrolateral side of the paroccipital process: this crest is usually regarded as the attachment site for *M. levator pterygoideus* (NORMAN, 1984; WEISHAMPEL, 1984). The rostroventral border of the opisthotic forms the caudal portion of the auditory foramen.

Prootic (CUST JV1251-57; GMH Hlj144) - The prootic (**Pro**) is fragmentarily preserved. It is fused to the opisthotic caudally and covered by the laterosphenoid rostrally; it contacts the parietal dorsally and forms a very large flange that extends ventrally to cover the lateral side of the sphenooccipital tubercle. The lateral side of the prootic bears the rostral portion of *crista otosphenoidale*. Its rostral margin is deeply notched by the caudal border of the large foramen for the trigeminal nerve (**c.n. V**).

Laterosphenoid (CUST JV1251-57) - The laterosphenoid (**Lsp**) is a very large and stout bone that forms the rostral portion of the lateral wall of the braincase. Caudally, it covers the rostrolateral wall of the braincase and participates in the rostral margin of the trigeminal foramen. It contacts dorsally the parietal. Its rostrodorsal portion is broken, so that its contact with the postorbital cannot be described. The lateral side of the laterosphenoid bears a prominent rounded sub-vertical ridge marking the separation between the orbit and the supratemporal fenestra. This crest extends ventrally to form an elongated and elliptical basal foot covering the lateral side of the alar process of the basipterygoid. Rostrally, the laterosphenoid forms a complex suture with the orbitosphenoid - presphenoid.

←

Fig. 4 — Holotype skull of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - A: dorsal view; B: left lateral view. AF, auditory foramen; AlP, alar process; Boc, basioccipital; Bpt, basipterygoid process; Fr, frontal; Lsp, laterosphenoid; Par, parietal; Po, postorbital; Poc, paroccipital process; Pro, prootic; So, supraoccipital; SphT, sphenooccipital tubercle; Sq, squamosal; VC, Vidian canal; V-XII, foramina for cranial nerves.

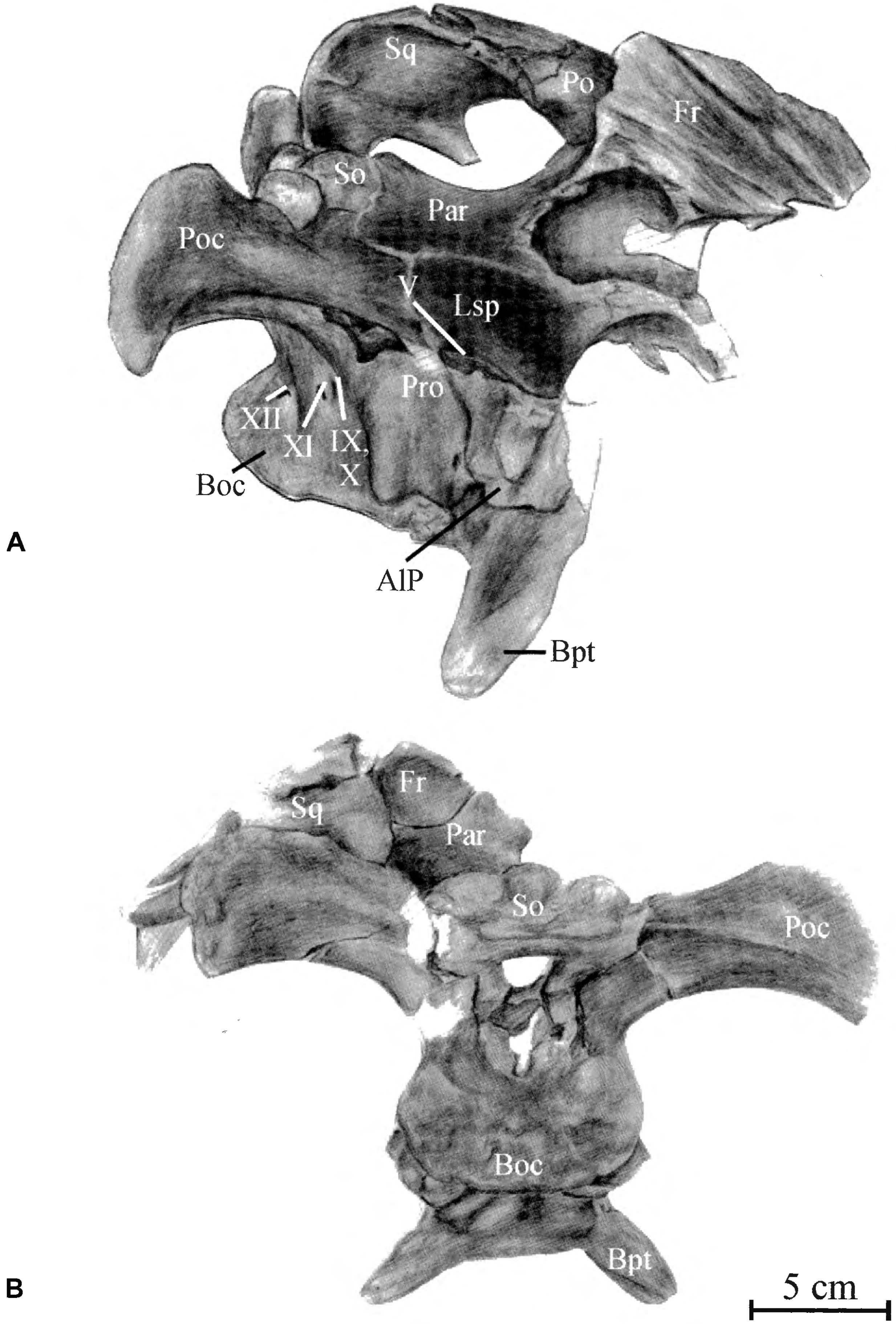
Orbitosphenoid and **presphenoid** (CUST JV1251-57) - These bones form the rostral wall of the braincase. They are unfortunately too incompletely preserved to provide any valuable information.

Supratemporal fenestra (CUST JV1251-57) - The supratemporal fenestra is trapezoidal in shape and proportionally short and wide. It is bordered medially and rostromedially by the parietal, rostrolaterally by the postorbital, laterally and caudally by the squamosal.

Parietal (CUST JV1251-57; GMH HljA12) - The parietal (**Par**) is relatively short and broad: its maximal width is much greater than its length. It clearly does not extend caudally towards the occipital surface of the skull. Its caudolateral borders are deeply truncated for reception of the very large supraoccipital knobs. Ventrally, the parietal forms a relatively straight suture with the opisthotic and the laterosphenoid. The rostral part of the parietal is not completely preserved; it can nevertheless be observed that it contacts the postorbital laterally and that it is completely fused with the frontal. The dorsal surface of the parietal, which forms the medial margins of the supratemporal fenestrae, is smoothly convex and does not bear any trace of a sagittal crest; only the caudal portion of the parietal, in contact with the median promontorium of the supraoccipital, is gently elevated. In ventral view, the depression for the cerebellum appears particularly large and deep.

Frontal (CUST JV1251-57) - The left frontal (**Fr**) is relatively well preserved in the holotype specimen. Although its rostral portion is broken, it appears relatively short and particularly wide. In ventral view, the mediocaudal corner of the frontal forms a very large and deep depression that enclosed the rostral portion of the cerebrum in life. This depressed area is surrounded by the elevated contact area for the laterosphenoid and the orbitosphenoid. Rostrolaterally, the ventral side of the frontal forms the roof of the orbit. The dorsal surface of the frontal is highly modified to form a very broad and excavated platform, strongly inclined forwards and inwards. Its dorsal surface bears long and deep longitudinal grooves. Laterally, the dorsal platform is bordered by a high and broad lateral wall, whose dorsal concave surface can be interpreted as a contact area for the nasal or the premaxilla. Parallel to this elongated facet, the lateral side of the frontal is excavated along its whole length by a concave contact area for the prefrontal. The frontal was therefore excluded from the orbital margin. The caudolateral part of the frontal projects dorsally and overhangs the rostral portion of the parietal and of the supratemporal fenestrae.

Prefrontal (CUST JV1251-57) - The left prefrontal is partly preserved in the holotype specimen. It is roughly crescent - shaped in outline. Its rostral portion is relatively thick, with a rounded lateral surface; its internal side is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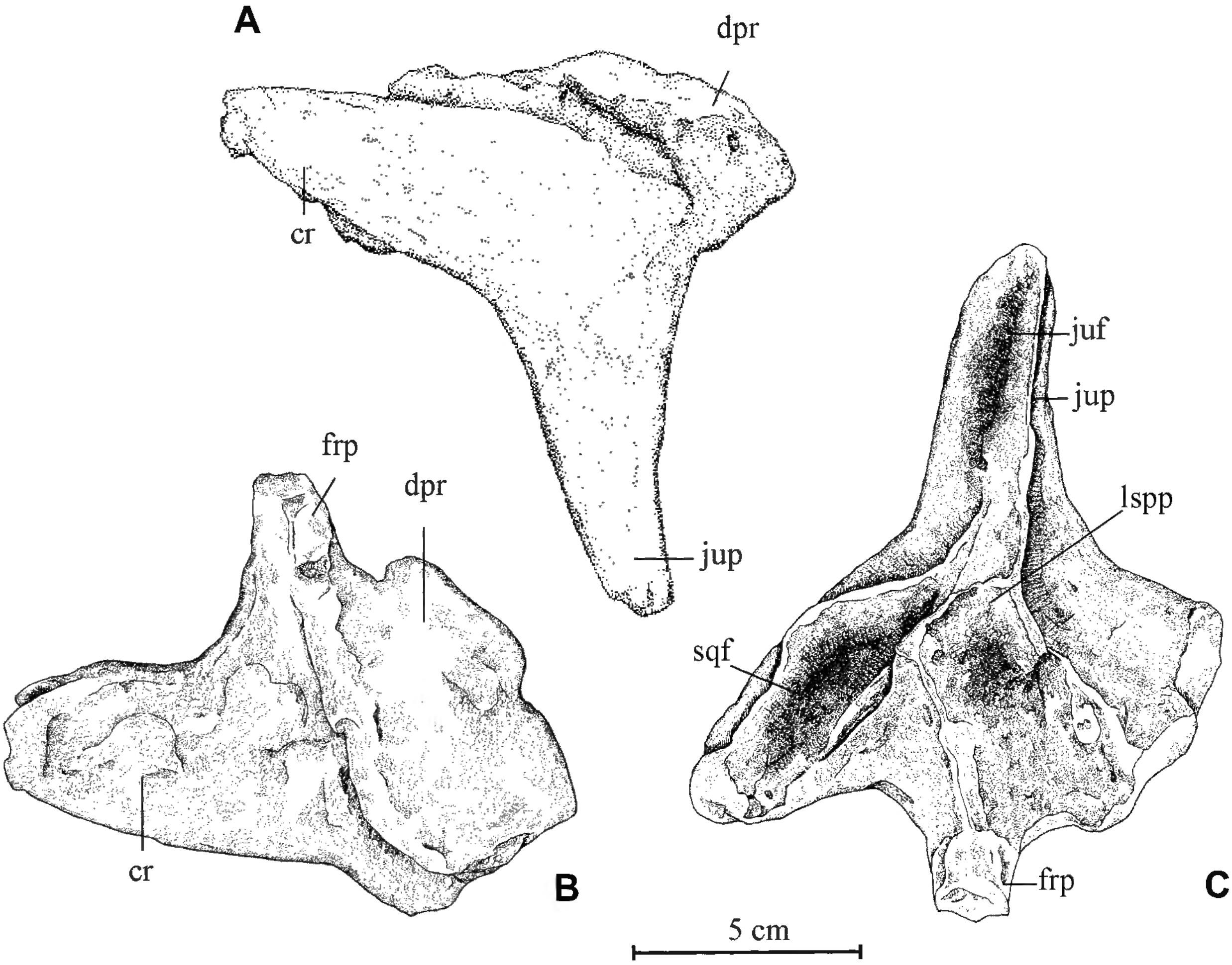

Fig. 6 — Right postorbital of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - A: lateral view; B: dorsal view; C: ventral view. cr, caudal ramus; dpr, dorsal promontorium; frp, frontal process; juf, jugal facet; jup, jugal process; lspp, laterosphenoid pocket; sqf, squamosal facet.

very roughened and excavated where it enclosed the nasal cavity. The caudal ramus is broken, but it apparently becomes progressively thinner and higher rearwards. Its internal side bears long and thin striations at this level. The lacrimal facet is broad and very roughened.

Postorbital (Fig. 6; CUST JV1251-57, CUST JV1258, GMH Hlj196, GMH Hlj197) - The postorbital of *Charonosaurus jiayinensis* is typically triradiate. The jugal process (**jup**) forms the caudal margin of the orbit and the rostrodorsal margin of the infratemporal fenestra. It is triangular in cross-section and gently curved rostroventrally. Its lateral side is flat, while its caudomedial side forms a large concave contact area for the ascending process of the jugal (**juf**). The internal orbital surface of the postorbital is very concave, but it does not form any caudal orbital sinus. The caudal ramus (**cr**) of the left postorbital is completely preserved in CUST JV1251-57. Rostrally, its ventral side is strongly excavated by a large articular surface for reception of the postorbital process of the squamosal (**sqf**). Caudally, it forms a very long, broad and thin blade that nearly completely covers the lateral side of the squamosal, reaching its caudal border. A thin frontal process (**frp**) extends medially to insert between the frontal and the parietal. At the angle between the jugal process and the frontal process, the ventral side of the postorbital forms a pocket-like depression for a synovial joint with the postorbital process of the laterosphenoid (**lspp**). In CUST JV1258 and GMH Hlj196, the dorsal side of the postorbital is very thickened and rough above the orbit and in front of the frontal process, forming a promontorium (**dp**), inclined rostrally. Together with the dorsal platform of the frontal, it probably formed the base of the broad supracranial crest. The dorsal promontorium is not developed in GMH Hj197, which apparently belongs to a very young specimen; however, the median articular surface is very thickened and turned upwards, indicating that the postorbital was partially covered by surrounding bones. Therefore, the

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Fig. 5 — Holotype skull of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - A: right lateral view; B: caudal view. AlP, alar process; Boc, basioccipital; Bpt, basipterygoid process; Fr, frontal; Lsp, laterosphenoid; Par, parietal; Po, postorbital, Poc, paroccipital process; Pro, prootic; So, supraoccipital; Sq, squamosal; V-XII, foramina for cranial nerves.

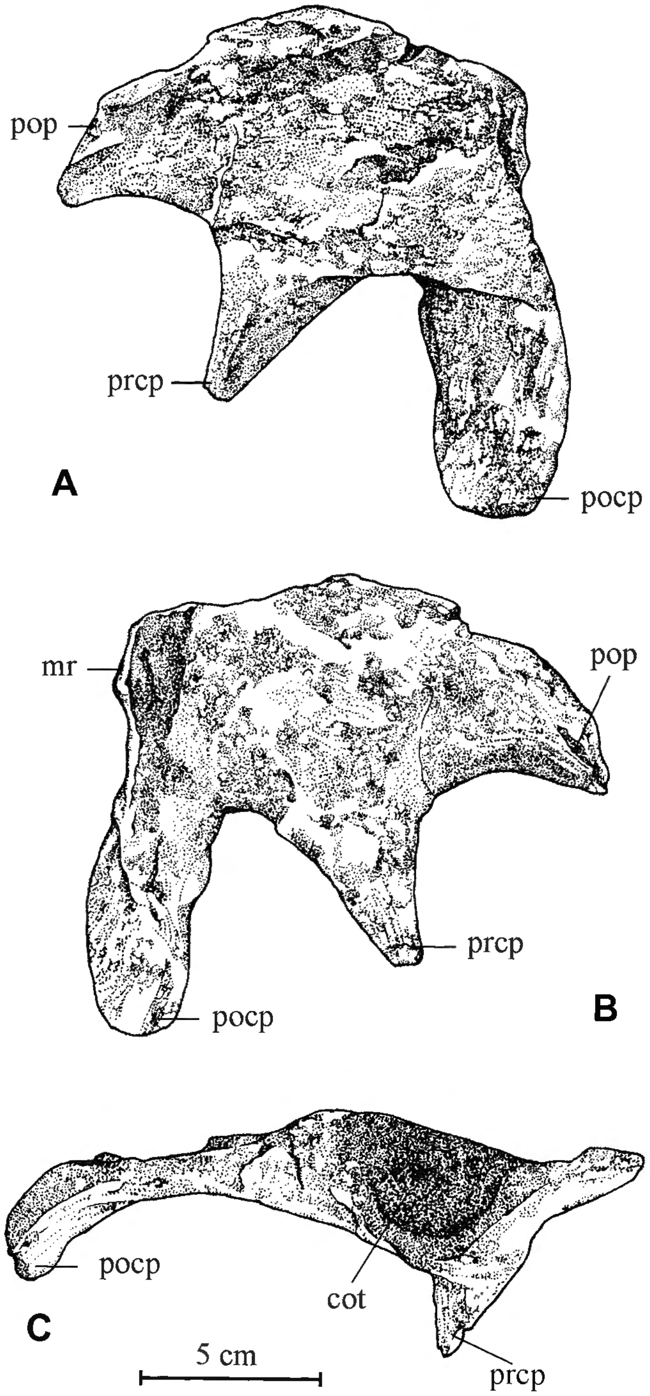

Fig. 7 — Left squamosal of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - A: lateral view; B: medial view; C: ventral view. cot, cotylus; mr, medial ramus; pocp, postcotyloid process; pop, postorbital process; prcp, precotyloid process.

development of the dorsal promontorium is here regarded as an ontogenetic character, linked to the development of a cranial crest, rather than as a diagnostic character permitting two hadrosaurid taxa to be distinguished within the studied sample.

Squamosal (Fig. 7; Pl. 3, Fig. 1; CUST JV1251-57, GMH Hlj101) - As usual in Iguanodontia, the squamosal of *Charonosaurus jiayinensis* is formed by four processes. The postorbital process (**pop**) is short, broad and slightly curved inwards. The precotyloid (or prequadratic) process (**prcp**) is relatively short, pointed at its distal end and triangular in cross-section; it extends rostroventrally to a 45° angle and is slightly curved inwards. The postcotyloid process (**pocp**) is broad, very short and very flattened, with an oblique great axis oriented caudolaterally; it extends ventrally and slightly laterally. Between the pre- and postcotyloid processes, the squamosal is deeply excavated to form a large cotylus (**cot**). The rostral and caudal sides of this cavity bear striations, marking ligamentous attachment with the quadrate. Above the cotylus, the body of the squamosal is particularly elevated. Its inner side is smooth, gently curved and inclined upwards and inwards to form the caudolateral angle of the supratemporal fenestra. Its lateral side is slightly excavated along its whole length by the broad articular facet for the caudal ramus of the postorbital. The medial ramus (**mr**) of the squamosal is not preserved on the studied material.

Jugal (Fig. 8; CUST JV1251-57) - The rostral process (**rpr**) of the jugal is rounded and very expanded dorsoventrally, with a high dorsal lacrimal process. In medial view, the maxillary facet of the rostral process is very excavated; its ventral portion bears deep scars indicating the insertion of strong ligaments. The caudodorsal part of the maxillary facet is bordered by a very elevated and convex maxillary process, bearing a small palatine facet. Because of the great dorso-ventral expansion of the rostral process, the neck of the jugal appears strongly contracted. The ascending process (**aspr**) is very inclined backwards, forming a 45° angle with the long axis of the jugal; this process is rather slender, triangular in cross-section and it gently tapers dorsally. Its dorsal portion bears a large flattened postorbital facet facing rostrally and laterally. The caudal process (**cpr**) is rather robust. Although broken, its ventral margin appears smoothly convex. Its medial side bears a large articular facet for reception of the rostral process of the quadratojugal.

Maxilla (Pl. 3, fig. 2; CUST JV1251-57, GMH Hlj178; YANG, 1986, pl. 1, figs. 4 & 6) - The maxillae are always fragmentary in the preserved material. Although always broken, the dorsal process appears large and elevated, lying behind the mid-point of the bone. An elongated groove along the rostrolateral side of the dorsal process marks the contact with the lacrimal. At the base of the lacrimal facet, a rather large canal penetrates the dorsal process and communicates with the excavated caudomedial area of this process. This foramen has been argued to represent the antorbital foramen among hadrosaurids (WEISHAMPEL & HORNER, 1990). Beneath the dorsal process, the lateral side of the maxilla forms a prominent jugal process, slightly inclined dorsally and rostrally. Two or three large foramina penetrate the maxilla ventrally and rostrally to the jugal process. A very prominent, rounded and horizontal ridge extends caudally from the jugal process and separates the ectopterygoid shelf from the dental battery. The ectopterygoid shelf is broad, dorso-ventrally concave and rostro-caudally undulatory. Rostrally to the dorsal process, the dorsal border of the

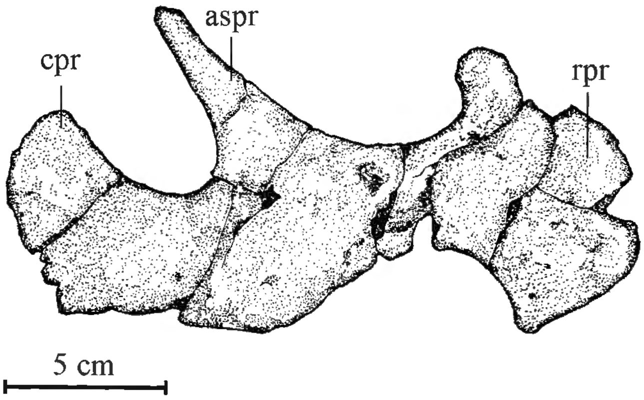

Fig. 8 — Right jugal of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - Lateral view. aspr, ascending process; cpr, caudal process; rpr, rostral process.

maxilla is widened to form a concave shelf upon which the premaxilla rested. The maxilla regularly tapers rostrally, but the rostralmost portion is always missing, so that it is not possible to know whether it forms a rostromedial maxillary process, as in Hadrosaurinae, or a true maxillary shelf, typical of Lambeosaurinae. The medial maxillary surface is flat and pierced by a series of special foramina interconnected by a groove along the whole length of the bone; they have been interpreted by EDMUND (1957) as foramina for the entry of blood vessels and sensory nerves into the dental lamina. The alveolar border of the maxilla is slightly concave. The dental battery contains up to 44 tooth rows.

Quadrate (Fig. 9; GMH "Hlj magnus", GMH Hlj124; YANG, 1986, pl. 1, figs. 1 & 3) - The quadrate of *Charonosaurus jiayinensis* is long, stout and slightly curved backwards. The proximal head is well rounded in lateral view, sub-triangular in cross-section and very flattened medio-laterally. Its caudal side bears a small buttress that lay against the rostrolateral side of the paroccipital process. The very thin pterygoid wing (**ptw**) is always broken in the studied material; however, it appears oriented rostromedially, forming an angle of about 45° with the jugal wing. The surface comprised between the rostrodistal part of the pterygoid wing and the lateral wall of the quadrate bears strong longitudinal striations, marking the insertion area of a very large fleshy *M. adductor mandibulae posterior* (OSTROM, 1961, fig. 46). The caudomedial side of the quadrate shaft bears a well-developed ridge, marking the contact with the quadrate ramus of the pterygoid. The jugal wing is slightly curved inwards and its rostral border is regularly rounded. The quadratojugal notch (**qjn**) is particularly long and deep beneath the jugal wing; its edge is rostromedially beveled by the articular surface for the quadratojugal (**qjf**) along nearly its whole height. This indicates that the quadratojugal notch was completely covered laterally by the quadratojugal and that the paraquadratic foramen was consequently absent. The distal head of the quadrate is dominated by a large hemispheric lateral condyle (**lcd**), triangular in cross-section, that fitted into the surangular component of the mandibular glenoid. A smaller medial condyle (**mcd**) is set more dorsally, at the base of the pterygoid wing; it articulated with the articular component of the mandibular glenoid.

Dentary (Fig. 10; Pl. 4; CUST JV1251, CUST JIII1221, CUSTJIV252, GMH HljA40; GMH Hlj278, GMH HljA40; YANG, 1986, pl. 1, figs. 7 & 9) - In adult specimens, the dentary is particularly long and robust. Its lateral side is very convex dorso-ventrally and pierced by a series of foramina for vessels and nerves. Viewed from above, the bone is strongly concave externally, as illustrated by STERNBERG (1935, pl. 2, fig. 1) for *Corythosaurus excavatus*. The coronoid process (**cpr**) is high, rather slender and slightly curved inwards. Its apex is distinctly inclined rostrally. Its lateral side is convex both rostro-caudally and dorso-ventrally, whereas its medial side is slightly concave. Its caudomedial side bears a smooth surangular facet (**saf**). Caudally, the coronoid process is deeply excavated by the rostrodorsal part of the adductor fossa. Under the coronoid process, the dentary is also very deeply excavated by the enormous rostral portion of the adductor fossa which enters the body of the bone towards the level of the tenth dental series; it extends rostrally as a deep mandibular groove (**mdg**) towards the level of the 22th dental series.

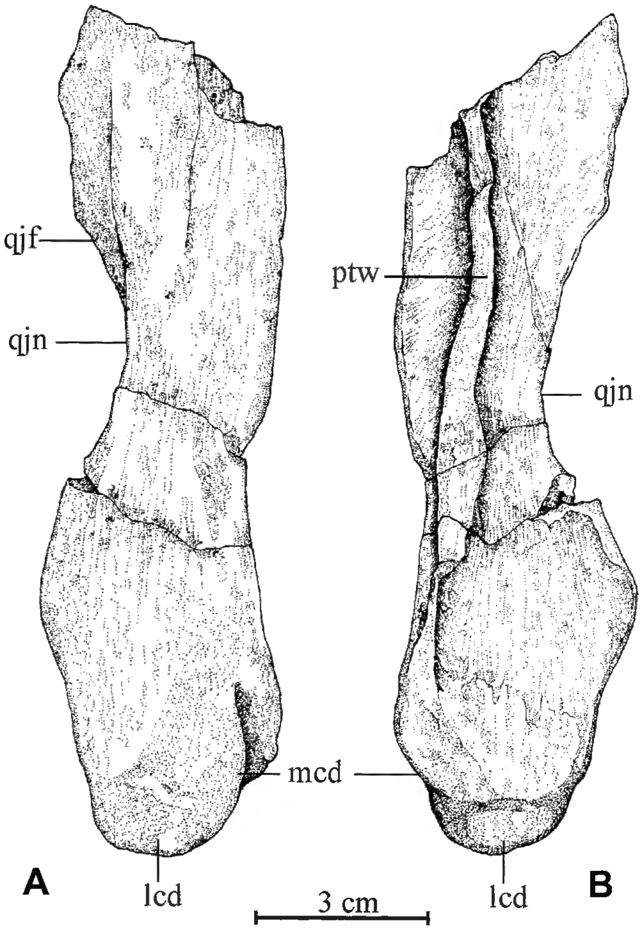

Fig. 9 — Left quadrate of *Charonosaurus jiayinensis* (GMH Hlj124), from the Yuliangze Formation of Jiayin - A: lateral view; B: medial view. lcd, lateral condyle; mcd, medial condyle; ptw, pterygoid wing; qjf, quadratojugal facet; qjn, quadratojugal notch.

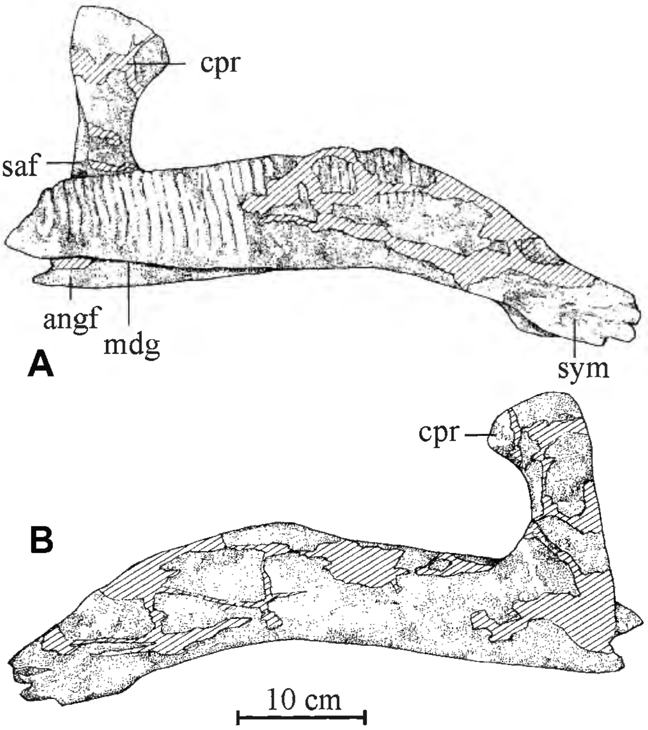

Fig. 10 — Left dentary of *Charonosaurus jiayinensis* (GMH HljA40), from the Yuliangze Formation of Jiayin - A: medial view; B: lateral view. angf, angular facet; cpr, coronoid process; mdg, mandibular groove; saf, surangular facet; sym, symphysis.

Under the mandibular groove, the medial side of the dentary bears a very elongated angular facet (**angf**). A triangular splenial facet lies at the caudoventral end of the coronoid process. The thin bony plate concealing the dental battery is not preserved in the specimens discovered up to now. The dental battery can be formed by more than 40 (GMH Hlj278) tooth rows, depending on the size of the dentary: the number of tooth rows is therefore clearly an ontogenetic character. Each tooth row is formed by 2 to 3 teeth, with 1 or 2 functional teeth. The rostral portion of the dentary is very strongly deflected ventrally, forming an angle of about 30° with the long axis of the bone; the deflection begins at the level of the rostral third of the dental battery. The rostral articular surface for the predentary is typically scoop-shaped and slightly inclined towards the sagittal axis of the mandible. The diastema is very short in juveniles and more extended in larger individuals: it is thus clearly an ontogenetic character, as previously noted by NORMAN (1998).

Surangular (Fig. 11; Pl. 3, Fig. 3; CUST JV1251-57, GMH Hlj195, GMH HljA1; YANG, 1986, pl. 1, figs. 2 & 5) - In dorsal view, the surangular component of the mandibular glenoid (**gl**) is not particularly deep and expanded; it forms a prominent lip on the lateral side of the surangular. The retroarticular process (**rapr**) is rather small, lobate and upturned above the glenoid. It is triangular in cross-section with very thin caudal and ventral edges. In front of the glenoid, the surangular bears a very high and thin plate, concave internally, which formed the caudolateral wall of the adductor fossa. Beneath the glenoid, the medial side of the surangular forms a large and concave insertion area for *M. pterygoideus dorsalis*, which extends caudally towards the inner side of the retroarticular process and rostrally towards the adductor fossa. A deep and elongated facet for the angular (**angf**) runs along the ventromedial side of the surangular. According to HORNER (1992), the horizontal shelf between the insertion area for *M. pterygoideus dorsalis* and the angular facet contacted the splenial.

Dentition (Fig. 12; Pl. 4, Fig. 2b) - Teeth of *Charonosaurus jiayinensis* are organised, as typical in hadrosaurids, into dental batteries. A maximum of four succeeding teeth can be observed within each row on the lower battery. The enamelled surface of the lower battery faces inwards and clearly curves outwards; that of the upper battery faces outwards and curves very slightly inwards. As usual in hadrosaurids (WEISHAMPEL & HORNER, 1990), the occlusal plane of both the upper

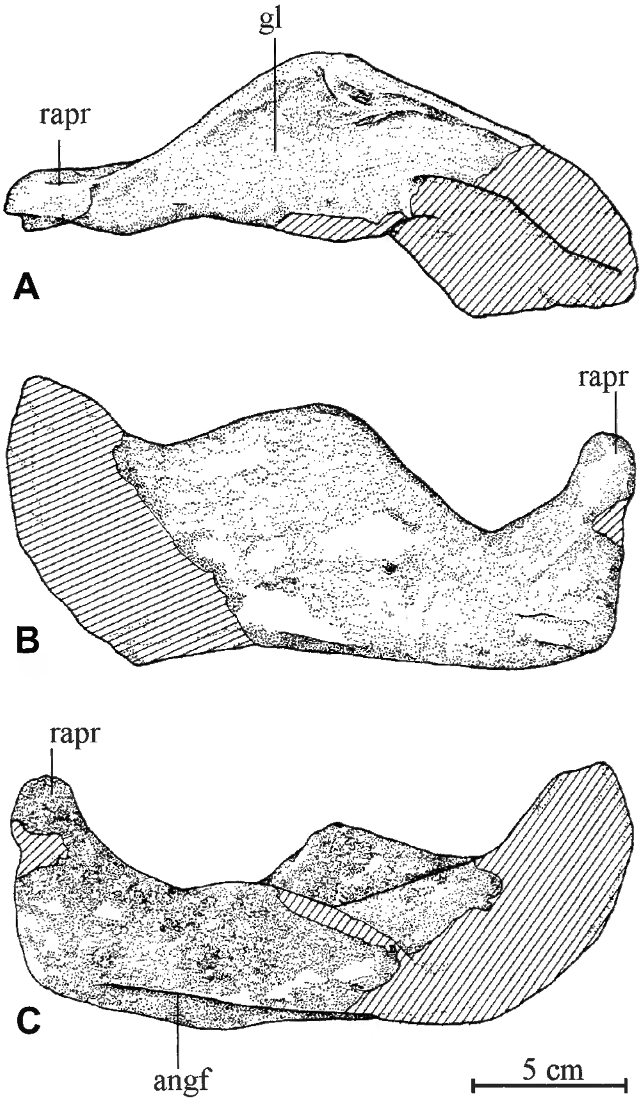

Fig. 11 — Left surangular of *Charonosaurus jiayinensis* (GMH Hlj195), from the Yuliangze Formation of Jiayin - A: dorsal view; B: lateral view; C: medial view. angf, angular facet; gl, glenoid; rapr, retroarticular process.

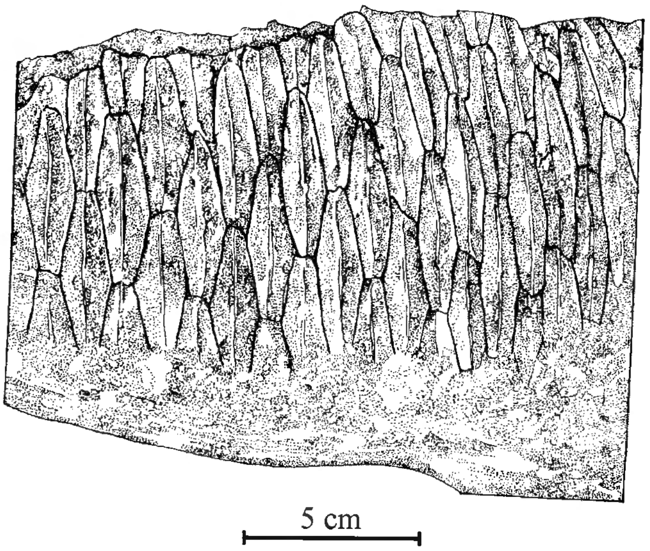

Fig. 12 — Detail of the dental battery on the dentary of *Charonosaurus jiayinensis* (GMH Hlj278), from the Yuliangze Formation of Jiayin.

and lower dental batteries is slightly undulatory and forms a 45° angle with the horizontal plane. The dental replacement pattern is that described by EDMUND (1960) in hadrosaurs (see also OSTROM, 1961, fig. 20A): the replacement of the worn teeth of alternate vertical rows progresses in wave-like fashion from the rear to the front of the battery; the replacement teeth become functional in alternate rows successively from the back forwards.

Individual tooth size depends on the position in the battery, teeth located centrally being the largest and those nearer the end of the battery being progressively smaller. In spite of this important variability, the dental crowns of *Charonosaurus jiayinensis* are characterised by their very high aspect, explaining the low number of teeth in vertical rows: in the dentary GMH Hjl278, for example, the largest dental crowns reach a height of 50 mm, for a height/maximal length ratio > 4. The maxillary teeth appear on average a little narrower than the dentary teeth, as usual in hadrosaurids (WEISHAMPEL & HORNER, 1990). The crowns are lanceolate in shape, perfectly straight and symmetrical. In dentary teeth, the enamel forms a strong sinuous median ridge. This ridge appears less strongly developed and straighter on the maxillary teeth. There is no true secondary ridges. The marginal denticles are very small. The crown-root angle of the dentary tooth cannot be measured with precision, but is clearly greater than 145°.

Axial skeleton:

The axial skeleton of *Charonosaurus jiayinensis* is very incompletely known because of the taphonomy of the locality. Many isolated centra and partial neural arches have been discovered, but the neural spines and the apophyses are always broken off because of post-mortem transport. The greatest part of the information is consequently unavailable. The neural arches are rarely fused to the centra, indicating that juveniles and young adults form the majority of the recovered material. The number of presacral and caudal vertebrae is unknown.

Cervical vertebrae - No atlas or axis material is known for *Charonosaurus jiayinensis*. The cervical centra are always strongly opisthocoelous, with a prominent hemispherical cranial articular surface and a deeply concave cup-shaped caudal articular surface. The centra are roughly triangular in cross-section because of the strong development of a longitudinal ventral keel. Above this keel, the lateral walls of the centrum are pierced by one or two pairs of nutritive foramina. The articular surfaces for the neural arch occupy the whole length of the centrum and are separated from each other by a very narrow groove, forming the floor of the neural canal. The cervical-dorsal transition appears progressive: the centra become stouter, sub-circular in cranial view and less strongly opisthocoelous.

Dorsal vertebrae and ribs - The dorsal vertebrae are very stout. The centra are very slightly opisthocoelous to perfectly amphiplatyan. The cranial and caudal articular surfaces are elliptical to sub-circular in shape. The middle part of the centrum is always constricted. The ventral keel is always less developed than on the cervical vertebrae and it is absent in numerous cases.

Dorsal ribs are unremarkable in their morphology. The capitulum is well-developed and supported by a long and gently curved neck. The elliptical tuberculum forms a shoulder region on the rib. The rib shaft is long, robust and it bears well-developed costal grooves.

Sacrum - One complete sacrum, housed in the Heilongjang Provincial Museum, has been described and figured by YANG (1986, pl. 1, figs. 1-3). Isolated material (CUST JV1260) complements this description. The sacrum is composed of nine vertebrae. The centra are proportionally short, low and wide. Their width gradually decreases cranially. Both proximal and distal articular surfaces are flat to slightly concave. Between the articular surfaces, the centra are strongly constricted. The ventral side of the sacrum is longitudinally grooved along its whole length. The zygapophyses are fused together. The diapophyses form stout transverse processes: their thickened and rounded ends are connected to the corresponding parapophysis by a prominent and rounded ridge. The neural spines are high and their basal part forms a nearly continuous plate; their dorsal portion remains unfused. The first four neural spines are curved forwards, whereas the distal four ones are curved backwards.

Seven sacral ribs are borne at the junction between adjacent co-ossified sacral centra. The base of each rib is firmly fused to the ventral surface of the transverse process; their distal ends are very expanded and fuse to form a continuous iliac bar, beginning at the level of the junction between the first and the second vertebrae and ending at the level of the junction between the seventh and the eighth vertebrae. The iliac bars gradually diverge from the vertebral column distally. Their lateral surface is concave and faces downwards, following the shape of the medial surface of the ilium.

Caudal vertebrae - Isolated caudals are known from several regions of the tail. All are amphiplatyan. The proximal centra are very short, but high, with sub-rectangular articular surfaces. The articular facets for the caudal ribs truncate the laterodorsal corner of these centra. Four large concave facets for the haemapophyses are developed on the ventral margin of the articular facets. Distally, the caudal centra become progressively smaller and proportionally more elongated; their articular surfaces become more rounded and the haemapophysial facets become less prominent.

Ossified tendons - A series of isolated fragments of ossified tendons is preserved (GMH Hlj87 and 207). They form very long rods with a fibrous appearance, bearing strong longitudinal striations around their whole circumference. They are usually rounded or elliptical in cross-section, but they can occasionally be very flattened.

Appendicular skeleton:

Scapula (Pl. 5, fig. 1; CUST JIII398, CUST "JIII", CUST "JIV", GMH "Hlj magnus"; YANG, 1986, pl. 2, figs. 4-5) - Although it is never completely preserved, the scapular blade appears relatively long and narrow, with sub-parallel craniodorsal and caudoventral borders. The proximal head is particularly robust. The coracoid suture is short, not particularly broadened and cup-shaped. Above this area, the lateral side of the proximal head bears a prominent acromial process that extends distally to form a short deltoid ridge. The dorsal part of the glenoid forms a long crescent-shaped depression under the coracoid suture. The ventrolateral side of the proximal head forms a prominent buttress which supported the caudodorsal margin of the glenoid. It is the insertion area for a powerful *M. triceps scapulare lateralis externum.*

Coracoid (Fig. 13; GMH Hlj174; GMH "Hlj magnus"; YANG, 1986, pl. 2, fig. 7) - The coracoid of *Charonosaurus jiayinensis* is short, stocky and more elongated dorso-ventrally than cranio-caudally. Very thick caudally, it gradually becomes thinner cranially. It terminates cranially in a very prominent hook-like process, pointing cranioventrally. The coracoid ridge arises from this hook, forms the rostral border of the coracoid and ends at the craniodorsal angle of this bone. At this level, the lateral side of the coracoid bears a very prominent knob, marking the insertion area for a very powerful *M. biceps* (**bik**). This feature is developed even in coracoids belonging to juvenile individuals (GMH Hlj174). The coracoid foramen (**corf**) is large, elliptical in shape and completely surrounded by the coracoid, close to the scapular suture. The thickened caudal side of the coracoid bears two distinct surfaces, forming together an angle of about 150° and separated by a narrow sulcus. The dorsal surface, forming the scapular articular facet (**scf**), is very rugose, with numerous knobs and depressions, and slightly convex; it faces dorsally and slightly medially. Ventrally, the glenoid surface (**gl**) is cup-shaped; it faces ventrally and slightly laterally.

Sternal (CUST JV"III", GMH "Hlj magnus"; YANG, 1986, pl. 6, figs. 4-5) - The sternals are not completely preserved in the studied material. They are typically hatchet-shaped, as usually observed in hadrosaurs. The enlarged proximal plate is very thin and nearly flat. It is relatively elongated dorso-ventrally, as observed, for example, in *Tsintaosaurus spinorhinus* (see YOUNG, 1958, fig. 22). Its ventral "handle" is longer, perfectly straight and dorso-ventrally flattened. Its distal end is distinctly blunt.

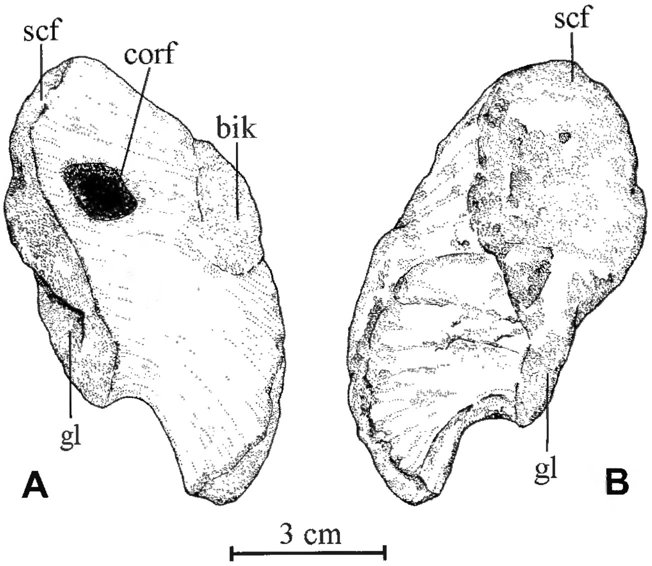

Fig. 13 — Right coracoid of *Charonosaurus jiayinensis* (GMH Hlj174), from the Yuliangze Formation of Jiayin - A: lateral view; B: medial view. bik, bicipital knob; corf, coracoid foramen; gl, glenoid; scf, scapular facet.

Humerus (Fig. 14; Pl. 5, figs. 2-3; CUST JVIII1247, CUST JV "III", GMH Hlj6, GMH Hlj143,GMH "Hlj magnus"; YANG, 1986, pl. 2, figs. 1 & 3) - The humerus of *Charonosaurus jiayinensis* is particularly robust. Its proximal end is very flattened cranio-caudally. The articular head (**ah**) is globular and supported by a buttress on the caudal side of the bone; it is usually separated from the inner tuberosity by a sulcus, but appears to be continuous with the outer tuberosity. In the very large GMH Hlj16, the articular head extends distally to form a very strong crest, parallel to the deltopectoral crest. This caudal crest is turned medially, limiting proximally a flattened triangular area, probably for insertion of a well-developed *M. scapulo-humeralis.* This crest is also present, but much less prominent in smaller individuals. Just medially to the distal portion of the caudal crest, a well-marked double elliptical facet marks the insertion of powerful *M. latissimus dorsi* and *M. teres major.* In CUST JIII1247, the lateral side of the caudal crest bears a scar marking the insertion of *M. triceps humeralis posticus.* The cranial side of the humerus forms a very wide and regularly concave bicipital sulcus (**bcsul**). From the inner tuberosity, the medial side of the humerus is regularly concave. From the outer tuberosity, the humerus develops a very prominent and angular deltopectoral crest (**dpc**), extending down below the mid-point of the bone. The border of this crest is thin, smoothly convex and turned cranially. Its cranial side bears a well-defined triangular scar for insertion of a strong *M. pectoralis*; its caudal side

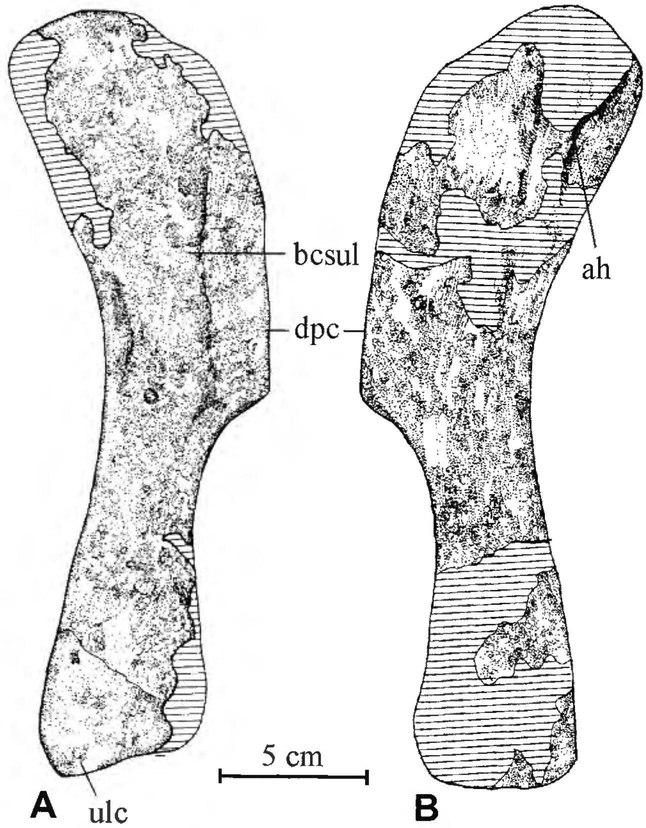

Fig. 14 — Left humerus of a juvenile specimen of *Charonosaurus jiayinensis* (GMH Hlj143), from the Yuliangze Formation of Jiayin - A: cranial view; B: caudal view. ah, articular head; bcsul, bicipital sulcus; dpc, deltopectoral crest; ulc, ulnar condyle.

bears a triangular scar for insertion of *M. deltoides clavicularis*. The distal portion of the humerus is slightly twisted outwards. The ulnar condyle (**ulc**) is by far more prominent and extends more distally than the radial condyle. The intercondylar groove is wider cranially than caudally. The muscular insertions are much less marked than on the proximal portion of the humerus. Along the craniomedial border of the humeral shaft, a smooth elliptical area can be interpreted as the insertion surface of *M. triceps humeralis medius*. Above the caudal internal groove, a large elliptical depressed area probably marks the insertion of *M. triceps humeralis lateralis*.

Ulna (Fig. 15; Pl. 6, Fig. 1; CUST JIII1715, CUST J"III", CUST J"IV", GMH Hlj "magnus") - The ulna of *Charonosaurus jiayinensis* is particularly long and slender: the ratio ''total length/maximal width of the proximal head'' is comprised between 6.3 and 6.7. The olecranon process (**ol**) is not very prominent and well rounded. Its caudal surface is very convex, whereas its cranial side is flattened. It is separated from the ulnar body by a concave sigmoidal sulcus. The proximal end of the ulnar body is very little enlarged medio-laterally when compared with the remainder of the bone. Its cranial side forms a concave sulcus for reception of the proximal head of the radius. It is bordered both medially and laterally by rather prominent ridges: the medial one (**mr**) is better developed than the lateral one (**lr**). The height of the ulna gradually decreases distally and its caudal surface becomes less convex. The distal end of the ulna is not enlarged and triangular in cross-section. Its craniomedial side bears a proximo-distally elongated facet for reception of the distal end of the radius.

Radius (Pl. 6, Fig. 2; CUST JIII1216, CUSTJIII1918, CUST J"III", CUST J"IV", GMH Hlj"magnus") - Like the ulna, the radius of *Charonosaurus jiayinensis* is particularly long and slender: the ratio ''total length/maximal width of the proximal head'' is comprised between 6.6 and 6.9. It is nearly perfectly straight, only slightly curved cranially. Both ends are very slightly expanded. The proximal end is semicircular in cross-section, its flattened caudal surface lodging into the cranioproximal gutter of the ulna. The distal end of the radius is triangular in cross-section; its flattened caudolateral side applied against the distal end of the ulna.

Metacarpals (Fig. 16; CUST J "III", GMH Hlj142, GMH Hlj"magnus") - All preserved metacarpals are very long and slender. The proximal head is rounded, sub-rectangular in cross-section, mediolaterally compressed and very roughened. The shaft of the metacarpals is perfectly straight: that of metacarpal III is elliptical in cross-section, whereas it is semicircular in metacarpals II and IV. The contact surfaces between adjacent metacarpals are flattened and scarred by ligaments that held the metacarpals together. The distal head is poorly developed and triangular in cross-section: it never forms an articular condyle, with flexor tendon groove, for the first phalanx.

Ilium (Fig. 17; Pl. 6, Fig. 3; CUST J"III", GMH Hlj77, GMH Hlj"magnus", Yang, 1986, pl. 7, fig. 2) - The following description is mainly based on GMH Hlj77, a particularly well-preserved complete left ilium. As usual in Hadrosauriformes, it forms an elongated and transversely compressed lamina. The preacetabular process (**pracp**) forms a very long and tapering projection from the craniodorsal edge of the iliac blade. It is moderately deflected ventrally and curved outwards; it is also twisted along its length, so that its lateral side faces dorsolaterally. The lateral side of the preacetabular process is perfectly flat. Its dorsal edge is very thickened and rounded, whereas its ventral edge is sharper. The caudal half of its medial side bears, at about the dorsal third of its height, a strong carina; its caudal end is flattened, forming a contact surface with the transverse apophysis of the first sacral vertebra. The main blade of the ilium is very high. Its dorsal edge is sigmoidal and thickened. At the level of the ischial peduncle, its dorsolateral border is folded to form a very prominent and roughened antitrochanter (**antr**). The dorsal part of the main blade of the ilium is medially thickened by a very developed oblique ridge, in continuity with that on the medial side of the preacetabular process. It fuses caudally with the dorsal border of the ilium, at the level of the ischial peduncle. The preacetabular notch is well developed and rather open, because of the slight ventral deflection of the preacetabular process. The pubic peduncle (**pupd**) is relatively short, not very massive and extends cranioventrally; contrary to *Iguanodon bernissartensis* (see Norman, 1980, fig. 63), its medial side

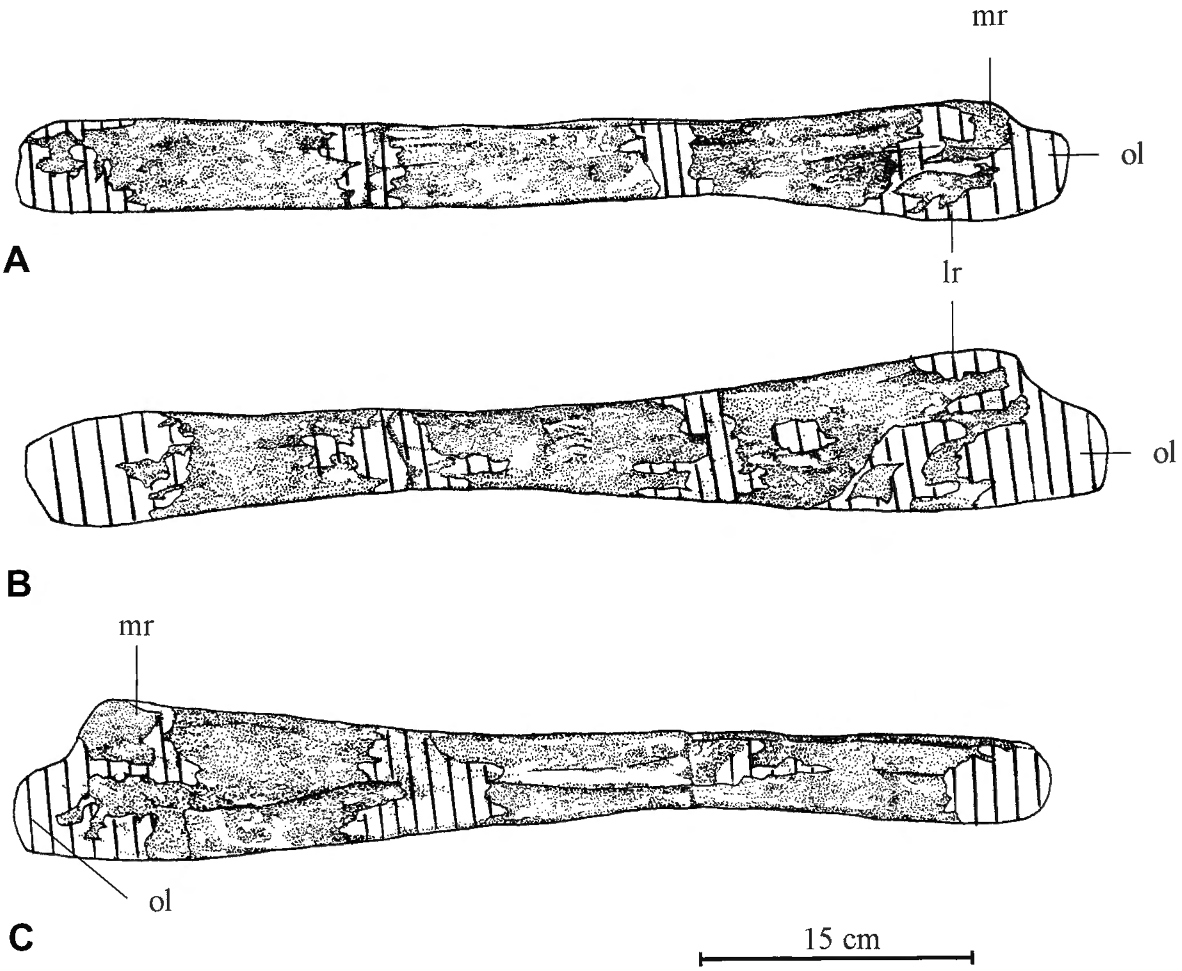

Fig. 15 — Left ulna of *Charonosaurus jiayinensis* (CUST JIII1715), from the Yuliangze Formation of Jiayin - A: dorsal view; B: lateral view; C: medial view. lr: lateral ridge; mr: median ridge; ol: olecranon process.

does not bear rugosities marking the contact with the first sacral rib and its caudal edge is smoothly convex, without developed acetabular surface. The iliac portion of the acetabulum is not very deep and asymmetrical. The ischial peduncle (**ispd**) is very elongated axially and oblique. Its articular surface faces caudoventrally and is formed by two sub-rectangular protrusions separated by a shallow depression. The postacetabular depression is less marked than the preacetabular one. The postacetabular process (**poacp**) is long, high and sub-rectangular in shape. Its dorsal border is rounded and convex; on the other hand, its ventral border is very sharp and slightly concave, so that the postacetabular process looks slightly deflected ventrally. Like the preacetabular process, the postacetabular process is slightly twisted along its length, so that its lateral side progressively faces dorsolaterally. Whereas the lateral side of the postacetabular process is perfectly flat, its medial side bears a low rounded oblique ridge, from the caudal corner of the ischial peduncle to the caudodorsal corner of the postacetabular process. The cranial and middle portions of this ridge are flattened by the contact area for the transverse process of distal sacral vertebrae.

Ischium (Fig. 18; Pl. 7, Fig. 1; CUST JV679 CUST JIV1225, CUST J"III", CUST J"IV", GMH HIj"magnus", YANG, 1986, pl. 7, fig. 3) - As usual in Hadrosauriformes, the proximal part of the ischium is expanded dorso-ventrally, flattened medio-laterally and triradiate. The iliac ramus (**ilr**), the largest of the three, is foot-like and very thickened, mainly medially. Its dorsal articular surface, which contacted the ischial peduncle of the ilium, is very rough, convex and elliptical in outline. The pubic ramus (**pur**) is partially preserved. It is very flat-

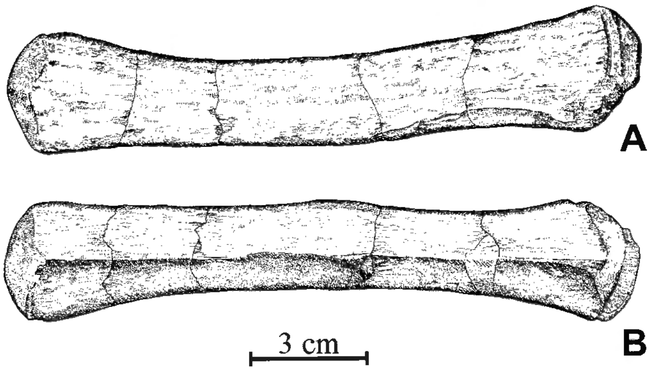

Fig. 16 — Right metacarpal IV of *Charonosaurus jiayinensis* (GMH HIj142), from the Yuliangze Formation of Jiayin - A: medial view; B: lateral view.

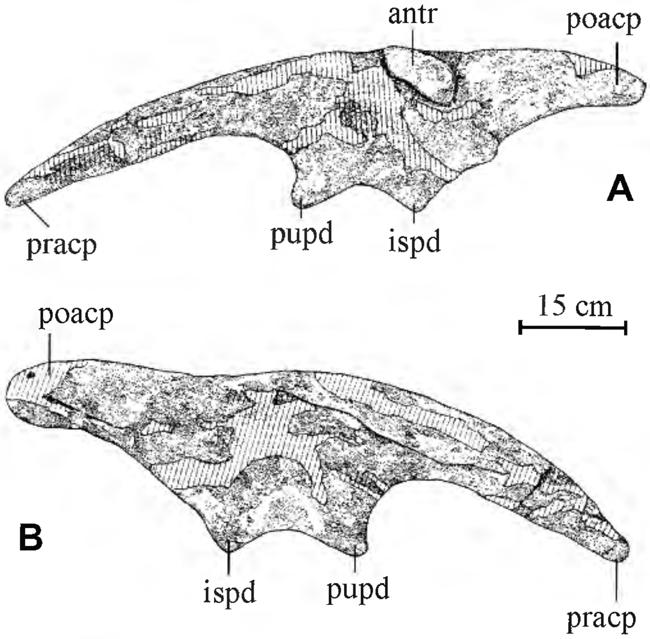

Fig. 17 — Left ilium of *Charonosaurus jiayinensis* (GMH Hlj77), from the Yuliangze Formation of Jiayin - A: lateral view; B: medial view. antr, antitrochanter; ispd, ischial peduncle; poacp, postacetabular process; pracp, preacetabular process; pupd, pubic peduncle.

tened medio-laterally and appears relatively short. Its concave dorsal border forms, in continuity with the ventral border of the iliac ramus, the caudal margin of the acetabulum. Distally to the pubic ramus, the obturator process (**obpr**) is not completely preserved, but was apparently well developed and turned medially. Between the pubic ramus and the obturator process, the obturator sulcus (**obsul**) is very elongated proximo-distally, but does not appear markedly excavated. The ischial shaft is perfectly straight and very stout. Its lateral side bears a strong dorsal ridge. Its medial side bears numerous longitudinal striations, indicating strong ligamentous attachment with the paired ischium. Its distal end forms a very expanded footed knob (**isfo**). Its distal surface is always by far too eroded to distinguish whether the distal foot is composed of a ''heel'' and a ''toe'' (*sensu* BRETT-SURMAN, 1975, 1989).

Pubis (CUST JIII1228, CUST J"III", CUST J"IV", GMH Hlj"magnus", YANG, 1986, pl. 7, figs. 5-6) - The prepubic blade is never completely preserved in the specimens collected at Jiayin. It appears relatively short and high, expanding abruptly in the cranial direction. The pubic shaft is also relatively short and well constricted. The middle portion of the pubis is usually better preserved. The iliac process is relatively prominent; its lateral side bears a strong and roughened ridge parallel to the regularly concave acetabular border of the bone, whereas its medial side bears a relatively well-marked triangular surface indicating a close contact with one of the cranialmost sacral ribs. The ischial peduncle is rather long, forming the caudoventral corner of the middle part of the pubis. The postpubic bar is never completely preserved. It starts medially to the ischial peduncle, so that both processes circumscribe a deep obturator foramen.

Femur (Fig. 19; Pl. 7, Fig. 2; CUST JIII1232, CUST J"III", GMH Hlj"magnus", YANG, 1986, pl. 5, figs. 1-3) - The femur of *Charonosaurus jiayinensis* is long, stout and straight. The femoral head (**fh**) is globular; its neck is short and stout, forming a 45° angle with the long axis of the bone. The greater trochanter (**grtr**) is relatively prominent on the lateroproximal angle of the femur, its apex lying above that of the femoral head. On the craniolateral side of the greater trochanter, the lesser trochanter is very poorly developed; both trochantera are separated by a shallow and narrow cleft, extending on the medial side of the proximal part of the femoral shaft. The femoral shaft is relatively long and essentially rectangular in cross-section, with a medio-lateral great-axis. The fourth trochanter (**4tr**) lies along the caudomedial side of the femoral shaft. It is triangular in shape, very elongated

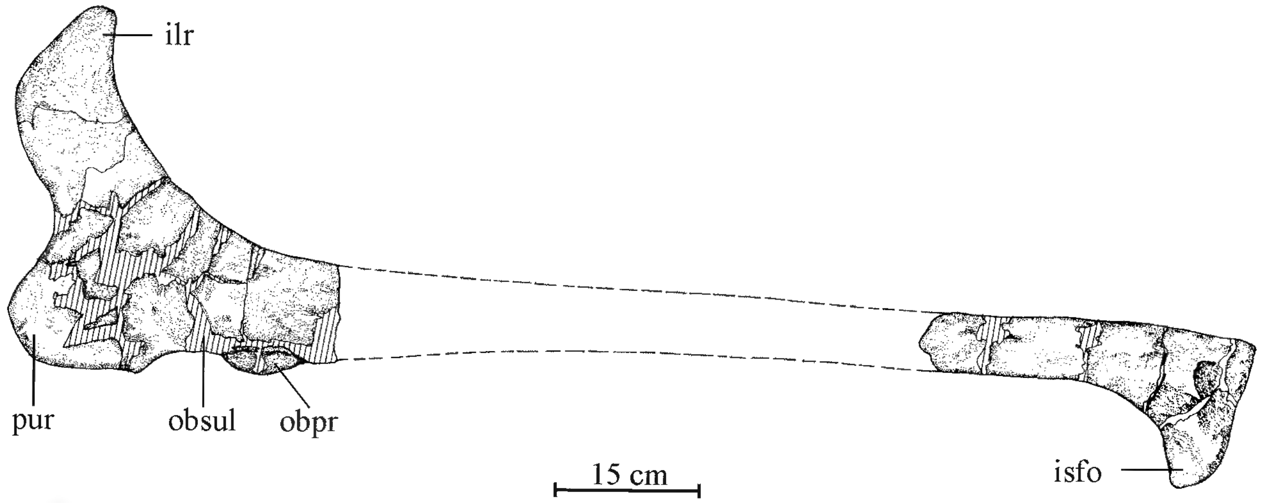

Fig. 18 — Reconstruction of a left ischium of *Charonosaurus jiayinensis*, from the Yuliangze Formation of Jiayin in lateral view, from CUST JV679 (proximal part) and CUST JIV1225 (distal part). ilr, iliac ramus; isfo, ischial foot; obsul, obturator sulcus; obpr, obturator process.

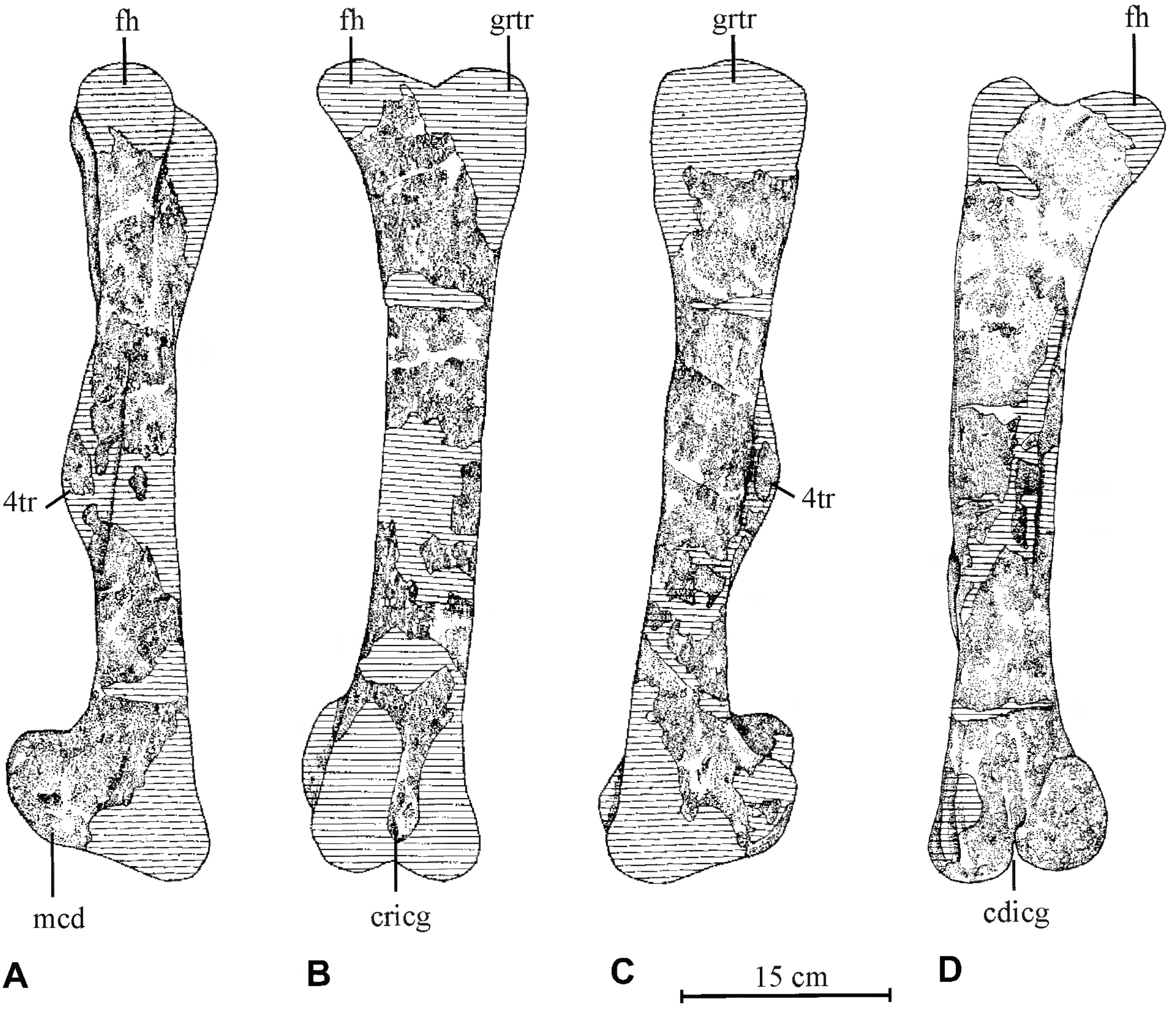

Fig. 19 — Left femur of *Charonosaurus jiayinensis* (CUST JIII1232), from the Yuliangze Formation of Jiayin - A: medial view; B: cranial view; C: lateral view; D: caudal view. cdicg, caudal intercondylar groove; cricg, cranial intercondylar groove; fh, femoral head; grtr, greater trochanter; mcd, medial condyle; 4tr, fourth trochanter.

proximo-distally, but not very prominent. The distal condyles are particularly widened cranio-caudally and saddle-shaped. The medial condyle (**mcd**) is the larger, but the lateral one extends further distally. A deep longitudinal groove runs along the caudolateral side of the lateral condyle, for reception of the distal tendon of *M. ilio-fibularis*. Caudally, both condyles are separated by a deep, but narrow intercondylar groove (**cdicg**). Cranially, they meet each other to form an intercondylar ''tunnel'' (**cricg**) that surrounded the distal tendon of *M. ilio-tibialis* on its way to the cnemial crest of the tibia. It must be noted that this intercondylar groove is apparently open in the holotype of *Mandschurosaurus amurensis* (RIABININ, 1930a, pl. 3, 2).

Tibia (Fig. 20; Pl. 8, Fig. 1; CUST JIII 1230, CUST JIII 1231, CUST J"III", CUST J"IV", GMH Hlj"magnus", YANG, 1986, pl. 5, fig. 5) - The tibia of *Charonosaurus jianinensis* is very massive. Its proximal head is very widened medio-laterally, because of the important development of the cnemial crest (**cncr**). This crest is clearly curved outwards and its widening is very gradual, beginning in the middle of the tibial shaft. The caudolateral angle of the tibial proximal head forms a prominent internal condyle (**icd**). The lateral condyle (**lcd**) is slightly larger than the internal one and is coupled, on its rostral side, to an accessory condyle (*sensu* THULBORN, 1972). The internal and lateral condyles are separated from each other by a narrow, but very deep intercondylar groove (**icdgr**). In proximal view, the medial side of the tibia is very convex; under the proximal head, this side forms a wide depressed area extending towards the proximal third of the bone. The tibial diaphysis is long, straight and ovoid in cross-section. Proximally, its long axis is oriented cranio-caudally because of the development of the cnemial crest; it gradually becomes wider medio-laterally towards the distal end of the bone because of the development of a prominent ridge along the lateral side of the external malleolus. The distal head of the tibia is very widened medio-laterally: its great axis forms a 120° angle with that of the proximal head. The external malleolus (**emal**) is very salient distally and its articular surface is

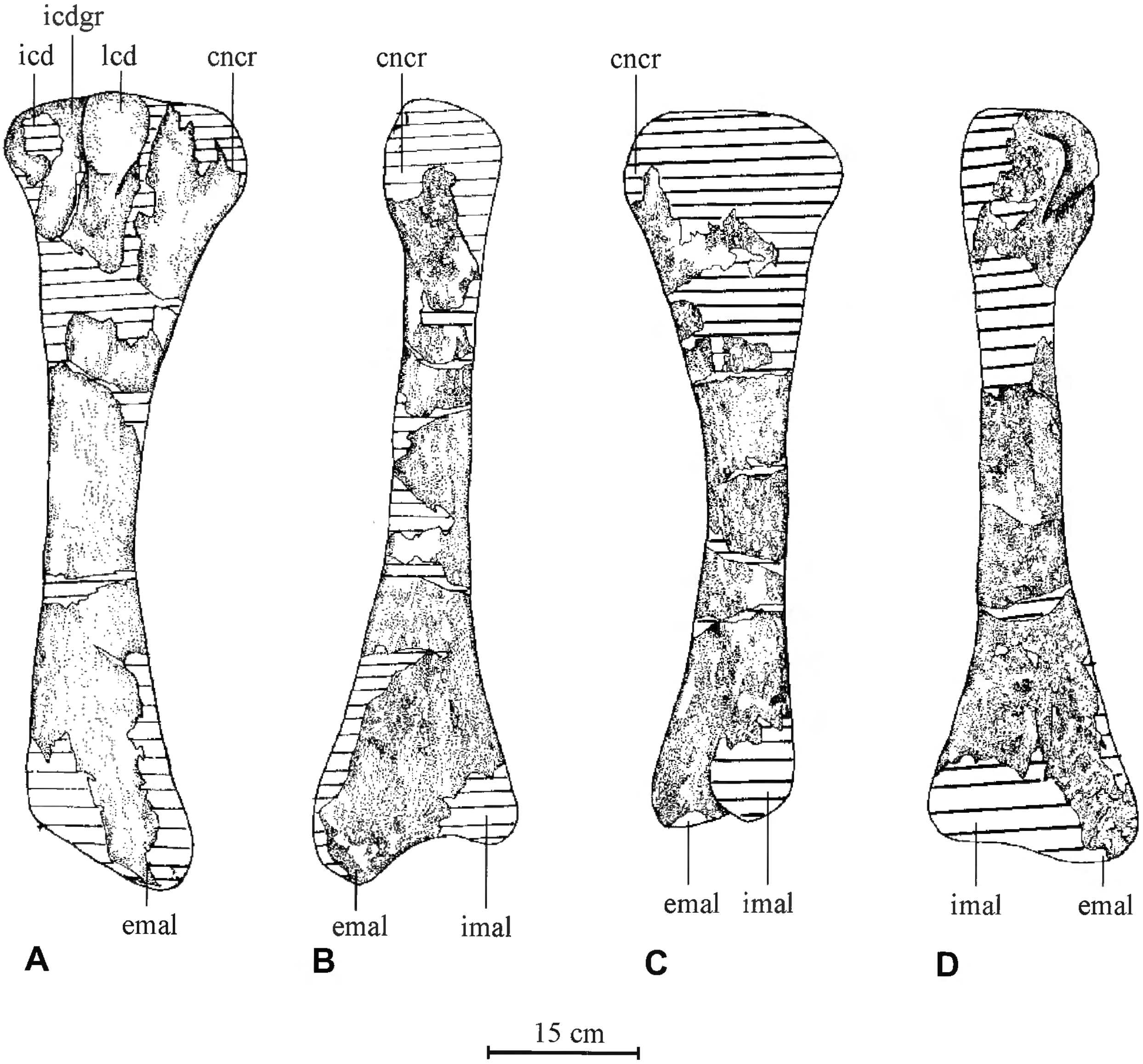

Fig. 20 — Right tibia of *Charonosaurus jiayinensis* (CUST JIII1230), from the Yuliangze Formation of Jiayin - A: lateral view; B: cranial view; C: medial view; D: caudal view. cncr, cnemial crest; emal, external malleolus; icd, internal condyle; icdgr, intercondylar groove; imal, internal malleolus; lcd, lateral condyle.

turned towards the caudal side of the tibia: its medial portion contacted the astragalus, whereas its lateral surface contacted the fibula. The internal malleolus (**imal**) is very salient mediolaterally; a large articular surface, turned cranially, fitted into the dorsal articular surface of the astragalus.

Fibula (Fig. 21; Pl. 8, Fig. 2; CUST JIII1248, CUST JIII1249, CUST J“III”, CUST J“IV”, GMH HIj“magnus”, Yang, 1986, pl. 5, figs. 4 & 6) - The fibula of *Charonosaurus jianinensis* is long, perfectly straight and very slender. Its proximal end is widened cranio-caudally and forms a characteristic cranial peg (**crp**). Whereas the lateral side of the proximal head is smoothly convex, its medial side is concave and bears longitudinal striations, marking the contact area with the proximal head of the tibia. The cranio-caudal diameter of the fibula progressively decreases distally along its shaft. Its outer side remains convex along its whole length. Its concave inner side can be subdivided into two distinct surfaces. The upper one occupies the proximal two-thirds of the fibular shaft; it has the shape of an elongated triangle, pointing distally, and bears very elongated striations for ligamentous contact with the tibia. It is bordered in its lower part by an oblique cranial crest. A second triangular surface, pointing proximally, occupies the distal third of the medial side of the fibula. It is also strongly striated and it faces caudomedially to fit against the external malleolus of the tibia. The distal head of the fibula (**dib**) is club-shaped and bulges forwards and outwards. Its distal articular surface is convex and roughened.

Astragalus (Fig. 22; Pl. 8, Fig. 3; CUST JIV924, CUST J“III”, GMH HIj“magnus”) - In dorsal view, the astragalus of *Charonosaurus jiayinensis* is nearly rectangular in shape and very widened medio-laterally. The articular

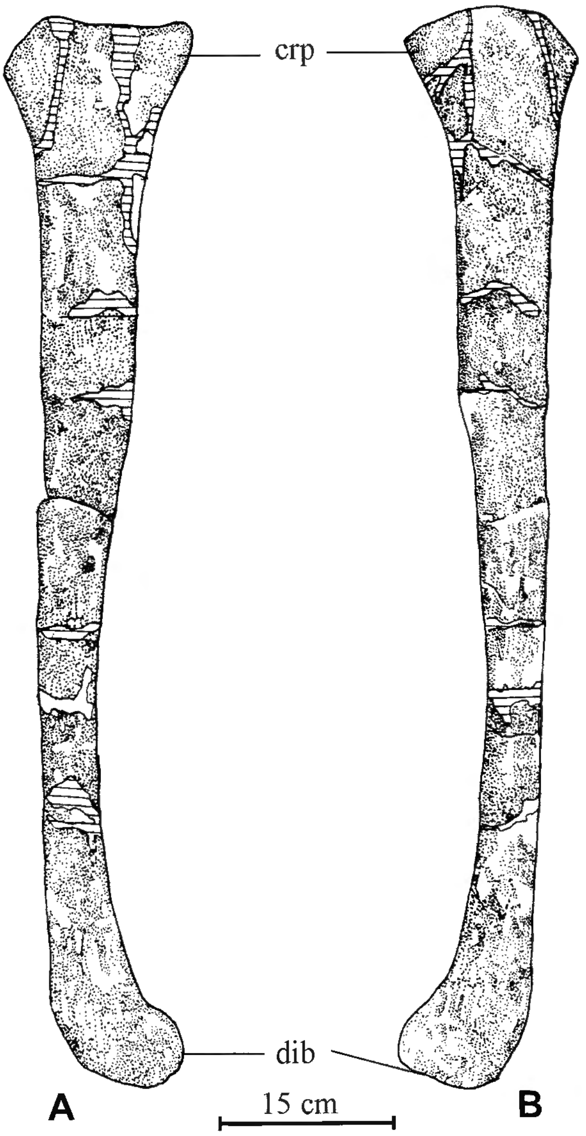

Fig. 21 — Left fibula of *Charonosaurus jiayinensis* (CUST JIV1249), from the Yuliangze Formation of Jiayin - A: medial view; B: lateral view. crp, cranial peg; dib, distal bulge.

surface for the internal malleolus of the tibia (**ast**) occupies the medial two-thirds of its dorsal side; this concave surface faces slightly craniomedially. The lateral third is formed by the articular surface for the external malleolus of the tibia; this surface strongly faces outwards. The wide caudal ascending process (**cdp**), accommodated against the caudal side of the tibia, is set on the caudomedial corner of the astragalus. The cranial ascending process (**crp**) is set on the craniolateral corner of the astragalus. It is less extended, but slightly higher than the caudal one. When viewed cranially, it forms an equilateral triangle. Both processes are connected together by a low, oblique and rounded crest that separates the medial and lateral articular surfaces. The ventral side of the astragalus is regularly convex cranio-caudally and concave medio-laterally.

Metatarsals (CUST JIII003, CUST JIII004, CUST JIII1233, CUST JIII1234, CUST JIV962, CUST JIV991, CUST J“III”, CUST J“IV”, GMH Hlj“magnus”) - Metatarsal II is the shortest of the three. Its proximal end is very compressed medio-laterally, but expanded planto-dorsally, so that it overhangs the shaft of the bone. The medial side of the proximal head is slightly convex, whereas its plantolateral side bears a wide triangular concave surface that reaches the mid-length of the bone and that bears longitudinal striations indicating strong ligamentous attachment with metatarsal III. The planto-dorsal diameter of the metatarsal shaft quickly lessens distally; the medial surface gradually becomes more convex, whereas the lateral side becomes flatter. Along the distal part of the shaft, a small lip-like projection from the laterodorsal surface reinforced the attachment between metatarsals II and III. Below this lip, the distal head of metatarsal II slightly diverges from metatarsal III; its lateral side bears a strongly concave triangular surface, bordered plantarly by a strong ridge. The distal articular surface is rough, convex planto-dorsally and forms a shallow trochlea.

Metatarsal III is the stoutest and the most symmetrical

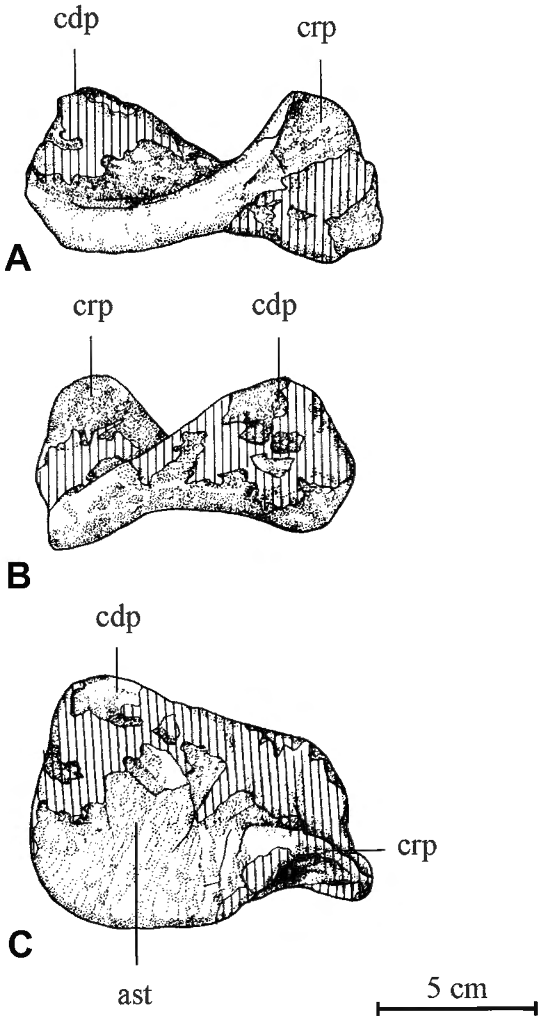

Fig. 22 — Left astragalus of *Charonosaurus jiayinensis* (CUST JIV1249), from the Yuliangze Formation of Jiayin - A: cranial view; B: caudal view; C: dorsal view. ast, articular surface for the tibia; cdp, caudal process; crp, cranial process.

of the metatarsals. Its proximal articular head is rectangular in outline, slightly more expanded planto-dorsally than medio-laterally. It bears a transverse, but slightly oblique concavity for articulation with the ventral surface of the astragalus. The medial border of the proximal head, which applied against metatarsal II, is slightly concave and rough; the lateral border, which articulated with metatarsal IV, is convex. The metatarsal shaft is roughly triangular in cross-section, with a very flattened and roughened medial side, a strongly convex lateral side and a strong rounded plantar ridge. The shaft expands distally to form a saddle-shaped articular condyle; it is rectangular in cross-section, longer medio-laterally than planto-dorsally and it bears a smooth, but wide intercondylar groove.

Metatarsal IV is larger than metatarsal II, but distinctly less stout than metatarsal III. Its proximal head is more expanded planto-dorsally than medio-laterally. Its proximal articular surface is cup-shaped. The medial side of the proximal part is very concave and bears longitudinal striations, indicating ligamentous contact with the proximolateral side of metatarsal III; on the other hand, its lateral side is strongly convex. Its plantar side bears a strong ridge extending from the proximomedial angle of the head halfway down the shaft. Beneath the proximal head, the metatarsal shaft is slightly constricted; in its middle portion, its dorsomedial side bears a strong knob that applied against the lateral side of metatarsal III. Under this knob, the shaft curves laterally away from metatarsal III. The distal articular condyle is rectangular in cross-section and very convex planto-dorsally. Its intercondylar groove is more developed than on metatarsals II and III. Its lateral side forms a deep cup-shaped depression.

Pes phalanges (CUST J"III", CUST J"IV", GMH Hlj"magnus") - The proximal phalanges of the three digits are block-like bones with a broad concave proximal surface and a saddle-shaped distal surface. The proximal phalanx of digit II is relatively more slender than that of the others. It is slightly asymmetrical: its lateral side is more convex, higher and more vertical than its medial side. Its dorsal side is regularly convex, whereas its plantar side is flat.

The proximal phalanx of digit III is the largest and the stoutest of the series. It is very compressed planto-dorsally and perfectly symmetrical in dorsal view. Its proximal articular surface is more concave and its distal trochlea is better developed than on the other elements of the series. Both its medial and lateral sides are steeply inclined, so that its concave plantar surface is much wider than its convex dorsal surface.

The proximal phalanx of digit IV is proportionally the shortest, but the thickest of the series. Its medial side is slightly concave and particularly elevated; its lateral side is slightly less high and vertical. Both its dorsal and plantar surfaces are nearly flat. Its proximal and distal articular surfaces are less developed than on the other elements of the series.

The ungual phalanges are proportionally wide and hoof-like. They are very arched and flattened planto-dorsally towards their tip. Well marked claw-grooves run along the plantar side, converging towards the tip of the unguals. The distal margin is regularly rounded and very roughened.

Phylogenetic relationships of *Charonosaurus jiayinensis*

Since SERENO's (1986) fundamental work, the phylogeny of Hadrosauriformes has been abundantly discussed by several authors, leading to a good understanding of the phylogenetic relationships between North American Hadrosauridae (WEISHAMPEL & HORNER, 1990; HORNER, 1992; WEISHAMPEL *et al.*, 1993; KIRKLAND, 1998), basal Hadrosauroidea (WEISHAMPEL & HORNER, 1993; GODEFROIT *et al.*, 1998; HEAD, 1998) and Iguanodontidae (NORMAN & WEISHAMPEL, 1990; NORMAN, 1990, 1998). With the exception of HORNER (1988, 1990, 1992), all these authors accept the monophyly of Hadrosauridae and, within this family, that of the subfamilies Hadrosaurinae and Lambeosaurinae. Therefore, it is not the purpose of the present paper to discuss the phylogeny of Hadrosauriformes in detail; we only wish to clarify the phylogenetic relationships of *Charonosaurus jiayinensis* on the base of the available material. For that reason, the proposed cladogramme is only based on characters that can be directly observed on the studied material. A revised list of characters supporting this cladogramme is first provided and discussed in detail.

Discussion of anatomical characters treated in the cladistic analysis

1. Occipital condyle inclined caudoventrally (0), or vertical (1) - According to GODEFROIT *et al.* (1998), the vertical articular surface of the occipital condyle, as observed in *Charonosaurus jiayinensis*, is a synapomorphy shared by *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 6), *Tanius sinensis* (see WIMAN, 1929, pl. 5), *Telmatosaurus transsylvanicus* (see WEISHAMPEL *et al.*, 1993, fig. 2), *Eolambia caroljonesa* (see KIRKLAND, 1998, fig. 3) and Hadrosauridae. In these taxa, the basioccipital neck supporting the occipital condyle is more or less shortened. Primitively in Ornithopoda, the condyle is more steeply inclined ventrally and the basioccipital neck usually appears relatively longer, as observed in *Camptosaurus dispar* (see GILMORE, 1909, fig. 5), *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 9), *I. atherfieldensis* (see NORMAN, 1986, fig. 18) and *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 14).

2. Basipterygoid processes short (0), or extending well below the level of the ventral border of the occipital condyle (1) - Primitively in Hadrosauriformes, the basipterygoid processes are shallowly declined (approximately 10°-30° from horizontal, according to WEISHAMPEL, 1984), so that the end of the basipterygoid processes and the base of the occipital condyle are nearly set in the same horizontal plane, as observed in *Camptosaurus dispar* (see GILMORE, 1909, fig. 5), *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 4) and *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 13). Among Hadrosauriformes, extension of the basipterygoid processes below the level of the occipital condyle can be regarded as a synapomorphy for Hadrosauroidea, as it is figured in *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 6), *Telmatosaurus transsylvanicus* (see WEISHAMPEL *et al.*, 1993, fig. 2), *Tanius sinensis* (see WIMAN, 1929, pl. 5), *Eolambia caroljonesa* (KIRKLAND, 1999, fig. 4d), *Parasaurolophus tubicen* (see SULLIVAN & WILLIAMSON, 1999, fig. 16), *Corythosaurus casuarius* (see OSTROM, 1961, fig. 12), *Edmontosaurus regalis* (see LAMBE, 1920, fig. 26), *Anatotitan copei* (pers. obs.) and *Prosaurolophus blackfeetensis* (see HORNER, 1992, pl. 8). WEISHAMPEL (1984) observed a wide range of basipterygoid processes declination among Hadrosauroidea. In *Tsintaosaurus spinorhinus*, the basipterygoid processes extend very low below the level of the occipital condyle and are distinctly curved backwards (YOUNG, 1958, fig. 3).

3. Parietal participating in the occipital aspect of the skull (0), or completely excluded from the occiput (1) - It has been shown that, in *Charonosaurus jiayinensis*, the parietal was probably not exposed on the occipital surface of the skull. This condition is also observed in *Parasaurolophus tubicen* (see SULLIVAN & WILLIAMSON, 1999). In other Lambeosaurinae, the parietal participates in the occipital aspect of the skull, as observed in *Corythosaurus casuarius* (OSTROM, 1961, fig. 54), in *Lambeosaurus lambei* (see GILMORE, 1924a), in *Tsintaosaurus spinorhinus* (see YOUNG, 1958, fig. 1), in the young *Hypacrosaurus* described by GILMORE (1937, fig. 30), and in embryonic and juvenile specimens of *H. stebingeri* (see HORNER & CURRIE, 1994). Hadrosaurinae show varying degrees of parietal interposition between the squamosals at the rear of the skull, but it usually forms a narrow caudal process in the midline of the occipital surface, as exemplified by *Edmontosaurus regalis* (see LAMBE, 1920, fig. 8), *Prosaurolophus blackfeetensis* (see HORNER, 1992, pl. 39b), *Kritosaurus navajovius* (see HORNER, 1992, pl. 45b), *Brachylophosaurus goodwini* (see HORNER, 1988, fig. 1d), or *Anatotitan copei* (pers. obs.). In *Saurolophus angustirostris*, the parietal separates the squamosals only in the young specimens (MARYAŃSKA & OSMÓLSKA, 1981a). The parietal usually participates in a largest part of the occipital surface in non-hadrosaurid Hadrosauriformes, as observed in *Iguanodon bernissartensis* (pers. obs.), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 11), or *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998).

4. Ratio "length /minimal width" of the parietal > 2 (0), or < 2 (1) - According to HORNER (1990) and WEISHAMPEL *et al.*, (1993), shortening of the parietal, as observed in *Charonosaurus jiayinensis*, is shared, within Hadrosauriformes, by *Ouranosaurus nigeriensis* and Lambeosaurinae. In *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Probactrosaurus gobiensis*, *Bactrosaurus johnsoni*, *Telmatosaurus transsylvanicus*, *Eolambia caroljonesa*, and hadrosaurines, on the other hand, the parietal is much longer than wide.

5. Deeply excavated frontal platform absent (0), occupying the rostral part of the frontal in adults (1), or extending above the rostral portion of the supratemporal fenestra (2); character treated as ordered - A deeply excavated rostral platform is typical of lambeosaurine frontals, as it is described and figured in *Parasaurolophus tubicen* (see SULLIVAN & WILLIAMSON, 1999, figs. 16-17), in a cranial roof probably belonging to *Corythosaurus* (see OSTROM, 1961, fig. 13), in a partial skull of *Lambeosaurus* (see GILMORE, 1924a, fig. 8), in a partial skull of an unidentified Lambeosaurinae (see GILMORE, 1937, fig. 32), *in Jaxartosaurus aralensis* (see ROZHDESTVENSKY, 1968, fig. 1) and in *Amurosaurus riabinini* (pers. obs.). All these specimens display short frontals forming a broad excavated base for the hollow crest and bearing pronounced longitudinal grooves for solid attachment of the nasals and premaxillae. However, in *Corythosaurus*, *Lambeosaurus*, *Jaxartosaurus* and *Amurosaurus* specimens in which this feature can be observed, this platform never occupies the whole dorsal surface of the frontal. In *Charonosaurus jiayinensis* and *Parasaurolophus tubicen*, on the other hand, it extends caudodorsally above the rostral part of the supratemporal fenestra. It can therefore be deduced that the crest of *Charonosaurus jiayinensis* was broader and extended more caudally than that of typical helmet-crested lambeosaurines. In *Parasaurolophus tubicen*, on the other hand, the crest was probably longer than that of *Charonosaurus jiayinensis*, as the dorsal platform is more steeply inclined and extends much more caudally above the supratemporal fenestra. In *Tsintaosaurus spinorhinus*, the rostral part of the frontals does not form an excavated platform, but their rostral end is upturned to participate in the posterior base of the supracranial spine (BUFFETAUT & TONG-BUFFETAUT, 1993).

In crested hadrosaurines, the rostral part of the frontal is also modified as a base for the ventral surface of the solid nasal crest. In *Prosaurolophus blackfeetensis*, the frontal forms an elongated rostral process, whose dorsal surface is strongly grooved where it received the caudal extension of the nasal (HORNER, 1992, pl. 9). In *Maiasaura peeblesorum*, the rostral end of the frontal is elevated and overhangs the caudal end of the nasal to form the caudal and dorsal portion of the solid crest (HORNER, 1983, fig. 2e-f). In *Saurolophus angustirostris*, the rostral end of the frontal sends a long and narrow process, extending backwards to fit into two grooves on the caudoventral surface of the nasal (MARYAŃSKA & OSMÓLSKA, 1981a, fig. 2); according to WEISHAMPEL (1984), such a process is also developed in *Saurolophus osborni* (*contra* OSTROM, 1961). In *Brachylophosaurus goodwini*, the rostrodorsal portion of the frontal bears longitudinal grooves where it articulates with the underside of the nasal (HORNER, 1988, fig. 1d).

It can be concluded that the development of a broad, excavated and steeply sloping rostral platform on the frontal constitutes a synapomorphy of Lambeosaurinae. In adult specimens of helmet-crested forms, but also in *Jaxartosaurus aralensis* and in *Amurosaurus riabinini*, this platform is limited to the rostral portion of the frontal. In *Parasaurolophus tubicen* and in *Charonosaurus jiayinensis*, it extends caudodorsally above the rostral part of the supratemporal fenestra.

6. Frontal participating in the orbital rim (0), or excluded by postorbital-prefrontal joint (1) - The distribution of articular facets along the lateral border of the frontal indicates that the frontal was excluded from the orbital rim in *Charonosaurus jiayinensis*. According to Weishampel (1984), Weishampel & Horner (1990) and Godefroit *et al.* (1998), exclusion of the frontal from the orbital rim by a postorbital-prefrontal joint is, among ornithopods, synapomorphic for Lambeosaurinae. In the latter group, the articular facets for the prefrontal usually forms a prominent roughened rostral platform on the dorsal surface of the postorbital, as observed in adult specimens of *Charonosaurus jiayinensis*, but also in *Parasaurolophus tubicen* (see Sullivan & Williamson, 1999, fig. 8a), *Lambeosaurus* sp. (see Gilmore, 1924a, fig. 8) and *Hypacrosaurus altispinus* (see Gilmore, 1924b, pl. 11). However, Horner (1992) showed that the frontal is also excluded from the orbital rim in some hadrosaurines. The dorsal surface of the hadrosaurine postorbital appears usually flatter, with the exception of *Saurolophus osborni* (see Brown, 1912, fig. 1).

7. Nasal forming a small part of the hollow crest (0), or half of the crest (1) - This character cannot be observed in *Charonosaurus jiayinensis*, but is added to the character-taxon matrix in order to clarify the phylogenetic relationships among Lambeosaurinae. From ontogenetic data, Weishampel *et al.* (1993) stated that ancestrally in lambeosaurines the nasal contributes in a small portion of the crest base, as observed in *Parasaurolophus*. Nasal forming half of the hollow crest is consequently regarded as a synapomorphy for the genera *Corythosaurus*, *Hypacrosaurus* and *Lambeosaurus*.

8. Caudal portion of the prefrontal oriented horizontally (0), or vertically (1) - Maryańska & Osmólska (1981a) showed that the hadrosaurid prefrontal is a coalescence of supraorbital I with the "true" prefrontal. The prefrontal of CUST JV-1251 is similar to those found in the Lambeosaurinae in its vertical nature, supporting the hollow supracranial crest (Weishampel & Horner, 1986, 1990). It must be noted that Buffetaut & Tong-Buffetaut (1993, fig. 1c) showed that the prefrontal of *Tsintaosaurus spinorhinus* is upturned as that of typical Lambeosaurinae. On the other hand, the prefrontals of Hadrosaurinae, including the forms that bear a solid crest, are oriented horizontally (see e.g. Lambe, 1920, fig. 3; Parks, 1920, pl. 3, fig. 1; Horner, 1988, fig. 1; 1992, pl. 16).

9. Lateral side of the squamosal low (0), or elevated (1) - The squamosal of *Charonosaurus jiayinensis* resembles that of North American Lambeosaurinae in being elevated above the cotyloid cavity: such a condition is encountered in *Corythosaurus casuarius* (see Ostrom, 1961, fig. 12), *Lambeosaurus lambei* (see Gilmore, 1924a, pl. 6), *Hypacrosaurus altispinus* (see Gilmore, 1924b, pl. 11) and *Parasaurolophus walkeri* (see Parks, 1922, pl. 3). The dorsal part of the squamosal is primitively distinctly lower in Hadrosauriformes, as observed in *Iguanodon bernissartensis* (see Norman, 1980, fig. 2), *I. atherfieldensis* (see Norman, 1986, fig. 3), *Ouranosaurus nigeriensis* (see Taquet, 1976, fig. 10), *Bactrosaurus johnsoni* (see Godefroit *et al.*, 1998, fig. 15), *Eolambia caroljonesa* (see Kirkland, 1998, fig. 5a-c), *Edmontosaurus regalis* (see Lambe, 1920, fig. 3), *Anatotitan copei* (pers. obs.), *Prosaurolophus blackfeetensis* (see Horner, 1992, pl. 12), *Saurolophus angustirostris* (see Rozhdestvensky, 1957, fig. 1), *Kritosaurus navajovius* (see Horner, 1992, pl. 44), *Brachylophosaurus goodwini* (see Horner, 1988, fig. 1), *Maiasaura peeblesorum* (see Horner, 1983, fig. 1), *Gryposaurus notabilis* (see Lambe, 1914, pl. 18) and *Tsintaosaurus spinorhinus* (see Young, 1958, fig. 2).

10. Rostral process of the jugal tapering in lateral view (0), or dorso-ventrally expanded (1) - According to Sereno (1986) and Weishampel *et al.* (1993), dorsoventral expansion of the rostral process of the jugal is a synapomorphy for *Ouranosaurus* + Hadrosauroidea. However, it can be observed that the rostral process is only slightly expanded in *Ouranosaurus* (see Taquet, 1976, fig. 19) and apparently tapers rostrally, more closely resembling the condition observed in iguanodontids (Norman, 1998), but also in *Bactrosaurus johnsoni* (see Godefroit *et al.*, fig. 13), *Protohadros byrdi* (see Head, 1998, fig. 5), *Eolambia caroljonesa* (see Kirkland, 1999, fig. 4e), *Tanius sinensis* (see Wiman, 1929, pl. 5, fig. 13) and *Gilmoreosaurus mongoliensis* (pers. obs.). This character is therefore regarded, in the present paper, as an synapomorphy shared by *Telmatosaurus transsylvanicus* and Hadrosauridae. However, the degree of dorso-ventral expansion is variable in this clade: it is better developed, for example, in Lambeosaurinae than in *Telmatosaurus transsylvanicus*.

11. Rostral process of the jugal angular (0), or rounded and symmetrical in lateral view (1), - Weishampel *et al.*, (1993) regarded the truncated, rounded rostral process of the jugal, as observed in *Charonosaurus jiayinensis*, as a lambeosaurine synapomorphy: it can indeed be observed in *Corythosaurus casuarius* (see Ostrom, 1961, fig. 7), *Lambeosaurus lambei* (see Gilmore, 1924a, pl. 8), *Hypacrosaurus altispinus* (see Gilmore, 1924b, pl. 11) and *Parasaurolophus walkeri* (see Parks, 1922, pl. 4). Nevertheless, the rostral process of the jugal looks also rather rounded and truncated in advanced hadrosaurine species, because of the strong development of the lacrimal process; however, in these three species, the rostral process of the jugal is very asymmetrical, contrary to that of lambeosaurines.

12. Jugal-ectopterygoid joint present (0), or absent (1) - Weishampel (1984) showed that the ectopterygoid contacts the medial side of the jugal in Hypsilophodontidae and Iguanodontidae. In the latter family, a contact facet for the ectopterygoid can be observed caudally to the maxillary process of the jugal in *Iguanodon atherfieldensis* (see Norman, 1986, fig. 15) and probably in *Ouranosaurus nigeriensis* (see Weishampel, 1984). This articular facet has also been observed in *Protohadros byrdi* (Head, 1998), but is absent in *Bactrosaurus johnsoni* (see Godefroit *et al.*, 1998; Head, 1998) and in all Hadrosauridae (Weishampel, 1984).

13. Antorbital fenestra surrounded by the jugal and/or the lacrimal (0), or completely surrounded by the maxilla (1) - The great elevation of the dorsal process of the maxilla and the concomitant migration of the antorbital fenestra along the upper reaches of the premaxillary articular surface of the maxilla are typical hadrosaurid synapomorphies (WEISHAMPEL & HORNER, 1990; WEISHAMPEL *et al.*, 1993). The maxilla remains rather low in *Telmatosaurus transsylvanicus* and *Protohadros byrdi* (*contra* WEISHAMPEL *et al.*, 1993 and HEAD, 1998), but these authors consider that the antorbital fenestra is completely enclosed in the maxillary dorsal process in both taxa, as in Hadrosauridae. The jugal and/or the lacrimal participate in the formation of the antorbital fenestra in *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 5), as in *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 2), *I. atherfieldensis* (see NORMAN, 1986, fig. 3) and *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 10).

14. Maxilla markedly asymmetrical (0), or nearly symmetrical (1) in lateral view. The shape of the maxilla in lateral view is usually regarded as different in Hadrosaurinae and Lambeosaurinae (GILMORE, 1933; WEISHAMPEL & HORNER, 1986, 1990): the dorsal process lies at about the middle of the bone in Hadrosaurinae, whereas it lies behind the mid-point in Lambeosaurinae. GODEFROIT *et al.* (1998) show that the latter condition, as observed in *Charonosaurus jiayinensis*, is in fact plesiomorphic in Hadrosauriformes, as it is also present in more basal Hadrosauriformes.

15. Ectopterygoid ridge faintly (0), or strongly (1) developed on the lateral side of the maxilla - The strong development of the horizontal ridge separating the ectopterygoid shelf is an hadrosaurid synapomorphy observed in *Charonosaurus jiayinensis*, as in *Edmontosaurus regalis* (see LAMBE, 1920, fig. 12), *Anatotitan copei* (pers. obs.), *Prosaurolophus blackfeetensis* (see HORNER, 1992, pl. 25*), Saurolophus osborni* (pers. obs.), *Brachylophosaurus canadensis* (see STERNBERG, 1953), *Gryposaurus latidens* (see HORNER, 1992, pl. 43), *Corythosaurus casuarius* (see STERNBERG, 1935, fig. 2), *Hypacrosaurus altispinus* (see GILMORE, 1924b, pl. 8), *Lambeosaurus lambei* (see GILMORE, 1924a, pl. 8), *Parasaurolophus tubicen* (see SULLIVAN & WILLIAMSON, 1999, fig. 14a) and *Tsintaosaurus spinorhinus* (see YOUNG, 1958, figs. 7-8), but also in *Telmatosaurus transsylvanicus* (see WEISHAMPEL *et al.*, 1993, fig. 3c). This ridge is much shorter and less prominent in *Camptosaurus dispar* (see GILMORE, 1909, fig. 7), *Iguanodon bernissartensis* (pers. obs.), *I. atherfieldensis* (see NORMAN, 1986, fig. 10), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 17), *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 11), *Eolambia caroljonesa* (see KIRKLAND, 1998, fig. 4a-c) and *Protohadros byrdi* (see HEAD, 1998, fig. 3c).

16. Paraquadratic foramen present (0), or absent (1) - Ancestrally in Hadrosauriformes, the quadratojugal articulates with the jugal in such a way that a free gap is developed between these bones: two articular facets are developed both ventrally and dorsally to the quadratojugal notch, as observed *in Iguanodon bernissartensis* (pers. obs.), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 22*), Altirhinus kurzanovi* (see NORMAN, 1998, fig. 10) and *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 14). The quadratojugal notch is absent in all Hadrosauridae (WEISHAMPEL, 1984) and also probably in *Telmatosaurus transsylvanicus* (see WEISHAMPEL *et al.*, 1993): a continuous elongated articular facet extends along the dorsal part of the quadratojugal notch, as observed in *Charonosaurus jiayinensis*, *Edmontosaurus regalis*. (LAMBE, 1920, fig. 16), *Prosaurolophus blackfeetensis* (see HORNER, 1992, pl. 18) and *Tsintaosaurus spinorhinus* (see YOUNG, 1958, fig. 6).

17. Distal head of the quadrate transversely expanded (0), or dominated by a large hemispheric lateral condyle (1). Ancestrally in Hadrosauriformes, the ventral head of the quadrate is transversely expanded, as observed in *Iguanodon bernissartensis* (see NORMAN, 1980), *I. atherfieldensis* (see NORMAN, 1986), *Ouranosaurus nigeriensis* (see TAQUET, 1976), *Protohadros byrdi* (see HEAD, 1998), *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998), *Eolambia caroljonesa* (see KIRKLAND, 1998) and *Telmatosaurus transsylvanicus* (see WEISHAMPEL *et al.*, 1993). In contrast, the ventral quadrate head of *Charonosaurus jiayinensis* and all Hadrosauridae is dominated by a large hemispheric lateral condyle that articulates with the surangular component of the mandibular glenoid; a smaller and more dorsal medial condyle articulates with the articular component of the mandibular glenoid.

18. Mandibular diastema absent (0), or well developed (1) in adult specimens - According to SERENO (1986), the development of an elongated diastema between the end of the predentary and the first dentary tooth, as observed in *Charonosaurus jiayinensis*, is a synapomorphy for *Ouranosaurus* and Hadrosauridae. More recent phylogenetic analyses rather regard it as a synapomorphy for Hadrosauridae, convergently acquired in *Ouranosaurus* and *Altirhinus* (WEISHAMPEL *et al.*, 1993; NORMAN, 1998; GODEFROIT *et al.*, 1998). The diastema is not developed in the non-hadrosaurid Hadrosauroidea *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998), *Telmatosaurus transsylvanicus* (see WEISHAMPEL *et al.*, 1993), *Eolambia caroljonesa* (see KIRKLAND, 1998, fig. 6) and *Gilmoreosaurus mongoliensis* (see WEISHAMPEL & HORNER, 1986), but appears relatively long in *Protohadros byrdi* (see HEAD, 1998). It must however be noted that the development of the diastema is clearly ontogenetic (see also NORMAN, 1990, 1998): within a determined species, small individuals have proportionally smaller diastema than larger specimens.

19. Coronoid process sub-vertical (0), or inclined rostrally (1) - Ancestrally in ornithopods, the coronoid process is vertical or inclined backwards. This condition is retained in all known non-hadrosaurid Hadrosauriformes (GODEFROIT *et al.*, 1998). OSTROM (1961) observed that in Hadrosauridae, on the other hand, the coronoid process extends upwards and forwards, towards the orbit rather than towards the supratemporal fenestra, as observed in *Charonosaurus jiayinensis*.

20. Surangular foramen present (0), or absent (1) - The absence of a surangular foramen near the mandibular glenoid is a synapomorphy shared by Hadrosauridae (WEISHAMPEL & HORNER, 1990), *Telmatosaurus transsyl-*

vanicus (see Weishampel *et al.*, 1993, fig. 1) and *Bactrosaurus johnsoni* (see Godefroit *et al.*, 1998, pl. 7, fig. 1). This foramen is primitively present in ornithopods, including *Iguanodon bernissartensis* (see Norman, 1980, fig. 2), *I. atherfieldensis* (see Norman, 1986, fig. 19), *Ouranosaurus nigeriensis* (see Taquet, 1976, fig. 32), *Altirhinus kurzanovi* (see Norman, 1998, fig. 17) and *Protohadros byrdi* (see Head, 1998, fig. 12a-b).

21. Two (0) or three, or more (1) dentary teeth for each position - Ancestrally in ornithischians, the dentary dentition is composed of a single functional tooth and, at most, a single replacement tooth per tooth position. The development of a dental battery, with up to five teeth per tooth position is probably the main synapomorphy for Hadrosauroidea, as it is observed in *Protohadros byrdi* (see Head, 1998), *Bactrosaurus johnsoni* (see Godefroit *et al.*, 1998), *Eolambia caroljonesa* (see Kirkland, 1998), *Telmatosaurus transsylvanicus* (see Weishampel *et al.*, 1993) and all Hadrosauridae. It is interesting to observe that the iguanodontid *Altirhinus kurzanovi* has three teeth in some of its alveoli (Norman, 1998).

22. Maxillary crowns broad, with subsidiary ridges (0), or miniaturised, with a single ridge (1) - Ancestrally in Hadrosauriformes, the maxillary teeth are relatively broad and the crown is asymmetrical in lateral view; the labial side is dominated by a prominent ridge, with a few subsidiary ridges. This plesiomorphic condition can be observed in *Iguanodon bernissartensis* (see Norman, 1980, fig. 21), *I. atherfieldensis* (see Norman, 1986, fig. 22), *Ouranosaurus nigeriensis* (see Taquet, 1976, pl. 20, fig. 1b) and *Altirhinus kurzanovi* (see Norman, 1998, fig. 21b). On the other hand, maxillary teeth are much narrower, with perfectly symmetrical lanceolate crowns devoid of subsidiary ridges in Hadrosauridae (see e.g. Weishampel, 1984), but also in *Protohadros byrdi* (see Head, 1998, fig. 13), *Bactrosaurus johnsoni* (see Godefroit *et al.*, 1998), *Eolambia caroljonesa* (see Kirkland, 1998, fig. 7a) and *Telmatosaurus transsylvanicus* (see Weishampel *et al.*, 1993). Thus, this character constitutes a synapomorphy for Hadrosauroidea.

23. Dentary crowns broad, with two sub-equal ridges (0), broad, with a dominant ridge and secondary ridges (1), or miniaturised (2); character treated as ordered - Ancestrally in Hadrosauriformes, the dentary teeth are relatively broad and their lingual enamelled surface is divided in three vertical channels by two sub-equal ridges, as observed in *Iguanodon bernissartensis* (see Norman, 1980, fig. 18), *I. atherfieldensis* (see Norman, 1986, fig. 21), *Ouranosaurus nigeriensis* (see Taquet, 1976, pl. 20, fig. 1a) and *Altirhinus kurzanovi* (see Norman, 1998, fig. 21). In non-hadrosaurid Hadrosauroidea, the dentary teeth are distinctly broader than the maxillary teeth and are sometimes slightly curved backwards; the medial surface of the crown bears a low and distally offset primary ridge, flanked by a smaller mesial secondary ridge and, sometimes, a third distal ridge, as exemplified by *Bactrosaurus johnsoni* (see Godefroit *et al.*, 1998, pl. 7, fig. 2b), *Protohadros byrdi* (see Head, 1998, fig. 13b), *Telmatosaurus transsylvanicus* (see Weishampel *et al.*, 1993, fig. 3g) and *Gilmoreosaurus mongoliensis* (pers. obs.). The situation is not clear in *Eolambia caroljonesa*, with dentary teeth described as miniaturised, although not tall and narrow (Kirkland, 1998: 295). However, the figured dentary teeth (Kirkland, 1998, fig. 7) closely resemble those of *Bactrosaurus johnsoni*. In Hadrosauridae, the dentary teeth are miniaturised like the maxillary ones and bear a strongly developed single carina (see e.g. Weishampel, 1984; Weishampel *et al.*, 1990), as observed in *Charonosaurus jiayinensis*. However, secondary ridges are often observed even in Hadrosauridae, such as *Parasaurolophus* sp. (see Horner, 1990, fig. 13.4d), *Gryposaurus latidens* (see Horner, 1992, pl. 42, fig. e), *Aralosaurus tuberiferus*, *Saurolophus angustirostris*, or *Amurosaurus riabinini* (pers. obs.).

24. Median carina of dentary teeth straight (0), or sinuous (1) - According to Weishampel & Horner (1990), a sinuous median carina on dentary teeth should constitute a synapomorphy for Lambeosaurinae. This character is indeed observed in *Charonosaurus jiayinensis*, but also in *Corythosaurus casuarius*, *Hypacrosaurus* sp., *Parasaurolophus* sp. (Horner, 1990, fig. 13.4) and *Tsintaosaurus spinorhinus* (Young, 1958, fig. 14). It is always straighter in other Hadrosauriformes, and particularly in Hadrosaurinae.

25. Angle between root and crown of dentary teeth more (0), or less (1) than 130° - Following Horner (1990), Weishampel *et al.* (1993) stated that a low angle (less than 130°) between the crown and the root is a synapomorphy for Hadrosaurinae, convergently evolved in *Iguanodon* species. However, personal observations in *Iguanodon bernissartensis* and *I. atherfieldensis* suggest that this angle, although variable, is usually higher than 130° in both taxa. In *Charonosaurus jiayinensis*, this angle is also higher than 130°, as also observed in *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus*, *Bactrosaurus johnsoni*, *Protohadros byrdi*, *Eolambia caroljonesa* and Lambeosaurinae (see also Godefroit *et al.*, 1998; Head, 1998; Kirkland, 1998).

26. A maximum of 7 (0), or a minimum of 9 (1) sacral vertebrae in adults - The sacrum of *Charonosaurus jiayinensis* is formed by nine fused vertebrae. Although fusion of the sacrum varies both ontogenetically (Brett-Surman, 1989) and between species, the sacrum in adult North American hadrosaurids consists of 10 to 12 vertebrae, including single dorsosacral and caudosacral contribution (Lull & Wright, 1942; Weishampel & Horner, 1990). In non-hadrosaurid Hadrosauriformes, the number of sacral vertebrae is always lower (7 in *Iguanodon bernissartensis* and *Bactrosaurus johnsoni*; 6 in *Iguanodon atherfieldensis* and *Ouranosaurus nigeriensis*).

27. Coracoid hook small and pointed ventrally (0), or prominent and pointed cranio-ventrally (1) - Primitively in Hadrosauriformes, the coracoid is sub-rectangular in shape, with a rudimentary hook pointing ventrally. The ratio of the cranio-caudal diameter to the

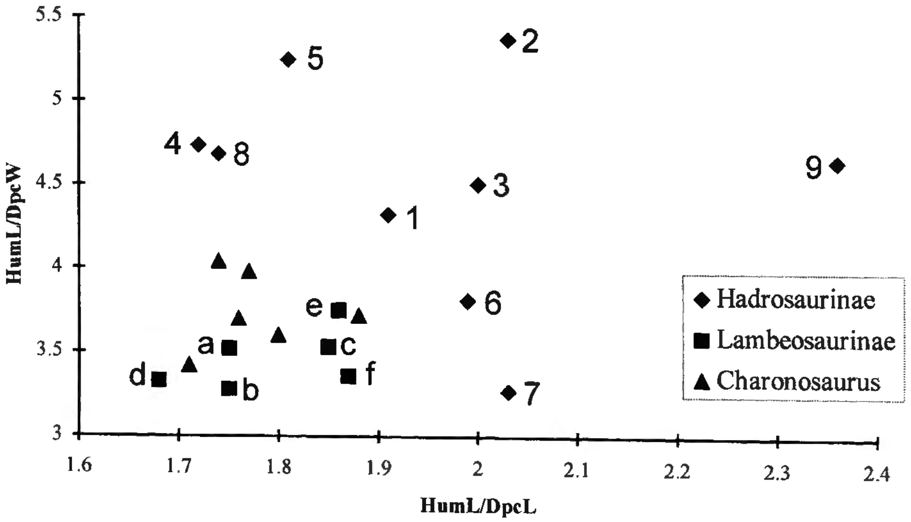

Fig. 23 — Morphometry of the hadrosaurian humerus - DpcL, length of the deltopectoral crest; DpcW, width of the deltopectoral crest; HumL, maximal length of the humerus. a, *Hypacrosaurus altispinus*; b, *Lambeosaurus lambei*; c, *Parasaurolophus cyrtocristatus*; d, *P. walkeri*; e, *Tsintaosaurus spinorhinus*; f, *Lambeosaurus magnicristatus*; 1, *Anatotitan copei*; 2, *Brachylophosaurus canadensis*; 3, *Edmontosaurus annectens*; 4, *E. edmontoni*; 5, *Gryposaurus incurvimanus*; 6, *Prosaurolophus maximus*; 7, *Saurolophus osborni*; 8, *Shantungosaurus giganteus*; 9, *Hadrosaurus foulkii*. Most of the measurements are taken from BRETT-SURMAN (1989).

dorso-ventral diameter < 1.3. This condition is observed in *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 53), *I. atherfieldensis* (see NORMAN, 1986, fig. 44), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 48) and *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, pl. 10, fig. 4). In Hadrosauridae, on the other hand, the coracoid terminates cranially in a large hook-like process pointing rather cranio-ventrally. The ratio of the cranio-caudal diameter to the dorso-ventral diameter is > 1.5.

28. Deltopectoral crest moderately (0), or strongly (1) developed on humerus - Robust humerus, with a wide deltopectoral crest extending below the midpoint of the bone, is sometimes regarded as a lambeosaurine synapomorphy (BRETT-SURMAN, 1975; WEISHAMPEL *et al.*, 1993). Nevertheless, BRETT-SURMAN (1989) showed that the deltopectoral crest length/width ratio is an insufficient feature to delineate subfamilies, as an important overlapping can be observed between Hadrosaurinae and Lambeosaurinae. Fig. 23 illustrates the differences in the shape of the humerus observed in selected lambeosaurine and hadrosaurine specimens. Most of the measurements are taken from BRETT-SURMAN (1975, 1989). The X-axis represents the humerus length/deltopectoral length ratio; the Y-axis represents the humerus length/deltopectoral width ratio. Fig. 24 represents the different points of measurements on the humerus. On the base of the combination of these three measurements, the lambeosaurine and hadrosaurine samples are well-separated from each other, in spite of the important variability observed within the hadrosaurine sample. It would therefore be possible to establish a discriminant function permitting a good separation of the hadrosaurine and lambeosaurine humeri on the base of these three measurements, but this further step needs a larger sample of measurements to be really useful. However, Fig. 23 clearly indicates that the humeri of the *Charonosaurus jiayinensis* specimens resemble,

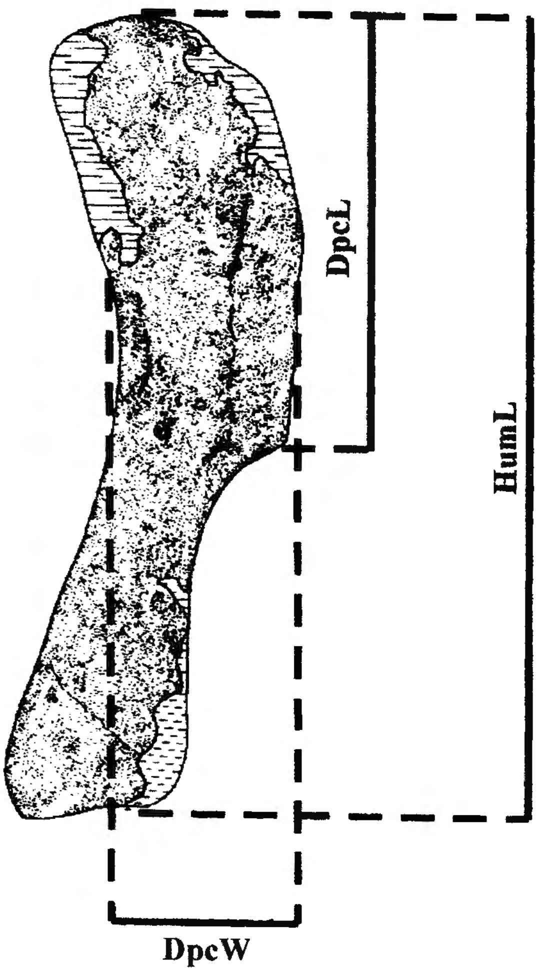

Fig. 24 — Measurements taken on the hadrosaurian humerus - DpcL, length of the deltopectoral crest; DpcW, width of the deltopectoral crest; HumL, maximal length of the humerus.

from a morphometrical point of view, those of typical lambeosaurine representatives in the strong development, both in relative length and width, of their deltopectoral crest. In non-hadrosaurid Hadrosauriformes, the deltopectoral crest is always less developed than in Lambeosaurinae, as observed in *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 57), *I. atherfieldensis* (see NORMAN, 1986, fig. 47), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 50), *Altirhinus kurzanovi* (see NORMAN, 1998, fig. 27), *Gilmoreosaurus mongoliensis* (see GILMORE, 1933, pl. 5, fig. 1), *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 28), or *Eolambia caroljonesa* (see KIRKLAND, 1998, fig. 9c).

29. Antitrochanter of ilium incipient (0), or prominent (1) - Although it is variable in size and shape, the ilium of all Hadrosauridae is characterised by a well-developed antitrochanter (BRETT-SURMAN, 1989). The antitrochanter is present, but always incipient, in non-hadrosaurid Hadrosauriformes, as observed in *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 63), *I. atherfieldensis* (see NORMAN, 1986, fig. 53), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 58), *Altirhinus kurzanovi* (see NORMAN, 1998, fig. 32), *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 30), or *Eolambia caroljonesa* (see KIRKLAND, 1998, fig. 10a).

30. Ischial peduncle of the ilium as a single knob (0), or formed by two small protrusions separated by a shallow depression (1) - The derived condition is observed in Hadrosauridae (BRETT-SURMAN, 1975). The ischial peduncle forms a large single knob in non-hadrosaurid Hadrosauriformes, as exemplified by *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 63), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 58) or *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 30).

31. Distal end of ischium forming a moderately expanded knob (0), tapering distally (1), or hypertrophied and footed (2); character treated as unordered - In non-hadrosaurid Hadrosauriformes, the shaft of the ischium terminates in a rounded knob that protrudes asymmetrically to the ventral side (BRETT-SURMAN, 1989; GODEFROIT *et al.*, 1998). In Hadrosauridae, the long, straight and thin shaft of the ischium usually tapers distally into a rounded point (BRETT-SURMAN, 1989). In Lambeosaurinae, on the other hand, the diameter of the shaft gradually increases distally where it terminates in an abrupt expansion into a structure resembling a "foot", as seen in *Charonosaurus jiayinensis*, *Parasaurolophus walkeri* (see PARKS, 1922, pl. 2), *Corythosaurus casuarius* (see BROWN, 1916, fig. 2), *Hypacrosaurus altispinus* (see GILMORE, 1924b, fig. 17), *Lambeosaurus lambei* (see STERNBERG, 1935, pl. 6) and *Tsintaosaurus spinorhinus* (see YOUNG, 1958, fig. 27), but also in *Eolambia caroljonesa* (see KIRKLAND, 1998, fig. 8a).

32. Cnemial crest restricted to the proximal head of the tibia (0), or extending on the diaphysis (1) - TAQUET (1976, fig. 63) observed that the cranio-caudal widening of the proximal head of the tibia is quite proximal in *Ouranosaurus nigeriensis*, as in *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 69), *I. atherfieldensis* (pers. obs.) and apparently in *Eolambia caroljonesa* (see KIRKLAND, 1998, Fig. 10b). This widening is more progressive and extends further on the proximal part of the tibial diaphysis in Hadrosauridae (TAQUET, 1976), but also in *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, pl. 13, fig. 2) and in *Gilmoreosaurus mongoliensis* (pers. obs., AMNH 6551).

33. Distal end of fibula moderately expanded into the shape of a ball (0), or greatly expanded and club-shaped (1) - The fibula of *Charonosaurus jiayinensis* resembles that of *Parasaurolophus cyrtocristatus* in its greatly expanded and club-shaped distal head. According to BRETT-SURMAN (1989), the distal head of the fibula is moderately expanded into the shape of a ball in all other hadrosaurids. This author hypothesised that the greatly enlarged distal end of the fibula may compensate for the lack of a calcaneum in *Parasaurolophus* or represents the fusion of the calcaneum with the fibula; however, this theory remains very conjectural, as the sample is not sufficient to exclude the possibility that the calcaneum was simply not fossilised in the *Parasaurolophus* and *Charonosaurus* specimens known to date.

34. Cranial ascending process of astragalus skewed laterally (0), or equilateral in shape (1) - BRETT-SURMAN (1989) distinguished two types of astragali in hadrosaurids. In *Charonosaurus jiayinensis* and *Parasaurolophus cyrtocristatus*, the cranial ascending process is rather reduced in size and equilateral. It resembles the generalised type, represented by all the genera except *Parasaurolophus*. In all the other Hadrosauridae, the cranial ascending process is skewed laterally into a 25-50-105 degree configuration; this configuration is plesiomorphic in Hadrosauriformes, as it is also observed in *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 65b) and *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 35b).

Previously cited features not retained in the present analysis

Below we discuss some anatomical features, culled from literature about Hadrosauriformes phylogeny, that we did not retained in the present analysis because they are ontogenetic, too variable, ill-defined, or require extensive revision. Other characters are also discussed by BRETT-SURMAN (1989).

Basioccipital excluded from the floor of the *foramen magnum* - According to WEISHAMPEL *et al.* (1993), the exoccipital condyloids nearly or completely exclude the basioccipital from the ventral margin of the *foramen magnum* primitively in Iguanodontia: this condition is encountered in *Iguanodon*, *Telmatosaurus* and Hadrosaurinae, but contrasts with that found in *Ouranosaurus* and Lambeosaurinae, in which the exoccipital condyloids are well-separated medially, allowing the basioccipital to form the floor of the *foramen magnum*. The validity of this character was discussed by GODEFROIT *et al.* (1998), who noted that well-separated condyloids are primitively present in *Hypsilophodon foxii* (see GALTON, 1974, fig. 8) and *Camptosaurus dispar* (see GILMORE, 1909) and that the basioccipital participates in the median part of the floor of the *foramen magnum* in *Iguanodon atherfieldensis* (see NORMAN, 1986), *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998), but also in several Hadrosaurinae such as *Anatotitan copei* (pers. obs.) or *Prosaurolophus blackfeetensis* (see HORNER, 1992). It can therefore be concluded that the important participation of the basioccipital in the floor of the *foramen magnum*, as observed in *Charonosaurus jiayinensis*, cannot be regarded as a synapomorphy shared with the Lambeosaurinae, but a variable feature among Hadrosauriformes that shows little consistency. Moreover, because of its important intraspecific variation, the degree of participation of the basioccipital in the formation of the floor of the *foramen magnum* is very difficult to quantify in a cladistic framework.

Lateral knobs on supraoccipital - According to HORNER (1990, 1992), the presence of lateral knobs on the supraoccipital for reception of the squamosal characterises his clade Lambeosauria, including *Ouranosaurus nigeriensis* and the Lambeosaurinae (his Lambeosauridae). However, these knobs are apparently not really developed in *Ouranosaurus nigeriensis* (TAQUET, 1976, fig. 13). Within Hadrosauridae, well-developed supraoccipital bosses, forming a ball and socket union with the squamosals, have been described in the Lambeosaurinae *Hypacrosaurus altispinus* (see HORNER, 1992), on a fragmentary lambeosaurine cranium (GILMORE, 1937, fig. 29) and on an isolated hadrosaurid supraoccipital (LANGSTON, 1960, pl. 34). *Aralosaurus tuberiferus*, usually regarded as a Hadrosaurinae (''gryposaur''), also possesses well-developed supraoccipital knobs (ROZHDESTVENSKY, 1968; HORNER, 1992). Pending further evidence, it is therefore too early to conclude that this kind of articulation is a lambeosaurine character. OSTROM (1961: 163) concluded that ''the fact that most well-preserved crania appear to be firmly united at this point and that no other similar articulations are exposed in existing hadrosaur material suggest that any mobility of this articulation probably existed only in the juvenile stage, which implies that a metakinetic condition existed early in hadrosaurian ontogeny, with a subsequent fusion and loss of mobility with the continued growth of the individual''. GODEFROIT *et al.* (1998) also showed that the development of supraoccipital knobs may be an ontogenetic character of poor phylogenetic significance in *Bactrosaurus johnsoni*.

Ventral deflection of the dentary - WEISHAMPEL & HORNER (1986, 1990) regarded the strong ventral deflection of the rostral end of the dentary as a lambeosaurine character; in Hadrosaurinae, on the other hand, the long axis of the dentary is considered as nearly straight. The ventral deflection of the lambeosaurine dentary may be plesiomorphic in Hadrosauriformes, as this character is also observed in *Altirhinus kurzanovi* (see NORMAN, 1998, fig. 3), *Bactrosaurus johnsoni* (see WEISHAMPEL & HORNER, 1986, fig. 2c), *Protohadros byrdi* (see HEAD, 1998, fig. 11) and, to a lesser degree, *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 2), *I. atherfieldensis* (see NORMAN, 1986, fig. 3) and *Telmatosaurus transsylvanicus* (see WEISHAMPEL *et al.*, 1993); the dentary appears nearly straight in *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 29). It must also be noted that a straight dentary is not observed in all Hadrosaurinae: it is distinctly deflected ventrally in *Prosaurolophus blackfeetensis* (see HORNER, 1992, pl. 34), *Gryposaurus notabilis* (see LAMBE, 1914, pl. 18) and *Brachylophosaurus canadensis* (see WEISHAMPEL & HORNER, 1990, fig. 26.3a). Therefore, it appears that this character is too variable and too ill-defined to be useful from a phylogenetic point of view. Moreover, it is also clearly an ontogenetic character: dentary are less deflected in juveniles than in larger specimens in Lambeosaurinae (pers. obs.).

According to BOLOTSKY & KURZANOV (1991), the dentary of *Amurosaurus riabinini* differs from that of *Corythosaurus casuarius* in the location of the ventral deflection, that begins more caudally in the former than in the latter. However, it appears that this character is variable within both species (maybe size-dependent) and cannot be used objectively.

Number of tooth rows - Although the number of tooth rows is higher in adult Hadrosauridae than in other ornithopods (see GODEFROIT *et al.*, 1998), this character is very variable in Hadrosauridae and essentially size-related. As noted by BRETT-SURMAN (1989: 54), ''the number of tooth rows may one day serve as an excellent indicator of age, if the rate of increase of rows can be shown to be consistent, but it must be abandoned in taxonomy''.

Relative height of dentary teeth - GILMORE (1924a) postulated that relatively high and narrow dentary teeth is a lambeosaurine character. However, the proportions of the teeth greatly vary within the dental battery of the dentary, the central teeth being higher than peripheral ones. Moreover, it is also clearly ontogenetic, juveniles having proportionally lower dentary teeth than larger specimens (pers. obs.). So, this character is too difficult to apply to be really useful in a phylogenetic point of view.

Ventral groove on the sacrum - A ventral haemal groove is observed along the fused sacrals of *Charonosaurus jiayinensis*. GILMORE (1933) observed that such a groove characterises the sacrum of Hadrosaurinae, while that of Lambeosaurinae bears a longitudinal ridge. This opinion was subsequently followed by WEISHAMPEL & HORNER (1990) and HORNER (1990). WEISHAMPEL *et al.* (1993), on the other hand, identified the ventral groove as a synapomorphy for Lambeosaurinae. GODEFROIT *et al.* (1998) and NORMAN (1998) showed that this feature is in fact not consistent in non-hadrosaurid Hadrosauriformes. It clearly requires revision in Hadrosauridae as well. Pending this, it has been decided not to include it in the present character matrix.

Very tall neural spines - According to HORNER (1990) and WEISHAMPEL *et al.*, this character is shared by *Ouranosaurus nigeriensis* and Lambeosaurinae. However, as noted by NORMAN (1998), this character is too ill-defined to be used objectively. Moreover, it is also probably ontogenetic (GODEFROIT *et al.*, 1998).

Table 1 — Character - taxon matrix for phylogenetic analyses of *Charonosaurus jiayinensis* - v, variable within the taxon.

Iguanodon	00000	00000	00000	00000	00000	00000	0000
Bactrosaurus	11000	00000	01000	00001	11100	00000	0100
Eolambia	11000	00000	0??00	?000?	11100	??00?	200?
Telmatosaurus	11000	00001	0?101	10001	11100	??0??	????
Hadrosaurinae	11000	v0001	01111	11111	11201	11011	1100
Charonosaurus	11112	10111	11101	11111	11210	11111	2111
Parasaurolophus	11112	10111	11101	11111	11210	11111	2111
Corythosaurus	11011	11111	11101	11111	11210	11111	2100
Hypacrosaurus	11011	11111	11101	11111	11210	1?111	2100
Lambeosaurus	1?011	11111	11101	11111	11210	1?111	210?
Tsintaosaurus	11010	10101	???01	11111	11210	11111	2100

Angular deltopectoral crest - According to WEISHAMPEL *et al.* (1993), the presence of an angular deltopectoral crest is a synapomorphy for Hadrosauridae (their "Euhadrosauria"). However, as noted by NORMAN (1998), this character is variable and appears sporadically among more basal ornithopods, including *Bactrosaurus johnsoni* (GODEFROIT *et al.*, fig. 28), *Gilmoreosaurus mongoliensis* (GILMORE, 1933, pl. 5, fig. 1), or *Tanius sinensis* (WIMAN, 1929, pl. 7, fig. 3).

Preacetabular process of ilium very deflected ventrally - GODEFROIT *et al.* (1998) regarded this character as synapomorphic for Hadrosauroidea, convergently acquired in *Iguanodon bernissartensis*. However, it appears too variable and too difficult to quantify to be really useful from a phylogenetic point of view. Where is the limit between a poorly deflected preacetabular process and a well deflected one? This is in many cases a subjective appreciation, as many intermediate cases exist in Hadrosauroidea. This character is also apparently ontogenetic in Hadrosauridae: in *Amurosaurus riabinini*, the preacetabular process is straighter in juveniles than in larger specimens (BOLOTSKY & GODEFROIT, in prep.).

Poorly excavated obturator sulcus on ischium - Following BRETT-SURMAN (1975), GODEFROIT *et al.* (1998) regarded the poorly excavated obturator sulcus, as observed in *Charonosaurus jiayinensis*, as a hadrosaurid character. Unfortunately, this character appears too variable and too difficult to quantify to be really a good diagnostic feature. Moreover, it is also probably an ontogenetic character: BRETT-SURMAN (1975) and WEISHAMPEL & HORNER (1990) indicated that the obturator foramen tends to close in older hadrosaurid individuals.

Shape of prepubic blade - The shape of the prepubic blade varies greatly within iguanodontids and hadrosaurids and may be useful in generic identification (BRETT-SURMAN, 1989; WEISHAMPEL & HORNER, 1990), but not in the establishment of phylogenetic relationships (GODEFROIT *et al.*, 1998). Moreover, it is very difficult to quantify in the framework of cladistic analysis. BRETT-SURMAN (1975) linked the shape of the prepubic blade in hadrosaurids to the general robustness of the animal: the most slender forms have the most elongated pubis, while the most robust forms have the shortest pubis.

Intercondylar canal on femur - The fusion of the rostral extensions of the distal condyles of the femur to form an intercondylar canal is, according to WEISHAMPEL & HORNER (1990), species dependent among ornithopods. On the other hand, BRETT-SURMAN (1989) suggested that the fusion of the condyles is an age-related feature in hadrosaurids and can occurs in all old individuals.

Robustness of metatarsals - BROWN (1913, fig. 7) observed that the pes of the type of *Hypacrosaurus altispinus* has relatively more robust metatarsals, but less robust phalanges than that of "*Diclonius mirabilis*" (= *Anatotitan copei*). BRETT-SURMAN (1989: 48) interpreted these differences as "... an adaptation of the hadrosaurines to a more heavily overgrown lowland environment, in contrast to the more open lambeosaurine environments where cursorial abilities would be at premium". However, the latter author (1989: 47) admitted that "The metatarsals of all hadrosaurids resemble one another closely. No consistent variation was observed among the genera, however, the sample size for complete and articulated metatarsals is insufficient at this time for any definitive statement".

Phylogenetic analysis

In order to clarify the phylogenetic relationships of *Charonosaurus jiayinensis*, a cladistic analysis was attempted, based on the 34 cranial, dental and postcranial characters discussed above and on 11 hadrosauroid genera. *Iguanodon* was used for outgroup comparisons. We only retained taxa sufficiently known by both cranial and postcranial material and accurately illustrated in literature. Autapomorphic features were excluded from the analysis. The character-taxon matrix is presented in Table 1. The data were treated using the Hennig 86 program (FARRIS, 1988). Analysis of the data matrix resulted in two most parsimonious trees, with a length of 37, a consistency index (CI) of 0.97 and a retention index (RI) of 0.98. The resulting consensus cladogramme is shown in Fig. 25.

The distribution of synapomorphies among the recognised nodes is summarised below, in reference to character list. For multistate features, the numbers between brackets refer to the character state.

- Hadrosauroidea are characterised by synapomorphies 1, 2, 12, 20, 21, 22, 23(1) and 32.
- *Telmatosaurus* + Hadrosauridae share the synapomorphies 10, 13, 15 and 16.
- Hadrosauridae are characterised by synapomorphies 17, 18, 19, 23(2), 26, 27, 29 and 30. However, it must be noted that the polarity of characters 26, 27, 29 and 30 is unknown in *Telmatosaurus*. So, it is also possible that some of these apomorphies characterise in fact the node *Telmatosaurus* + Hadrosauridae.
- Hadrosaurinae are characterised by synapomorphies 14, 25 and 31(1).
- Lambeosaurinae are characterised by synapomorphies 4, 6, 8, 24, 28 and 31(2).
- With the exclusion of *Tsintaosaurus*, all the other Lambeosaurinae share the synapomorphies 5(1) and 9. The state of character 11 is still unknown in *Tsintaosaurus* and, in the current state of our knowledge, also characterises the Lambeosaurinae.
- ''Corythosaurs'' (*Corythosaurus*, *Hypacrosaurus* and *Lambeosaurus*) are characterised by synapomorphy 7.
- Within Lambeosaurinae, *Charonosaurus* is the sister-taxon of the North American genus *Parasaurolophus*. Both share a parietal completely excluded from the occipital aspect of the skull (synapomorphy 3), a frontal platform extending above the rostral part of the supratemporal fenestra (synapomorphy 5(2)) and, consequently, probably a similar kind of supracranial hollow crest, a greatly expanded and club-shaped distal end of fibula (synapomorphy 33) and an equilateral cranial ascending process of astragalus (synapomorphy 34).

From this cladogramme, several points need to be more deeply discussed. Notwithstanding the discussions about the nature of its supracranial crest (see e.g. BUFFETAUT & TONG-BUFFETAUT, 1993), *Tsintaosaurus* is grouped within the Lambeosaurinae, as it shares cranial (characters 4, 6 and 8), dental (character 24) and postcranial (characters 28 and 31(2)) synapomorphies with typical representatives of this subfamily. However, it is regarded as the sister-group for North American Lambeosaurinae and *Charonosaurus*, as it presents the plesiomorphic conditions for two characters: the rostral part of its frontal is not broadly excavated (character 5) and its squamosal is not particularly elevated (character 9).

KIRKLAND (1998) regarded *Eolambia caroljonesa*, from the Albian - Cenomanian of Utah, as the oldest and most primitive Lambeosaurinae; lambeosaurine synapomorphies observed in this taxon would include the absence of a premaxillary foramen, the external nares partially surrounded by premaxillae, the development of a maxillary shelf, a truncated rounded rostral process of the jugal and the presence of very tall caudal neural spines. However, most of these characters require discussion. External nares partially surrounded by premaxillae is not a lambeosaurine character, as premaxillae also participate in the rostrodorsal margin of the external nares in other Hadrosauriformes, including *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 2), *I. atherfieldensis* (see NORMAN, 1986, fig. 3), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 16), or *Protohadros byrdi* (see HEAD, 1998, fig. 3b). As illustrated, the rostral part of the best preserved maxillae of *Eolambia caroljonesa* looks greatly damaged (see KIRKLAND, 1998, fig. 4a-c); consequently, the apparent lack of a rostrodorsal maxillary process may result from post-mortem breakage. Moreover, the rostrodorsal surface is not really developed into a maxillary shelf, as observed in typical Lambeosaurinae (compare with HORNER, 1990, fig. 13d-f). The rostral process of the jugal of *Eolambia caroljonesa* is not truncated and

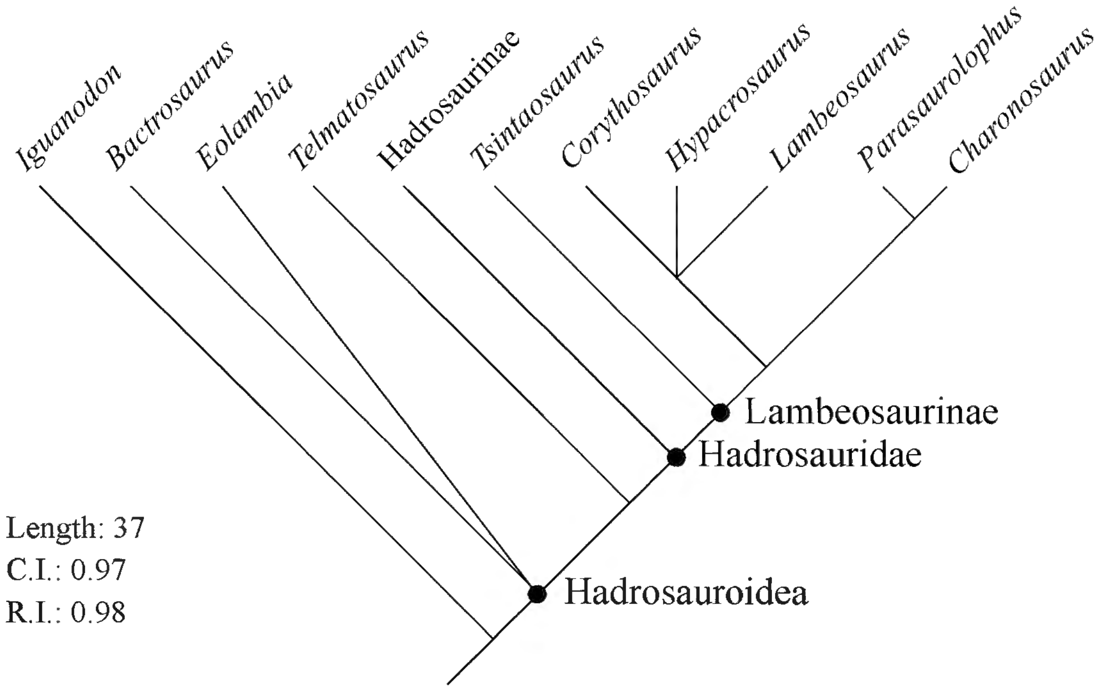

Fig. 25 — Cladogramme showing the phyogenetic relationships of *Charonosaurus jiayinensis*.

rounded, as postulated by KIRKLAND (1998, fig. 4e), but more closely resembles the plesiomorphic condition observed in non-hadrosaurid Hadrosauroidea (see above). It has been shown above that the relative height of the neural spines is not a good phylogenetic character, as it is very variable and difficult to quantify; however, the neural spines of the proximal caudal vertebrae of *Eolambia caroljonesa* do not appear particularly elongate (see KIRKLAND, 1998, fig. 8n-o). The present phylogenetic analysis suggests that *Eolambia caroljonesa* might rather represent a non-hadrosaurid Hadrosauroidea, as this taxon lacks a number of synapomorphies that diagnose *Telmatosaurus* + Hadrosauridae (characters 10 and 15), Hadrosauridae (characters 17, 18, 19, 23(2) and 29), Hadrosaurinae (characters 14 and 25) and Lambeosaurinae (characters 4, 6, 8, 24 and 28). The hypertrophied and footed distal end of the ischium (character 31(2)) and the absence of premaxillary foramina (not treated in the present analysis and very difficult to observe in not well-preserved material) are herein regarded as lambeosaurine synapomorphies convergently evolved in *Eolambia caroljonesa.*

Discussion on autapomorphic features in Charonosaurus jiayinensis

Short parocccipital and postcotyloid processes - The paroccipital processes extending only to the level of the mid-height of the *foramen magnum* appear autapomorphic in *Charonosaurus jiayinensis.* In other Hadrosauriformes, they have a more pending aspect, extending ventrally well below the base of the *foramen magnum,* as observed in *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 4), *I. atherfieldensis* (see NORMAN, 1986, fig. 5), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 13), *Bactrosaurus johnsoni* (see GILMORE, 1933, fig. 22), *Tanius sinensis* (see WIMAN, 1929, pl. 5, fig. 5), *Corythosaurus casuarius* (see OSTROM, 1961, figs. 9-10), *Edmontosaurus* (see LAMBE, 1920, fig. 6), *Anatotitan copei* (pers. obs.), *Prosaurolophus maximus* (see BROWN, 1916, fig. 1), *Prosaurolophus blackfeetensis* (see HORNER, 1992), *Saurolophus angustirostris* (see MARYAŃSKA & OSMÓLSKA, 1981a, pl. 1, fig. 1d) and *Tsintaosaurus spinorhinus* (see YOUNG, 1958, fig. 1). This is probably not an ontogenetic character, as a similar paroccipital process morphology can be observed in both juvenile (AMNH 5461) and adult (AMNH 5461) specimens of *Corythosaurus casuarius*. The postcotyloid process of the squamosal appears also particularly short in *Charonosaurus jiayinensis,* when compared with other Hadrosauriformes: this condition can be related to the shortness of the paroccipital processes, as previously described.

Rounded dorsal surface of parietal - The regularly rounded dorsal surface of the parietal, without any trace of a sagittal crest, characterises *Charonosaurus jiayinensis* among Hadrosauriformes: indeed, this crest is well developed in *Iguanodon bernissartensis* (see NORMAN, 1980, fig. 3), *I. atherfieldensis* (see NORMAN, 1986, fig. 4), *Ouranosaurus nigeriensis* (see TAQUET, 1976, fig. 11), *Probactrosaurus gobiensis* (see ROZHDESTVENSKY, 1966, fig. 3), *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 8), *Telmatosaurus transsylvanicus* (see WEISHAMPEL *et al.*, 1993, fig. 1), *Edmontosaurus* species (see LAMBE, 1920, fig. 8), *Anatotitan copei* (pers. obs.), *Saurolophus osborni* (pers. obs.), *Prosaurolophus blackfeetensis* (see HORNER, 1992, pl. 1), *Brachylophosaurus goodwini* (see HORNER, 1988, fig. 1d), *Gryposaurus incurvimanus* (see PARKS, 1920, pl. 3), *Kritosaurus navajovius* (see HORNER, 1992, pl. 44-45), *Parasaurolophus tubicen* (see WIMAN, 1931, pl. 1, fig. 5), *Lambeosaurus* sp. (see GILMORE, 1924a, fig. 8), *Corythosaurus casuarius* (see OSTROM, 1961), *Hypacrosaurus altispinus* (see GILMORE, 1924b), and *Tsintaosaurus spinorhinus* (see YOUNG, 1958, fig. 4). WEISHAMPEL & HORNER (1990) remarked that this character may be ontogenetic, as the crest is only slightly developed in hatchlings and juveniles. However, the sagittal crest is never developed in *Charonosaurus jiayinensis,* even in large adult specimens.

Very extended caudal ramus of postorbital - In *Charonosaurus jiayinensis,* the caudal ramus of the postorbital is thin, very long and high and nearly completely covers the lateral side of the squamosal. Usually in ornithopods, the medial squamosal tapers rostrally, while the lateral postorbital tapers caudally (WEISHAMPEL, 1984). The caudal ramus of the postorbital is always less extended in other hadrosaurids, as observed in *Maiasaura peeblesorum* (see HORNER, 1983), *Brachylophosaurus goodwini* (see HORNER, 1988, fig. 1A), *Prosaurolophus blackfeetensis* (see HORNER, 1992, pl. 10), *Saurolophus osborni* (see BROWN, 1916, fig. 2), *Edmontosaurus regalis* (see LAMBE, 1920, fig. 3), *Anatotitan copei* (pers. obs.), *Corythosaurus casuarius* (see OSTROM, 1961, pl. 6), *Lambeosaurus lambei* (see GILMORE, 1924a, fig. 9), *Hypacrosaurus altispinus* (see GILMORE, 1924b, fig. 13), *Parasaurolophus walkeri* (see SULLIVAN & WILLIAMSON, 1999, fig. 4), or *Tsintaosaurus spinorhinus* (YOUNG, 1958, fig. 2).

Alar process of basisphenoid very prominent and symmetrical - The alar process of the basisphenoid is implicated in ornithopod intracranial mobility, as attachment site for *M. protractor pterygoideus* (NORMAN, 1984; WEISHAMPEL, 1984). Usually in hadrosaurids, this process is rather small and projects caudally, as observed in *Edmontosaurus regalis* (see LAMBE, 1920, fig. 26), *Prosaurolophus blackfeetensis* (see HORNER, 1992, pl. 8, B), *Corythosaurus casuarius* (see OSTROM, 1961, fig. 12), or *Parasaurolophus tubicen* (see SULLIVAN & WILLIAMSON, 1999, fig. 16). In *Charonosaurus jiayinensis,* on the other hand, the alar process is distinctly more prominent and formed by two nearly symmetrical wings, a rostral one and a caudal one.

Strong caudal crest on the humerus - The development of a relatively strong caudal crest on the proximal part of the humerus is unusual and has never been reported in Hadrosauriformes. This character is probably linked to the great elongation of the forearm in *Charonosaurus jiayinensis.* However, this character must be regarded very cautiously because it displays an important ontogenetic variability, being very developed in "old adults" only. As previously noted by BRETT-SURMAN (1989: 75), "Old {hadrosaurid} individuals can be recognised by the

Table 2 — Values for ulna and radius "total length/maximal width of the proximal head" ratios in selected Hadrosauriformes.

Taxon	Ulna	Radius
Charonosaurus jiayinensis	6.3-6.7	6.6-6.9
Tsintaosaurus spinorhinus	6.5	6.6
Edmontosaurus regalis	6	6.6
Gryposaurus incurvimanus	5.9	6
Parasaurolophus cyrtocristatus	5.5	-
Parasaurolophus walkeri	-	5.9
Hypacrosaurus altispinus	5.5	5.9
Saurolophus angustirostris	5.1	6.4
Prosaurolophus maximus	4.7	-
Iguanodon atherfieldensis	5.3	5.3
Iguanodon bernissartensis	5	6
Ouranosaurus nigeriensis	5.2	5.6
Bactrosaurus johnsoni	4	5.7

greater deposition of bone on articular surfaces, ridges, and processes well beyond anything in younger animals".

Radius and ulna elongated and slender - The forearm of *Charonosaurus jiayinensis* appears particularly elongated and slender when compared to other Hadrosauriformes. The ratio "total length /maximal width of the proximal head" is an estimation of the robustness of the ulna and the radius. Table 2 compares these ratios in several Hadrosauriformes (measurements are culled from literature). These values are, of course, subject to intraspecific, including ontogenetic, variations. The bones resemble, by their slenderness, those of *Tsintaosaurus spinorhinus* and *Edmontosaurus regalis*. These values may be useful in generic identification, but not in the establishment of phylogenetic relationships, as they greatly vary within Lambeosaurinae and Hadrosaurinae subfamilies and in-non hadrosaurid Hadrosauriformes as well.

Elongated preacetabular process of ilium - Morphometrical comparisons of the ilium in Hadrosauridae are illustrated in Figure 26. The X-axis represents the ilium length/height ratio, whereas the Y-axis represents the ilium length/preacetabular length ratio. The ilium of *Charonosaurus jiayinensis* resembles that of *Parasaurolophus* species in its general robustness, with a very low ilium length/height ratio. On the other hand, the postacetabular process of the ilium is distinctly lower in *Charonosaurus jiayinensis* (length/height ratio of the postacetabular process = 2.53 in GMH HIj77) than in *Parasaurolophus* (1.5 in *P .cyrtocristatus* and 1.66 in *P. walkeri*, according to BRETT-SURMAN, 1975). Moreover, the pubic peduncle is not cranioventrally developed as in *P. walkeri* (see PARKS, 1922, pl. 6). Figure 26 also shows that the preacetabular process of the ilium is diagnostic in *Charonosaurus jiayinensis* in being proportionally longer than in any other known Hadrosauridae, with a ilium length/preacetabular process length ratio of 2.18.

Comparisons with other Asian Lambeosaurinae

Besides *Tsintaosaurus spinorhinus* and *Charonosaurus jiayinensis*, other Lambeosaurinae were previously described from more fragmentary material discovered in other Asian localities. All are distinctly different from *Charonosaurus jiayinensis.*

Jaxartosaurus aralensis **RIABININ, 1939** - The holotype of his species consists of an isolated skull roof and partial braincase from the Dabraszinskaya Formation in southern Kazakhstan. Differences with *Charonosaurus jiayinensis* include a much shorter frontal platform, a well-developed

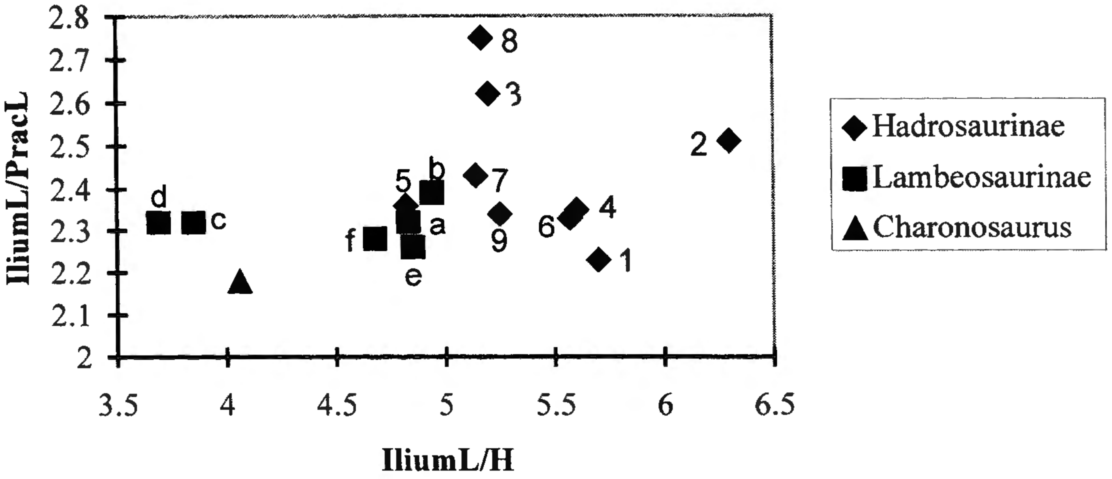

Fig. 26 — Morphometry of the hadrosaurian ilium - IliumL, ilium length; H, ilium height; PracL, length of preacetabular process. a, *Hypacrosaurus altispinus*; b, *Lambeosaurus lambei*; c, *Parasaurolophus cyrtocristatus*; d, *P. walkeri*; e, *Corythosaurus casuarius*; f, *Tsintaosaurus spinorhinus*; 1, *Anatotitan copei*; 2, *Edmontosaurus annectens*; 3, *E. edmontoni*; 4, *E. regalis*; 5, *Gryposaurus incurvimanus*; 6, *Prosaurolophus maximus*; 7, *Saurolophus osborni*; 8, *S. angustirostris*; 9, *Secernosaurus koerni*. Most of the measurements are taken from BRETT-SURMAN (1989).

sagittal crest, long paroccipital processes, a very asymmetrical alar process of the prootic, a much broader lateral supratemporal bar and a parietal that takes a large part in the occipital surface.

Procheneosaurus convincens **Rozhdestvensky, 1968** - This species, considered as a possible junior synonym of *Jaxartosaurus aralensis* by Weishampel & Horner (1990: 558), is based on the well-preserved skeleton of a juvenile specimen from Upper Cretaceous deposits in the vicinity of Tashkent (Uzbekistan). Comparisons with *Charonosaurus jiayinensis* are difficult to establish because of important ontogenetic differences and because the postcranial skeleton of the holotype needs to be described in detail. However, the sagittal crest is very developed on the parietal, the paroccipital processes have a pending aspect and the alar process of the prootic is much less prominent and asymmetrical.

Barsboldia sickinskii **Maryańska & Osmólska, 1981b** - This species is represented by one series of dorsal and sacral vertebrae with associated ilium from the Nemegt Formation of P.R. Mongolia. Because of the scarcity of the type-material and of the lack of autapomorphies, it is considered by Brett-Surman (1989: 106) as a *nomen dubium*. The sacrum of *Barsboldia sickinskii* is formed by 9 co-ossified vertebrae as in *Charonosaurus jiayinensis*. However, the ilium body appears proportionally higher and the preacetabular process, although incompletely preserved, shorter than in the latter.

Nipponosaurus sachalinensis **Nagao, 1936** - This species is based on a partial skull and skeleton of a single specimen from the Miho Group of Sachalin Island. The length of its hindlimb and the presence of cranial material indicate that it is a juvenile individual, so that comparisons with *Charonosaurus jiayinensis* are difficult to establish. It is also possible that *Nipponosaurus sachalinensis* might be the juvenile of another Asian Lambeosaurinae. While the postcranial skeleton closely resembles that of other Lambeosaurinae, the carpal elements are rather reminiscent of those of iguanodontids: the third metacarpal is well expanded at both ends and its shaft is slightly curved (Brett-Surman, 1989). This material is presently under study by Suzuki, Minoura and Weishampel.

Amurosaurus riabinini **Bolotsky & Kurzanov, 1991** - The holotype of this species is a partial skull from the Tsagayan Formation of Blagoveschenck (Amur Region, Russia). Many differences can be observed with the skull of *Charonosaurus jiayinensis*, including a shorter frontal platform, a well-developed sagittal crest, longer paroccipital processes, a longer parietal and particularly well-separated squamosals. In the meantime, numerous new specimens have been discovered at Blagoveschensk. The study of this material is in preparation by Bolotsky and Godefroit.

Posture and gait in *Charonosaurus jiayinensis*

As discussed above, *Charonosaurus jiayinensis* is known from fragmentary skeletons or isolated bones belonging to several individuals and mixed together after sub-aerial maceration and transportation. The bones were not cautiously reported on precise maps during excavations by local Chinese teams, so that it is currently impossible to determine whether the skeletons exhibited in the different museums are really based on a single skeleton or on several individuals. The proportions between the different portions of the skeleton consequently remain very conjectural, pending the discovery of more complete specimens.

Since the first attempts of skeletal reconstruction of dinosaurs in the 19th century, the natural posture of advanced ornithopods intrigued many palaeontologists, who tried to determine whether iguanodontids and hadrosaurids were biped or quadruped (see, e.g., Dollo, 1883; Galton, 1970; Norman, 1980; Alexander, 1985; Bultynck, 1993). Today, some kind of compromise is generally adopted. Hadrosaurids for example would be able to "switch between biped and quadruped gaits according to circumstances" (Thulborn, 1989: 48) and "when all evidence is taken together, {they} appear to have been primarily bipedal at higher speeds, but probably often walked on four legs while walking and browsing on low vegetation" (Forster, 1997: 297). Fig. 27 is a full skeletal reconstruction of *Charonosaurus jiayinensis*, both in walking quadruped pose and in running biped pose.

Because the available material is abundant, complete and exceptionally well preserved, posture and locomotion was studied in detail in *Iguanodon* (Norman, 1980, 1986). On the basis of this work, it has been decided to compare some anatomical features, linked to gait and locomotion, observed in *Charonosaurus* with those described in *Iguanodon*.

Comparisons of pectoral girdle and forelimb structures

In obligate quadruped dinosaurs, scapula and coracoid usually fuse in adult specimens, as observed in sauropods, ankylosaurs, or neoceratopsians. In *Iguanodon bernissartensis*, Norman (1986) observed that the scapula/coracoid suture is well-developed and transversely thickened to increase its strength, suggesting an adaptation towards receiving the vertical thrust from the head of the humerus. The two elements are even completely fused in some larger specimens from Bernissart (*contra* Norman, 1980). Between the sternal bones, a large irregular intersternal ossification is frequently found in the sternal area between the coracoids and the sternal bones (Norman, 1980, figs. 55-56). Therefore, the pectoral girdle of larger *Iguanodon* forms a kind of continuous solid arch, particularly well adapted for weight supporting during quadruped locomotion. Contrary to running mammals in which the left and right scapulae are independently movable on the rib cage, the pectoral girdle of quadruped dinosaurs may have moved as a whole relative to the rib cage, but the scapulae cannot have moved independently (Alexander, 1985). The pectoral girdle of *Charonosaurus jiayinensis* and other hadrosaurids appears less well adapted for weight supporting: the coracoid is smaller and more slender, the scapula/coracoid suture is less

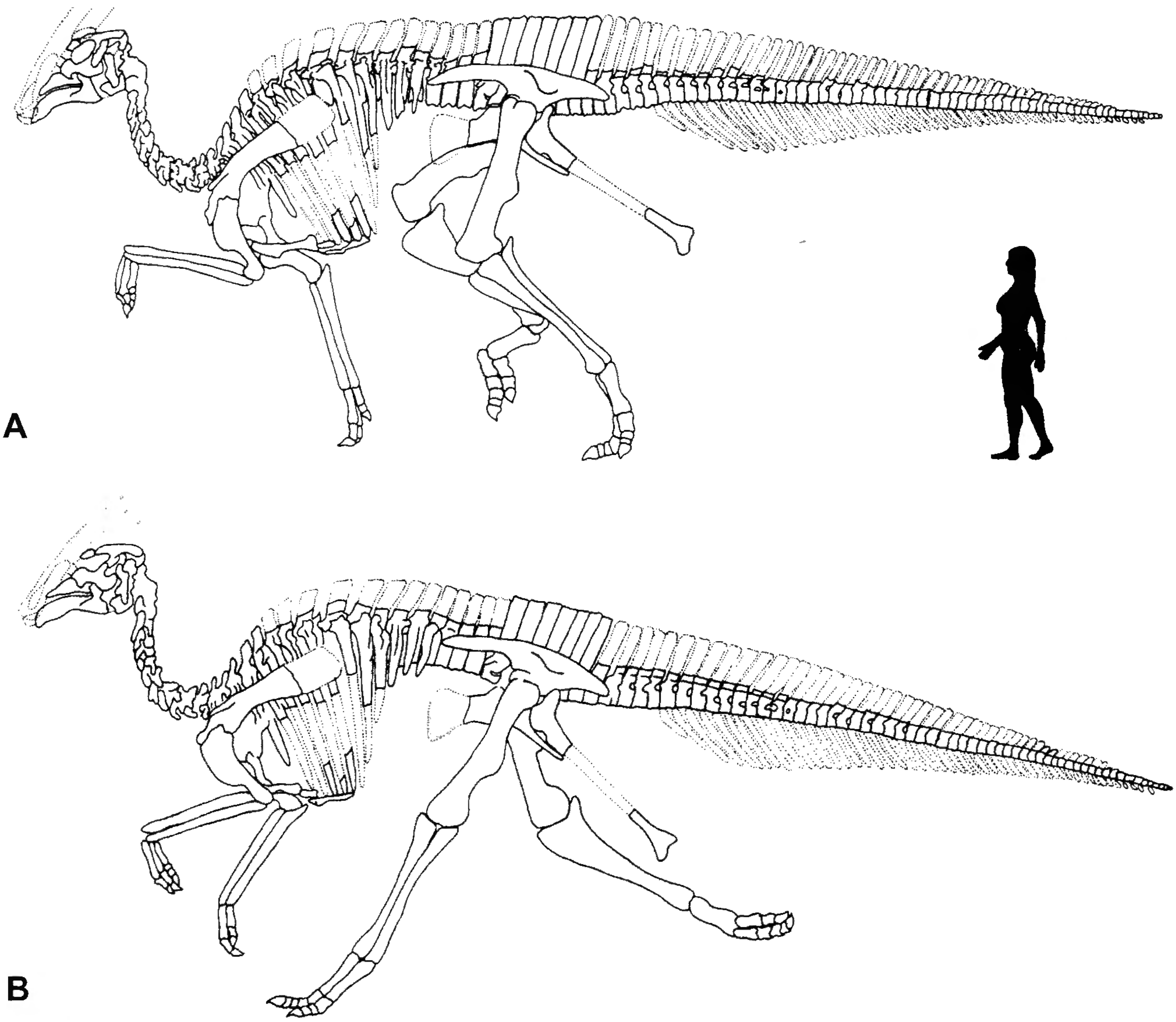

Fig. 27 — Reconstruction of the whole skeleton of *Charonosaurus jiayinensis*, from the Yuliangze Formation of Jiayin - A: in walking quadruped gait; B: in running biped gait.

thickened transversely and intersternal ossifications have not been observed.

The pectoral girdle of advanced ornithopods is remarkable for its curved and extremely elongated scapular blade. *M. dorsalis scapulae*, an important limb protractor as well as an abductor, inserts along the cranial part of its lateral side and *M. teres major*, a major limb retractor, along the caudoventral part of its lateral side. WALKER & LIEM (1994) compare the entire forelimb of terrestrial vertebrates with a single lever that is retracted by *M. teres major* (Fig. 28). The fixed point — or fulcrum — is represented by the shoulder joint. The out-lever arm (L_O) is the distance from the shoulder joint to the distal end of the limb and the out-force (F_O) is delivered downward and backward, perpendicular to the out-lever; the in-lever arm (L_I) is the perpendicular distance from the shoulder joint to the line of action of *M. teres major* exerting an in-force F_I. This is a third-order lever, as both the in- and out-forces are applied on the same side of the fulcrum, with the in-force closer to the fulcrum. At equilibrium, the following relationship between lever arms and forces applies:

$$F_O \text{ X } L_O = F_I \text{ X } L_I$$

An increased value for the out-force can therefore be obtained by increasing the length of the in-lever arm relative to the out-lever arm. On the other hand, WALKER & LIEM (1994) showed that an increased value for the velocity at the end of the out-lever arm can be obtained by lengthening of the out-lever arm, or by shortening of the in-lever arm by a proximal shift in the point of attachment of the retractor muscles, as observed in running quadruped mammals. The gear ratio, which represents the relationship between force and velocity at the end of the out-lever arm, can be expressed as the length of the out-lever arm divided by the length of the in-lever arm (L_O/L_I). When the ratio is low, force is emphasised at the expense of velocity; when it is high, velocity is emphasised at the expense of force. In advanced ornithopods, the great elongation and curvature of the scapular blade

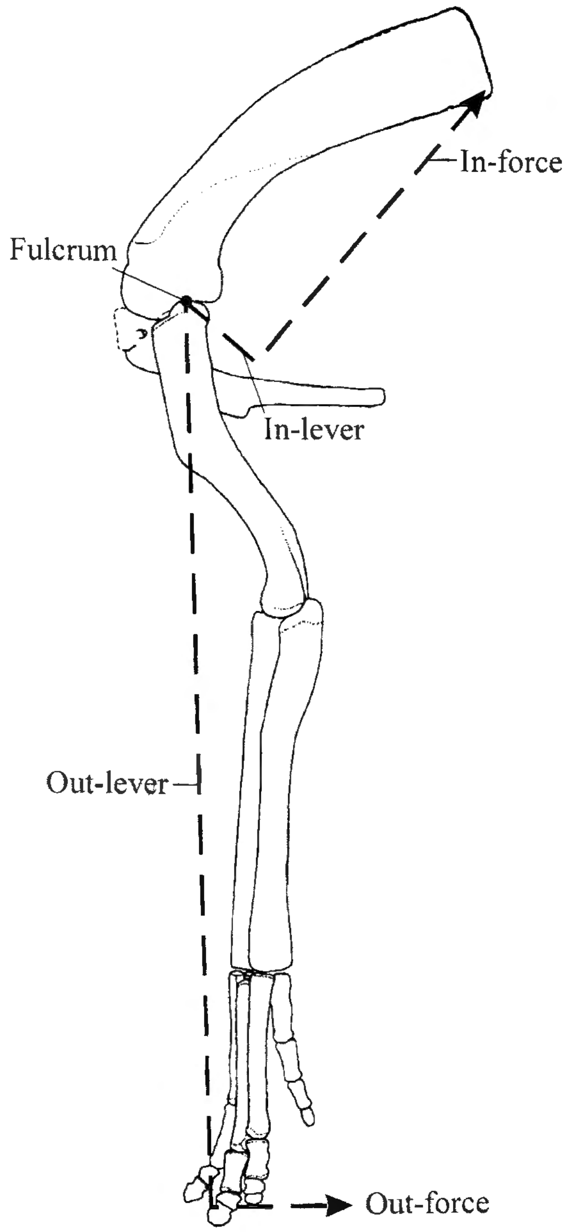

Fig. 28 — Retraction of the forearm of an hadrosaurian dinosaur at the shoulder, as a third-order lever (modified from DILKES, 2000).

implies a distal shift in the point of attachment of *M. teres major*. The in-lever arm is consequently particularly long and the gear ratio low. It implies that the ornithischian forelimb was rather designed for power than for high velocity.

The arm can also be compared to a third-order lever; retracted by *M. biceps*, the fulcrum is represented by the elbow articulation. Because the forearm is particularly elongated in *Charonosaurus jiayinensis*, the gear ratio of the arm was lower than in *Iguanodon bernissartensis*, and velocity of the forearm was therefore emphasised at the expense of force. To compensate the relative loss of force due to the elongation of the forearm, *M. biceps* was apparently particularly well developed in *Charonosaurus jiayinensis*, as indicated by the wide bicipital sulcus on the cranial side of the humerus and particularly by the very prominent knob on the craniodorsal angle of the coracoid, interpreted as the proximal insertion area for *M. biceps*.

When compared to that of *Iguanodon bernissartensis*, the humerus of *Charonosaurus jiayinensis* and of other lambeosaurines is characterised by the great development of its deltopectoral crest that extends distally down below the mid-point of the bone. This crest provided wide insertion areas for *M. pectoralis* and *M. deltoidesclavicularis*. In *Iguanodon atherfieldensis*, *M. brachialis* apparently originates along the lateral edge of the humerus, distal to the deltopectoral crest. The distal extension of this crest in lambeosaurines probably provided a widest and strongest attachment area for *M. brachialis*.

According to NORMAN (1980), the index of forelimb proportion, derived by multiplying together the ratios of the lengths radius/humerus and metacarpal III/humerus, allows to distinguish biped from quadruped dinosaurs. If used as prehensile organ, the distal segment of the limb tends to become more elongate, whereas if the limb is primarily weight supporting, the distal segment tends to become shorter. Unfortunately, this index cannot be accurately calculated for the material discovered at Jiayin, as it consists in disarticulated specimens. It cannot be certified that all the bones from the reconstructed skeletons exhibited in the different museums really belong to the same specimens: no detailed maps from the different excavations are currently available. However, all the ulnae, radii and metacarpals from Jiayin are characterised by their important elongation and it can be confidently asserted that the index of forelimb proportions was rather high in *Charonosaurus jiayinensis*. It must also be noted that the forearm space was probably very small in this species, so that pronation and supination were very limited.

The wrist of *Iguanodon bernissartensis* seems to be constructed so as to resist compression stresses which are produced by weight-support (NORMAN, 1980, fig. 59): carpals form block-like elements reinforced in larger specimens by ossified ligaments and connective tissue. In all hadrosaurs, on the other hand, the carpus is reduced to two small ossicles. However, GALTON (1970) noted that the two carpal bones are also quite small in the ceratopsian *Monoclonius*, so a lack of ossification in the wrist region need not have impeded the weight-carrying capacity of the forelimb.

In *Iguanodon bernissartensis*, the metacarpals are stout and firmly bound together along their whole length to produce a firm rectangular palm against which the phalanges articulate; moreover, they are slightly curved dorso-ventrally and their phalangeal articular surface extends onto the dorsal surface of the shaft, thereby allowing the phalanges to be hyperextended in weight-bearing position. In *Charonosaurus jiayinensis*, on the other hand, the metacarpals are extremely slender and perfectly straight. They do not bear extended striated surfaces indicating firm ligamentous attachment. There is no extension of the phalangeal articular surface onto the dorsal side of the shaft.

It can therefore be concluded that neither the pectoral girdle nor the forelimb of *Charonosaurus jiayinensis*, and of hadrosaurids in general, display the weight-supporting adaptations observed by NORMAN (1980) in *Iguanodon bernissartensis*. It confirms GALTON's (1970) hypothesis that hadrosaurs were primarily bipeds. However, the forelimb of *Charonosaurus jiayinensis* was particularly powerful, although the movements were apparently rather limited.

Comparisons of pelvic girdle and hindlimb structures

NORMAN (1980) showed that *Iguanodon bernissartensis* did not hold its vertebral column exclusively in a horizontal position: this dinosaur could have raised the thorax so that the vertebral column was normally held at between 40° and 50° to the horizontal. Indeed, the rather robust pubic peduncle of its ilium bears a well-marked acetabular surface on its lateral side, whereas its medial surface was strengthened by the first sacral rib through which the thrust from the femur is transmitted to the vertebral column. Therefore, the pubic peduncle was probably well able to support the femoral head when the vertebral column was inclined. On the other hand, GALTON (1970) claimed that the sacrum of hadrosaurids was held more or less horizontal, with very limited movements. Indeed, as observed in *Charonosaurus jiayinensis*, the pubic peduncle was distinctly less developed than in *Iguanodon bernissartensis* and does not bear any concave acetabular surface; moreover, the pubic peduncle region is not reinforced by the first sacral rib, as the latter contacted the ischial peduncle of the pubis. Therefore, the pubic peduncle of the ischium was probably too weak in *Charonosaurus jiayinensis* to carry the upward thrust of the femoral head if the sacrum was inclined from the horizontal.

The main difference between the ilium of *Iguanodon bernissartensis* and that of *Charonosaurius jiayinensis* is the great development of the antitrochanter, a synapomorphy for Hadrosauridae (see above). This structure is interpreted as an attachment site for *M. ilio-femoralis*, a femur protractor in dinosaurs (NORMAN, 1986). Thus, this muscle was probably much more powerful in hadrosaurids than in more basal ornithopods. However, DILKES (2000) indicated that *M. ilio-fibularis* is equally likely to have had an origin from the antitrochanter.

M. ilio-tibialis 1 is an important retractor of the tibia. In ornithopods, it probably inserted proximally along the preacetabular process of the ilium and distally along the cnemial crest of the tibia (NORMAN, 1980; DILKES, 2000). The great elongation of the preacetabular process of the ilium observed in *Charonosaurus jiayinensis* together with the greater development and distal shift of the cnemial crest along the shaft of the tibia observed in all Hadrosauroidea increases the length of the in-lever arm, and consequently the power of *M. ilio-tibialis 1*.

Therefore, the anatomy of the pelvic girdle and of the hindlimb bones of *Charonosaurus jiayinensis* reveals that the musculature of the hindlimb was particularly powerful. This species, as other Hadrosauridae, was probably better adapted for biped stance than was *Iguanodon bernissartensis*.

Function of the distal ischial foot in Lambeosaurinae

The significance of the ischial foot, very developed in *Charonosaurus jiayinensis* as in other lambeosaurines, remains enigmatic. LULL & WRIGHT (1942) hypothesised that the ischial foot was used as a seat when the lambeosaurine was resting. BRETT-SURMAN (1975) disagreed with this theory: the ischial shaft was not thick enough to support the posterior part of the animal. Moreover, the force of weight of the animal travelling up the ischial shaft would have shorn the pelvis at the ischial-iliac junction, as both bones meet in a plane that lies parallel to the ischial shaft. According to BRETT-SURMAN (1975), the development of the ischial foot is related to ovoviviparity in lambeosaurines: this structure would be preadapted as a support for large eggs and the corresponding musculature needed to hold them in the cloaca. However, HORNER & CURRIE (1994) described embryonic and nestling specimens of *Hypacrosaurus stebingeri*, associated with numerous eggs, showing that Lambeosaurinae where in fact oviparous.

In reptiles, *M. rectus abdominis* is a very large median muscle originating from the caudal edge of the sternum and the distal ends of the thoracic ribs and inserting along the caudal end of the pubis. This muscle helps to support the abdomen. It has also a very important respiratory function in crocodiles, as diaphragmatic muscles derive from *M. rectus abdominis*. These diaphragmatic muscles, which extend from the liver to the distal end of the pubes and to the last pair of gastralia, pull the liver caudally in a piston-like manner to enlarge the pleural cavity (WALKER & LIEM, 1994). RUBEN *et al.* (1994) described a crocodile-like ventilation of the lungs, with an hepatic-piston diaphragm, in theropod dinosaurs. In birds, the lungs are ventilated by rocking movements of the sternum, which alternately expand and compress the bellows-like air sac; *M. rectus abdominis*, arising along the caudal margin of the sternum and inserting on the distal ends of the pubes, has therefore also an important ventilatory function, as it pulls the sternum backwards. In advanced ornithopods, and especially in hadrosaurs, the postpubic bar is too short and too slender to have supported a very long and powerful *M. rectus abdominis*. According to NORMAN (1986), the insertion of this muscle would have been on the more robust distal end of the ischium. This would explain why this part of the ischium is so enlarged and foot-like in Lambeosaurinae. In these dinosaurs, the development of large hollow supracranial crests greatly increases the size of the nasal apparatus: the entire route of the nasal passage is more than 2 m long in some *Parasaurolophus* specimens (WEISHAMPEL, 1981a & b; FORSTER, 1997). Consequently, ventilation of the lungs needed to be efficient enough to inspire a sufficient amount of fresh air from the outside to the lung through such a long way. Thus, *M. rectus abdominis*, that very probably helped in inspiration movements also in lambeosaurines, had to be particularly powerful. The development of the ischial foot provided an enlarged insertion area for such a strong abdominal musculature.

BRETT-SURMAN (1975) propounded an alternative hypothesis: in hadrosaurids, powerful *M. rectus abdominis* would have inserted along the enlarged prepubic blade to help in respiration. However, there is no palaeontological evidence nor examples in living amniotes indicating that this muscle could insert on the proximal part of the pubis. On the other hand, GALTON (1969) and NORMAN (1986) found evidence suggesting that the lateral abdominal muscles inserted along the ventral edge of the prepubic blade, respectively in *Hypsilophodon* and *Iguanodon*. As these muscles also help in respiration in living lacertilians and birds (WALKER & LIEM, 1994), it is not unreasonable to think that the great development of the prepubic blade in lambeosaurines (especially in *Parasaurolophus*) may also be related to the hypertrophy of the nasal passage.

Comparisons with other late Maastrichtian dinosaur faunas

Lambeosaurine bones largely dominate the Jiayin assemblage, representing more than 90 % of the recovered fossils. Other groups are represented by isolated hadrosaurine, theropod, turtle and crocodile bones. The synchronous Blagoveschensk and Kundur dinosaur localities, in the neighbouring Russian Far East (see Fig. 1), are similarly dominated by lambeosaurines. However, significant differences can be observed between the three hadrosaurian faunas. The corythosaur-like *Amurosaurus riabinini*, the dominant lambeosaurine at Blagoveschensk, is not represented at Jiayin. On the other hand, *Charonosaurus jiayinensis* is apparently not represented at Blagoveschensk (BOLOTSKY & GODEFROIT, in prep.). Preliminary excavations reveal that *Amurosaurus* is also represented at Kundur and that hadrosaurines are apparently more abundant at Kundur than at Jiayin and Blagoveschensk. The *Wodehouseia spinata - Aquilapollenites subtilis* palynozone of Sakhalin Island has also yielded the incomplete skeleton of a juvenile lambeosaurine *Nipponosaurus sachalinensis* (MARKEVICH & BUGDAEVA, 1997). It can therefore be concluded that the vertebrate faunas of the *Wodehouseia spinata - Aquilapollenites subtilis* palynozone in north-eastern Asia are dominated by lambeosaurine dinosaurs; these lambeosaurines appear rather diversified.

If it can be demonstrated that the *Wodehouseia spinata - Aquilapollenites subtilis* palynozone of north-eastern Asia is really synchronous to the *Wodehouseia spinata* palynozone of North America, as postulated above, the Late Cretaceous dinosaur assemblages from the Amur Region can directly be compared to typical Late Maastrichtian ("Lancian") faunas from western North America. In the latter area, late Maastrichtian dinosaur assemblages are dominated either by ceratopsians or titanosaurids (LEHMAN, 1987). Hadrosaurs are represented by the large hadrosaurines *Edmontosaurus* and *Anatotitan*. While different kinds of dinosaur communities can be recognised in late Maastrichtian deposits of North America, in relation to different sedimentary/environmental provinces, none of them are dominated by hadrosaurs (see LEHMAN, 1987, figs. 5-8). Moreover, the presence of Lambeosaurinae in late Maastrichtian localities in North America is not substantiated. SULLIVAN & WILLIAMSON (1999) demonstrated that, with the possible exception of one fragmentary specimen (see WEISHAMPEL & JENSEN, 1979) whose age remains equivocal, all the currently known *Parasaurolophus* specimens come in fact from strata dated between 76 and 73 Ma. The youngest North American Lambeosaurinae would consequently be *Hypacrosaurus altispinus*, from the early Maastrichtian Horseshoe Canyon Formation in Alberta (EBERTH, 1997). It may consequently be assumed that important faunal exchanges occurred by late Campanian or early Maastrichtian times between north-eastern Asia and western North America, including migrations of both *Parasaurolophus*-like and *Corythosaurus*-like lambeosaurines, probably from east to west, and giving rise respectively to *Charonosaurus jiayinensis* (this paper) and *Amurosaurus riabinini* (BOLOTSKY & GODEFROIT, in prep.). The development of radically different kinds of dinosaur communities by late Maastrichtian times may reflect some kind of geographical isolation between eastern Asia and western North America during this period or drastic differences in climatic and palaeoecological conditions.

In Europe, potential late Maastrichtian dinosaur faunas are, as in eastern Asia, dominated by Hadrosauroidea, although titanosaurids dominate early Maastrichtian European assemblages (LE LOEUFF *et al.*, 1993, 1994; LAURENT *et al.*, 1997). However, it must be kept in mind that stratigraphic correlation of Late Cretaceous dinosaur localities of Europe is often problematic (see BUFFETAUT & LE LOEUFF, 1991) and that it is impossible in many cases to determine the exact position of the dinosaur localities within the Maastrichtian. On the other hand, hadrosaur remains discovered in well-dated late Maastrichtian marine deposits from Belgium and The Netherlands are too fragmentary to be identified with sufficient precision (WEISHAMPEL *et al.*, 1999). Only two hadrosauroid species may be regarded as valid in Europe (see e.g. BRINKMANN, 1988; CASANOVAS *et al.*, 1999a & b). *Telmatosaurus transsylvanicus* (NOPCSA, 1900), from the Hateg Basin in Romania, is a non-hadrosaurid Hadrosauroidea (WEISHAMPEL *et al.*, 1993; see also cladogramme in the present paper, Fig. 25).The only European lambeosaurine described to date is *Pararhabdodon isonensis* CASANOVAS, SANTAFE & ISODRO, 1993, from northern Spain. Although known by fragmentary material, this species appears rather primitive (CASANOVAS *et al.*, 1999a). The age of the holotype is probably comprised between the late Campanian and the base of the late Maastrichtian (Pereda Suberbiola, pers. com.). LAURENT *et al.* (1997) referred to *Pararhabdodon* sp. a series of cranial and postcranial bones from the late Maastrichtian of south-western France. However, the published material is clearly not diagnostic, even at the family level, so that further investigations are needed to confirm this identification (LAURENT, in prep.). CASANOVAS *et al.*, 1999b described another taxon of Hadrosauroidea from the late Maastrichtian of northern Spain, but do not name it. This hadrosauroid is regarded as more derived than *Telmatosaurus transsylvanicus*, but lacks a number of characters that diagnose Hadrosauridae (their Euhadrosauria). The latest Cretaceous hadrosaurian faunas from Europe may therefore be regarded as primitive, as compared to western North American and Asian ones: this is usually explained in terms of geographical isolation during the Late Cretaceous. (WEISHAMPEL *et al.*, 1993; CASANOVAS *et al.*, 1999a & b).

A more analytical, cladistic-based, study of the Hadrosauroidea biogeography, with estimation of ghost lineage duration (see e.g. WEISHAMPEL *et al.*, 1993; WEISHAMPEL, 1996), would bring new insights about the history of hadrosaurs by latest Cretaceous times. However, it has been decided to delay such study after the full completion of the study of hadrosaurian material from the Russian Far East (BOLOTSKY & GODEFROIT; SUZUKI *et al.*, in prep.): indeed, available information about Maastrichtian hadrosaurs from north-eastern Asia is too fragmentary to date. For the time being, it may be concluded that the study of lambeosaurine-dominated ''late'' Maastrichtian localities in north-eastern Asia suggests that different kinds of dinosaur communities existed outside North America and Europe just before the K/T crisis. Future developments in the study of these localities would lead to a better understanding of the real dinosaur biodiversity during the late Maastrichtian. These new data are very important to clarify the extinction pattern of non-avian dinosaurs, some 65 Ma ago.

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Caption of the plates

PLATE 1

Holotype skull of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - A: rostral view; B: dorsal view; C: caudal view. Scale bar = 5 cm.

PLATE 2

Fig. 1 — Holotype skull of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - A: left lateral view; B: right lateral view. Scale bar = 5 cm.

Fig. 2 — Right jugal of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - Lateral view. Scale bar = 5 cm.

Fig. 3 — Left postorbital of *Charonosaurus jiayinensis* (GMH Hlj196), from the Yuliangze Formation of Jiayin - A: medial view; B: lateral view. Scale bar = 3 cm.

PLATE 3

Fig. 1 — Left squamosal of *Charonosaurus jiayinensis* (CUST JV1251-57), from the Yuliangze Formation of Jiayin - A: medial view; B: lateral view. Scale bar = 4 cm.

Fig. 2 — Left maxilla of *Charonosaurus jiayinensis* (GMH Hlj178), from the Yuliangze Formation of Jiayin - A: lateral view; B: medial view. Scale bar = 5 cm.

Fig. 3 — Left surangular of *Charonosaurus jiayinensis* (GMH Hlj195), from the Yuliangze Formation of Jiayin - A: dorsal view; B: medial view. Scale bar = 5 cm.

PLATE 4

Left dentaries of *Charonosaurus jiayinensis*, from the Yuliangze Formation of Jiayin.

Fig. 1 — GMH HljA40 - A: lateral view; B: medial view. Scale bar = 10 cm.

Fig. 2 — GMH Hlj278 - A: lateral view (scale bar = 10 cm); B: detail of the dental battery (scale bar = 3 cm).

PLATE 5

Fig. 1 — Right scapula of *Charonosaurus jiayinensis* (CUST JIII398), from the Yuliangze Formation of Jiayin - A: medial view; B: lateral view. Scale bar = 15 cm.

Fig. 2 — Left humerus of a juvenile specimen of *Charonosaurus jiayinensis* (GMH Hlj143), from the Yuliangze Formation of Jiayin - A: cranial view; B: caudal view. Scale bar = 5 cm.

Fig. 3 — Left humerus of *Charonosaurus jiayinensis* (CUST JVIII1247), from the Yuliangze Formation of Jiayin - Cranial view. Scale bar = 5 cm.

PLATE 6

Fig. 1 — Left ulna of *Charonosaurus jiayinensis* (CUST JIII1715), from the Yuliangze Formation of Jiayin - A: dorsal view; B: lateral view; C: medial view. Scale bar = 10 cm.

Fig. 2 — Right radius of *Charonosaurus jiayinensis* (CUST JIII1216), from the Yuliangze Formation of Jiayin - A: cranial view; B: caudal view. Scale bar = 10 cm.

Fig. 3 — Left ilium of *Charonosaurus jiayinensis* (GMH Hlj77), from the Yuliangze Formation of Jiayin - A: lateral view; B: medial view. Scale bar = 15 cm.

PLATE 7

Fig. 1 — Left ischia of *Charonosaurus jiayinensis*, from the Yuliangze Formation of Jiayin in lateral view- A: CUST JV679 (proximal part; scale bar = 10 cm); B: CUST JIV1225 (distal part; scale bar = 5 cm).

Fig. 2 — Left femur of *Charonosaurus jiayinensis* (CUST JIII1232), from the Yuliangze Formation of Jiayin - A: medial view; B: cranial view; C: lateral view; D: caudal view. Scale bar = 15 cm.

PLATE 8

Fig. 1 — Right tibia of *Charonosaurus jiayinensis* (CUST JIII1230), from the Yuliangze Formation of Jiayin - A: lateral view; B: cranial view; C: medial view; D: caudal view. Scale bar = 10 cm.

Fig. 2 — Left fibula of *Charonosaurus jiayinensis* (CUST JIV1249), from the Yuliangze Formation of Jiayin - A: lateral view; B: medial view. Scale bar = 15 cm.

Fig. 3 — Left astragalus of *Charonosaurus jiayinensis* (CUST JIV1249), from the Yuliangze Formation of Jiayin - A: cranial view; B: caudal view; C: dorsal view. Scale bar = 5 cm.

PLATE 1

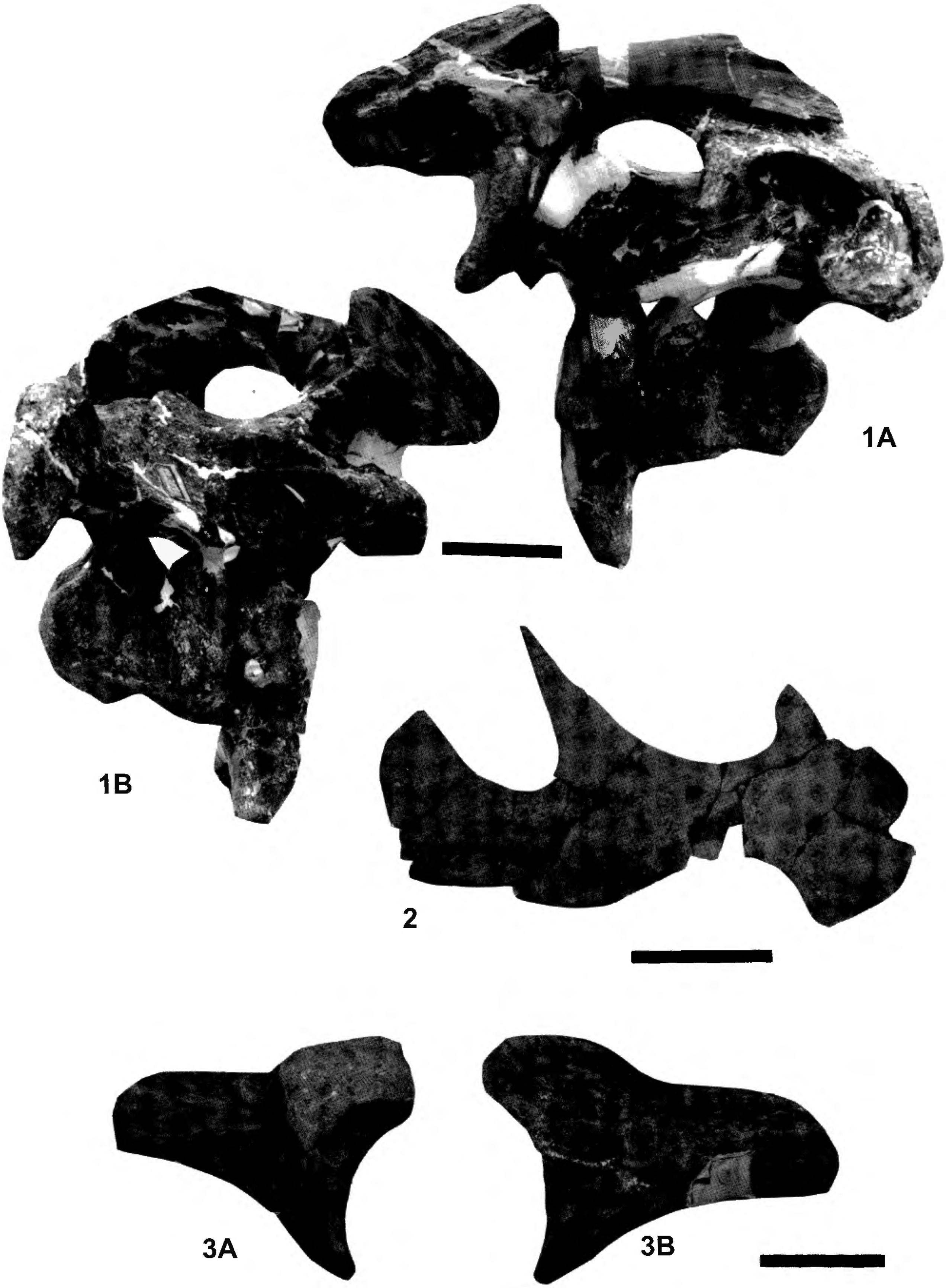


PLATE 2

PLATE 3

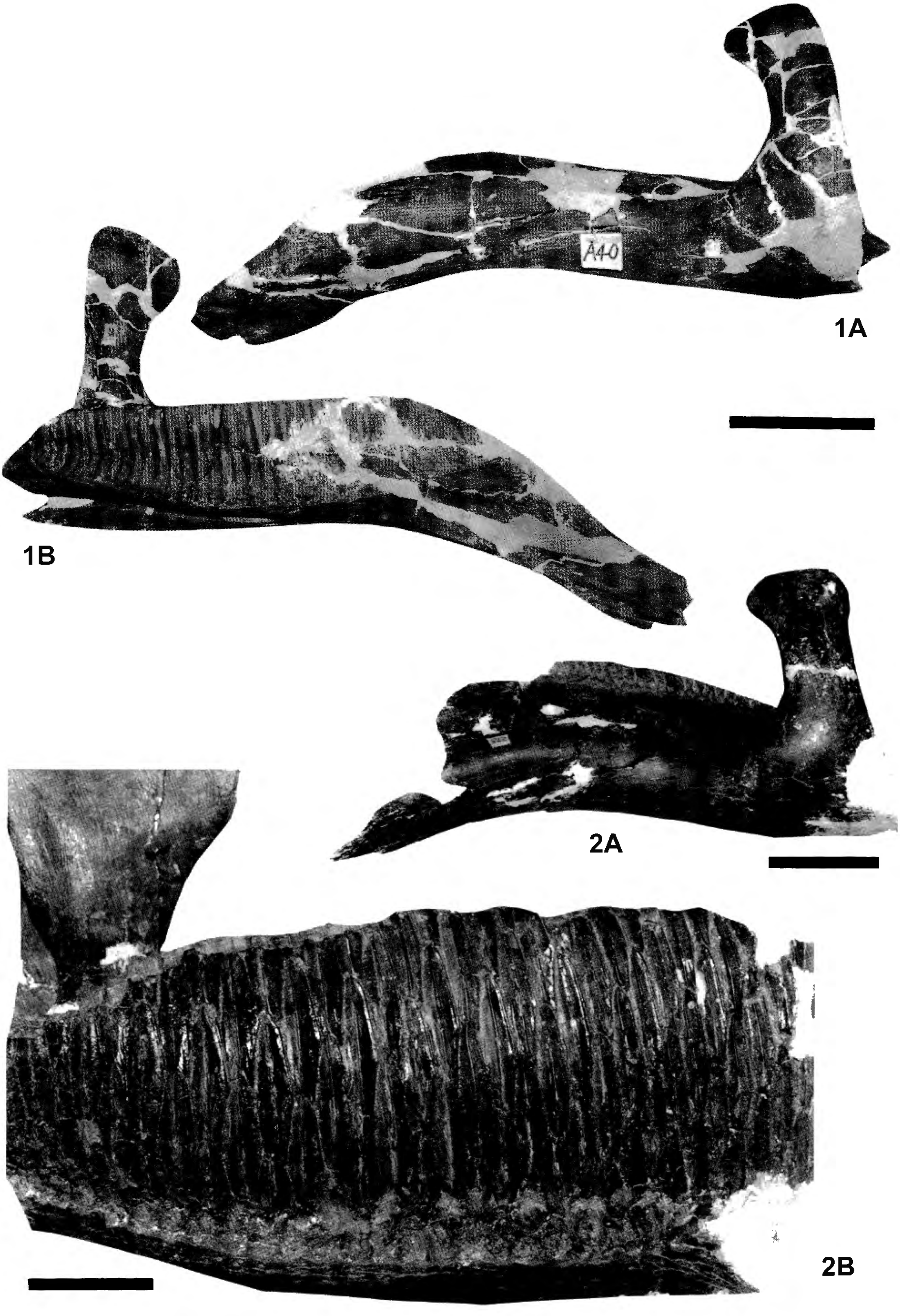
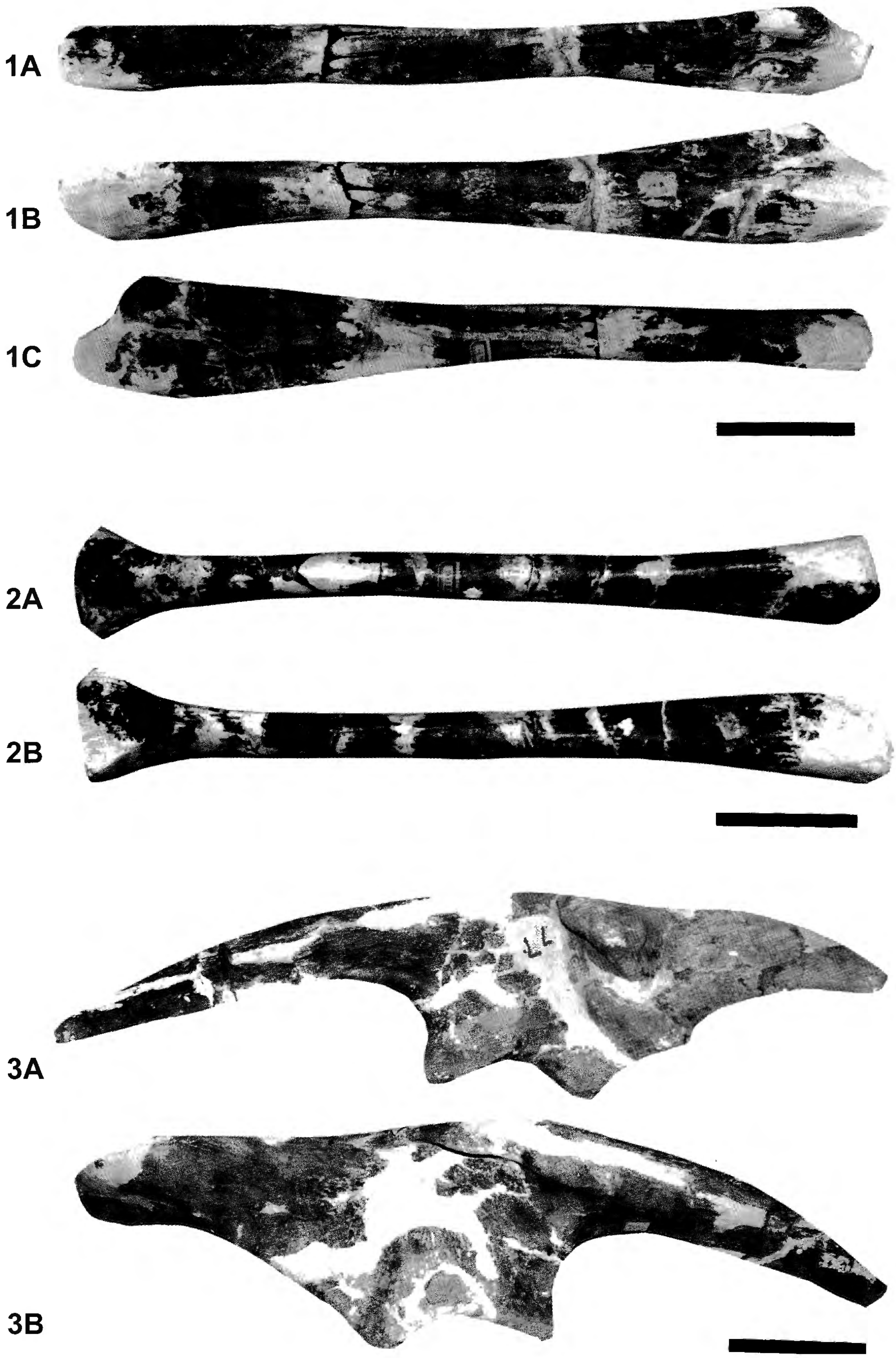


PLATE 4

PLATE 5



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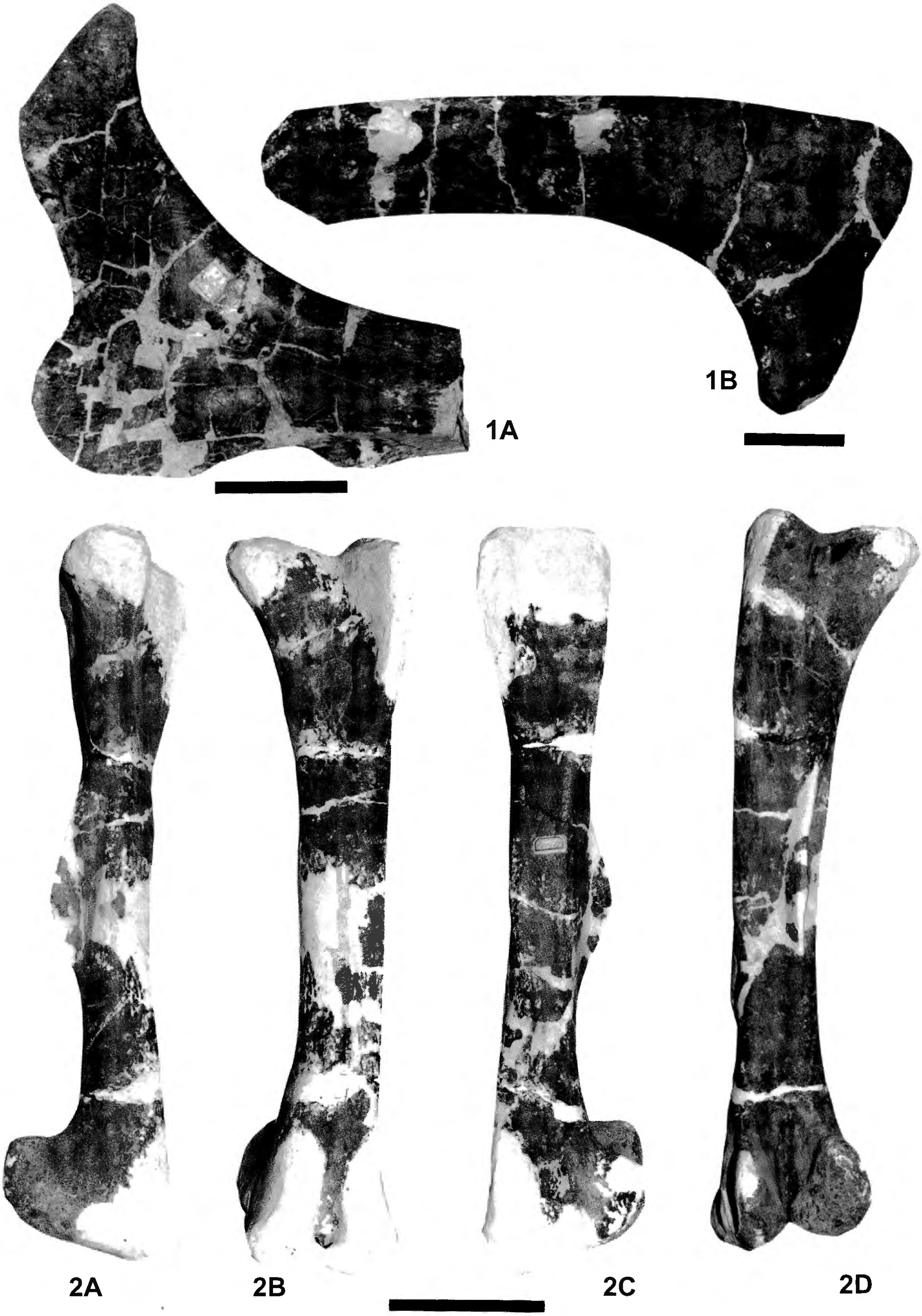

PLATE 7

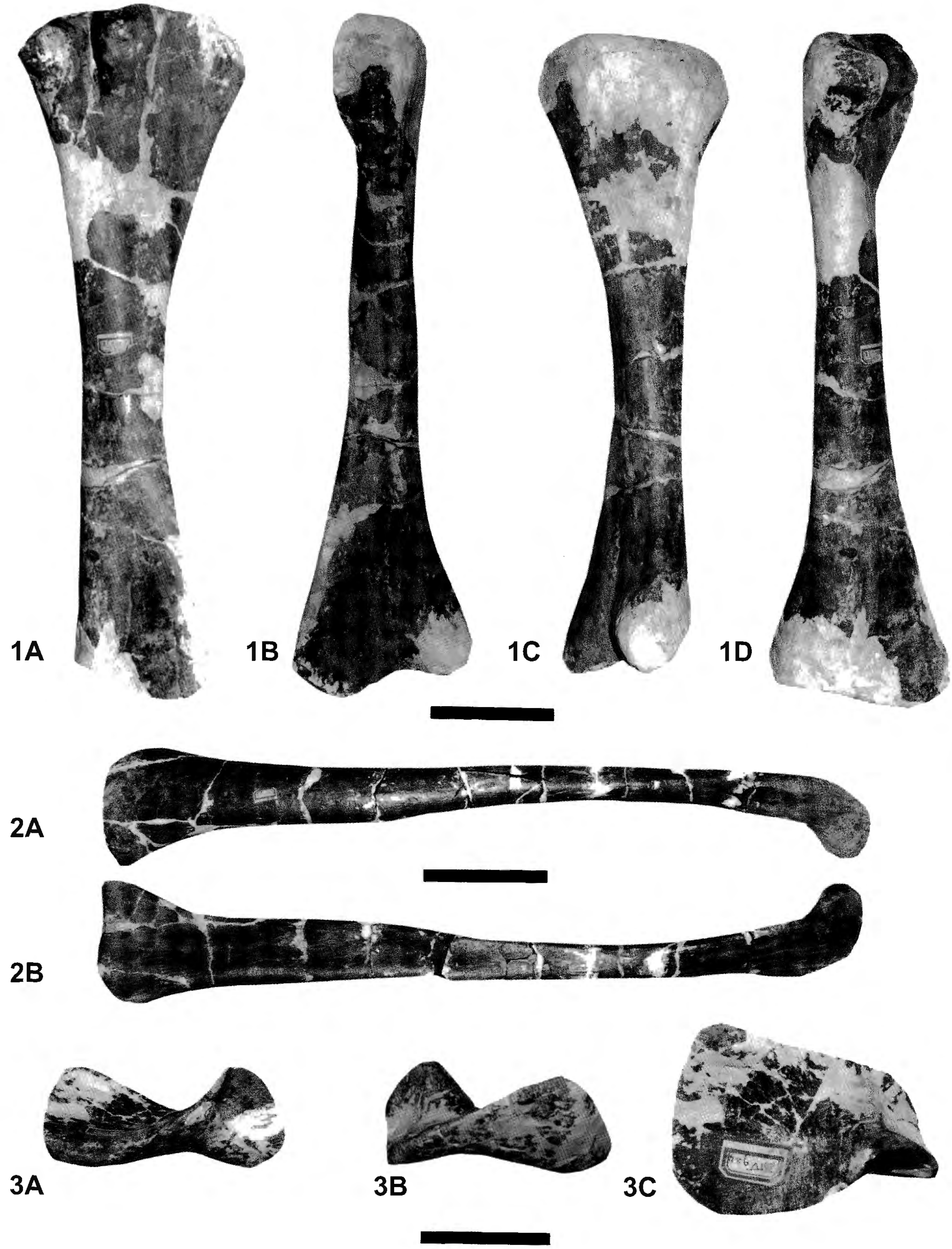

PLATE 8