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ANKYLOSAURIDAE (DINOSAURIA) FROM MONGOLIA

(plates 19—36)

Abstract. — The paper deals with Asian Ankylosauria, assigned to the family Ankylosauridae, BROWN. New material collected by the Polish-Mongolian expeditions to Mongolia in three Late Cretaceous formations (Djadokhta, Barun Goyot and Nemegt) is described. Two new genera and species: *Saichania chulsanensis* and *Tarchia kielanae*, both from the ?Campanian Barun Goyot Formation, are described. Revised diagnoses of all Mongolian ankylosaurid species are given. An ossified conchal system in nasal cavities of *Saichania chulsanensis*, a unique feature among the extinct lower tetrapods is described. The postfrontal, epipterygoid, and additional ossifications in the antorbital wall closing the orbit in the front, as well as four pairs of secondary ossifications of dermal origine, which cover partly the skull bones, are found in the skull of *Pinacosaurus grangeri* and *Saichania chulsanensis*. Presented reconstruction of the hyoid apparatus of *Saichania chulsanensis* differs from that known in *Psittacosaurus* and *Protoceratops* and shows similarities to that of Squamata. In the pectoral girdle of *Saichania chulsanensis* the fusion of the coracoid with the transverse process of the first dorsal vertebra is stated. A morphological (and possibly also phylogenetical) sequence of Mongolian Ankylosauridae, beginning with an unnamed Early Cretaceous specimen from Khovboor, through *Talarurus*, *Pinacosaurus*, *Saichania* to “*Dyoplosaurus*” is presented. The position of Ankylosauria within the Ornithischia is discussed. It is presumed that the quadrupedality in Ankylosauria is primary. The origin of Ankylosauria from Pseudosuchia, independent from the line of bipedal and cursorial Ornithopoda seems possible. Common origin of Ankylosauria and Stegosauria is suggested.

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INTRODUCTION

Ankylosauria from the Cretaceous of Asia have been studied only preliminarily. A monograph of COOMBS (MS) devoted to ankylosaurs contains few data about Asiatic representatives. The first note on the occurrence of the armored dinosaurs in Asia come from MATLEY (1923) who has described *Lametasaurus indicus* from the Cretaceous of Jubbulpore (Lameta Beds). Assignment of *Lametasaurus* to the Ankylosauria has been questioned (CHAKRAVARTI, 1935). Notes by WIMAN (1929) and GILMORE (1933*a*) pertain to the occurrence of remains of the true Ankylosauria in China. These fragmentary findings did not allow more precise identification. *Pinacosaurus grangeri* GILMORE described on the basis of a deformed skull (AMNH 6523) from the Djadokhta Formation of Shabarakh Usu (Bayn Dzak) was the first Asiatic species undoubtedly belonging to Ankylosauria (GILMORE, 1933*b*). In 1935 YOUNG described *Pinacosaurus ninghsiensis* from the Cretaceous of Ninghsia (China).

In the USSR RIABININ (1939) has found ankylosaur's in the Upper Cretaceous near Tashkent. It seems also probable that the remains described by him as possible Ceratopsia (*l.c.*, table 11, figs 1, 1*a*, 4, 4*a*; table 12, figs 4, 5; table 14, figs 2, 2*a*) belong also to the Ankylosauria. On the basis of incomplete and badly preserved materials found during 1930—1931 by the Sino-Swedish expeditions, BOHLIN (1953) reported the occurrence of the ankylosaurs in several sites of Cretaceous age in the eastern Kansu and has described three new genera and species: *Sauroplices scutiger*, *Heishansaurus pachycephalus* and *Peishansaurus philemys*, as well as a new genus and species *Stegosaurides excavatus* assigned to ?Stegosauria. MALEEV¹ (1956), ROMER (1966), STEEL (1969) and others assigned *Stegosaurides excavatus* to the Ankylosauria. Not all species established by BOHLIN can be regarded as valid because of their incomplete type specimens. Data pertaining to occurrence of Ankylosauria in China are supplemented by the reports of the 1960 Sino-Soviet Palaeontological Expeditions (ROZHDESTVENSKY, 1961*a*, 1961*b*). Two skeletons of ankylosaurs have been excavated near Maortu (Alashan). This material so far undescribed is housed in Peking. Occurrence of ankylosaurs has also been noted in Inner Mongolia (Young, 1964) and in Nanhsiung (Kwantung) in the Nanhsiung Formation of Late Cretaceous age (YOUNG, 1965; CHENG *et al.*, 1973).

Abundant and well preserved remains of ankylosaurs have been excavated from the Upper Cretaceous of Mongolia by Soviet expeditons during 1946—1949 (MALEEV, 1952*a*, 1952*b*, 1952*c*, 1954*b*, 1956). Remains from Bayn Shireh (Bayn Shireh svita, see p. 132) described by MALEEV (1952*b*) as *Talarurus plicatospineus* include numerous specimens housed in the Palaeontological Institute in Moscow. MALEEV (1952*a*) established a new family, the Syrmosauridae (regarded herein as a synonym of the Ankylosauridae) with one genus *Syrmosaurus* (type species *Syrmosaurus viminicaudus*) from the Djadokhta Formation. MALEEV (1952*b*) has also described *Syrmosaurus disparoserratus* from Sheeregeen Gashoon (Bayn Shireh svita) and *Syrmosaurus* sp. from Oshi.

¹ Referred to in previous publications as MALEYEV.

The new ankylosaurs were discovered in the Upper Cretaceous of Mongolia by the Polish-Mongolian Palaeontological Expeditions of 1963—1971 (KIELAN-JAWOROWSKA & DOVCHIN, 1969; KIELAN-JAWOROWSKA & BARSBOLD, 1972; MARYAŃSKA 1970, 1971). A rich and interesting collection of ankylosaurs was discovered by the Soviet-Mongolian Expeditions to Mongolia in 1970—1971. The latter collection contains Upper Cretaceous forms from e.g. Alag Teg (TVERDOCHLEBOV & TSYBIN, 1974) and Khermeen Tsav (KRAMARENKO, 1974) as well as Lower Cretaceous forms from the vicinity of Khovboor (KRAMARENKO, *l.c.*) and (?) Khuren Dukh (KALANDADZE & KURZANOV, 1974). Fragmentary undescribed remains of ankylosaurs from several sites in Kazakhstan (e.g. Shakh-shakh) housed in the Laboratory of Palaeobiology of Kazakh Academy of Sciences in Alma Ata and remains from Yakutia (USSR) housed in the Palaeontological Museum in Moscow complete the collection of ankylosaurs from Asia (see table 1 and text-fig. 1).

The present paper is devoted to ankylosaurs collected in the Mongolian People's Republic by Polish-Mongolian Palaeontological Expeditions in 1963—1971, and housed in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw and in Geological Institute Section



Fig. 1

Diagrammatic map of Asia showing the localities in which ankylosaurs were found. 1 — Bayn Dzak, 2 — Alag Teg, 3 — Altan Ula, 4 — Nemegt, 5 — Khulsan, 6 — Khermeen Tsav, 7 — Sheeregeen Gashoon, 8 — Khovboor, 9 — Bayn Shireh, 10 — Baga Tarjach, 11 — Baysheen Tsav, 12 — NW Ninghsia, 13 — Chia-yü-kuan, 14 — Hui-hui-pu, 15 — Ehr-hia wu-kuan, 16 — Maortu, 17 — Tsondolein Khuduk, 18 — Tebch, 19 — Iren Dabasu, 20 — Khuren Dukh, 21 — Oshi Nur, 22 — Jubbulpore, 23 — Alym Tau, 24 — Shakh-shakh, 25 — Djara Khuduk, 26 — Laiyang, 27 — Nanhsiung, 28 — Kemptenday.

I d e n t i f i c a t i o n		Museum cat. no	Locality (for explanation of numbers see Text-fig. 1)
original	in this paper		
	" <i>Dyoplosaurus</i> " <i>giganteus</i> MALEEV	PIN, undescribed specimen, no catalogue number	Khermen Tsav (6)
<i>Dyoplosaurus</i> cf. <i>giganteus</i> (MARYAŃSKA, 1970)	"Dyoplosaurus" <i>giganteus</i> MALEEV	ZPAL MgD-I/43, housed now in GISPS, Ulan Bator	Altan Ula (3)
<i>Dyoplosaurus</i> sp. (MARYAŃSKA, 1970)		ZPAL MgD-I/42, and MgD-I/49, MgD-I/113	
<i>Dyoplosaurus giganteus</i> MALEEV (MALEEV, 1956)	"Dyoplosaurus" <i>giganteus</i> MALEEV	PIN 551-29	Nemegt (4)
<i>Pinacosaurus</i> (KRAMARENKO, 1974)	<i>Saichania chulsanensis</i> gen. n., sp. n.	PIN, undescribed specimen, no catalogue number	Khermeen Tsav II (6)
ankylosaurid (KIELAN-JAWOROWSKA & BARSBOLD, 1972)		ZPAL MgD-I/114	
ankylosaurid (KIELAN-JAWOROWSKA & BARSBOLD, 1972)	<i>Saichania chulsanensis</i> gen. n., sp. n.	GI SPS 100/151 holotype	Khulsan (5)
ankylosaurid (KIELAN-JAWOROWSKA & BARSBOLD, 1972)	<i>Tarchia kielanae</i> gen. n., sp. n.	ZPAL MgD-I/111 holotype	
<i>Pinacosaurus ninghsiensis</i> YOUNG (YOUNG, 1935)	<i>Pinacosaurus grangeri</i> GILMORE	Inst. Vert. Paleont., Peking, no catalogue number	NW of Ninghsia (12)
ankylosaurs KUROCHKIN & KALANDADZE 1970)	<i>Pinacosaurus grangeri</i> GILMORE	PIN, undescribed specimens, no catalogue numbers	Alag Teg (2)
<i>Pinacosaurus grangeri</i> GILMORE (GILMORE, 1933)	<i>Pinacosaurus grangeri</i> GILMORE	AMNH 6523 holotype	Bayn Dzak (1)
<i>Syrmosaurus viminicaudus</i> MALEEV (MALEEV, 1952)		PIN 614	
<i>Pinacosaurus grangeri</i> GILMORE (MARYAŃSKA, 1971)		ZPAL MgD-II/7 ZPAL MgD-II/9 ZPAL MgD-II/31 ZPAL MgD-II/32 ZPAL MgD-II/27	
ankylosaurs (ROZHDESTVENSKY, 1972)	ankylosaurids	undescribed remains housed in Paleobiol. Lab. in Alma Ata	Shakh-shakh (24)
Nodosauridae gen. et sp. indet. (RIABININ, 1939)	ankylosaurids	PIN, no catalogue number	Alym Tau (23)

ble 1

remains from Asia

Associated vertebrate fauna	Formation and/or other stratigraphic data	Presumable age
<i>Therizinosaurus cheloniformis</i> <i>Tarbosaurus bataar</i> , hadrosaurs, sauropods	Upper white beds of Khermeen Tsav (GRADZIŃSKI & JERZYKIEWICZ, 1972)	Contemporaneous with Nemegt Formation
<i>Gorgosaurus lancinator</i> , <i>Tarbosaurus bataar</i> , <i>Gallimimus bullatus</i> , <i>Deinocheirus mirificus</i> , <i>Saurolophus angustirostris</i> , turtles	Nemegt Formation (GRADZIŃSKI, 1970; MARTINSON <i>et al.</i> , 1969; GRADZIŃSKI & JERZYKIEWICZ, 1972)	Upper Campanian or Lower Maastrichtian (MARYAŃSKA & OSMÓLSKA, 1975) Maastrichtian (MARTINSON, 1975)
<i>Tarbosaurus bataar</i> , <i>Gallimimus bullatus</i> , <i>Gorgosaurus novõjilovi</i> , <i>Therizinosaurus cheloniformis</i> , <i>Nemegtosaurus mongoliensis</i> , <i>Saurolophus angustirostris</i> , <i>Prenocephale prenes</i> , <i>Homalocephale calathocercos</i> , <i>Paraligator ancestralis</i>	Nemegt Formation (GRADZIŃSKI, 1970; MARTINSON <i>et al.</i> , 1969; GRADZIŃSKI & JERZYKIEWICZ, 1972)	Upper Campanian or Lower Maastrichtian (MARYAŃSKA & OSMÓLSKA, 1975) Maastrichtian (MARTINSON, 1975)
<i>Bagaceratops rozhdestvenskyi</i> , small therapods, oviraptors, <i>Cherminisaurus kozlowskii</i> , <i>Erdenetesaurus robinsoni</i> , <i>Darchansaurus estesi</i> , <i>Macrocephalosaurus gilmorei</i> and other lizards. <i>Djadochtatherium catapsaloides</i> , <i>Nemegtbaatar gobiensis</i> , <i>Barunlestes butleri</i> , <i>Asioryctes nemegtensis</i> , <i>Deltatheridium pretrituberculare tardum</i> and other mammals	Red beds of Khermeen Tsav (GRADZIŃSKI & JERZYKIEWICZ, 1972) Khermeen Tsav formation (KIELAN-JAWOROWSKA, 1975a)	Contemporaneous with Barun Goyot Formation (KIELAN-JAWOROWSKA, 1975a)
? <i>Protoceratops kozlowskii</i> , <i>Tylocephale gilmorei</i> , <i>Velociraptor</i> sp., carnosaur indet., sauropod indet., <i>Zangerlia testudinimorpha</i> , <i>Gobipterix minuta</i> , <i>Naransaurus chulsanensis</i> , <i>Macrocephalosaurus</i> and other lizards, <i>Djadochtatherium catapsaloides</i> , <i>Nemegtbaatar gobiensis</i> , <i>Barunlestes butleri</i> , <i>Asioryctes nemegetensis</i> and other mammals	Barun Goyot Formation (MARTINSON <i>et al.</i> , 1969; GRADZIŃSKI & JERZYKIEWICZ, 1974)	Upper Santonian — Campanian (MARTINSON, 1973) ? Middle Campanian (KIELAN-JAWOROWSKA, 1974b, 1975a, b)
—	—	? Contemporaneous with Djadokhta Formation
carnosaurs, sauropods turtles	unnamed formation (TVERDOCHLEBOV and TSYBIN, 1974) Barun Goyot svita (SHUVALOV, 1975)	? Contemporaneous with Djadokhta Formation
<i>Protoceratops andrewsi</i> , <i>Velociraptor mongoliensis</i> , <i>Sauronithoides mongoliensis</i> , <i>Oviraptor philoceratops</i> , Hadrosauridae indet., <i>Shamosuchus ajadochtaensis</i> , <i>Gobiosuchus kielanae</i> , <i>Adamisaurus magnidentatus</i> , <i>Macrocephalosaurus ferrugineus</i> and other lizards, <i>Djadochtatherium matthewi</i> , <i>Kryptobaatar dashevegi</i> , <i>Deltatheridium pretrituberculare pretrituberculare</i> , <i>Zalambdalestes lechei</i> and other mammals	Diadokhta Formation (BERKEY & MORRIS, 1927) LEFELD, 1972) Barun Goyot svita (SHUVALOV, 1975; SOCHAVA, 1975)	Upper Santonian-Campanian (Rozhdestvensky, 1971) ? Santonian (KIELAN-JAWOROWSKA 1974b) Turonian-Lower Senonian (SOCHAVA, 1975) Campanian-Maastrichtian (SHUVALOV 1975)
<i>Aralosaurus tuberifrons</i> , carnosaur, sauropods, turtles, <i>Kansajsuchus borealis</i>	Beleutinska svita (ROZHDESTVENSKY, 1964)	Turonian (ROZHDESTVENSKY, 1974)
<i>Jaxartosaurus aralensis</i> , theropods, sauropods	Beleutinska svita (ROZHDESTVENSKY, 1971)	Coniacian (ROZHDESTVENSKY, 1974)

Identification		Museum cat. no	Locality (for explanation of numbers see Text-fig. 1)
original	in this paper		
Ankylosauria (ROZHDESTVENSKY, 1953)	ankylosaurs	PIN, no catalogue number	Djara-Khuduk (25)
<i>Heishansaurus pachycephalus</i> BOHLIN (BOHLIN, 1953)	<i>nomen dubium</i> ankylosaurid	Inst. Vert. Paleont., Peking, no catalogue number	Chia-yü-kuan (13)
Nodosauridae gen. et sp. indet. (BOHLIN, 1953)	ankylosaurid	Inst. Vert. Paleont., Peking, no catalogue number	Tsondolein-Khuduk (17)
<i>Syrmosaurus disparoserratus</i> MALEEV (MALEEV, 1952)	<i>Talarurus disparoserratus</i> (MALEEV)	PIN 554 holotype	Sheeregeen Gashoon (7)
		ZPAL MgD-I/115	
<i>Talarurus plicatospineus</i> (MALEEV, 1952)	<i>Talarurus plicatospineus</i> MALEEV	PIN 557, holotype PIN 557-3	Bayn Shireh (9)
—		PIN, undescribed specimen, no catalogue number	Baga Tarjach (10)
dinosaur ex group <i>Ankylosaurus</i> (SHUVALOV, 1976)		PIN, undescribed specimen, no catalogue number	Bayshin Tsav (11)
Nodosauridae gen. et sp. indet. (GILMORE, 1933)	ankylosaurs	AMNH 6367	Iren Dabasu (19)
Ankylosaurs (ROZHDESTVENSKY, 1961)	ankylosaurs	Peking, undescribed specimen from Soviet-Chinese Exped.	region Maortu (16)
Nodosauridae gen. et sp. indet. (CHENG <i>et al.</i> , 1973)	ankylosaurs	China (?), no catalogue number	Nanhsiung (27)
<i>Sauroplices scutiger</i> BOHLIN (BOHLIN, 1953)	<i>Sauroplices scutiger</i> BOHLIN	Inst. Vert. Paleont., Peking, no catalogue number	Tebch (18)
ankylosaur (KRAMARENKO, 1974)	(?) ankylosaurid (see p. 94)	PIN, undescribed specimen, no catalogue number	Khovboor (8)
ankylosaurs (KURZANOV & KALANDADZE, 1974)	?ankylosaurid	PIN, no catalogue number	Khuren Dukh (20)
ankylosaurs (ROZHDESTVENSKY, 1973)	ankylosaurid	PIN, undescribed specimen, no catalogue number	Kempenday (28)
Nodosauridae gen. et sp. indet. (GILMORE, 1933)	ankylosaur	?	Layang (26)
<i>Peishansaurus philemys</i> BOHLIN (BOHLIN, 1953)	<i>nomen dubium</i> ?ankylosaur	Inst. Vert. Paleont., Peking, no catalogue number	Ehr-chiawutung (15)

Associated vertebrate fauna	Formation and/or other stratigraphic data	Presumable age
<i>Itemirus medullaris</i> hadrosaurs, ornithomimids, turtles, <i>Kansajsuchus borealis</i>	see ROZHDESTVENSKY, 1964 Beleutinska svita (EFIMOV, 1975)	Turonian (ROZHDESTVENSKY, 1964)
<i>Microceratops sulcidens</i> , <i>Chiayüsauros lacustris</i> , <i>Chiayüsuchus cingulatus</i> , turtles	—	possibly older than the Djadokhta Formation (MARYAŃSKA & OSMÓLSKA, 1975)
<i>Microceratops gobiensis</i> , " <i>Stegoceras</i> " <i>bexelli</i>	—	older than the Djadokhta Formation (MARYAŃSKA & OSMÓLSKA, 1975)
<i>Microceratops gobiensis</i> , ornithomimid indet., hadrosaurs indet.	Bayn -Sihreh svita (SHUVALOV, 1975)	Upper Cenomanian-Lower Santonian (MARTINSON, 1975; SHUVALOV, 1975) older than the Djadokhta Formation (MARYAŃSKA & OSMÓLSKA, 1975)
hadrosaurs, turtles	Bayn Shireh svita (BARSBOLD, 1972; MARTINSON, 1973)	Upper Cenomanian-Lower Santonian (MARTINSON, 1973)
	Bayn Shireh svita (KHAND & STANKEVITCH, 1975)	Upper Cenomanian-Lower Santonian (MARTINSON, 1975)
hadrosaurs, theropods, <i>Basilemys orientalis</i>	Bayn Shireh or Barun Goyot svita see SHUVALOV, 1976	Upper Cenomanian-Lower Santonian (MARTINSON, 1975) Santonian-Campanian (SHUVALOV, 1976)
<i>Bactrosaurus johnsoni</i> , <i>Alectrosaurus olseni</i> , <i>Archornithomimus asiaticus</i>	Iren Dabasu Formation (GILMORE, 1933)	Cenomanian (ROZHDESTVENSKY, 1977)
sauropods, hadrosaurs		Cenomanian (ROZHDESTVENSKY, 1961)
sauropods, carnosaurs, coelurids	Upper part of Nanhsiung Formation (CHENG <i>et al.</i> , 1973)	Upper Cretaceous (CHENG <i>et al.</i> , 1973)
<i>Psittacosaurus mongoliensis</i> , <i>Prodeinodon</i> sp.	—	Lower Cretaceous
<i>Psittacosaurus mongoliensis</i> , <i>Changaiemys hoburensis</i> , <i>Mongolemys</i> sp. <i>Kielantherium gobiensis</i> and other not described mammals	see KALANDADZE and KURZANOV, 1974 and SHUVALOV, 1974	Lower Cretaceous: Aptian-Albian (SHUVALOV, 1974)
<i>Psittacosaurus</i> sp., <i>Iguanodon orientalis</i> , <i>Thoiria namsarai</i> , <i>Changaiemys hoburensis</i>	see SHUVALOV, 1974 and NOVODVORSKA, 1974	Lower Cretaceous: Neokomian (ROZHDESTVENSKY, 1977) Aptian-Albian (SHUVALOV, 1974)
	Sangarska svita (ROZHDESTVENSKY, 1973)	Lower Cretaceous: Neocomian (ROZHDESTVENSKY, 1973)
?	?	Cretaceous
?	?	Cretaceous

Identification		Museum cat. no	Locality (for explanation of numbers see Text-fig. 1)
original	in this paper		
<i>Stegosaurides excavatus</i> BOHLIN (BOHLIN, 1953)	<i>nomen dubium</i> ?ankylosaur	Inst. Vert. Paleont., Peking, no catalogue number	Hui-hui-pu (14)
<i>Lametasaurus indicus</i> MATLEY (MATLEY, 1923)	<i>nomen dubium</i> part ?ankylosaur	?	
<i>Brachypodosaurus gravis</i> CHAKRAVARTI (CHAKRAVARTI, 1934)	<i>nomen dubium</i> ?ankylosaur	Geol. Mus. Benares Hindu University, V. 9	Jubbulpore (22)
	ankylosaur	AMNH 1959	

* Quoted after: BOHLIN, 1953; DASZHEVEG, 1975; EFIMOV, 1975*a*, 1975*b*; ELŻANOWSKI, 1974; GILMORE, 1933*a*; 1943; KIELAN-JOWOROWSKA, 1969, 1970, 1974*b*, 1975*a*, 1975*b*; KONZHUKOVA, 1954; KURZANOV 1976; MALEEV, 1952*a*, 1952*b*, 1965*b*, 1956, 1955; MARYAŃSKA & OSMÓLSKA, 1974, 1975; MLYNARSKI, 1972; MOOK, 1924; NOWIŃSKI, 1971; OSBORN, 1924; OSMÓLSKA, 1972; OSMÓLSKA & RONIEWICZ, 1970, OSMÓLSKA *et al.*, 1972; ROZHDESTVENSKY 1955, 1957, 1968; SULIMSKI, 1972, 1975; YOUNG, 1958, 1935.

of Palaeontology and Stratigraphy in Ulan Bator. The collection of the Palaeontological Institute of the USSR Academy of Sciences in Moscow served as supplementary material. Some conclusions concerning the development of ankylosaurs in Asia have been based on the new material collected by the Soviet-Mongolian expeditions. The latter material is housed in the Palaeontological Institute in Moscow as will be studied by Soviet palaeontologists. Publication of some data on this collection is done here through kind permission of Dr. A. K. ROZHDESTVENSKY.

Abbreviations used for Institutions:

- AMNH — American Museum of Natural History, New York.
 BM (NH) — British Museum (Natural History), London.
 GI SPS — Geological Institute Section of Palaeontology and Stratigraphy, the Academy of Sciences of the Mongolian People's Republic, Ulan Bator.
 NMC — National Museum of Canada, Ottawa.
 NMNH — National Museum of Natural History, Washington.
 PIN — Palaeontological Institute of the USSR Academy of Sciences, Moscow.
 ZPAL — Institute of Paleobiology (Zakład Paleobiologii) of the Polish Academy of Sciences, Warsaw.

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Associated vertebrate fauna	Formation and/or other stratigraphic data	Presumable age
sauropods, theropods	?	Cretaceous
sauropods, carnosaurs	Lameta Beds	Upper Cretaceous

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MATERIAL

Talarurus plicatospineus MALEEV

PIN 557 — fragments of postcranial skeletons of at least six individuals and two fragments of skulls. On these specimens MALEEV (1952) distinguished *Talarurus plicatospineus*; Bayn Shireh, Eastern Mongolia, Upper Cretaceous, Bayn Shireh svita Cenomanian — Lower Santonian according to BARSBOLD, 1972.

PIN, no catalogue number — undescribed incomplete skull with cranial roof, occipital part and brain case; Bayshin Tsav, Eastern Mongolia, Upper Cretaceous, Bayn Shireh svita.

PIN, no catalogue number — undescribed fragment of maxilla with eight teeth; Baga Tarjach, Eastern Mongolia, Upper Cretaceous, Bayn Shireh svita.

Talarurus disparoserratus (MALEEV)

PIN 554/1—2 — fragments of right maxilla and PIN 554/1—1 — left maxilla of the same specimen, described by MALEEV (1952*b*) as a holotype of *Syrmosaurus disparoserratus*; Sheeregeen Gashoon, Mongolia, Upper Cretaceous, Bayn Shireh svita.

PIN 554/2—1 — basicranial fragment with occipital condyle, basioccipital and basisphenoid. Same "formation" and locality.

ZPAL MgD-I/115 — right ilium. Same "formation" and locality.

Pinacosaurus grangeri GILMORE

ZPAL MgD-II/1 — almost complete postcranial skeleton with skull of a young individual; Dayn Dzak, Mongolia, Upper Cretaceous, Djadokhta Formation, ?Santonian according to KIELAN-JAWOROWSKA, 1974*a*, 1974*b* (GRADZIŃSKI *et al.*, 1968, text-fig. 29, no 5; MARYAŃSKA, 1971).

ZPAL MgD-II/9 — fragments of a shoulder girdle, almost complete manus, pelvic girdle, sacral

and caudal vertebrae, hind limb (GRADZIŃSKI *et al.*, 1969, text-fig. 29, no 6). Same formation and locality.

ZPAL MgD-II/31 — fragments of shoulder girdle, dorsal, sacral and caudal vertebrae, pelvic girdle, hind limbs, fragments of an armour. Same formation and locality.

ZPAL MgD-II/32 — fragments of caudal portion of vertebral column. Same formation and locality.

ZPAL MgD-II/2 — fragments of an armour. Same formation and locality.

PIN 614 — almost complete skeleton without skull, specimen described by MALEEV (1952) as a holotype of *Syrmosaurus viminicaudus*. Same formation and locality.

PIN, no catalogue number — undescribed fragments of skulls and postcranial skeletons of several individuals of various individual age (TVERDOCHLEBOV & TSYBIN, 1974). Alag Teg, Mongolia, Upper Cretaceous, unnamed "formation", stratigraphic equivalent of Djadokhta Formation.

Saichania chulsanensis gen. n., sp. n.

GI SPS 100/151 — skull and anterior part of postcranial skeleton: complete cervical and dorsal vertebrae, shoulder girdle, forelimb and armour in natural arrangements. Khulsan, Mongolia, Upper Cretaceous, Barun Goyot Formation, ?Middle Campanian according to KIELAN-JAWOROWSKA, 1974*b* (GRADZIŃSKI & JERZYKIEWICZ 1972, text-fig. 4, no 11).

ZPAL MgD-I/114 — fragment of skull roof and armour. Khermeen Tsav II, Mongolia, Upper Cretaceous, Khermeen Tsav "formation" of KIELAN-JAWOROWSKA, 1975*b*, stratigraphic equivalent of Barun Goyot Formation.

PIN, no catalogue number — undescribed, almost complete postcranial skeleton with skull. Same "formation" and locality.

Tarchia kielanae gen. n., sp. n.

ZPAL MgD-I/111 — incomplete skull with skull roof, occipital part and brain case. Khulsan, Mongolia, Upper Cretaceous, Barun Goyot Formation (?Middle Campanian according to KIELAN-JAWOROWSKA, 1974*b*) GRADZIŃSKI & JERZYKIEWICZ, 1972, text-fig. 4, no. 6.

"Dyoplosaurus" giganteus MALEEV

ZPAL MgD-I/43 — caudal portion of vertebral column with tail-club. Altan Ula IV, Mongolia, Upper Cretaceous, Nemegt Formation, ?Upper Campanian — Lower Maastrichtian (GRADZIŃSKI *et al.*, 1968, text-fig. 4, no 5; MARYAŃSKA, 1970). This specimen is now housed in GI SPS in Ulan Bator.

ZPAL MgD-I/42 — caudal portion of vertebral column with tail-club and fragments of armour. Same formation and locality. (GRADZIŃSKI *et al.*, 1969, text-fig. 4, no 7; MARYAŃSKA, 1970).

ZPAL MgD-I/49 — right humerus. Same formation and locality (GRADZIŃSKI *et al.*, 1969, text-fig. 4, no 3).

ZPAL MgD-I/113 — incomplete postcranial skeleton without skull. Altan Ula III, Mongolia, Upper Cretaceous, Nemegt Formation.

PIN 551—29 — free caudal vertebrae, metacarpals and phalanges of manus, fragments of armour. This specimen has been described by MALEEV (1956) as holotype of *Dyoplosaurus giganteus*. Nemegt, Mongolia, Upper Cretaceous, Nemegt Formation.

PIN, no catalogue number — an undescribed skeleton with skull from upper white beds of Khermeen Tsav I, Mongolia, Upper Cretaceous, stratigraphic equivalent of Nemegt Formation.

Table 4

Measurements of the pectoral girdle and fore limb (in mm)

	<i>Talarurus plicatospineus</i>		<i>Pinacosaurus grangeri</i>		<i>Saichania chulsanensis</i>
	PIN 557-20 left	PIN 557-91 left	PIN 614 left	ZPAL MgD-II/1 left	GI SPS 100/151 right
Scapulocoracoid:					
total length of scapulocoracoid	600	ca 550	580	ca 300	580
length of scapula	430	ca 380	390	ca 190	400
proximal width of scapula	122	180	90	50	75
distal width of scapula	ca 150	150	ca 80	—	157
Humerus					
	PIN 557-71 left	PIN 557-91 left	PIN 614 left	ZPAL MgD-II/1 left	GI SPS 100/151 left
length	300	320	290	ca 160	300
maximum width of proximal end	ca 135	150	135	ca 75	212
maximum width of distal end	137	150	125	ca 65	163
maximum width of shaft	53	60	51	31	73
Ulna					
	PIN 557-80 left	PIN 557-91 left	PIN 614 left		GI SPS 100/151 left
length	215	220	ca 210		210
maximum width of proximal end	81	120	83		125
maximum width of distal end	67	57	48		78
maximum width of shaft	33	43	32		50
Radius					
	PIN 557-85 left	PIN 557-91 left	PIN 614 right	ZPAL MgD-II/1 left	GI SPS 100/151 left
length	188	171	174		182
maximum width of proximal end	77	64	62	39	84
maximum width of distal end	75	73	60	—	81
maximum width of shaft	37	33	30	18	41

Table 5

Measurements of metacarpal bones (in mm)

	<i>Talarurus plicatospineus</i>	<i>Pinacosaurus grangeri</i>	<i>Saichania chulsanensis</i>
	(MALEEY, 1956) PIN 557-3	ZPAL MgD-II/9	GI SPS 100/151
Length of metacarpals:			
I	59	34	51
II	65	35	46
III	67	37	56
IV	—	ca 33	58
V	—	—	49
Maximum width of proximal end of the metacarpals:			
I	30	22	39
II	41	23	41
III	41	22	41
IV	—	19	43
V	—	18	38
Maximum width of distal ends of the metacarpals:			
I	35	19	45
II	32	17	40
III	33	14	42
IV	28	—	35
V	—	—	28

Table 6

Measurements of metatarsal bones (in mm)

	<i>Talarurus plicatospineus</i> (MALEEV, 1956) PIN 557-3	<i>Pinacosaurus grangeri</i> ZPAL MgD-II/9	" <i>Dyoplosaurus</i> " <i>giganteus</i> (MALEEV, 1956) PIN 551-29
Length of the metatarsals:			
I	—	29	—
II	81	ca 45	80
III	89	42	70
IV	87	—	—
Maximum width of the metatarsals:			
I	—	23	—
II	57	ca 25	70
III	40	ca 27	95
IV	47	—	35
Maximum width of the metatarsals:			
I	39	24	—
II	67	—	74
III	53	22	60
IV	51	—	55

GENERAL REMARKS ON SYSTEMATICS

The systematics of Ankylosauria proposed by COOMBS (MS) is here applied. Two families are distinguished: the Ankylosauridae (including Ankylosauridae BROWN, 1908; Ankylosaurinae NOPCSA, 1923; Syrmosauridae MALEEV, 1952) and the Nodosauridae (including among others Nodosauridae MARSH, 1890; Edmontoniinae RUSSELL, 1940; Acanthopholididae NOPCSA, 1902; Panoplosaurinae NOPCSA, 1923). COOMBS' conclusion that the range of the Nodosauridae is restricted to Europe and North America is here confirmed. A comparison of the Asiatic and North American Ankylosauridae shows that *Talarurus*, *Pinacosaurus* and *Saichania* are less advanced in some respects (e. g. degree of development of cranial sinuses and tooth morphology) than the North American *Euoplocephalus* and *Ankylosaurus*, but some Mongolian Ankylosauridae show characters unknown in American forms. These are: completely ventral orientation of the occipital condyle and associated special structure of the atlas; very strongly developed ventral armour and sternal complex. Such differences make it necessary to supplement COOMBS' (*l.c.*) diagnosis of the Ankylosauridae. COOMBS regards as valid only two ankylosaurid genera in North America: *Euoplocephalus* and *Ankylosaurus*. He regards *Dyoplosaurus*, *Scolosaurus* and *Anodontosaurus* as synonyms of *Euoplocephalus*. I do not discuss this problem, because I have not had an opportunity to study North American specimens. On the basis of my studies of described specimens of *Talarurus plicatospineus* (MALEEV, 1952*a, b*, 1956) and of undescribed specimens of this genus in the PIN collections I consider *Talarurus* as a valid genus not congeneric with *Pinacosaurus* as suggested by COOMBS (MS). The new genera *Saichana* and *Tarchia* described in this paper, the generic diversity of *Talarurus* and *Pinacosaurus* and the validity of *Sauroplices* (regarded by COOMBS as *nomen dubium*) all demonstrate greater diversification of the Ankylosauridae in Asia than in North America.

Identification of some ankylosaur species described by BOHLIN (1953) from China is difficult. Very incomplete and badly preserved material of *Stegosaurides excavatus* and *Peishansaurus philemys* is the main basis for the view that these two species are *nomina dubia*. There is no certainty about their affiliation to Ankylosauria. Assignment of *Sauroplices scutiger* (BOHLIN,

1953) to the Ankylosauria is unquestionable. Newly discovered sites with the ankylosaurids, or related forms, at Khovboor and (?) Khuren Dukh in Mongolia and Kempenday in USSR confirm the occurrence of this group in Asia in Early Cretaceous. A characteristic ornamentation of the armour of *Sauroplices scutiger* allows one to distinguish it from other ankylosaurid species. *Heishansaurus pachycephalus* (BOHLIN, 1953) must be regarded as *nomen dubium*. Its teeth are larger than those of all known ankylosaurids which makes assignment to the Ankylosauridae difficult. On the basis of that character it may be supposed that *Heishansaurus pachycephalus* is the only representative of the Nodosauridae in Asia, but the structure of the occipital condyle suggests its affinity to the Ankylosauridae, and existence of a W-shaped folding of the cingulum on some teeth is reminiscent of *Talarurus*.

Syrmosaurus (MALEEVE, 1952a) needs special discussion. Its type species *Syrmosaurus viminicaudus* is a junior synonym of *Pinacosaurus grangeri* GILMORE (MARYAŃSKA, 1971). New materials allow one to assign the second species — *Syrmosaurus disparoserratus* MALEEVE to *Talarurus* (see also p. 99). The third representative of *Syrmosaurus* — *Syrmosaurus* sp. belongs to *Psittacosaurus* (ROZHDESTVENSKY, 1955). It follows that there is no basis for maintaining the genus *Syrmosaurus* or the family Syrmosauridae. The generic affinity of *Dyoplosaurus giganteus* MALEEVE is an open question. Coombs (MS), regarding *Dyoplosaurus* as a synonym of *Euoplocephalus*, identifies *D. giganteus* as *Euoplocephalus giganteus*. The material on which MALEEVE (1956) described this species does not furnish evidence in favour of assigning it to the North American *Dyoplosaurus*. On the basis of the materials collected by the Polish-Mongolian expeditions (ZPAL MgD/I/43, 42, 113) assignment of *Dyoplosaurus giganteus* to *Talarurus*, *Saichania* or *Pinacosaurus* is excluded. An almost complete skeleton of the species, with skull, collected by the Soviet-Mongolian expeditions of 1972, is housed at the PIN in Moscow, and will be described by Soviet palaeontologists. Occipital and basicranial parts of that specimens have a structure similar to *Tarchia* (nov.) Until a detailed study of the above mentioned PIN specimen is done the name "*Dyoplosaurus*" *giganteus* is here used.

Undescribed ankylosaurs from the Early Cretaceous at Khovboor and Kempenday housed at the PIN in Moscow are tentatively assigned to the Ankylosauridae. A detailed examination will determine its assignment either to the Ankylosauridae or to a new primitive ankylosaurian family from which the proper Ankylosauridae are derived.

CHECK-LIST OF ASIAN ANKYLOSAURIA

Family Ankylosauridae BROWN, 1908

Early Cretaceous:

Sauroplices scutiger BOHLIN, 1953

Unnamed and undescribed specimen from Khovboor in PIN collection.

Late Cretaceous:

Talarurus plicatospineus MALEEVE, 1952

Talarurus disparoserratus (MALEEVE), 1952

Pinacosaurus grangeri GILMORE, 1933

Saichania chulsanensis gen. nov., sp. n.

Tarchia kielanae gen. n., sp. n.

Species of erroneous generic assignment:

"*Dyoplosaurus*" *giganteus* MALEEVE, 1956

Heishansaurus pachycephalus BOHLIN, 1953

Species of doubtful validity: *Peishansaurus philemys* BOHLIN, 1953; *Stegosaurides excavatus* BOHLIN, 1953.

DESCRIPTIONS

Suborder **Ankylosauria** OSBORN, 1923Family **Ankylosauridae** BROWN, 1908

Diagnosis (partly based on COOMBS, MS, emended). — Ankylosaurs with broad skulls, width nearly equal to or surpassing length more or less triangular in dorsal view; back wide and squarely truncated; dorsal surface of skull covered by a large number of grooves which show little bilateral symmetry and which remain distinct in large individuals. Posterolateral corners of skull and nasal region with coossified dermal plates, the former tend to protrude forming horn-like, pyramidal projections; greatest width of skull either across the tips of the posterolateral "horns" or across the distal ends of the jugal projections; nostrils variable, elongate or suboval slits openings facing strongly anteriorly (*Pinacosaurus*, *Saichania*, *Euoplocephalus*) or small circular openings facing laterally (*Ankylosaurus*); nostrils divided by a septum which separates the true respiratory passage from an opening into an accessory cranial sinus; respiratory passage within skull associated with paired sinuses; occipital condyle fitted closely against the brain case, and directed postero-ventrally or ventrally; lateral temporal fenestra and quadrate cotylus hidden in lateral view by a postero-ventral projection of the jugal and coossified dermal plate; quadrate cotylus well separated from the quadratojugal; lateral extremities of paroccipital processes do not extend beyond the posterior margin of the skull roof; epipterygoid occasionally present; ectopterygoid and adjacent mandibular ramus of pterygoid directed laterally; teeth small, basal cingulum small or absent, but base of tooth swollen; distal caudal vertebrae with elongate interlocking zygapophyses and long interlocking haemal arches; large terminal tail-club of dermal armour, often associated with a mass of ossified tendons; scapular spine located on extreme anterior edge of scapular blade; coracoid small relatively to scapula; capitulum of humerus ovate, and very slightly elevated above the shaft; ischium nearly straight or with slight anterior curvature; fourth trochanter distal to femoral mid-length; keeled armour plates usually deeply excavated on medial surface; large conical spines rare or absent.

Genus *Talarurus* MALEEV, 1952

Type species: Talarurus plicatospineus MALEEV, 1952a.

Distribution: Upper Cretaceous of Asia, Bayn Shireh "formation" (= svita).

Included species: type species and *Talarurus disparoserratus* (MALEEV, 1952a).

Diagnosis (partly based on MALEEV, 1953, emended). — Ankylosaurid up to 5—6 m long, skull small, relatively long and narrow, parietal posteriorly incurved along the medial line making occipital condyle and supraoccipital partly visible in dorsal view; articulating surface of occipital condyle variously developed, always directed ventro-posteriorly; exoccipital high, perpendicular to the skull roof; maxillary teeth with more or less developed cingulum-like thickening always cut by W-shaped furrows on external side; curvature of tooth row small; horizontal palatal shelf in posterior position; weakly developed horizontal maxillary shelf bordering internal nares anteriorly; separate cranial openings for exists or nerves situated posteriorly to foramen ovale; trunk relatively weakly dorso-ventrally flattened; manus pentadactyl, pes tetradactyl.

Remarks. — COOMBS' (MS) suggestion to regard *Talarurus* as synonym of *Euoplocephalus* is unacceptable because of essential anatomic differences and different proportion of the two genera. *Talarurus* differs from *Euoplocephalus* in different shape of the skull, in the structure of the palatal region and in having a tetradactyl pes.

The reasons for assignment of *Syrmosaurus disparoserratus* to *Talarurus* are given on p. 101. In addition to *Talarurus plicatospineus* and *T. disparoserratus*, the only form showing presence

of W-shaped folding of cingulum on maxillary teeth is *Heishansaurus pachycephalus* BOHLIN (1953); however, material of *H. pachycephalus* is too fragmentary to defend assignment to *Talarurus*.

Talarurus plicatospineus MALEEV, 1952

(pl. 26, fig. 2; text-fig. 11A)

1952 *Talarurus plicatospineus* sp.n.; MALEEV, p. 273, text-figs 1, 2 and 3.

1956 *Talarurus plicatospineus* MALEEV; MALEEV, p. 56, text-figs 1—32.

Holotype: fragmentary skull with posterior part of skull roof, occipital region and basicranium. PIN 557—91, MALEEV, 1952*b*, p. 273; MALEEV, 1956, p. 56, figs 1—3.

Type horizon: Upper Cretaceous, Bayn Shireh "formation" (= svita).

Type locality: Bayn Shireh, Eastern Mongolia.

Revised diagnosis. — *Talarurus* with occipital condyle ventro-posteriorly oriented, visible in both lateral and dorsal views; condyle articulating surface narrow, crescent-shaped; cingulum-like swelling of maxillary teeth better developed lingually than labially; maxillary teeth with weakly marked W-shaped folding of cingulum labially; pectoral glenoid deep, short; humeral head situated dorso-terminally; characteristic furrow-rib ornamentation of armour elements; tail-club weakly developed.

Material. — see p. 93.

Measurements. — see tables 4, 5 and 6.

Remarks. — MALEEV (1956, p. 56) designated "a fragment of the skull (posterior part of the skull roof, occipital region, basicranium) and postcranial skeleton" as the type specimen of *Talarurus plicatospineus* (PIN 557). Examination of the rich bone material belonging to this species in the PIN collections shows that the specimen chosen as the type specimen of *T. plicatospineus* by MALEEV (1956) consists, in fact, of bones belonging to at least three individuals. Sorting of the bones into proper skeleton is impossible at the moment, so it seems appropriate to regard as the holotype only the skull fragment described and illustrated by MALEEV (1952*b*, p. 273; 1956, p. 56, figs 1—3, PIN 557—91).

The shape of the articular surface and the relatively strong backward shift of the occipital condyle distinguish *Talarurus plicatospineus* from *?T. disparoserratus* and from all other Upper Cretaceous ankylosaurids of Asia and North America. Detailed comparison of all skeletal elements of *T. plicatospineus* with other ankylosaurids is presented in the second part of this paper.

Distribution. — See table 1.

Talarurus disparoserratus (MALEEV), 1952

(pl. 26, fig. 1)

1952 *Syrmosaurus disparoserratus* sp.n.; MALEEV, p. 134.

1954 *Syrmosaurus disparoserratus* MALEEV; MALEEV, p. 162, fig. 15.

Holotype: two fragments of right maxilla (PIN 554/1—2) and left maxilla (PIN 554/1—1) of one individual.

Type horizon: Upper Cretaceous, Bayn Shireh "formation" (= svita).

Type locality: Sheergeen Gashoon, Southern Mongolia.

Revised diagnosis. — *Talarurus* with subspherical occipital condyle oriented ventro-posteriorly; maxillary teeth with strongly developed W-shaped folding of cingulum labially.

Material. — see p. 93.

Remarks. — MALEEV (1952*a*, fig. 15) erroneously identified maxillary fragment as belonging to mandibles. His fig. 15 (1954) shows not a right mandible but a left maxilla.

Despite the paucity of material, the fragments of maxilla and basicranium allow some

conclusions about the development of a secondary palate and the pattern of cranial nerve openings. The labial side of the maxilla is low along the whole tooth row with a slight posterior rise toward the palatinum. Therefore along almost the whole length of tooth row the palatal vacuities are laterally bordered by a vertical core of maxilla. The horizontal palatal shelf of the maxilla is very small. The poorly developed posterior shelf is opposite the posterior third of the tooth row. Lack of an anterior horizontal shelf of the maxilla proves that the secondary palate was weakly developed and the palatal vacuities were very large.

Assignment of this species to *Talarurus* is tentative because of incompleteness of the material and is based mainly on similarities in general basicranial pattern, on maxillary structure and on presence of folding of the cingulum. *T. disparoserratus* differs from *T. plicatospineus* in stronger cingulum development on maxillary teeth, in more distinct labial folding of the cingulum, and in shape and position of the articular surface of the occipital condyle. Considering *Syrmosaurus disparoserratus* as a synonym of *Pinacosaurus grangeri* as suggested by COOMBS (MS) seems completely unjustified. *Syrmosaurus* differs from *Pinacosaurus* in more primitive structure of the palate, different structure of the teeth, and different distribution of cranial nerve openings. The two genera occur in formations of different age. As *Talarurus* is the only ankylosaurid genus in Mongolia in which the nerves from IX to XII possess separate openings and this is the case also in *T. disparoserratus* (PIN 554/2—1), the assignment of *S. disparoserratus* to *Talarurus* seems to be justified.

Distribution. — See table 1.

Genus *Pinacosaurus* GILMORE, 1933

Type species: Pinacosaurus grangeri GILMORE.

Genus monotypic, diagnosis and distribution as for the type species.

Pinacosaurus grangeri GILMORE, 1933

(Pls. 19—26, text-figs 2, 3 and 11B)

1933 *Pinacosaurus grangeri* n.sp.; GILMORE, p. 3, figs 1—3.

1935 *Pinacosaurus ninghsiensis* n.sp.; YOUNG, p. 5, pls 1—3.

1952 *Syrmosaurus viminicaudus* n.sp.; MALEEV, p. 137, figs 1—3.

1954 *Syrmosaurus viminicaudus* MALEEV; MALEEV, p. 147, figs 1—4, 6, 10, 12, 13 (non figs 1, 5, 7—9, 11).

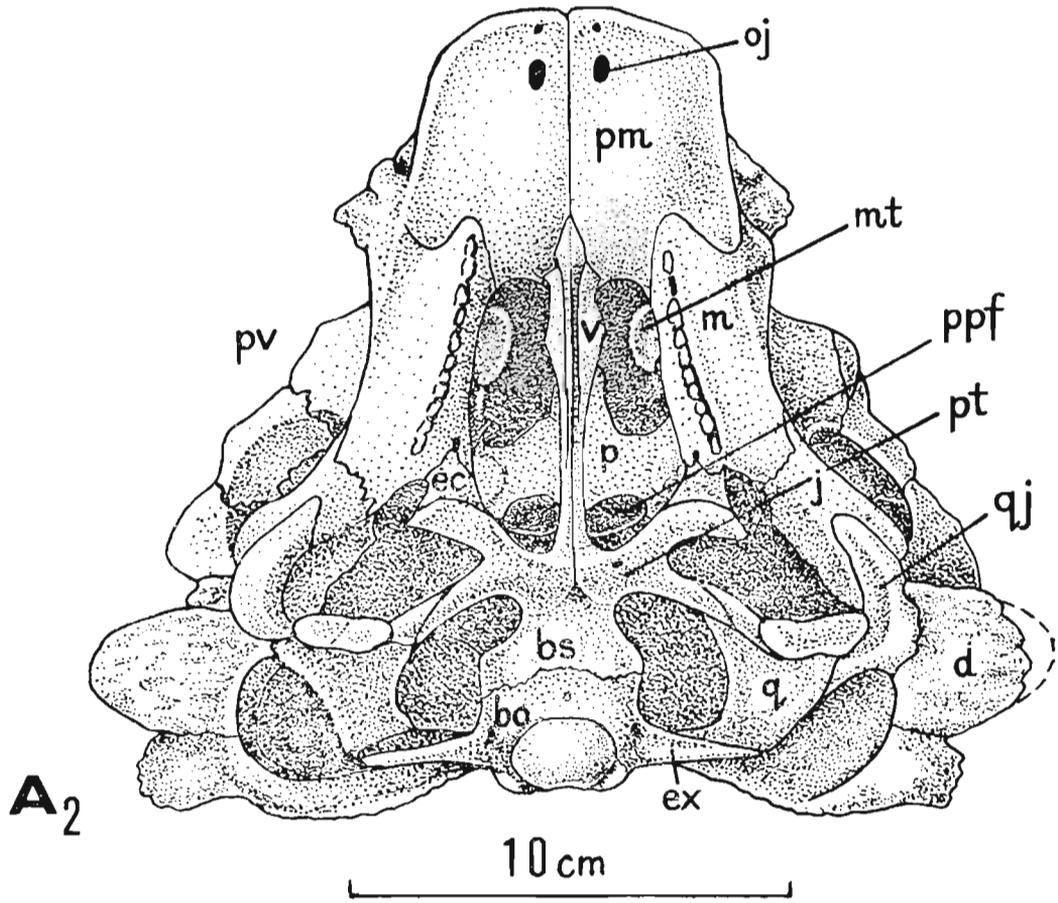
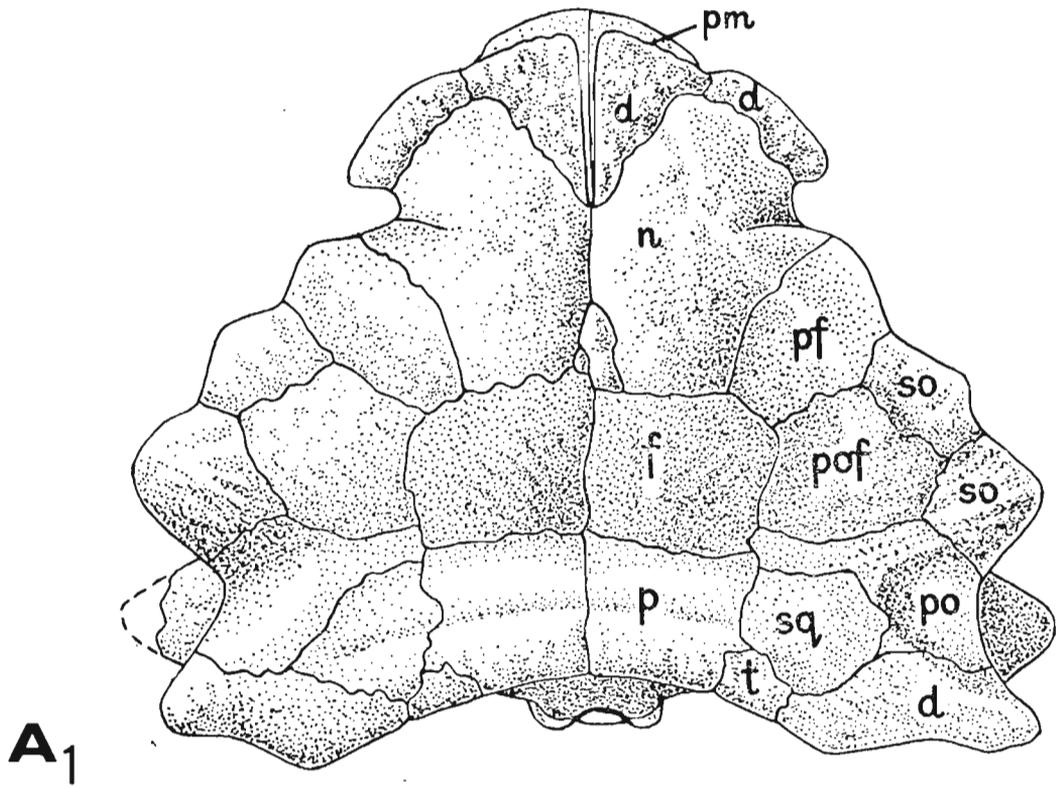
1971 *Pinacosaurus grangeri* GILMORE; MARYAŃSKA, p. 45, text-fig. 1, pls 6 and 7.

Holotype: AMNH 6523, crushed skull and jaws, atlas and axis vertebrae, and a few dermal bones.

Type horizon: Upper Cretaceous, Djadokhta Formation.

Type locality: Bayn Dzak (Shabarkh Usu), Gobi Desert, Mongolia.

Revised diagnosis. — Ankylosaur attaining 5 m in length; nostrils situated anteriorly, suboval, separated by horizontal premaxillary septum; septum separates a dorsal foramen leading to the respiratory passage, from a ventral foramen leading to the premaxillary sinus; young individuals show third foramen in nasal area situated laterally and leading to vast premaxillary sinus; premaxilla not completely covered by nasal or accessory dermal "plate", without ornamentation; subspherical occipital condyle oriented ventro-posteriorly; exoccipital slightly oblique to skull roof, causing occipital part of skull to be on same level as posterior margin of skull roof; quadrate not coossified with paroccipital process, slightly oblique anteriorly; mandibular cotylus of quadrate situated at level of posterior margin of orbit; width of premaxillary beak larger than distance between posteriormost maxillary teeth; in palatal region both anterior and posterior horizontal maxillary shelves poorly developed; palatinum relatively strongly developed anteriorly; maxillary and dentary teeth with labial cingulum and slight basal swelling lingually; orbits not completely closed; postcranial skeleton rather light, limb bones slender, manus pentadactyl, pes tetradactyl.



Material. — See p. 93-94.

Measurements. — See tables 2, 4, 5 and 6.

Remarks. — *Pinocosaurus grangeri* differs from all other ankylosaurids in postcranial structure, particularly in slenderness of the limbs. The description of *Syrmosaurus viminicaudus* as presented by MALEEV (1954) has been partly illustrated by drawings of bones belonging in fact to *Talarurus plicatospineus*: fig. 7 of MALEEV (*l.c.*) shows a scapula of *Talarurus plicatospineus* (PIN 557—20/1); fig. 8 — a humerus of the same species (PIN 557—97/1) but diminished 1/2, not 1/3 as stated in the caption; fig. 9 — radius (PIN 557—81/1) turned at 180° and ulna (PIN 557—101/1) of the same species. The remaining figures show bones of *S. viminicaudus* and only fig. 1 illustrating a tooth is incorrect, not resembling the original. The above errors pertain only to illustrations. MALEEV'S descriptions relate to bones of *S. viminicaudus* housed in the collections of the PIN. For a detailed comparison of the bones of postcranial skeleton see the section "Anatomy" of this paper.

A comparison of skulls of *P. grangeri* with those of *Talarurus plicatospineus* and *T. disparoserratus* reveals that the skull of *P. grangeri* is relatively shorter and broader, the bony palate is much stronger, teeth do not show a folding of cingulum, the occipital region does not protrude beyond the skull roof, and the openings of nerves IX—XII show a tendency to fusion. The study of the skull of a young individual of *Pinacosaurus grangeri* (ZPAL MgD-II/1) which is unusually well preserved, allowed me to recognize the presence of cranial structures previously unknown in Ankylosauria. These are discussed in detail in the section "Anatomy".

Distribution. — See table 1.

Genus *Saichania* nov.

Type species: Saichania chulsanensis sp.n.

Derivation of the name: after Mongolian "saichan" — beautiful.

Diagnosis. — Genus monotypic, diagnosis and distribution as for type species.

Saichania chulsanensis sp. n.

(pls 28—36, text-figs 4—8 and 11C)

Holotype: Skull with jaws and complete anterior part of postcranial skeleton, GI SPS 100/151.

Type horizon: Upper Cretaceous, Barun Goyot Formation.

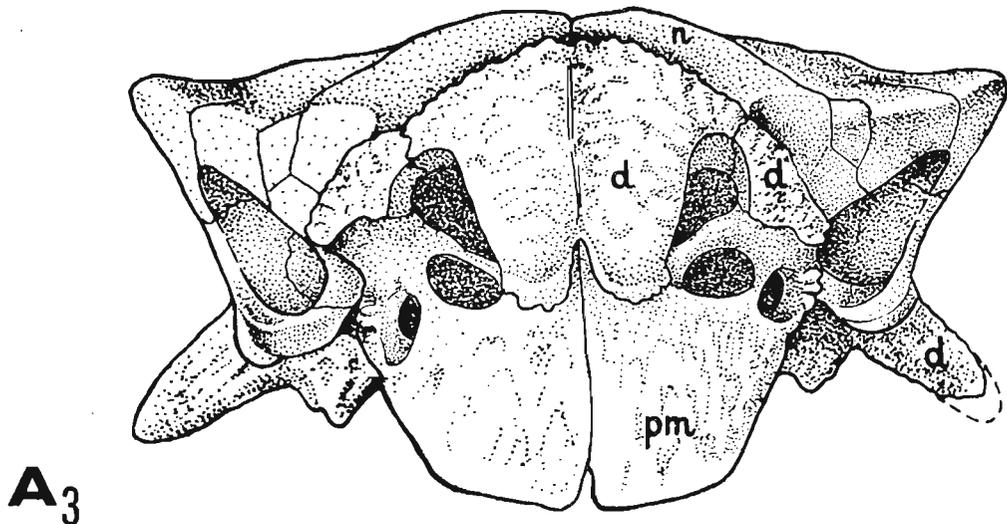
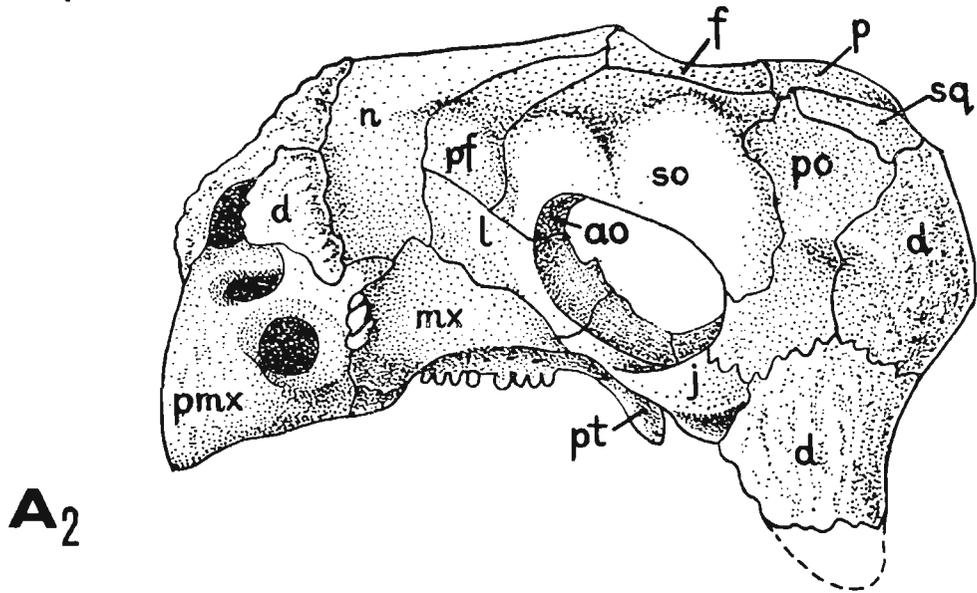
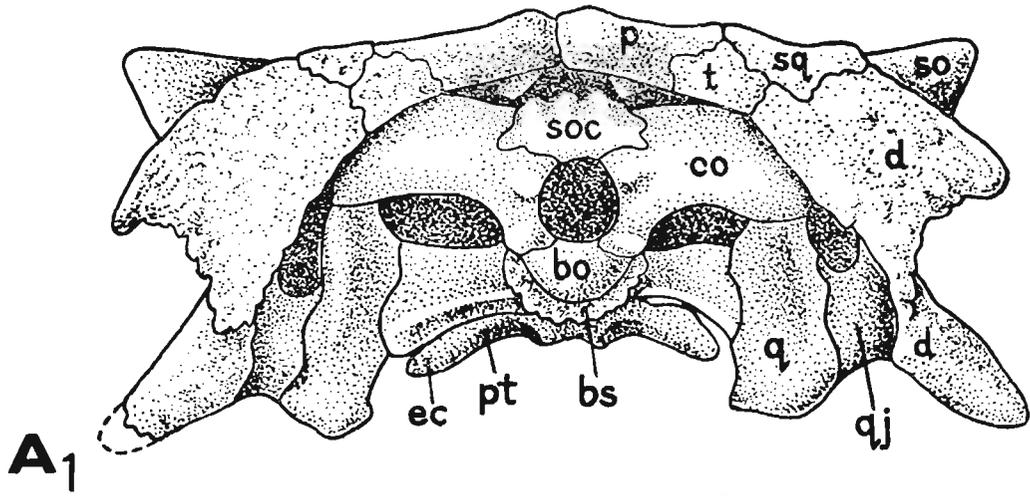
Type locality: Khulsan, Nemegt Basin, Gobi Desert, Mongolia.

Derivation of the name: after the type locality.

Diagnosis. — Ankylosaurid attaining 7 m in length; large, oval external nostrils situated terminally, divided by horizontal septum; septum separates large, suboval, dorsally situated foramen of true air passage from ventro-medially positioned passage leading to premaxillary sinus; premaxillary part of the snout relatively narrow; premaxillae partly covered by well developed secondary dermal plates; occipital condyle weakly convex, directed ventrally; epipterygoid present; exoccipital low, its dorsal part perpendicular to skull roof, its ventral

Fig. 2

Pinacosaurus grangeri GILMORE. The skull (ZPAL MgD-II/1) A_1 — in dorsal view, A_2 — in palatal view. Abbreviations: *bo* — basioccipital, *bs* — basisphenoid, *d* — secondary dermal bone, *ec* — ectopterygoid, *eo* — exoccipital, *cp* — epipterygoid, *f* — frontal, *fo* — fenestra ovalis, *ic* — internal carotid foramen, *j* — jugal, *l* — lacrimal, *ls* — laterosphenoid, *m* — maxilla, *mt* — maxilloturbinal, *n* — nasal, *oj* — supposed opening of Jacobson's organ, *or* — orbitosphenoid, *p* — parietal, *pa* — exit of palatine artery, *pf* — prefrontal, *pl* — palatine, *pm* — premaxilla, *po* — postorbital, *pof* — postfrontal, *pos* — postocular shelf, *ppf* — posterior palatal foramen, *pr* — prootic, *prs* — presphenoid, *pt* — pterygoid, *pv* — palatal vacuity, *q* — quadrate, *qj* — quadratojugal, *so* — supraorbital, *soc* — supraoccipital, *t* — "tabular" *v* — vomer, *vf* — vascular foramen, *vs* — venal sinus, I—XII exits of cranial nerves.



10 cm

part strongly deflected anteriorly; quadrate oblique, with mandibular cotylus at level of middle part of orbit; orbits anteriorly and posteriorly closed by partly neomorphic bones; skull roof overhanging occipital region; palatal region with strongly developed anterior and posterior maxillary shelves; main body of maxilla surrounds palatal vacuities over small area laterally; width of premaxillary beak almost equal to distance between posteriormost maxillary teeth; one opening for nerves IX—XII; atlas and axis fused; strongly developed secondary plate-like intercostal ossifications along latero-ventral part of the trunk; limb bones very massive, fore limb strongly flexed, manus pentadactyl.

Material. — See p. 94.

Measurements. — See tables 2—6.

Remarks. — *Saichania chulsanensis* sp. n. differs from *Pinacosaurus grangeri* by a more advanced development of accessory cranial sinuses and a much stronger ossification of the palatal region. In these characters it differs also from *Talarurus*. Other differences from *Talarurus* are: different structure of the occipital region and presence (in *Saichania*) of a single foramen for nerves IX—XII situated posterior to the foramen ovale.

The horizontal septum dividing the external nasal opening is depressed in *Saichania*, but in *Pinacosaurus grangeri* it is situated more externally. Essential differences are in the occipital region. Ventral parts of the paroccipital processes of *Pinacosaurus* are deflected slightly posteriorly from the skull roof, but in *Saichania chulsanensis* these processes are oriented strongly anteriorly. The occipital condyle of *Saichania* is strongly pressed into the brain case without any trace of a neck, and faces completely ventrally, invisible in lateral and dorsal views. Well developed bones in the orbital region almost completely close the orbit of *Saichania*. The new species also differs from *Pinacosaurus grangeri* in the strong anterior tilt of the quadrate and its ossification with the paroccipital process. Pectoral girdle and fore limbs of *Saichania chulsanensis* are the most massive and its metacarpals are the shortest of any Asian ankylosaurid. Unusually strong development of fusion between pectoral girdle and first dorsal rib, development of additional ossifications in the sternal complex and intercostal plates, coossification of atlas and axis and fusion of the quadrate and paroccipital process distinguish the new species from all the known ankylosaurids. *Saichania chulsanensis* differs from the North American *Euoplocephalus tutus* in the shape and structure of the nostrils, and in particular in the position of the accessory nasal foramen. This foramen in *E. tutus* is situated laterally, leads to a maxillary sinus, and is separated from the true nares by a vertical septum. An essential difference is in the position of nerve openings and in the occipital condyle, which in *E. tutus* is directed ventro-posteriorly.

Coossification of the quadrate with the paroccipital process and of the atlas with the axis observed in *Saichania chulsanensis* have not been previously reported in the Ankylosauridae. In this respect *Saichania* resembles some representatives of the Nodosauridae. Fusion of quadrate to paroccipital process is common among nodosaurids, but fusion of the atlas and axis has been reported only in *Panoplosaurus* and *Edmontonia* (a synonym of *Panoplosaurus* according to COOMBS, MS).

Distribution. — See table 1.

Genus *Tarchia* nov.

Type species: *Tarchia kielanae* sp.n.

Derivation of the name: Mongolian "tarchi" — brain, because of a relatively large brain case.

Diagnosis. — Genus monotypic, diagnosis and distribution as for the type species.

Fig. 3

Pinacosaurus grangeri GILMORE. The skull (ZPAL MgD-II/1), *A*₁ — occipital view, *A*₂ — lateral view, *A*₃ — anterior view. Abbreviations as in fig. 2.

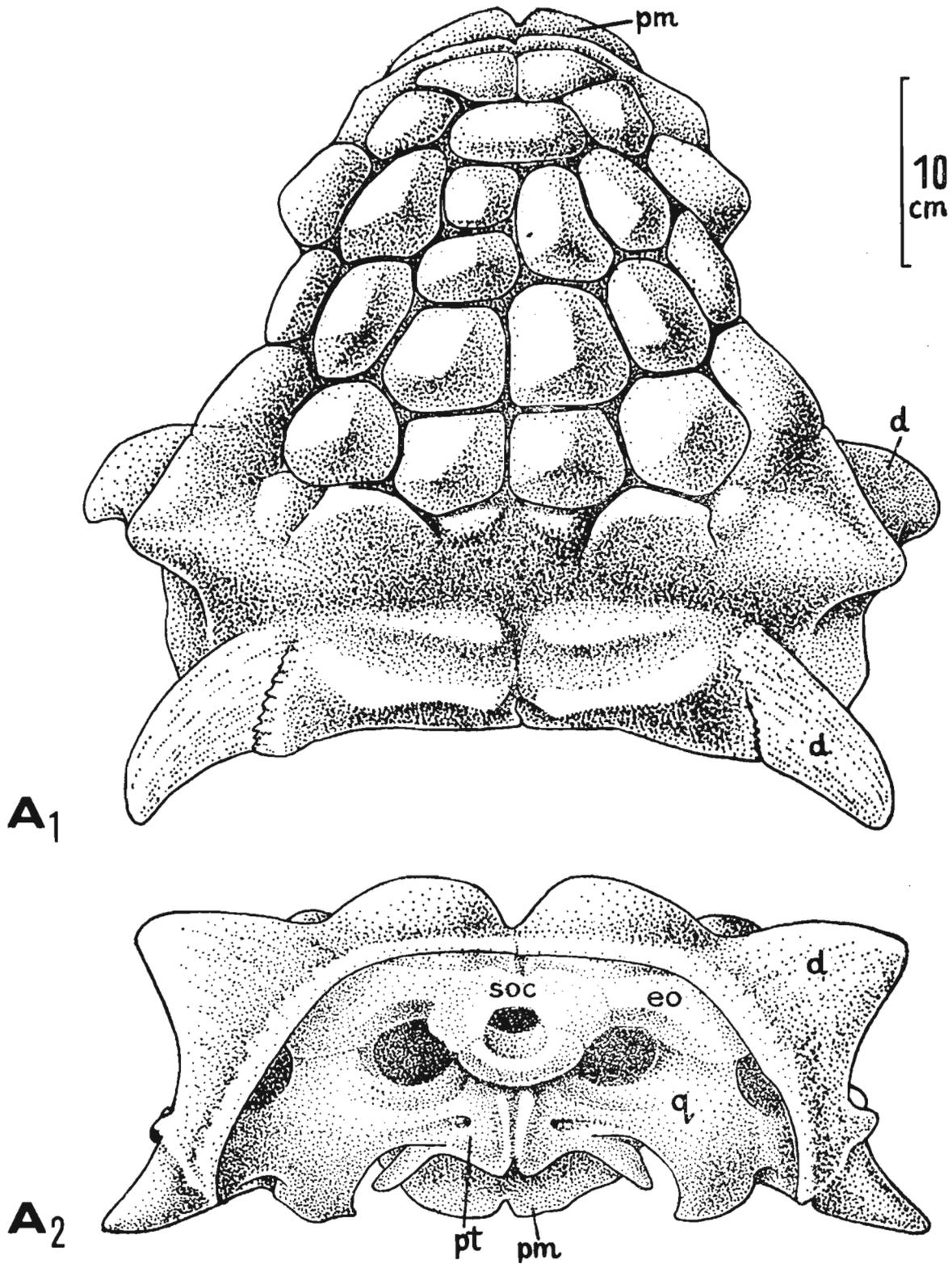


Fig. 4

Saichania chulsanensis gen.n., sp.n. The skull, holotype specimen (GI SPS 100/151). *A*₁ — dorsal view, *A*₂ — occipital view. Abbreviations as in fig. 2.

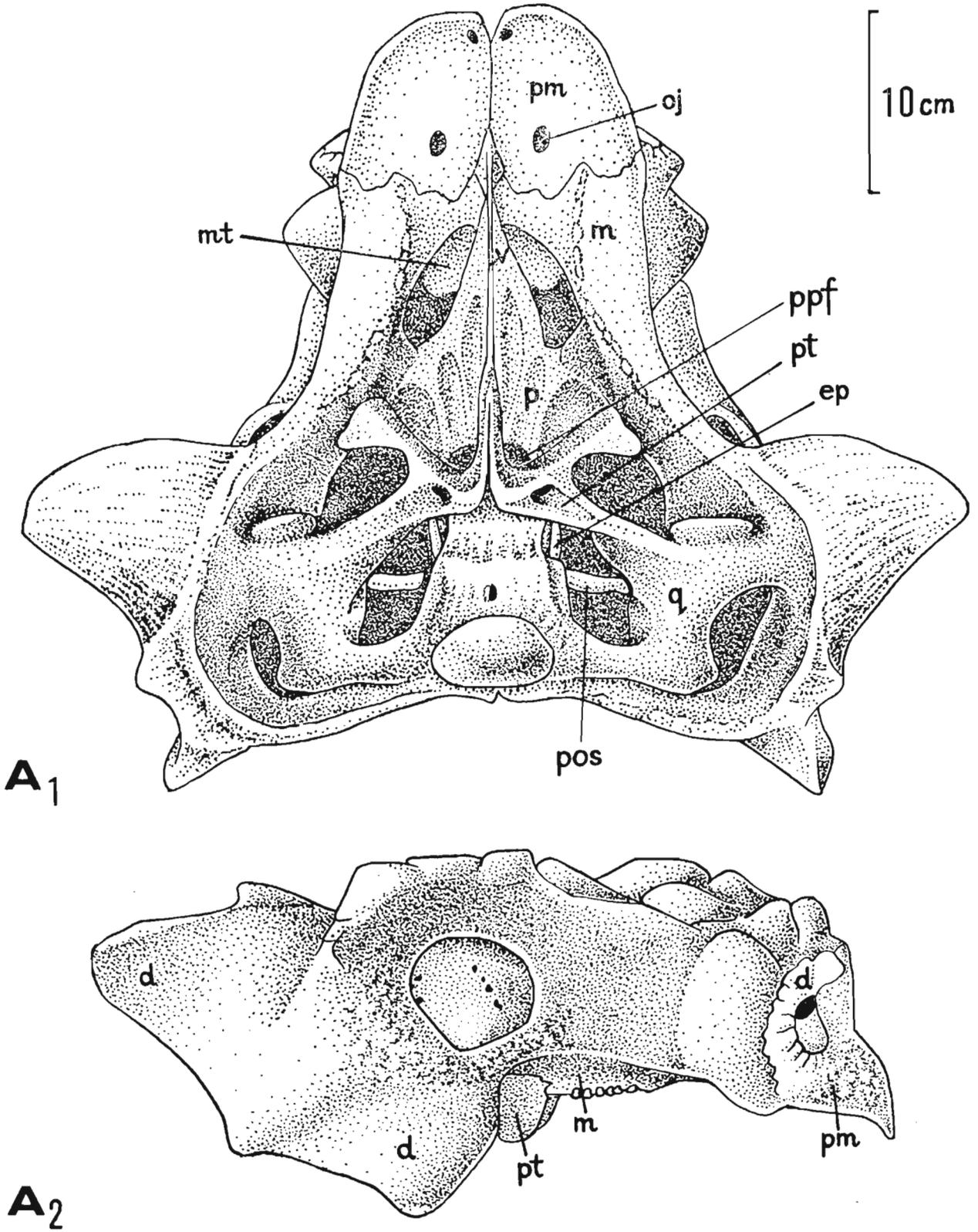


Fig. 5

Saichania chulsanensis gen.n., sp.n. The skull, holotype specimen (GI SPS 100/151) in: A₁ — palatal view, A₂ — lateral view. Abbreviations as in fig. 2.

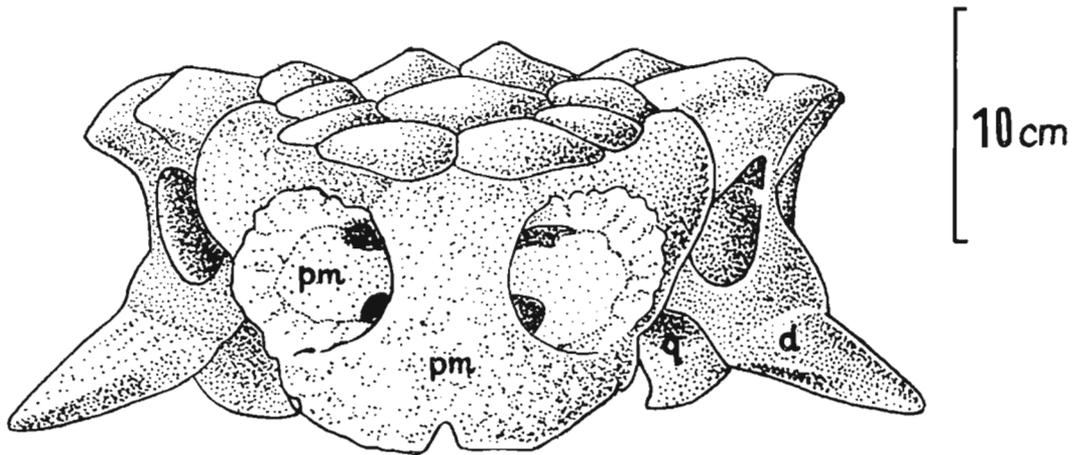


Fig. 6.

Saichania chulsanensis gen.n., sp.n. The skull, holotype specimen (GJ SPS 100/151) in anterior view. Abbreviations as in fig. 2.

Tarchia kielanae sp. n.

(pl. 27)

Holotype: posterior part of skull with roof, brain case and occipital region, ZPAL MgD-I/111.

Type horizon: Upper Cretaceous, Barun Goyot Formation.

Derivation of the name: in honour of Prof. ZOFIA KIELAN-JAWOROWSKA in recognition of her work on Mongolian vertebrates.

Diagnosis. — Large ankylosaurid; orbits not completely closed; exoccipital high and short, perpendicular to the skull roof; occipital condyle directed ventro-posteriorly; foramen magnum higher than wide; brain case very high; occipital part of skull and occipital condyle partly visible in dorsal view; one openings for nerves situated posterior to foramen ovale.

Material. — See p. 94.

Measurements — See table 2.

Remarks. — The only specimen of this species is an incomplete skull which makes detailed comparisons to other ankylosaurs impossible. *Saichania chulsanensis* has a skull almost the same size as *Tarchia kielanae*, but the latter has a larger brain case, almost twice the height of *S. chulsanensis*. The width of the occipital part in both skulls is the same, but the position and size of the paroccipital processes and the shape and size of the foramen magnum differ considerably. The essential difference is that the occipital part in *Saichania chulsanensis* is obscured by the overhanging skull roof, whereas in *Tarchia kielanae* the occiput is shifted slightly backwards beyond the skull roof as in *Talarurus plicatospineus*. Unusually thick skull bones and almost invisible cranial sutures of *Tarchia kielanae* prove that it is an adult skull. Consequently one can tentatively state that the bony wall of the orbits and the nasal septum were not so strongly ossified as in *Saichania chulsanensis*. In the development of these ossifications *Tarchia* resembles *Pinacosaurus grangeri*. *Tarchia kielanae* has some similarities to other Mongolian ankylosaurids. However, the mixture of these characters in the skull of *Tarchia kielanae* and the characters of the brain case prevent assignment of this species to any known Mongolian genus.

Distribution. — See table 1.

ANATOMY

A detailed description of the skull and postcranial skeleton of the ankylosaurs, based mostly on the material from North America, has been presented by COOMBS (MS). To avoid repetitions in osteological descriptions only those skeletal elements are discussed here that are somewhat

different in the Asiatic ankylosaurids or could be studied in detail for the first time. As the genera *Pinacosaurus*, *Saichania* and *Tarchia* are monotypic, and two species of *Talarurus* (*T. plicatospineus* and *T. disparoserratus*) do not differ in gross anatomy, for the sake of brevity in anatomical descriptions I use only the generic names.

OSTEOLOGY OF THE SKULL

In general the shapes of *Talarurus*, *Pinacosaurus* and *Saichania* skulls have the characteristics of ankylosaurid skulls given by COOMBS (MS). Horn-like protuberances on squamosals and jugals in *Saichania* are well pronounced and thus resemble *Ankylosaurus* more than *Euoplocephalus*. Squamosal "horns" are less pronounced in *Talarurus* which has relatively the longest skull of Asiatic Ankylosauridae. The skull of a young individual of *Pinacosaurus* (ZPAL MgD-II/1) has secondary elements of dermal origin covering the jugals, squamosals and the region of the external nares that must appear early in development. Skull roof ornamentation of *Saichania* and *Tarchia* differs from that of *Euoplocephalus*, *Ankylosaurus* and *Talarurus*. Skulls of *Saichania* and *Tarchia* are dorsally covered by numerous grooves, the areas between them are smooth and elevated. Bilateral symmetry of ornamentation is distinctly marked. As all the studied species are represented by single specimens, thin sections of skull roof bones have not been done. Thus I do not discuss the problem of the character of thickening of the skull roof (see COOMBS, MS). External nares of both *Pinacosaurus* and *Saichania* are visible both in ventral and dorsal views of the skull (pl. 19, fig. 1c; pl. 20, fig. 1b; pl. 28, fig. 1a and 1b), and in this respect they differ from *Euoplocephalus* (in which the external nares are visible only in dorsal view) and from *Ankylosaurus* (in which they are visible only in ventral view).

Individual bones

Supraoccipital. The contacts of the supraoccipital are visible only in *Pinacosaurus* (ZPAL MgD-II/1) (pl. 19, fig. 1b; text-fig. 3). The small supraoccipital connects suturally with exoccipitals, and reaches the dorsal margin of the foramen magnum for a short distance. It articulates with the parietal in *Pinacosaurus*. In other Mongolian ankylosaurids the supraoccipital and the parietal are coossified. Inside the brain case the supraoccipital contributes to the wall of the inner ear cavity just above the suture with the exoccipital.

Exoccipital. The exoccipitals are differently developed in the several genera of Mongolian ankylosaurids. In *Pinacosaurus* (ZPAL MgD-II/1) exoccipitals are rather high (text-fig. 3), compressed antero-posteriorly, and loosely joined to the quadrate and squamosal. They slant obliquely backward to the skull roof and therefore are visible in a dorsal view of the skull. Similar oblique orientation of the exoccipitals is characteristic of *Talarurus* (PIN 557). In *Talarurus* the exoccipital is completely fused to the squamosal. In *Saichania* (text-fig. 4) the exoccipitals are relatively long and low, antero-posteriorly flattened in the dorsal part, and perpendicular to the skull roof. Ventrally they are strongly bent forward. The paroccipital process in *Saichania* is completely fused to the squamosal. In *Tarchia* the exoccipitals are rather high and short, and completely fused to the skull roof and at least in part dorsally fused to the quadrates. The role of the exoccipital in the structure of the occipital condyle and foramen magnum is distinct in *Pinacosaurus*. Only the dorso-lateral margins of the occipital condyle are formed by exoccipitals, which make there two small protrusions distinctly separated from the basioccipital articular surface of the occipital condyle. In *Pinacosaurus* the exoccipitals form less than a quarter of the condyle. The entire lateral and part of the upper border of the foramen magnum are made up by the exoccipitals. In the laterodorsal part of the foramen magnum the exoccipitals in *Pinacosaurus* and *Saichania* form two nodes pointing medio-posteriorly with distinct muscular scars. It seems that the contribution of the exoccipital to the structure of the occipital condyle is insignificant in *Saichania*. In *Pinacosaurus* the exoccipital

is perforated by the exit for nerve XII just above the basioccipital contact. The exit for the nerves IX—XI is situated antero-ventrally to the exit of nerve XII and almost at the suture with the basioccipital. The exoccipital forms the postero-ventral margin of the fenestra ovalis. Inside the brain case the exoccipital forms a part of the posterior wall of the inner ear cavity, and contacts the opisthotic. A vast contact of the antero-medial part of the exoccipital with the prootic is free in *Pinacosaurus*.

Contacts of the exoccipital with surrounding bones are obscured in other Mongolian ankylosaurids. There is an important difference in the number of nerve exits situated posterior to the fenestra ovalis. In *Pinacosaurus* there are two openings, one probably for nerves IX—XI, and another one for nerve XII. Inside the brain case are two corresponding foramina for the entrance of these nerves. In *Talarurus* four separate exits are present posteriorly and four corresponding separate entrances inside the brain case. In *Saichania* (text-fig. 7) and *Tarchia* (pl. 27) one foramen exists for exits of the nerves IX—XII situated posterior to fenestra ovalis. Within the brain case are two entrances corresponding to the single outer foramen.

Basioccipital. A massive basioccipital forms most of the occipital condyle. Contact of the basioccipital with the basisphenoid is completely fused in the young specimen of *Pinacosaurus* as in all other ankylosaurids, but lateral sutures with the exoccipitals are clearly marked. The ventral surface of the basioccipital is transversally concave. Along a short distance the basioccipital contributes to the ventral margin of the foramen magnum. In *Talarurus* the narrow, crescent-shaped articular surface of the occipital condyle is oriented posteriorly, whereas in *Pinacosaurus* (pl. 19) the surface is oval and oriented postero-ventrally. In *Saichania* (pl. 28, fig. 1b) the articular surface is large, almost flat, and directed ventrally, and in *Tarchia* it is strongly convex and directed postero-ventrally. The foramen magnum in *Talarurus*, *Pinacosaurus* and *Saichania* is oval, long axis horizontal, whereas in *Tarchia* the height exceeds the width. There is a small unrecognized foramen at the centre of the concave ventral surface of the basioccipital in a young specimen of *Pinacosaurus* (ZPAL MgD-II/1). In *Saichania* (GI SPS 100/151) a small distinctive pouch is present in the same position, whereas in the old specimen of *Tarchia* (ZPAL MgD-I/111) a large gap leading to the endocranial cavity is observed. It is probable the dimensions of this foramen depend on individual age and increase through resorption of the bone.

Opisthotic. This small thin bone is partially visible in *Pinacosaurus* (ZPAL MgD-II/1). Tracing of its contacts cannot be done precisely because of damage. It lines the exoccipital in the region of inner ear cavity forming part of its posterior wall. It has a short contact dorsally with the supraoccipital. The opisthotic forms a very thin bar over the fenestra ovalis. Anteriorly it contacts the basioccipital.

Prootic. The prootic is a relatively large, massive bone. In *Pinacosaurus* it contacts the exoccipital posteriorly, the laterosphenoid antero-dorsally, the basisphenoid antero-ventrally, the opisthotic ventrally and the supraoccipital postero-medially. All contacts are loose with the exception of the last mentioned. A large foramen for exit of nerve V occurs in the anterior part of the prootic just at the laterosphenoid contact. Posterior to the exit of nerve V, at the contact of the prootic and basisphenoid, there is the exit of nerve VII. The medial surface of the prootic takes part in the structure of lateral wall of the inner ear cavity. In *Saichania* there are two separate openings interpreted herein as exits for three branches of the nerve V (text-fig. 7). The smaller dorsal foramen is for V₁, and the large exit located close to the basisphenoid is for V₂ and V₃. The entrance for nerve V is very large. The exit of nerve VII in *Saichania* is located in large opening that also contains exits of nerves V₂ and V₃ but which is distinctly separated by a bony bridge from exit of the ramus maxillaris and the ramus mandibularis. The entrance of nerve VII is in the same position as in *Pinacosaurus*. A contact of the prootic with the epipterygoid is clearly visible in both *Pinacosaurus* and *Saichania*, being particularly distinct in the latter where the epipterygoid contacts the prootic ventral to the exit of V₁ just above the large exit of V₂ and V₃.

Basisphenoid. The basisphenoid is small, massive and strongly compressed antero-posteriorly. In ventral view it forms slightly thickened, coarsely rugose basal tubera at the border with the basioccipital. It sends short, massive basipterygoid processes antero-ventrally. Contact of the pterygoid processes of the basisphenoid with the basisphenoid processes of the pterygoid is movable only in the young specimen of *Pinacosaurus* (text-fig. 2). In *Saichania* these bones are fused. Anteriorly the basisphenoid contacts the parasphenoid. In the lateral wall of basisphenoid, below the laterosphenoid contact, there is a foramen for nerve VI, and a more ventral foramen for the carotid artery. A canal leading out of this foramen inside the basisphenoid opens in the bottom of the hypophyseal cavity. The exit of the palatine artery is situated anterior to the exit of nerve VI. A foramen, probably for the exit of nerve III, is situated ventrally to the exit of the palatine artery. The fragmentary basisphenoid of *Pinacosaurus* appears to form the ventral border of the exit of the palatine artery, but the dorsal border is formed by the orbito-presphenoidal complex which also contains the exit of nerve III. Two centrally situated furrows, probably corresponding to median palatine arteries, are visible on the ventral side of the brain case, anterior to pituitary cavity, in the wall made of basisphenoid. The pituitary

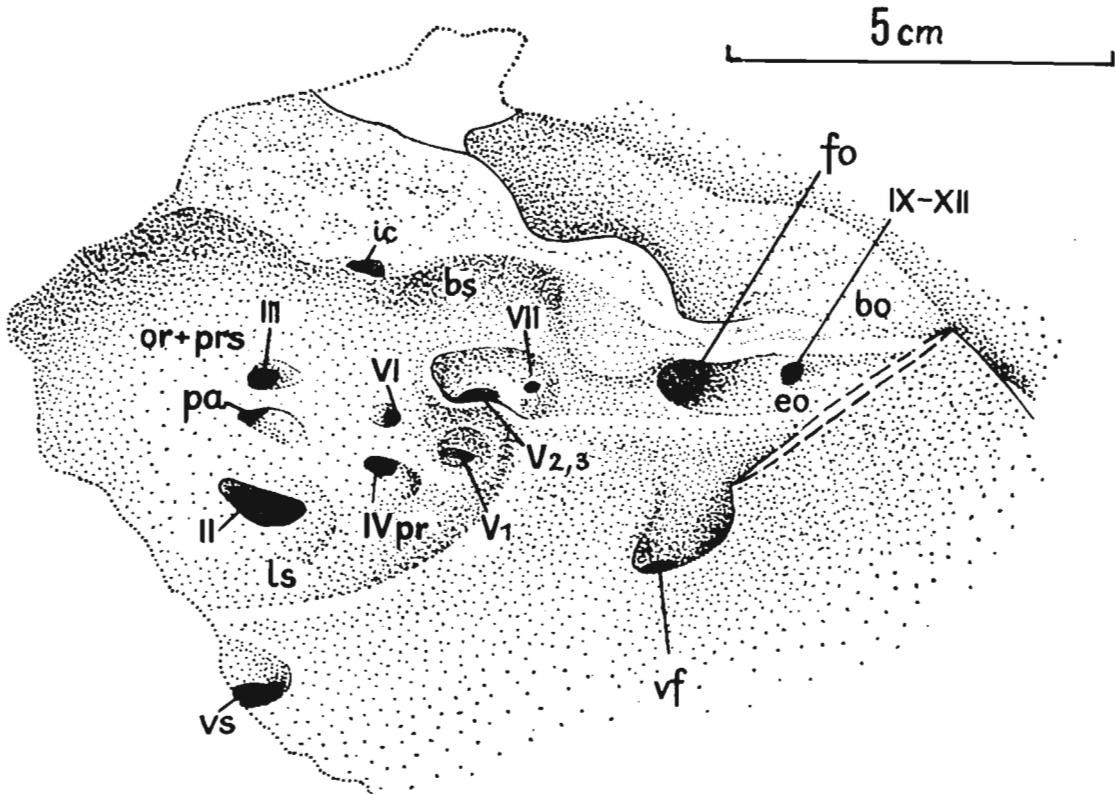


Fig. 7

Saichania chulsanensis gen.n., sp.n. Holotype specimen (GI SPS 100/151). Diagrammatic drawing of the right side of brain case showing the distribution of exits of cranial nerves and arteries. Oblique latero-anterior view, upside down. Abbreviations as in fig. 2.

cavity is relatively large and deep. The dorsum sellae in *Pinacosaurus* (pl. 20, fig. 3) and *Tarchia* is low and narrow, and in *Saichania* is broad and high. Because of differences in the height of dorsum sellae, it is pierced by nerve VI only in *Saichania*. A foramen for carotis interna is visible at the bottom, and the exit of nerve VI in the lateral wall of the pituitary fossa. A distinct perpendicular furrow situated at the level of the exits of nerve II, above and in front of the pituitary fossa in *Saichania*, corresponds most probably to the optic chiasma.

Laterosphenoid. Only the posterior part of the laterosphenoid is preserved in *Pinacosaurus*

(ZPAL MgD-II/1). It is loosely attached to the skull roof and to the prootic and basisphenoid, as well as to other bones of the brain case. A well preserved laterosphenoid is to be observed in *Saichania* and in *Tarchia*. In the latter it is completely fused to adjoining bones. The laterosphenoid consists of two parts — a massive main body that contacts the skull roof and a lateral wing. The broad contact of the laterosphenoid with the roof covers the frontal-parietal suture and extends laterally to the postocular shelf. In *Pinacosaurus* the contact with the postocular shelf is free, but in *Saichania* and *Tarchia* these bones are fused, and the main body of the laterosphenoid forms a prolongation of the postocular shelf toward the brain case. Within the laterosphenoid near its contact with orbito-presphenoidal complex there is a large exit for nerve II, and postero-ventrally to it the exit of nerve IV.

Parasphenoid. The parasphenoid has been preserved only in *Saichania* where it is not clearly visible. A laterally flattened parasphenoidal rostrum wedges between the palatal wings of the pterygoid and the vomer, making a continuation of the interpalatal septum formed by the vomer.

Orbitosphenoid and presphenoid. This region is not preserved in *Pinacosaurus*. Existence of a complete interorbital septum in *Saichania* suggests the presence of these bones. The orbito-presphenoidal complex is well preserved in *Tarchia* where it occupies a region situated antero-dorsal to the parasphenoid. This complex forms a lateral margin of the olfactory channel. The shape and position of the presphenoid-orbitosphenoid complex is different in *Saichania* and *Tarchia*. In *Saichania* these bones are relatively low but greatly expanded antero-posteriorly, whereas in *Tarchia* they are rather short and high, a difference correlated with different brain case heights in these genera. In *Saichania* the orbito-presphenoidal complex contacts the additional ossification of the anterior wall of the orbit. A large foramen in the dorsal part of the interorbital septum probably pierces the orbito-presphenoidal complex. This foramen is situated antero-dorsally to the exit of nerve II and leads to a cavity below the skull roof that opens toward the brain case. Presumably the foramen is vascular, possibly for the ophthalmic artery or it may have housed a venous sinus.

Parietal. This bone contacts the frontal anteriorly, the squamosal laterally, and the “tabular” postero-laterally. The interparietal suture is very distinct. The parietal forms the central part of the posterior skull roof margin and overhangs the occipital region. The contact of the parietal with the supraoccipital in *Pinacosaurus* is movable (pl. 19, fig. 1*b*; text-fig. 3). An unossified gap between the parietals and the occiput occurs only in *Pinacosaurus*. All contacts of the parietal are visible on the internal side of the skull roof. In its posterior part, the parietal forms two nodes that fit into corresponding depressions in the supraoccipital.

Frontal. In *Pinacosaurus* a relatively small, almost square frontal is separated from the parietals by a transverse suture. The naso-frontal suture is very distinct and is directed transversely (pl. 20, fig. 1*b*; text-fig. 2). The frontal contacts the prefrontal antero-medially, whereas it meets the postfrontal laterally. The frontal postorbital contact is short. There is a distinct interfrontal suture. All contacts of the frontal are visible on the inner side of the skull roof. Keel-like ridges on the inner surface of the frontals diverge anteriorly and constitute the medial extremity of the preorbital septum. More medially, transverse keel-like ridges of the frontals form the anterior limit of the brain case. The contact of the frontal with the laterosphenoid close to the suture with the parietal is loose and is marked by numerous fine furrows.

Premaxilla and secondary dermal ossification of the narial region. Only in the *Pinacosaurus* specimen ZPAL MgD-II/1 is the premaxilla well exposed (pl. 19, fig. 1*c*; pl. 20, fig. 1 and 2; text-figs 2 and 3). My former description (MARYAŃSKA, 1971) of the premaxilla of that specimen needs some corrections. The premaxilla forms half of the preorbital part of the skull. Laterally the premaxilla-maxilla suture runs vertically in its ventral part. More dorsally the premaxilla protrudes backward as a process wedged between the maxilla and the nasal but not reaching the lacrimal. Antero-laterally three pairs of external openings pierce the premaxillae above the toothless beak (pl. 20, fig. 2). Two ventrally situated pairs are completely surrounded by

premaxilla, which also forms ventral margin of the third pair of openings. Along the midline the premaxilla has a narrow dorsal process that has a very short suture with the nasal. Dorsal and dorso-lateral rims of the third, dorsally positioned openings are formed by secondary dermal ossifications. The latter contact the nasals with a distinct suture and overlap the premaxilla anteriorly. In effect, the nasals are excluded from the dorsal margin of the dorsally situated nasal openings. Because of these secondary ossifications the external nares open far to the front, as otherwise they would open much farther posteriorly on the dorsal side of the skull. It may be presumed that similar relations exist in all other ankylosaurids. It seems probable that the dorsal surface of the premaxilla of *Ankylosaurus* is secondarily hidden also by strongly developed secondary dermal ossifications of that region. All known ankylosaurs have a concave ventral surface on the premaxilla except a young individual of *Pinacosaurus* in which it is convex, probably a juvenile character. Important differences between *Pinacosaurus* (text-fig. 3), *Saichania* (text-fig. 6) and *Euoplocephalus* concern the number and distribution of openings through the premaxilla in the external nasal region. *Ankylosaurus* is not mentioned here because of the lateral position of its nares and lack of the data concerning the number and situation of the particular openings. As mentioned above, a juvenile *Pinacosaurus* has three pairs of openings, whereas *Euoplocephalus* and *Saichania* have but two of them. These are, however, positioned differently in these two genera. In all three genera the opening situated dorsally leads to true dorsal air passage and the other openings lead to accessory cranial sinuses. In *Euoplocephalus* the additional foramen is situated laterally in relation to the dorsal foramen and leads (according to COOMBS, *l.c.*) to a maxillary sinus. In *Saichania* this second foramen is situated ventromedially and leads to a premaxillary sinus. *Pinacosaurus* has two foramina leading to the premaxillary sinus, the lateral one leading to that part of premaxillary sinus which is directly connected with the maxillary sinus. The location of these foramina in *Pinacosaurus* seems to suggest that one of them may correspond to that of *Saichania*, and the other to that of *Euoplocephalus*. Closing of lateral foramen in *Saichania* and of the medio-ventral one in *Euoplocephalus* may be explained by different development of accessory cranial sinuses in these genera. The premaxillary sinus is most extensive in *Saichania*, whereas in *Euoplocephalus* the maxillary sinus is larger.

Maxilla and maxillary sinus. Maxillary contacts with surrounding bones are visible only in *Pinacosaurus* (pl. 21, fig. 1). Laterally the maxilla does not reach the external nasal openings. The maxilla-nasal contact is distinct but short. In palatal view the maxilla of *Pinacosaurus* shows the incipient anterior palatal shelf (text-fig. 2). A small process of the maxilla just at its contact with the premaxilla is situated antero-laterally to the palatal vacuity and does not reach the vomer, so that the anterior border of palatal vacuity is formed by the premaxilla. The posterior palatal shelf of the *Pinacosaurus* maxilla is weakly developed. The palatal shelves of the maxilla are very well developed in *Saichania* (text-fig. 5) as in *Euoplocephalus*. Development of palatal maxillary shelves forming a secondary palate results in a decrease in participation of the main body of the maxilla in the lateral rim of the palatal vacuity. An internal maxillary protuberance in the air passage region is visible through the palatal vacuity of both *Pinacosaurus* and *Saichania*. The maxillary sinus present in all Ankylosauridae is divided by a vertical septum at approximately mid-length. Both parts of the sinus open to the nasal cavity. The bony process separates the last eight maxillary teeth from the anterior ones in the maxilla in *Saichania*, creating a sort of diastema placed exactly at the level of the internal septum in the sinus. The "diastema" corresponds in length to about one and a half of alveola. I have mentioned a connection between maxillary and premaxillary sinuses in *Saichania*.

The number of teeth in a maxillary row differs in genera of Ankylosauridae. There are 19 teeth per row in *Talarurus*, 17 — in the young specimen of *Pinacosaurus*, 22 — in *Saichania*, whereas 22 — in *Euoplocephalus* and 35 — in *Ankylosaurus*.

Lacrimal. This bone is well exposed only in the young specimen of *Pinacosaurus* (ZPAL MgD-II/1). Antero-ventrally it contacts the maxilla along a suture that slants obliquely upward,

and anteriorly it contacts the nasal (text-fig. 3, pl. 19). The lacrimal does not reach the premaxilla from which it is distinctly separated by a maxilla-nasal contact. Dorsally the lacrimal contacts the prefrontal and supraorbital; postero-ventrally below the orbit it contacts the jugal. The inner wing of the lacrimal forms the antero-lateral orbital wall. The lacrimal foramen is clearly visible. Medially the inner orbital wing of the lacrimal contacts the accessory orbital ossification of the anterior orbital wall.

Jugal. The jugal is well exposed in a young specimen of *Pinacosaurus*. It forms the ventral boundary of the orbit. Anteriorly, it contacts the lacrimal laterally and within the orbit (text-fig. 3). Contact with the maxilla is latero-ventral, just at the maxilla-ectopterygoid suture. Posteriorly, on the lateral side of the skull and within the orbit, the lacrimal contacts the post-orbital. The ventro-lateral margin of the jugal is overlapped by the quadratojugal. Posteriorly, a horizontal wing of the jugal protrudes into the orbit to form the postocular shelf (HASS, 1969). In the young specimen of *Pinacosaurus* the secondary dermal plate is not coossified to the jugal, but only to the quadratojugal and squamosal. However, the jugal of adult individuals of *Saichania* and "*Dyoplosaurus*" is partly covered by that dermal plate.

Quadrate. This bone is developed differently in Mongolian ankylosaurids than in the North American genera (COOMBS, MS). The only Mongolian ankylosaurid in which the junction of quadrate and squamosal is streptostylic is the young individual of *Pinacosaurus* (ZPAL MgD-II/1). In all other representatives of the Ankylosauridae (*Saichania*, *Tarchia*, "*Dyoplosaurus*") the quadrate and squamosal are fused. The contact between the quadrate and the paroccipital process is free in young *Pinacosaurus* and in adult "*Dyoplosaurus*" (PIN, undescribed specimen, no catalogue number) and probably in *Tarchia*. In *Saichania* the paroccipital process is firmly fused to the quadrate. The pterygoid-quadrate junction is fused in *Saichania*, *Tarchia* and "*Dyoplosaurus*", and only in the young *Pinacosaurus* does the quadrate process of pterygoid freely overlap the pterygoid process of the quadrate. A coossification of the quadrate with the squamosal and with the paroccipital process stated in Mongolian ankylosaurids resembles the conditions in the Nodosauridae (COOMBS, *l.c.*).

The quadrate is directed somewhat anteriorly in *Pinacosaurus* and strongly anteriorly in *Saichania*. In *Tarchia* and "*Dyoplosaurus*" it is almost vertical and perpendicular to the skull axis.

Quadratojugal. In *Pinacosaurus* the quadratojugal is a small bone with two narrow projections. The anterior horizontal one underlines the jugal ventro-medially along the posterior half of suborbital bar. The longer, posterior projection is almost vertical and embraces about 3/4 the length of the lateral margin of the quadrate. The ventral margin of quadratojugal-quadrate contact is definitely above the mandibular cotylus. Laterally, the vertical projection of the quadratojugal reaches the medial surface of the postorbital. Externally the quadratojugal is covered by a secondary dermal plate. In *Saichania* all contacts of the quadratojugal are obscured.

Squamosal. The squamosal in *Pinacosaurus* (ZPAL MgD-II/1) is a small bone that contacts the postorbital, the parietal, the secondary dermal-squamosal, and the "tabular". Ventrally on the squamosal is an articular socket for the quadrate. In *Pinacosaurus* the squamosal-quadrate junction is streptostylic, in *Saichania* these bones are fused, but with distinct boundaries between them; and in *Tarchia* the fusion of the squamosal and the quadrate is so complete that the boundaries are untraceable. This character is probably connected with age of the individuals.

Postorbital. The postorbital is a relatively large bone developed in three planes. Suturally it is distinguishable only in *Pinacosaurus* (ZPAL MgD-II/1). The horizontal wing is incorporated into the skull roof and contacts the postfrontal and posterior supraorbital anteriorly, the frontal medially, the squamosal medioposteriorly, and the secondary dermal plate, which forms postero-lateral corner of the skull, also medio-posteriorly. The vertical wing of the post-orbital forms the posterior part of the orbit and contacts the jugal and secondary dermal-jugal bone ventrally. The third, internal wing of the postorbital forms the postocular shelf. This structure extends dorsally from the horizontal wing of the postorbital to the brain

case contacting both parietal and laterosphenoid. In *Pinacosaurus* the contact of the postocular shelf with the laterosphenoid is loose. Ventrally in the orbit the postorbital part of the postocular shelf contacts the ventral wing of the jugal, thus forming the postero-ventral wall of the orbit. In the young specimen of *Pinacosaurus* the postocular shelf is low; in *Saichania* it is more massive and more ventrally expanded. It follows from an examination of the skull of *Pinacosaurus*, that the ventral part of the postocular shelf is built of the jugal, but the posterior part is composed of postorbital. Contact of postorbital with the squamosal is visible on the ventral side of skull roof just posterior to the postocular shelf.

Prefrontal. The suturally distinct prefrontal of *Pinacosaurus* is a relatively large bone that contributes to the construction of the skull roof. Antero-medially it contacts the nasal; postero-medially its contact with the frontal is short. Postero-laterally the prefrontal contacts the postorbital and laterally the supraorbital. The contribution of the prefrontal to the structure of the lateral wall of the skull is insignificant. Ventrally it has an almost horizontal suture with the lacrimal.

Supraorbitals. Two supraorbitals are evidently incorporated into the skull roof in *Pinacosaurus*. They form the upper orbital margin and protrude over the orbit as horns (text-fig. 2). The anterior supraorbital contacts the lacrimal, the prefrontal, and the postfrontal; the posterior one contacts the postfrontal and the postorbital. A suture between the supraorbitals is well visible. Unlike *Euoplocephalus* (COOMBS 1972) in Mongolian ankylosaurids the bony eyelids do not occur.

Postfrontal. The bone here called the postfrontal has been found in *Pinacosaurus* (ZPAL MgD-II/1). It takes part in the structure of the skull roof and is the only skull bone that forms the roof of the orbit (text-fig. 2; pl. 20, fig. 1b). In dorsal view, it contacts medially the frontal, and anteriorly the prefrontal, posteriorly the postorbital, and laterally two supraorbitals. On the internal side of the skull all the sutures of this bone are distinct. Aside of its contacts visible on the dorsal side of the skull, the postfrontal contacts in the orbital region an additional ossification that forms the anterior wall of the orbit. The contact of the postfrontal with the frontal is situated slightly lateral to the contact between the frontal and laterosphenoid. The bone described here as the postfrontal is regarded by COOMBS (MS) as a third palpebral. Extensive participation of this bone in the structure of the skull roof and the orbital roof as well as the fact that it attaches to the brain case preclude identification as a palpebral (or supraorbital).

Nasal. The largest bone in the skull of *Pinacosaurus* (ZPAL MgD-II/1) is the nasal which reaches far backward in the skull roof (pl. 19; text-fig. 2). A transverse naso-frontal suture runs approximately opposite the mid-point of the orbit. The nasal-prefrontal contact is long, and passes from the dorsal to the lateral side of the skull. In the lateral wall of the skull the nasal contacts posteriorly the lacrimal, ventrally along a short distance the maxilla, and posteriorly the premaxilla. The nasal-premaxilla contact is well exposed only on the lateral wall of the skull. Antero-dorsally along its whole width the nasal contacts the secondary dermal nasal ossification with a distinct suture. This secondary ossification covers the premaxilla-nasal in that region. Under this ossification in the median line of the skull, the nasal contacts the narrow ascending premaxillary process. Development of an extensive secondary dermal nasal ossification excludes the true nasal from the rim of any opening in the nasal region. The internasal suture is distinct and incised. Inside the nasal region along the whole length of the nasal bones, a well developed internasal bony septum is present. In *Pinacosaurus* it is formed presumably at least in part by the nasals. There is a massive bony plate situated medially within the nasal cavity at the internasal suture. This plate is in close contact with its fellow and forms a medial section of the internasal septum. The anterior prolongation of this septum is made by the premaxilla. As along the whole length of the nasal, the internasal septum is definitely paired and is formed by the internal wings of the nasal; it cannot be regarded as an ossification within septum nasi. As it may be observed on the skull of a young specimen of *Pinacosaurus* the septum between two air passages has nothing in common with the vomer. There is a distinct gap between the

vertical vomeral keel extending high dorsally and the nasal septum hanging down the skull roof in *Pinacosaurus*. Because of the immaturity of the specimen of *Pinacosaurus* there are no ossifications within the septum nasi to complete the internasal septum. In *Saichania* a complete internasal septum is developed in which both nasals and other ossifications within septum nasi as well as those of the ethmoidal region take part. This internasal septum in *Saichania* attains the vomeral keel.

Pterygoid. In both young *Pinacosaurus* (ZPAL MgD-II/1) and in adult *Saichania* (GI SPS 100/151) contact of the basiptyergoideal tuber with the pterygoid is very distinct but fused. The overlapping contact of the quadratic wing of the pterygoid with the quadrate is loose only in a young *Pinacosaurus* (text-fig. 3) but fused in adult *Saichania* (text-fig. 5). Anteriorly, thin vertical pterygoidal sheets form posterior sections of the palatal wall and in the median line of the palatal region are overlapped by the vomer. Contact of the pterygoid with the palatinum is clearly visible in both specimens in question. It is situated in the vertical wall that forms the posterior limit of the palatal region. The pterygoid extensively overlaps the palatinum, so that a large part of the posterior palatal wall is formed by two very thin bones. The ventral pterygoid part of this wall is pierced by an opening. In the posterior part of a highly roofed palatal region where palatal septum is formed of pterygoids, there are relatively large posterior palatal foramina, present in both *Pinacosaurus* and *Saichania*. They are separated in the median line by the pterygoids and the parasphenoid. The vomer forms their antero-medial margin whereas the antero-lateral, lateral and postero-lateral borders are formed by the palatinum, and the postero-medial border by the pterygoid. Contact of the pterygoid with the small ectopterygoid is visible in *Pinacosaurus* on the laterally directed mandibular processes. Distinct contact of the pterygoid with a bone here named the epipterygoid is visible in *Saichania*. The dorsal part of the quadratic wing of the pterygoid is embraced by the epipterygoid just at the base, lateral to contact with the basisphenoid.

Epipterygoid. The bone here called the epipterygoid was not found in the Ankylosauria and among other Ornithischia it occurs only in the Pachycephalosauria (MARYAŃSKA & OSMÓLSKA, 1974). It is a rod-like bone of small diameter extending almost parallel to the brain case (pl. 28, fig. 1b). It embraces anteriorly the pterygoid with its two small processes, and rests upon the prootic posteriorly and slightly dorsally, in front to the exit of the nerve V. This very delicate bone is preserved completely only in *Saichania* (GI SPS 100/151) and in the PIN undescribed specimen, no catalogue number, collected at Khermeen Tsav. Its presence is a result of the perfect state of preservation of the whole skull as in *Prenocephale* (MARYAŃSKA & OSMÓLSKA, *l.c.*). A distinct trace of it is observed in *Pinacosaurus* (ZPAL MgD-II/1). I have found it also in *Euoplocephalus* in the specimen BM (NH) R. 8588 which is a cast of AMNH 5403. It seems probable that it was characteristic of all the Ankylosauridae.

Ectopterygoid. This small triangular bone is distinct only in a young specimen of *Pinacosaurus*. It joins the pterygoid with the maxilla and reaches the palatinum on the palatal side.

Palatine. The palatine is well visible in *Pinacosaurus* and in *Saichania* (pl. 21, fig. 3 and pl. 30, figs 1 and 2). It is a part of the highly vaulted palate. Contact of the palatine with the vomer runs on the lateral wall of the palate just beneath its roof, so the palatine forms lateral wall of the V-shaped palate. The palatine forms posterior and medio-posterior margins of the palatal vacuity. Distinct sutural contact of the palatine with the maxilla is visible posterolaterally to the palatal vacuity. The contact with ectopterygoid is very short. The palatine is situated lower posteriorly than anteriorly. In *Pinacosaurus* the palatine contacts the main body of the maxilla along the last 4—5 maxillary teeth. Contacts of the palatine with the pterygoid is very distinct in *Pinacosaurus*. The palatine underlies the vertical wall that divides the palatal region posteriorly. Dorso-posteriorly the palatine contacts the parasphenoid. In *Saichania* the palatine-maxilla contact is more medially situated and the palatine does not contact the main body of the maxilla, but rather the posterior horizontal palatal shelf of the maxilla. This contact is broader than in *Pinacosaurus* and corresponds to the part of the maxilla occupied by

8—9 last maxillary teeth. Among Mongolian ankylosaurids the horizontal palatal part of palatine is best developed in *Saichania* and less in *Talarurus* in which the palatine contacts the main body of maxilla far posteriorly along the last 2—3 maxillary teeth. Presence of numerous pits and chambers in the posterior part of the palatine is characteristic of all specimens examined. These pit structures are best developed in *Saichania* (pl. 30, fig. 1). In *Pinacosaurus* they are present only in the posterior part of the palatine, whereas in *Saichania* the entire palatal part of palatine is covered by these structures. The palatine forms a system of chambers and pits separated one from another by thin walls. During preparation of the palatal region it appeared that the whole palatine surface was covered with fine bone debris, so it seems probable that the pits and chambers may have been closed in life and formed a kinds of closed gas-filled cavities. This pneumatization of the palatine may be connected with a tendency to lighten the heavy skull, or these chambers may have been resonance boxes.

Vomer. On the well preserved Mongolian specimens it is demonstrated that the vomer did not reach the skull roof. This pertains to *Pinacosaurus* (ZPAL MgD-II/1), *Saichania* (GI SPS 100/151) and *Talarurus* (PIN, undescribed specimen, no catalogue number, from Baynsheer Tsav) in which the vomer and the skull region situated dorsally to vomer are preserved. The very thin and deep vertical plates of the vomer form a septum within a highly vaulted palatal region and do not pass to skull roof dorsally. The vomeral septum extends far ventrally. In *Pinacosaurus* (ZPAL MgD-II/1) it attains the ventral line of tooth row of the maxilla and in *Saichania* the ventral margin of that septum is situated below the ventral line of the tooth row. The lateral extension of the dorsal part of the vomer is strongest at the contact with the premaxilla. In *Saichania* a laterally directed wing of the vomer joins anterior palatal shelf of the maxilla, both bones forming the anterior margin of the palatal vacuity. The vomer of *Pinacosaurus* does not attain the maxilla (text-fig. 2). In the anterior part of the palatal region the vomer dorsally contacts a massive internasal septum. In the postero-dorsal part of the palatal region the vomer embraces the parasphenoid. Contact of the vomer with the pterygoid is clearly visible in *Pinacosaurus* and *Saichania*. Posteriorly, the vomers evidently overlap very thin plates of the pterygoid which form the posterior part of the palatal septum. The vomer attains the interpterygoid foramen.

Mandible. Some information can be added to the description of the mandible of ankylosaurids given by COOMBS (MS). The main differences between the structure of the mandible of the North American and Mongolian ankylosaurids is the position of the angular. In *Pinacosaurus* (ZPAL MgD-II/1) the angular is a small ornamented bone, the anterior process of which hardly attains the penultimate alveolus. Small dimensions of the angular in *Pinacosaurus* may be attributed to the young age of the individual. In an adult individual of *Saichania* the angular attains but half the length of the tooth row. This bone is definitely shorter in Mongolian ankylosaurids than in North American genera in which it terminates at about the level of the anteriormost alveolus. Some differences are also observed in the structure of the coronoid. Both in *Pinacosaurus* and *Saichania* the coronoid is a relatively large bone the anterior wing of which attains more than a third of the length of the tooth row. The posterior, vertical wing of the coronoid forms a relatively high process definitely higher than the coronoid process of the surangular. The articular of *Pinacosaurus* is an extremely small bone limited to the glenoid. In *Saichania* the articular did not continue at the bottom of the mandibular fossa. Differences in mandibular shape in *Pinacosaurus* and *Saichania* (pl. 22, fig. 8; pl. 29, fig. 1) is probably related to differences in age of the individuals. In the former the mandible is rather low and equally high almost over its length (excluding symphyseal part) with a slightly marked angular protuberance.

Seventeen functional teeth are present in the right ramus, and 16 in the left ramus of *Saichania* mandibles; 16 teeth are preserved in the left ramus of a *Pinacosaurus* mandible. Some differences may be noted in the structure of mandibular teeth in *Pinacosaurus* and *Saichania*. Tooth crowns of *Pinacosaurus* are higher relative to their width and have a weakly marked basal swelling on the lingual side (pl. 22, fig. 7). In *Saichania* this swelling takes the form of a distinct cingulum

which is very prominent both on the lingual and labial sides. Also the manner in which the central cusp passes into a flat broad keel on lingual side of tooth is better marked in *Pinacosaurus* than in *Saichania*.

Accessory ossification in antorbital wall. A completely ossified antorbital wall occurs in *Saichania* (GI SPS 100/151). First stages of the development of this wall are observed in *Pinacosaurus* (ZPAL MgD-II/1). An additional ossification situated perpendicular to the skull roof contacts the orbital wing of the lacrimal laterally and the prefrontal, the supraorbital and the postfrontal dorsally. Its postero-medial continuation is the preorbital crest on the internal surface of the frontal. Probably this ossification originates within lamina orbitonasalis and in *Saichania* increases its size and closes the orbit in the front, or joins other additional ossification of this region.

Accessory ossification in posterior border of the skull roof. In *Pinacosaurus* the posterior border of the skull roof, which overhangs the occiput, contains a small bone bordered by distinct sutures. It is here designed the "tabular" (text-fig. 4, pl. 20, fig. 1). It contacts the parietal antero-medially, the squamosal anteriorly and the secondary dermal bone laterally. The homology of this bone is uncertain as its presence has not previously been reported in the Ornithischia.

Secondary dermal ossifications. A young individual of *Pinacosaurus* has additional secondary ossifications of dermal origin which cover partly the skull bones. Two pairs of secondary bones are present in the nasal region (text-fig. 2 and 3). One of them, situated centrally in front of the nasals, partly covers the premaxilla. Another pair overhangs the dorsal nasal opening from dorso-lateral side. Another two pairs of dermal ossification occur in the posterior region of the skull. One of them is coossified with the squamosal and the postorbital and forms horn-like protuberances at the posterior skull margin. The second pair forms lateral bony projections contacting the squamosal, jugal and postorbital. Aside from these four pairs of large dermal bones, in various parts of the skull there are fine bony tubercles that can be observed e.g. on internasal suture and near the maxilla-premaxilla suture on lateral side of the skull.

Accessory elements

Auditory apparatus. A part of the left stapes is preserved in the young specimen of *Pinacosaurus* (pl. 20, fig. 4). The bone is rod-shaped, 15 mm long as preserved with a diameter of 2 mm. The expanded foot plate is not preserved.

Hyoid apparatus. A part of hyoid apparatus is preserved in *Saichania* (GI SPS 100/151). It consists of two bent, rod-like bones and a central, unpaired bone that is bifurcated distally and has a convex dorsal surface (text-fig. 8; pl. 29, figs 6 and 7). Fragments of thin, battered bony sheets touch distal ends of the central unpaired bone. Paired, rod-like elements of the hyoid apparatus may be compared with those found in *Panoplosaurus* and *Euoplocephalus* (COOMBS, MS) and in *Protoceratops* and *Psittacosaurus* (COLBERT 1945) interpreted as first ceratobranchials. In *Saichania* no element resembling the second ceratobranchial of *Protoceratops* or *Psittacosaurus* (COLBERT, *l.c.*) has been found. The unpaired centrally located bone of *Saichania* is interpreted herein as the corpus (basihyal and basibranchial) with strongly developed, narrow lingual process (entoglossal process). The rod-like bones represent probably the first ceratobranchials. The fragments of the bony sheets situated near the posterior ends of the corpus may correspond to cornu hyale of FÜRBRINGER (1922), and ceratohyale of CAMP (1923). Some of these fragments may be derived from second ceratobranchials. If the position of the above sheets is natural, the first interpretation is more probable. It is also possible that the distal ends of the corpus may represent second ceratobranchials, but there is not the slightest trace of coossification of these elements with the corpus, which makes such an interpretation doubtful. The hyoid apparatus of *Saichania* is probably the first known so completely ossified apparatus in dinosaurs. A reconstruction of the hyoid apparatus of *Saichania* shown in fig. 11 differs considerably from that given by COLBERT (1945) for *Psittacosaurus* and *Protoceratops*. COLBERT

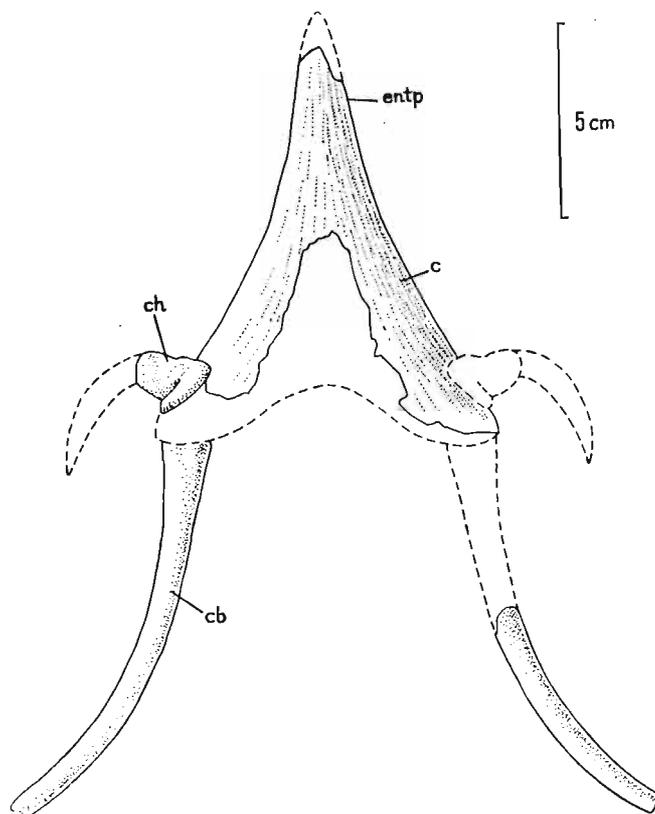


Fig. 8

Saichania chulsanensis gen.n., sp.n. Holotype specimen (GJ SPS 100/151). Reconstruction of the hyoid apparatus. Abbreviations: *c* — corpus, *ch* — ceratohyal, *cb* — ceratobranchial I, *entp* entoglossal process.

(*l.c.*) bases his reconstruction on the hyoid apparatus of recent crocodiles in which the cartilaginous corpus is broad without well developed entoglossal process. The structure of ossified elements of that apparatus in *Saichania* clearly shows that it is closer to that of *Sphenodon* (FÜRBRINGER, 1922) or *Lacerta* (GOODRICH, 1930).

Bony nasal structures

Nasal cavities of *Pinacosaurus grangeri* and of *Saichania chulsanensis* were easily emptied of loose sandy sediments. There are differences in the structure of nasal cavities in the above forms, both in the number and dimensions of ossifications. It is difficult to say whether differences are correlated with different ontogenic stages or are taxonomic variables, because only one specimen of a young *Pinacosaurus* (ZPAL MgD-II/1) and an adult *Saichania* (GI SPS 100/151) were at my disposal. In *Pinacosaurus* a well developed bony ridge is present along the whole length of the internal surface of the nasal in the dorso-lateral part of the nasal cavity. Similar pattern of longitudinal ridges along the underside of the nasals is found in some Theriodontia, e.g. cynodonts (*Diademodon*, *Nyctosaurus*), gorgonopsids (*Leontocephalus*), whaitsioids (*Moschowhatsia*) and tritilodonts (*Oligokyphus*) (WATSON, 1913; KEMP, 1969; TATARINOV, 1963, 1974; KÜHNE, 1965). In theriodonts such ridges are compared to the bony ones occurring in mammals (crista nasoturbinalis), and their presence is taken as evidence for existence of nasoturbinals. The same interpretation can be applied to the ridges on the nasals of *Pinacosaurus*. In the anterior part of nasal cavity in *Pinacosaurus* the nasal ridge joins a massive bony protuberance on the level of the lateral wing of the nasal, lacrimal, and maxilla (text-fig. 2) slightly posterior to the lateral premaxilla-maxilla suture. This conchal protuberance is convex anteromedially, and concave postero-laterally. Its third wall is bowl-like, and ventro-posteriorly

oblique. Along the skull roof this ossification forms a sharp, posteriorly directed ridge that passes into the nasal ridge described above. This ossification was described in *Pinacosaurus* (MARYAŃSKA, 1971) and interpreted as a maxilloturbinal. The whole bony structure in question is clearly visible both within the external nares and through the palatal vacuity. A partial bony internasal septum is another characteristic feature of the nasal cavity of *Pinacosaurus*. The anterior part of this septum is formed by a median ascending process of the premaxilla and the posterior part by massive, vertical wings that arise medially along the whole length of the nasal. These wings adhere closely one to another in the median line of the skull roof. They are high anteriorly, and diminish gradually toward the rear. In fossil reptiles known to me the nasal septum is never formed by the nasals. In some theriodonts only few ridges are formed by them.

Saichania chulsanensis. The nasal cavity of *Saichania* is very large and occupies the entire preorbital length of the skull (text-fig. 9). Three bony structures (crista naso-turbinalis, maxilloturbinal, and nasal septum) present in *Pinacosaurus* attain a much higher degree of the ossifica-

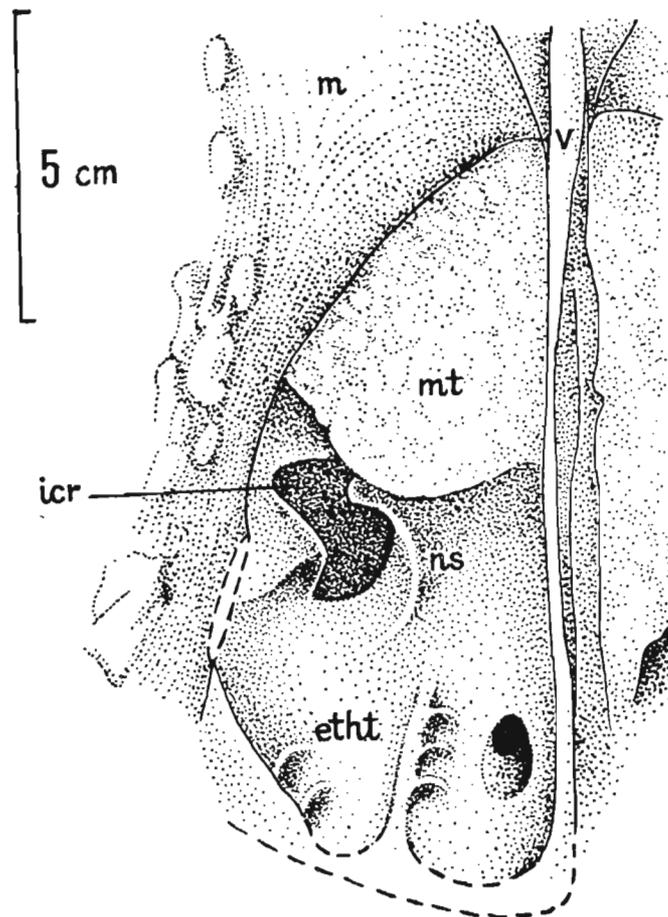


Fig. 9

Saichania chulsanensis gen.n., sp.n. Holotype specimen (GJ SPS 100/151). Ossified conchal system in palatal view. Part of the right maxilla, pterygoid and palatine removed. Abbreviations: *mt* — maxilloturbinal, *nt* — nasoturbinal, *etht* — ethmoturbinal region, *icr* — interconchal recess; other abbreviations as in fig. 2.

tion in *Saichania*. In addition *Saichania* has bony lamellae situated postero-dorsally in the nasal cavity. The nasal cavity of *Saichania* is completely divided into two pairs (right and left) by massive bony septum. Anteriorly, the internasal septum is composed of premaxilla and nasal and attains the vomeral keel ventrally. The parasphenoidal rostrum and an additional ossification

within the septum nasi are located antero-dorsally and take part in formation of internasal septum posteriorly. This ossification is here identified as an ethmoidal ossification. It extends anteriorly up to the part of the septum made by the nasal. Posteriorly the nasal cavity is closed by ossifications within the lamina orbitonasalis which forms the anterior orbital wall. The posterior part of the nasal cavity lies very close to the telencephalon; hence the olfactory lobes were very short. BROWN and SCHLAIKJER (1943) pointed out the existence of very short olfactory lobes in ankylosaurs and noted their complete coverage by ossifications of the frontal part of the brain case.

The description given below is based on the structure of the right half of the nasal cavity which is better preserved. The external nasal opening of *Saichania* is horizontally divided by a premaxillary sheet. The large dorsal foramen leads directly to the nasal cavity. The second foramen situated ventro-medially leads to the premaxillary sinus. The vast nasal cavity has two levels that contact one another only in the posterior part. A wide bony canal located just under the skull roof leads posteriorly from the dorsally positioned external nasal opening. It is called here the dorsal air passage. The bony internasal septum forms its medial wall. The ventral wall of this passage is made anteriorly by the premaxilla. Posteriorly the ventral and lateral walls are formed by ossified, maxilloturbinal and nasoturbinal elements (see below). At the distal termination of the nasal cavity the dorsal air passage bends latero-ventrally and reaches the second part of the nasal cavity which is positioned ventro-laterally to the above described dorsal canal. The route of the dorsal air passage is clearly visible in *Euoplocephalus* (see COOMBS, MS, fig. 21). The second part of the nasal cavity situated ventrally is broader than the dorsal canal and is located above and posterior to the palatal vacuity. This ventral part of the nasal cavity is interpreted here as a „cavum nasi proprium”. As it is located above the palatal vacuity, its anterior part is visible in palatal view of the skull, whereas the posterior part is obscured by the palatine. The cavum nasi proprium is closed anteriorly by a massive protuberance at the level of the lateral wing of the nasal, maxilla, and lacrimal that forms a base for a bowl-like ossification recognized as a maxilloturbinal (observed also in *Pinacosaurus*). The maxilloturbinal of *Saichania* is much stronger in anterior, ventral and median directions. It attains the frontal shelf of the maxilla anteriorly. Medially it contacts the internasal septum. The medial and dorsal surfaces of expanded maxilloturbinal form the lateral and ventral wall of the dorsal air passage along the whole of its length. Posterior to the maxilloturbinal on the medial part of the cavum nasi proprium there is a labyrinthine ossification, here interpreted as a bony nasoturbinal, which is supported by sagittal crest of the nasal. The crista nasoturbinalis of *Saichania* is very high and constitutes the latero-posterior wall of the dorsal air passage. The horizontal part of the nasoturbinal reaches the internasal septum and forms the posterior ventral wall of the dorsal air passage. A vertical ridge is present lateral to the horizontal part of the nasoturbinal. A deep interconchal recess which extends to the skull roof is located anteriorly between that ridge and the maxilloturbinal. This recess is closed on the lateral side by a thick scroll-shaped bone which forms a postero-lateral prolongation of the vertical nasoturbinal ridge. This bony element reaches the lateral wall of the nasal cavity and is located slightly above the postero-lateral region of the palatal vacuity. As the posterior part of the cavum nasi proprium could not be prepared through the palatal vacuity, the ventral part of the orbito-nasal wall was removed just above the vertical wall that closes the palatal vault posteriorly. This revealed a vertical bony crest and thin scroll-like bony sheets in the postero-dorsal part of the cavum nasi. These elements are interpreted here as the ethmoturbinals.

I could not trace in detail all connections of the sinus maxillaris with the nasal cavity without partial destruction of the single skull of *Saichania* at my disposal. A ventro-medially situated nasal opening leads to a premaxillary sinus that has a connection with the maxillary sinus (see p. 113). In this way a second air passage is being formed that is located below and laterally to the dorsal one. A connection of the anterior part of the sinus maxillaris with the cavum nasi

proprium has been described. It seems probable that the posterior part of the sinus maxillaris communicated with the nasal cavity as well, and the lacrimal duct opens into the nasal cavity in this region.

Another organ, as far unknown in ankylosaurs, was probably present in *Pinacosaurus* and *Saichania*. External nasal openings (see p. 103) are horizontally divided by premaxillae. The dorsal foramen is a true air passage. A ventro-medially situated foramen in *Saichania* and *Pinacosaurus* leads to a multichambered premaxillary sinus. A bony cavity distinguishable within the premaxillary sinus is situated dorso-medial to other premaxillary chambers and reaches the internasal septum. A deep vascular groove internally on the median wall of this cavity leads to a foramen located on the palatal side of the premaxilla. Similar foramina situated in that region are also present in other ankylosaurs (e.g. *Euoplocephalus* AMNH 5405, *Panoplosaurus* AMNH 5665, NMNH 11868, NMC 8531). Their existence was reported by GILMORE (1930) but was not explained. The position of this bony cavity in front of the nasal capsule and its connection with the oral cavity show in my opinion that this was a vomero-nasal organ (Jacobson's organ).

Remarks on the nares and the nasal cavities

Pinacosaurus grangeri and *Saichania chulsanensis* differ from all other known dinosaurs, and indeed all known fossil and living reptiles, in the unusual structure of their nares and nasal cavities which contain numerous ossifications. However, PARSONS (1970, p. 152) stated: "the nasal anatomy of the various extinct groups of reptiles is almost totally unknown". Distinct bipartition of the paired external nasal openings in *Saichania* (tripartition in *Pinacosaurus*), as well as the complicated structure of the premaxilla within the nares, has no counterpart in other Ornithischia. In gross anatomy the closest structural resemblance of the external nasal region is to be encountered in some mammal-like reptiles, as e.g. some theriodonts (TATARINOV, 1974; BRINK, 1960*a, b*) and pelycosaurus, in particular *Ennatosaurus tecten* (TATARINOV & EREMINA 1975). In addition to the premaxilla, the septomaxilla also forms part of the narial region of theromorphs. No separate septomaxilla can be seen in *Pinacosaurus* or *Saichania*, but TATARINOV & EREMINA (1975) interpreted the theromorph *Ennatosaurus* as having a septomaxilla contributing to the wall of a cavity for a lateral nasal gland within the lower margin of the nares, an interpretation which could be applicable to ankylosaurs as well. Taking such an interpretation into account, the third, laterally situated foramen in the external narial region of *Pinacosaurus* (see p. 103) and the smooth surface of premaxilla situated within the external narial region lateral to the air foramen in *Saichania* may have contained a lateral nasal gland. The exit of the naso-lacrimal duct in that region of the nose in *Pinacosaurus* and *Saichania* was not observed. Only the entrance of that duct, situated within the orbital wing of the lacrimal, is discernible. It is possible that the naso-lacrimal duct attains the nasal cavity in its posterior part, in the region of posterior part of maxillary sinus.

The terminology used herein for describing the structures of the nasal cavities in *Pinacosaurus* and *Saichania* is that of mammals and suggests homologies with elements of mammals. Use of mammalian terminology seems justified because the high degree of organisation of the particular elements is comparable to structures of the nasal cavity of mammals rather than to those of reptiles. My opinion is based mainly on the following features: 1) The first bony element to appear (in young *Pinacosaurus*) is a protuberance of the maxilla, nasal, and lacrimal on which an additional ossification is based. In mammals the maxilloturbinal is an additional ossification based upon the crista maxilloturbinalis, which is the earliest to appear in ontogeny; 2) Bony crests on the internal surface of the nasals in ankylosaurids and therapsida are regarded as a counterpart of the crista nasoturbinalis of mammals and prove the existence of a nasoturbinal. In *Pinacosaurus* as in theriodonts there is only a crest on the nasals corresponding to crista nasoturbinalis, but in *Saichania* the whole concha nasalis has been ossified: 3) Both

the location and structure of the third turbinal element correspond to the ethmoturbinals of mammals. The structure of the bony nasal septum is still another argument. In *Pinacosaurus* the internal bony septum is incomplete and consists entirely of the nasal and premaxilla. In *Saichania* this septum is fully ossified down the whole length of the nasal cavity. In the degree of ossification of the internasal septum *Saichania* resembles mammals rather than reptiles. Also, along the nasal suture of some mammals (e.g. : Felicidae) the nasal forms an internal protuberance which forms the base for the internasal septum. The proximity of the nasal cavity to the anterior part of the brain resembles mammals more than reptiles (PARSONS, 1956a, 1959b, 1967, 1970). Three conchal formations (preconcha, concha, and postconcha) develop in the cavum nasi proprium only in crocodiles among recent reptiles. The first element that appears in ontogeny is the concha. It is a projection on the lateral caval wall. Later it becomes subdivided into preconcha and concha. The concha is homologized with the maxilloturbinal of mammals (PARSONS, 1970). It seems that the only element of *Saichania* which is a counterpart of the lateral projection of nasal wall is the maxillo-turbinal. As that element appears in ankylosaurs very early in an ossified state, it may be presumed that it had been present in a cartilaginous state. It is probable that the maxilloturbinal of *Saichania* corresponds to the preconcha and concha of crocodiles. The postconcha of crocodiles is a convexity of the postero-lateral caval wall. In *Saichania* the ethmoturbinal system seems to be connected with the dorso-posterior wall. Both its structure and connection with the posterior wall suggest that it has no counterpart in modern reptiles. Homologies of various conchae among the different groups of living tetrapods are uncertain (PARSONS, 1970) and the grounds for homologizing conchal structures of extinct and modern tetrapods are even more ambiguous.

The only element of the nasal cavity of ankylosaurids resembling that of some recent reptiles is the dorsal air passage leading from external nares to the posterior part of the cavum nasi proprium. The dorso-medial position of that passage, in relation to the cavum nasi proprium with its posterior outlet to the cavum nasi, resembles the location of the vestibulum of some iguanids and agamids, that live in sandy areas (e.g. *Dipsosaurus*, *Callisaurus*, *Phrynosoma*, *Uma*) (STEBBINS, 1948; PARSONS, 1970). The vestibulum of these genera may form a long and curved tube. This comparison is based only on gross anatomy. It is possible that a large part of the supposed vestibulum of ankylosaurs may have been lined with olfactory epithelium as in the case in some agamids (e.g. *Otocryptis*), in which the vestibulum distinguished on the basis of gross anatomy does not correspond to that distinguished on histological grounds. A different interpretation of the dorsal air passage in *Saichania* is accepted in this paper. Because of its position between the skull roof and the nasoturbinal, the dorsal passage can be compared with the meatus nasi superior (*s. olfactorius*) of mammals. This interpretation is supported by the fact that the passage introduced air directly to the olfactory part of the cavum nasi proprium. In this case the ventrally located air passage leading from the additional nasal opening through the sinus maxillaris to the cavum nasi would be a counterpart of the meatus nasi medium which brings air to the anterior respiratory part of the cavum nasi proprium. Such an interpretation seems to be supported by a connection of that air passage with the sinuses surrounding the nasal cavity. It follows that the anterior, short and broad part of the nasal duct situated external to the horizontal premaxillary septum which divides the nostrils could be regarded as the vestibulum. The position of the lateral nasal gland suggested above seems to support this view. It may be supposed that the structure of the nasal cavity in *Pinacosaurus* and *Saichania* described above is more or less characteristic for all ankylosaurs. COOMBS (MS, fig. 21), in describing and illustrating sections of the cranial sinuses of *Euoplocephalus tutus*, has shown paired premaxillary sinuses, nasal sinuses, maxillary sinuses and two pairs of major cranial sinuses. The paired premaxillary sinus, nasal and maxillary sinuses are present also in *Saichania*. From the position of the transverse section, as shown by COOMBS (*l.c.*), the major cranial sinuses recognized by him may correspond among others to cavities inside the turbinal ossifications. A dorsally located major cranial sinus of *Euoplocephalus* corresponds probably to the interconchal

recess of *Saichania*, and the ventrally situated one is a section through a lateral part of nasoturbinal. The differences are due to more extensive development of secondary bony palate in *Euoplocephalus*.

The structure of the nasal cavity distinguishes ankylosaurids from all other dinosaurs as well as from all other fossil reptiles. Among extinct reptiles the Therapsida have been regarded as closest to mammals in development of the olfactory apparatus. Since the nasoturbinals in theromorphs are known mainly in carnivorous forms, the ankylosaurs are the only group of fossil herbivorous tetrapods (see also p. 139) showing a high organization of the nasal cavity. Presence of nasoturbinals in theriodonts has been interpreted as evidence of expansion of the olfactory surface (e.g. TATARINOV, 1974). In mammals both maxilloturbinal and nasoturbinal play a respiratory role and are not lined with sensory epithelium. As ankylosaurids have ossified ethmoturbinals, which undoubtedly executed sensory function, it may be supposed that maxilloturbinal and the nasoturbinal in *Saichania* played only a respiratory role as is the case in living reptiles and mammals. Similarly, the dorsal and ventral air passages in ankylosaurids prepared the air to enter the lungs as in present-day mammals. I suppose that the dorsal air passage of ankylosaurids was analogous to the narial passage in hadrosaurs. It is highly probable that within the hadrosaurs cavum nasi proprium (e.g. *Corythosaurus* and *Procheneosaurus*) a system of turbinals was developed, but was not ossified as in ankylosaurs. I regard interpretations by STERNBERG (1942, 1953) and RUSSELL (1946) of the hadrosaurian crest as a trapping mechanism more probable than that of OSTROM (1961, 1962) who assumed an olfactory function for that passage. It seems probable that only the posterior part of this crest may be lined with the olfactory epithelium (near the olfactory part of the cavum nasi proprium), but as in the ankylosaurs all anterior part prepared inhaled air and played the respiratory role. I think HEATON's (1972) interpretation of hadrosaurian crest as "resonating devices producing individually recognizable cells" (*l.c.*, p. 203) is probable, but only as additional and secondary function of that passage.

OSTEOLOGY OF THE POSTCRANIAL SKELETON

Vertebral column and ribs

Cervical vertebrae. The entire cervical region (7 vertebrae) is preserved in *Saichania* (GI SPS 100/151). The atlas and axis are fused with full coossification of the zygapophyses and incomplete fusion of the intercentrum of the atlas and the odontoid process of the axis (pl. 32, fig. 1). The neural arch and the single headed atlantal ribs are completely fused with a short intercentrum. The almost horizontal neural arch of the atlas is directed strongly posteriorly. There is no neural spine. The postzygapophyses are slightly oblique anteriorly so that their articular surfaces are almost horizontal. A strong, sharp midventral spine on the intercentrum is directed anteriorly and ventrally. The body of the axis is strongly depressed laterally with a well marked ventral crest. The posterior articular face is concave, circular and vertical. The neural arch is massive, rising obliquely backward with a strong antero-median crest. The neural spine is flattened antero-posteriorly, laterally terminated by swellings situated antero-dorsal to the postzygapophyses. The heavy neural arch is positioned perpendicular to the posterior part of the body. The neural canal is large. The incisions between the postzygapophyses are broad. The diapophyses are short and distinctly ventro-anteriorly directed. The strong axial ribs are two headed and articulate with the diapophyses and parapophyses.

Cervical vertebrae from the third to the seventh differ little in general structure (pl. 32, fig. 2). Their centra are strongly biconcave and depressed laterally below the diapophyses. The broad ventral crest is well marked. Centra of all vertebrae have offset, oblique articular surfaces such that the anterior surface is located below the posterior. This displacement of articular surfaces

is best developed on the third and fourth vertebrae. The sixth vertebra is almost straight. Gradual changes in the shape of articular surfaces can be noted backward from a circular posterior surface on the axis to a strongly dorso-ventrally flattened and oval one of the sixth vertebra. Neural arches are massive; boundaries of the arches and centra are hardly discernible. The neural canal is high and broad. At $2/3$ of the arch length, at the front of each vertebra, the canals are closed by thin horizontal sheets on which a median suture is clearly visible. Massive, transversely flattened, moderately tall neural spines rise upward and obliquely anteriorly at the posterior third of the arches. The neural spines are terminated with tubercular swellings that protrude slightly above the level of the postzygapophyses. These tubercles are separated from the neural spine tuber by a distinct, strongly marked depression on all cervical vertebrae. Pre- and postzygapophyses are prominent; their articular surfaces slant obliquely medially and protrude strongly backward and forward, so that large spaces remain between vertebrae. Diapophyses of all vertebrae are strongly flattened dorso-ventrally and directed laterally and slightly ventrally. Cervical ribs are preserved on all vertebrae. The ribs of the atlas are directed ventro-posteriorly, the axial ribs ventrally and slightly backward and the ribs of third to seventh vertebra are directed latero-posteriorly. Only the broadened distal terminations of the latter are bent forward. Ribs of third and fourth vertebrae have an articular connection. Ribs of fifth to seventh are completely fused.

A complete cervical region is not preserved in *Pinacosaurus*. There are some differences between the cervical vertebrae of *Pinacosaurus* (ZPAL MgD-II/1) and *Saichania*: 1) in *Pinacosaurus* the vertebral centra are more oblique than in *Saichania* and their anterior surface is situated lower than the posterior one; 2) The neural spines on first vertebra of *Pinacosaurus* are very low and completely reduced on posterior vertebrae; 3) The zygapophyses of *Pinacosaurus* are longer than in *Saichania*. The preserved cervicals of *Talarurus disparoserratus* have massive neural spines and weak diapophyses. Also the ventral crests of the centrum and the supra-articular tubercles near the postzygapophyses are weakly developed. Different displacement of the articular surfaces of the centra in *Talarurus* is observed. The anterior surfaces of cervicals are situated higher than the posterior ones, as is in nodosaurids (GILMORE, 1930). Among known ankylosaurids, *Saichania* is the only known in this moment genus in which the atlas and axis are fused, and *Pinacosaurus* the only genus in which the neural spines completely disappeared in the posterior cervicals.

Dorsal vertebrae. In no Mongolian ankylosaurid is the complete dorsal region perfectly preserved. In *Saichania* ten vertebrae are preserved. The first dorsal vertebra has a typical dorsal centrum, but its diapophyses and short ribs are coossified with the coracoid. The neural process of that vertebra is located transversely and thus resembles neural spines of cervical vertebrae. The second dorsal vertebra has a short rib backwardly pointing rib fused to the diapophyses. All dorsal centra are long, spool-like, and almost amphiplatyan. Neural arches are well developed; neural canals high. Transverse processes point obliquely upwards. Prezygapophyses are fused to form single, furrow-like articular surfaces. The postzygapophyses are fused, forming rod-like structure. Starting with third vertebra the ribs are loosely joined.

Differences in the structure of dorsal vertebrae of Mongolian ankylosaurids pertain chiefly to the height of neural arches and neural spines. In *Pinacosaurus* the neural arches are very high as compared to the length of centrum. The neural processes of *Talarurus* are massive and broadened at top. The degree of development of the ventral crest on the centrum varies. In *Pinacosaurus* the crest is weakly developed; in *Talarurus* it is broad; in *Saichania* it is particularly strongly marked in the anterior part of centrum. The posterior dorsal vertebrae are preserved in *Pinacosaurus* and *Talarurus*. The centra of four or five last vertebrae are fused, forming the presacral rod.

Dorsal ribs. The first ten dorsal ribs are preserved in *Saichania* (GI SPS 100/151). The first two pairs differs in shape from others and resemble the cervical ribs. The first rib is fused to the coracoid. The short second dorsal rib is directed strongly posteriorly (pl. 34). The third

and fourth ribs are flattened antero-posteriorly in ventral part and dorso-ventrally in dorsal. They are directed strongly posteriorly and almost parallel to the vertebral column. Starting with the fifth, ribs are flattened antero-posteriorly over their whole length and have a strong convex arch. Ventrally the ribs bend strongly inward so that they embrace the trunk of the animal from the sides and almost meet ventrally. In the dorsal part they are directed laterally. The ribs from the second to fifth are movable, from the sixth rib they are ankylosed to their vertebrae. Starting with the fifth rib a plate-like bony process appears on the posterior margin of the latero-ventral part of each rib. These plate-like processes (pl. 33, figs 3, 4 and 5) of dermal origin overlap the lateral side of the next rib. Each of these plates is fused to the rib at a few points (2-4). The overlapping plates form a uniform bony cover over the trunk along a latero-ventral line. Posterior to the fifth rib the position of these processes changes from lateral to ventral. Presumably these processes may occur in other ankylosaurs as well and are not a distinctive feature of *Saichania*. Similar structures are fragmentarily preserved in *Edmontonia rugosidens* (GILMORE, 1930) and in *Ankylosaurus* (BROWN, 1908, fig. 14).

Sacrum and sacral ribs. The sacral vertebrae are preserved in *Pinacosaurus* and *Talarurus*. The sacrum consists of four vertebrae with low, broad centra which are fused together. The neural canal is broad and high. The neural spines relatively low, laterally flattened and fused together. In *Pinacosaurus* (ZPAL MgD-I/31) broad transverse processes of the two first vertebrae are vertical and anteriorly oblique. Processes of the next two are horizontal. Ribs are coossified to transverse processes and contact the ilium along a distance corresponding to the length of the acetabulum. The difference between the sacrum in *Pinacosaurus* and *Talarurus* lies in the longer transverse processes and sacral ribs of *Pinacosaurus*. In connection with this, iliac blades of *Talarurus* are relatively closer together than in *Pinacosaurus* in which they are widely spaced.

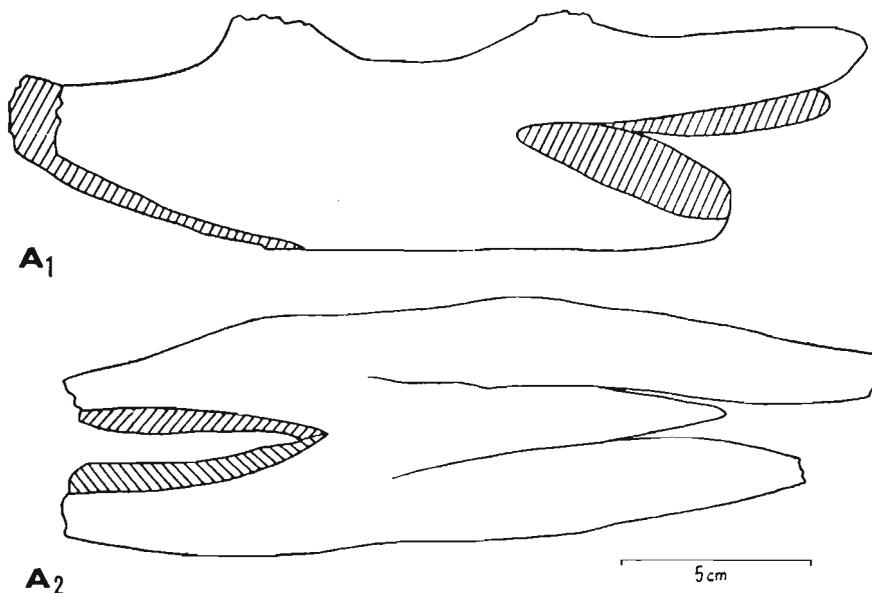


Fig. 10

“*Dyoplosaurus*” *giganteus* MALEEV (PIN 551—29). Chevron of the middle caudal vertebra in A_1 — lateral view, A_2 — ventral view. The articular surfaces shaded.

Caudal vertebrae and ribs. An entire caudal series of vertebrae is preserved in *Pinacosaurus* (ZPAL MgD-II/9, ZPAL MgD-II/31, PIN 614), and a fragmentary tail is known for *Talarurus plicatospineus* and „*Dyoplosaurus*”. The complete caudal region of *Pinacosaurus* has 40 vertebrae. Centra are slightly biconcave. Proximal vertebrae are of almost the same height and width, and short in comparison with dorsal centra. Distally the centra become elongate and lower, their shape

changes from oval in cross section to square. Natural arches of proximal caudals are very high. Coossification of the arch with the body varies. Neural arches are free in many cases. Distally they become considerably lower and starting with the fifteenth are very low and lack rising neural spines. Dorsal surfaces of the arches become concave. Prezygapophyses are relatively long on the first vertebra and laterally embrace short postzygapophyses. From the fifteenth vertebra the zygapophyses become distinctly V-shaped and their anterior bifurcated part closely embraces wedge-shaped postzygapophyses (pl. 25, fig. 5) along their whole length. The first two or three caudal vertebrae have long, strong transverse processes that contact the posterior part of the ilium. Posteriorly, these processes diminish and by the eighth caudal, disappear. Chevrons appear on the third caudal. Chevron shape varies greatly onto the centrum and hang down as V-shaped, laterally flattened trabecules. Distal chevrons become lower, strongly elongated antero-posteriorly, and flattened on ventral side. On the fifteenth vertebra at the base of the chevrons bony projections appear which are directed forward and backward to form articulations between the hemal arches similar to zygapophyseal articulations. In this region the chevrons resemble in morphology the neural arches. Ossified tendons closely winding round the caudals appear at fifteenth caudal. Because of the modification of the neural arches and the chevrons, distal parts of the tail have very limited possibilities of movement and form a tail-club, a structure typical in ankylosaurs (text-fig. 10 and 11, *B₈*).

The tail structure in all Mongolian ankylosaurids is similar to that of *Pinacosaurus*. Differences in *Pinacosaurus*, *Talarurus* and "*Dyoplosaurus*" in coossification of some parts of individual vertebrae as well as the degree of fusion of the arches with the centra seem to be individual variations rather than taxonomic characters. In all Mongolian ankylosaurids the tail-club is terminated by bony plates. These are best developed in "*Dyoplasaurus*" (MARYAŃSKA, 1970). It follows from a comparison of a young *Pinacosaurus* with an adult one, that the degree of ossification of tendons and dermal armour plates around the tail may serve as an indicator of individual age.

Sternum. The sternal plates of *Pinacosaurus* and *Talarurus* were described by MALEEV (1954, 1956). In both, they form a single rhomboidal plate formed by fusion of right and left segments, with a blunt process directed postero-laterally which contacts the coracoid. In *Saichania* (ZPAL MgD-I/112) the sternal plates are more extensively developed (pl. 32, fig. 3 and 4, pl. 33, fig. 1). There is the single medio-anterior part which corresponds to the preserved parts of the sternum in *Pinacosaurus* and *Talarurus*. Anterior to this part, divergent, relatively short pointed plates are developed, and posteriorly there are strongly expanded plates not completely fused along their midventral line. At least four or five pairs of ribs are connected with the sternum. This very strong ossification of the sternal complex in *Saichania* is unique not only within the ankylosaurids but also among Ornithischia.

Pectoral girdle and fore limb

Pectoral girdle. The scapula of Mongolian ankylosaurids is completely fused to the coracoid as is the case in North American forms. In *Saichania* (GI SPS 100/151) the scapular blade (pl. 35, fig. 3) is slightly convex outwards. The broadened distal end of the scapula is bent ventrally. Along approximately half the length of the scapula its dorso-anterior border is flat and broad and at the level of the glenoid forms an acromial process oriented at right angle to the scapular blade. This process is most expanded at the line of the coracoid-scapula contact. The ventral margin of the scapula is broad proximally and sharp posteriorly. The glenoid cavity is formed of the coracoid and scapula. It is shallow, open, and crescent-shaped. The scapula is very low behind the glenoid.

The coracoid in *Saichania* is very small and strongly bent medially behind the glenoid. In natural position the coracoids almost contact one another. A characteristic feature of the

coracoid of *Saichania* is its fusion with transverse process and rib of the first dorsal vertebra.

The scapulocoracoid of *Pinacosaurus* (PIN 614) is more convex externally, and the coracoid is not directed as strongly medially, as in *Saichania* (pl. 26, fig. 5). The scapulocoracoid of a young individual (pl. 23, figs 4 and 5) is relatively long. That of *Talarurus* differs much; the scapula is relatively long with a weakly developed acromion process. The coracoid in *Talarurus* is much larger and straight and the glenoid is deep and more closed than in *Saichania* and *Pinacosaurus*.

Humerus. The humerus of *Saichania* is very massive. Its proximal termination is strongly expanded and almost straight. Medial to the humeral head a strong process is developed, and laterally is the proximal part of deltopectoral crest. The humeral head is flattened, lies on the extensor surface, and wraps around onto the medial process. On the proximal edge of the deltopectoral process, just lateral to humeral head, a smooth depression is developed. It resembles a mammalian sulcus intertubercularis which is connected with biceps muscle. A strong deltopectoral process begins lateral to humeral head and extends down the shaft to terminate distal to humeral mid-length (pl. 35, fig. 1). The shaft is poorly separated from deltopectoral crest, and strongly flattened dorso-ventrally. The whole bone is slightly convex dorsally. The distal termination is less expanded than the proximal. The distal articular surface lies on flexor surface. Both epicondyles are developed. The radial condyle is oval and situated at the centre of distal expansion. The ulnar groove is relatively shallow. A broad articular surface for the ulna is also developed on the flexor surface of the entepicondyle. This surface wraps around onto the flexor surface adjacent to the capitulum. The supinator process is prominent. Axes of the proximal and distal expansions lie at an angle of 15° to each other, so torsion along the shaft is present.

The humerus of *Pinacosaurus* (text-fig. 11, *B*₁ pl. 23, fig. 1; pl. 26, fig. 4) is more slender than in *Saichania* and *Talarurus* as a result of a lesser expansion of the proximal termination and, especially, of the median process. Also, the deltopectoral crest is less developed, especially in its proximal part. The humeral shaft is better distinguished and less flattened than in *Saichania*. The ulnar groove in *Pinacosaurus* is better marked. The humeral head is developed on extensor surface but wraps around onto the proximal end. The humerus of *Talarurus* is more massive than that of *Pinacosaurus*, but not so massive as in *Saichania*, with a less developed proximal expansion and a very well developed ulnar groove. The humerus of *Saichania* is more massive than in the North American *Euoplocephalus* and *Ankylosaurus*, and has a more expanded proximal end and a larger delto-pectoral crest. A strongly concave, smooth surface on the proximal margin, lateral to humeral head is characteristic of *Saichania*, and is not present in other ankylosaurids. In *Saichania* it is developed in a place which in *Euoplocephalus* and *Ankylosaurus*, according to COOMBS (MS) is the insertion of scapular deltoid muscle. Both the shape of the humeral head and the presence of a bony connection between the pectoral girdle and the vertebral column prove that the motion mechanics of the fore limb of *Saichania* must have been different from that of other ankylosaurs. This problem will be dealt with in another paper.

Ulna. The ulna of *Saichania* is very massive with a broad proximal termination and an antero-posteriorly flattened distal end. The olecranon process is relatively low. The sigmoidal notch is strongly open and shallow. The processes bordering it meet at an angle of about 120° . The posterior process is more extensive than the lateral. The proximal articular surface is very large, and oriented at an angle of $30\text{--}40^\circ$ to the longitudinal axis. Because of a very strong development of the posterior process of the proximal part of the ulna, the obliquely situated articular surface embraces about $2/3$ of the ulnar length (pl. 29, fig. 5). The distal termination is narrow, the distal margin sharp, and the articular surface is oblique latero-medially and parallel to the proximal articulation.

The ulna of *Pinacosaurus* (pl. 23, fig. 2; pl. 26, fig. 3) differs from that of *Saichania* in the lesser expansion of its proximal part and in having a distinct shaft which embraces about $1/2$ of the

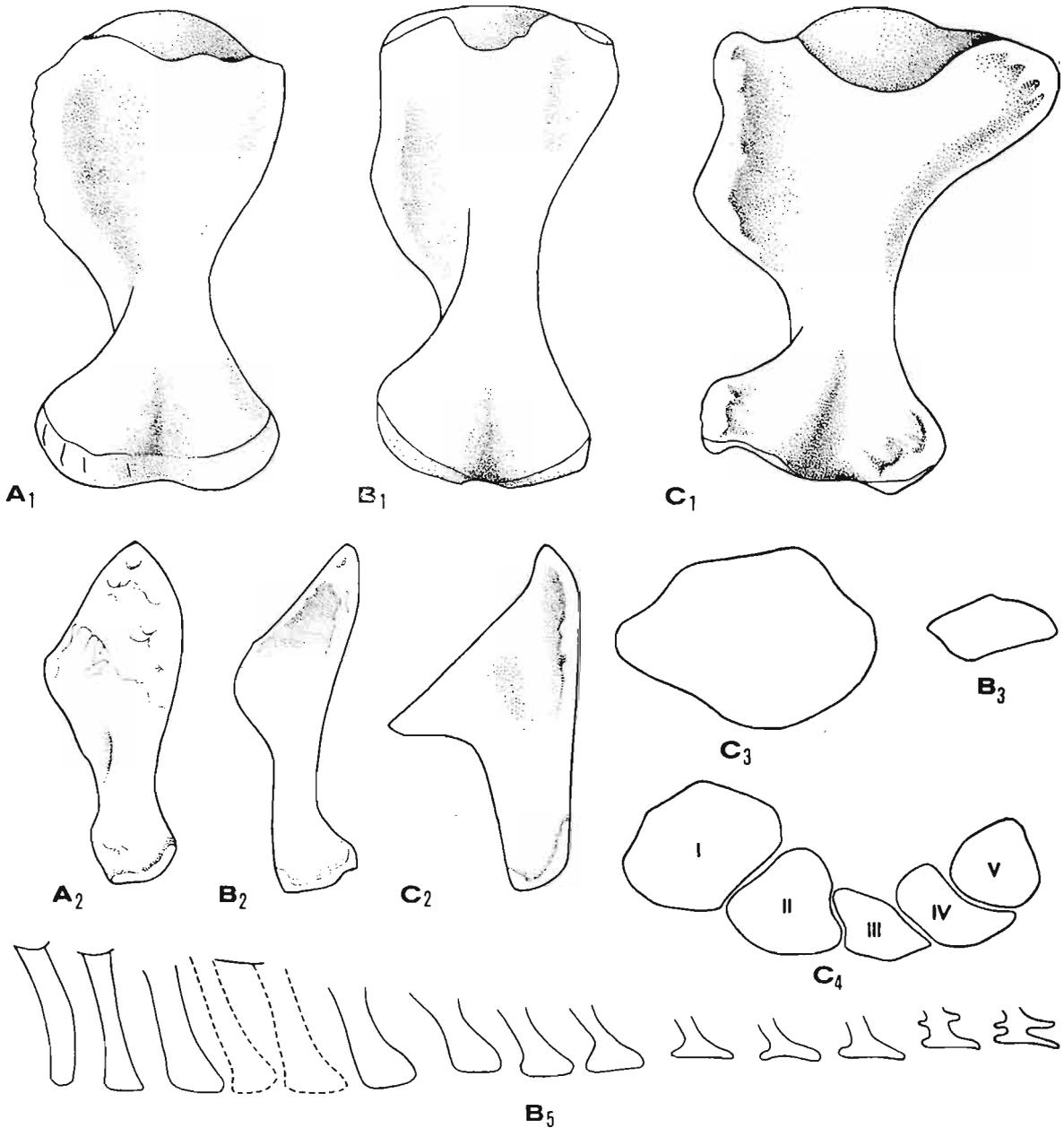


Fig. 11

Diagrammatic drawing showing the outlines of some bones in Asian Ankylosauridae. *A* — *Talarurus plicatospineus*, *B* — *Pinacosaurus grangeri*, *C* — *Saichania chulsanensis*, 1 — left humerus in dorsal view, 2 — right ulna in posterior view, 3 — proximal surfaces of the left radius, 4 — proximal surfaces of the left metacarpals, 5 — the chevrons of caudals (third to sixteenth from left to right). Not to scale.

ulnar length. The olecranon is very tall and sharp. The sigmoidal notch is less open than in *Saichania* and the processes bordering it are equally developed and meet at an angle of 70°. The olecranon is less developed in a young *Pinacosaurus* (ZPAL MgD-II/1) than in an adult (PIN 614). The ulna of *Talarurus* is more massive than in *Pinacosaurus* but more slender than in *Saichania*, except that its distal termination is more expanded and articular surface more terminally positioned (pl. 26, fig. 2; text-fig. 11, 2).

Radius. The radius of *Saichania* is straight, massive, slightly broadened at proximal termination, and strongly expanded distally. The proximal articular surface is oval, slightly concave

and terminally positioned. The bone is flattened antero-posteriorly. The entire distal termination of the radius protrudes considerably beyond the ulna. This protrusion together with the oblique distal articular surface of the ulna indicates a strong oblique orientation in the forearm. The radius of *Pinacosaurus* (pl. 23, fig. 3) is more slender than in *Saichania*. The proximal articular surface is very narrow (text-fig. 11, 3) especially in the young individual. The radius of *Talarurus* is almost as massive as in *Saichania*.

Manus. Aside of the intermedium mentioned by MALEEV (1954a) none of the carpal elements are present in any Mongolian specimen. Metacarpals I—V are preserved in natural arrangement in *Saichania* (GI SPS 100/151) and in *Pinacosaurus* (ZPAL MgD-II/9). The metacarpals I—V of *Saichania* (pl. 36, fig. 2) are very massive and flattened antero-posteriorly. Metacarpal I is the widest; its proximal articular surface (text-fig. 11, 4) is slightly concave and subquadrangular. A strong protuberance exists on the posterior side of the proximal end of the shaft. The distal articular surface has a strong internal condyle. Metacarpal II has a subtriangular, slightly concave proximal articular surface. A broad crest extends upward and outward from the shaft on the side of internal condyle. The distal articular surface has equally developed condyles. Metacarpal III is the longest. Its proximal surface is strongly convex and oblique posteriorly. The shaft is flattened with a broad crest running on the posterior side from internal condyle. A distinct tuber is present on the slightly concave anterior side of the shaft near the lateral margin. Distal surfaces of metacarpals I and II are convex with well developed condyles and are situated in a plane perpendicular to the long axis of the bone; the articular surface of metacarpal III is distinctly shifted to the anterior side of bone. Metacarpal IV is flattened laterally and has crescent-shaped, convex proximal surface. A strong depression in the shaft is present proximally on the lateral side of metacarpal V. Metacarpal V is the smallest of all metacarpals. The distal termination is narrow, the condyles not developed. In natural arrangement the metacarpals form an arch with metacarpal V shifted distinctly backward.

Not all the phalanges are preserved. They are very short with shallow proximal articular surfaces. Their distal terminations have strongly divided condyles. Ligamental depressions are not developed. The distal articular surface is more expanded on the dorsal than on the ventral side, suggesting greater extension than flexion movements. At metacarpal I a partial and at metacarpal II a complete small crescent-shaped bone is preserved, each having a concave articular surface for the metacarpal and convex distal articulation. These bones articulate with the metacarpals to form an extension of distal articular surface on the anterior side. I recognize them as sesamoid bones (pl. 36, fig. 4). There is no trace of sesamoids at metacarpals III and IV in which the distal articular surfaces are well developed anteriorly.

The general shape and position of articular surfaces of metacarpals in *Pinacosaurus* (ZPAL MgD-II/9) is similar to that of *Saichania*. Slenderness of *Pinacosaurus* metacarpals (pl. 24, fig. 5) is an essential difference. First phalanges are preserved at metacarpals I—IV; they are long, unlike those of *Saichania*, and have strongly developed lateral condyles. The second phalanx of digit III is low and the ungual has the form of a very small nail. The phalangeal formula of *Pinacosaurus grangeri* is unknown. It can be only stated that its third digit has three phalanges, not four as it was claimed by MALEEV (1954). Most probably a phalangeal formula of that genus was 2 : 3 : 3 : 3 : 2 as in *Talarurus*. Comparison of *Saichania*, *Pinacosaurus* and *Talarurus* shows that the manus of *Saichania* was most massive, that of *Talarurus* more slender, and the longest and most slender was that of *Pinacosaurus*.

Pelvic girdle and hind limb

The pelvic girdle and hind limb in *Saichania* (GI SPS 100/151) are not preserved. Descriptions of these in *Pinacosaurus* and *Talarurus* by MALEEV (1954, 1956) are supplemented below. In *Pinacosaurus* and *Talarurus* the subacetabular and postacetabular portions of the ilium lie horizontally, whereas the narrow preacetabular part of the ilium is oblique, particularly in

Pinacosaurus. A thin, narrow, dorsal plate is situated horizontally, and the massive preacetabular ilium is located along dorso-lateral body line. Strong divergence of the preacetabular ilium is characteristic of *Pinacosaurus*, and suggests the trunk of that genus was very wide. The acetabulum has a more prominent border in *Talarurus*, whereas in *Pinacosaurus* it is hardly marked. Bony connection of the ilium with sacral vertebrae in both genera takes place along the length of the acetabulum. The first sacral rib joins the ilium at the front of the acetabulum, the fourth — behind its posterior border.

The ischium of *Talarurus* differs from that of *Pinacosaurus* in being wider proximally and having a greater backward curvature of the shaft.

The material under study does not furnish any new data about the structure of the ilium and hind limb in comparison with the description of MALEEVA (1954, 1956). It must be corrected that the femur illustrated by MALEEVA (1954, p. 158, fig. 11) does not belong to *Syrmosaurus* (= *Pinacosaurus*) but to *Talarurus* (PIN 517—101).

Pes. Fragments of the pes are preserved in the skeleton of *Pinacosaurus* (ZPAL MgD-II/9). Metatarsal I is preserved together with the phalanges of digit I as well as the fragments of metatarsals II and III and phalanges of the fourth digit. The phalangeal formula is unknown, but it is possible to state that the pes of *Pinacosaurus* has four well developed metatarsals (pl. 24, fig. 5), not three as stated by MALEEVA (1954). The preserved phalanges are very low with strongly developed articular surfaces that are deeply concave proximally and convex with double condyles distally. Ligamental fossae are distinctly marked. The terminal hoof-like unguals (pl. 24, fig. 7) are large and broad with well developed proximal articulations.

As compared to the pes of *Talarurus* (MALEEVA, 1956), metatarsals of *Pinacosaurus* are more slender and the unguals broader. A phalangeal formula of 2 : 3 : 4 : 5 : 0 for *Talarurus* was proposed by MALEEVA (*l.c.*), but I doubt this is correct. The pes which served as a basis for this formula was completed with bones belonging, in fact, to several individuals, and it is likely that the fourth digit consisted of four, not five, phalanges. The complete pes of "*Dyoplosaurus*" is unknown. The preserved fragments suggest that it has four digits as in other Mongolian ankylosaurids.

Dermal armour

A complete armour of the anterior part of the body in natural arrangement is preserved in *Saichania* (GI SPS 100/151). It consists of two uniform belts, a cervical and a pectoral, and numerous loose elements that covered the body both dorsally and ventrally. Cervical and pectoral half-rings have identical construction. They consist of two bony layers (pl. 36, fig. 1). The deeper half-ring is a uniform, bony bar thickened at its end. This deeper layer is covered by a superficial half-ring formed of three pairs of large, keeled, sharply pointed plates that are joined one with another by square coossified fields of fine, oval, tubercular ossifications. These two layers of each half ring are fused together along the anterior margin at 1/3 of its length. The central and distal parts of the belts are free. Both layers are fused as well by bony bridges along the posterior margin. Keeled plates that take part in the structure of the external layer of the pectoral girdle are much larger than those of the cervical girdle and small fields of fine ossifications are not so closely set as in the cervical half-ring.

Posterior to the pectoral girdle the armour plates are symmetrically arranged into half-rings and longitudinal belts (see KIELAN-JAWOROWSKA & BARSBOLD, 1972, pl. 2, fig. 1). However, they floated freely in the skin and did not possess a continuous lower bony layer. Many types of plates and scales may be distinguished among the armour elements (pl. 36, figs 6—11); the most common are: 1) large keeled thin-walled, sharp-pointed plates; 2) smaller, keeled thick-walled plates; 3) conical scales slightly hollowed at the base; 4) crest-like, laterally flattened large scutes of narrow base and sharp, peripherally situated peak; 5) oval, low, asymmetrical sharp-pointed scales; and 6) various fine ossifications. Almost every one of the larger plates

is surrounded by a ring of fine tubercular ossifications. In top view the different types of scales are set in symmetrical longitudinal belts to the sides of the median body line. Symmetrical conical scales evidently resting on the neural spines are placed along the median line. Lateral to them is a belt of large, keeled, thin-walled plates with their peaks pointing backwards. These large plates rest on ribs and intercostal tendons. Interspaces are covered with numerous fine ossifications. The sides of the body are very strongly armoured by plates and scales arranged in several rows. Each large element is surrounded by smaller, conical scales. Flattened keeled plates are arranged midway on the flanks of the body with their peaks pointing backwards. Ventral to them there is a row of large plates, the peaks of which also point backwards, and below this there is another row with peaks pointing forward.

The armour of *Pinacosaurus* was probably similar in structure as may be determined from preserved elements. Both two-layered half-rings, cervical and pectoral, are distinct in a young individual. The armour of *Talarurus* consists of cervical and pectoral half-rings, but they are narrower than in *Saichania*, and similar pelvic armour. Rib-groove ornamentation is characteristic in the armour elements of *Talarurus*. Armour plates of *Sauroplices* (BOHLIN, 1953) are ornamented in a similar way. The preserved armour elements of "*Dyoplosaurus*" have been described (MARYAŃSKA, 1970).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION OF ASIATIC ANKYLOSAURIA

There are at least 26 Asiatic sites from which the remains of ankylosaurs are known, in the sediments of the Lower and Upper Cretaceous. All these sites are situated roughly between 63°—130° east of Greenwich and 23°—62° latitude north, in the area of the Mongolian People's Republic, China, USSR and (?) India (text-fig. 1 and table 1).

The present knowledge of continental Cretaceous sediments of Central Asia does not allow precision in determining relative and absolute age. Table 1 shows a compilation of recent data. Temporal positions are based on studies of continental faunas (invertebrates, mammals and some cases of dinosaurs) which in most cases are endemic to Asia, and therefore the stratigraphic conclusions must be regarded as tentative. Only three Upper Cretaceous units can be formally accepted. These are: The Djadokhta Formation (BERKEY & MORRIS, 1927; LEFELD, 1971), Barun Goyot Formation and Nemegt Formation (MARTINSON *et al.*, 1968; GRADZIŃSKI *et al.*, 1969; GRADZIŃSKI & JERZYKIEWICZ, 1972). Stratigraphic units called "svita" distinguished by Soviet geologists in Mongolia do not always correspond to units of international classification, and consequently an informal terminology is here applied to such units (e.g. Bayn Shireh „formation" —svita). A compilation of recent results obtained by the Soviet geologists in Mongolia has been presented by MARTINSON (1973, 1975) who has distinguished the following svitas in the Upper Cretaceous: Sayn Shand (Lower Cenomanian), Bayn Shireh (Upper Cenomanian to Lower Santonian), Barun Goyot (Upper Santonian to Campanian) and Nemegt (Maastriichtian). MARTINSON (*l.c.*) does not distinguish a separate stratigraphic unit for the sediments of, among others Bayn Dzak (Djadokhta Formation of American and Polish authors), but has included them into the Barun Goyot svita. BARSBOLD (1972) in the stratigraphic scheme of the Upper Cretaceous of Mongolia mentions the Djadokhta svita isochronous with the Barun Goyot svita. According to the results of the Polish-Mongolian expeditions to the Gobi Desert in Mongolia (GRADZIŃSKI *et al.*, 1969; LEFELD, 1970; GRADZIŃSKI & JERZYKIEWICZ, 1972; KIELAN-JAWOROWSKA, 1974a, 1975a, 1975b; MARYAŃSKA & OSMÓLSKA, 1975) both the litology and faunal contents of Bayn Dzak sediments prove without doubt that they should be regarded as a separate lithostratigraphic and biostratigraphic unit (Djadokhta Formation), older than the Barun Goyot Formation.

Sediments at Bayn Shireh that contained remains of *Talarurus plicatospineus* were regarded by MALEEV (1952c) as the youngest Cretaceous sediments in Mongolia, i.e. Maastrichtian in age. This opinion was not confirmed by later investigations. An Upper Cenomanian to Lower Santonian age ascribed to these sediments by Martinson (1973, 1975) is more probable. The same pertains to Sheeregeen Gashoon sediments, the age of which was initially determined by MALEEV (1952c) and KONZHUKOVA (1955) as Maastrichtian. According to new data (MARTINSON, 1973; BARSBOLD, 1972; SHUVALOV, 1975) these sediments or at least a part of them, represent the Bayn Shireh svita and are Upper Cenomanian to Lower Santonian in age. According to MARYAŃSKA & OSMÓLSKA (1975) the sediments at Sheeregeen Gashoon containing *Microceratops gobiensis* (and remains of ankylosaurs) should be regarded as older than the Djadokhta Formation which yields *Protoceratops andrewsi*.

The oldest sediments containing ankylosaurs in Asia are at Khovboor (see text-fig. 1 and plate 1) in Mongolia (undescribed remains in the collections of PIN) and at Tebch in China (*Saurolites scutiger*, BOHLIN, 1953). At all these sites the ankylosaurs are associated with, among other things, psittacosaurs, which suggests a Lower Cretaceous age. Undoubtedly younger are the sediments of the so-called Bayn Shireh svita containing *Talarurus plicatospineus* and, among other things, remains of primitive hadrosaurs. The Djadokhta Formation with *Pinacosaurus grangeri*, other dinosaurs, and mammals (table 1) seems to be still younger. The Barun Goyot Formation and its chronological counterparts contain *Saichania chulsanensis* gen.n., sp.n. and are younger than the Djadokhta Formation. The youngest Cretaceous sediments in Mongolia containing ankylosaurs ("*Dyoplosaurus*" *giganteus*) are those of the Nemegt Formation. The above scheme of relative geochronology of Cretaceous sediments is based on investigations of ankylosaurs. It confirms the results of KIELAN-JAWOROWSKA (1974b, 1975a, 1975b) based on studies of mammals and the data obtained by MARYAŃSKA and OSMÓLSKA (1974, 1975) based on studies of the Pachycephalosauria and the Protoceratopsidae. This scheme agrees only in part with suggestions of MARTINSON (1973, 1975) based on studies of invertebrates.

The ankylosaurs are represented in Asia only by the Ankylosauridae (*sensu* COOMBS, MS). The Nodosauridae (*sensu* COOMBS, *l.c.*) are unknown from Asia. Abundance of Ankylosauridae in post-Middle Campanian Late Cretaceous sediments has been noted (e.g. GILMORE, 1923, 1930; NOPCSA, 1928; PARKS, 1924; SAHNI, 1972; STERNBERG, 1929; COOMBS, MS) in North America (Two Medicine Formation, Oldman Fm., Judith River Fm. Edmonton Fm.). In Asia, Ankylosauridae are present earlier in the Late Cretaceous or even in the Early Cretaceous. The earlier appearance of Ankylosauridae in Central Asia than in North America may suggest that the former area is the center of their early radiation. Comparison of the latest Cretaceous ankylosaurian fauna of Asia and North America (Santonian — Late Campanian or Maastrichtian in Asia and Middle Campanian — latest Maastrichtian in North America) shows that in this interval of time the Ankylosauria were represented on both continents not only by different genera of Ankylosauridae but partly also by different families. KIELAN-JAWOROWSKA (1974a, 1974b) on the basis of study of Cretaceous mammals from both continents has concluded that Asia and North America during the latest Cretaceous were separated by a barrier, possibly by marine straits, and interchange of mammals had taken place by means of a sweepstakes route. Existing currents allowed occasional migration of mammals from Asia to America but not vice versa. Nevertheless, the problem of migration of dinosaurs is more complicated. The earliest record of an ankylosaurid in North America is in the Middle Campanian. Approximately at the same time the Protoceratopsidae and Pachycephalosauridae made their appearance on that continent. Possible migration of these dinosaurs from Asia to America may have taken place prior to the Campanian. The study of this problem needs detailed investigations of the relations between the Asiatic and North American dinosaurs such as *Saurolophus angustirostris* and *S. osborni* and the genera *Tarbosaurus* and *Tyrannosaurus* and *Albertosaurus*. ROZHDESTVENSKY (1968, 1974) suggested a close relationship between these forms and bidirectional migration

of dinosaurs between Asia and America during post-Campanian times. The question of Early Cretaceous migrations of dinosaurs between the continents poses another problem. Absence of certain groups on one or another continent neither proves nor precludes migration (*sensu* land connection) but rather proves existence of other barriers (e.g. ecological ones) that have hampered or prevented migrations of certain groups. For example, the Nodosauridae are well represented in the Cretaceous both in Europe (since the Wealden) and in North America (since the Arundel and Cloverly Formations). The Nodosauridae penetrated into Asia neither during Early nor Late Cretaceous, although the Pachycephalosauridae and the Iguanodontidae did. But the oldest and most primitive representatives of both latter families occur in the Wealden of Europe together with the Nodosauridae. Migration of pachycephalosaurs and iguanodonts from Europe to Asia proves that such routes were possible. However, they were used neither by the Early Cretaceous European nodosaurids and hypsilophodonts, nor by the Asian psittacosaurids. Possibly faunistic differences between Central Asia and other continents during Cretaceous times depended on different ecological conditions connected with distance from the sea and differences in vegetation. Possibly the absence of the Ceratopsidae in the late Cretaceous of Asia (taking into account the differentiation of the Protoceratopsidae — MARYAŃSKA & OSMÓLSKA, 1975) is connected with unfavourable living conditions rather than with lack of opportunity for migration.

EVOLUTION OF ASIATIC ANKYLOSAURIDAE

A comparison of the relatively rich osteological material of the Mongolian Ankylosauridae beginning with *Talarurus*, through *Pinacosaurus* and *Saichania* to "*Dyoplosaurus*" reveals some trends in the evolution of their skeletons (text-fig. 12). These are: the changes in skull structure toward greater massiveness attained by shortening relative to width, by stronger ossification of the orbital region involving the neomorphic bones, and by stronger ossification of the palate. The latter is attained through development of horizontal maxillary shelves and expansion of the palatine forward and the maxilla backward. The tendencies toward greater massiveness of the skull are reflected in the structure of the neurocranium. Forms with relatively light skull (*Talarurus*) are characterized by separate openings for nerves and blood vessels posterior to the foramen ovale. In intermediate forms (*Pinacosaurus*) a reduction in the number of openings is observed and in the most advanced forms (*Saichania*, *Tarchia*) a single, common opening is formed. A complication of cranial sinuses parallels these changes. This is expressed by development of multichambered premaxillary and maxillary sinuses. Studies of Mongolian Ankylosauridae do not support the generally accepted opinion on a tendency to general increase in body size (STEEL, 1968). Not a single form in Mongolia has attained size of the North American ankylosaurs such as *Ankylosaurus* or the largest individuals of *Euoplocephalus*. This pertains both to skull size and body size. A general tendency toward greater massiveness existed in the postcranial skeleton, but it was not consistent through all forms. For example, *Pinacosaurus* is characterized by a relatively light skeleton and slender limbs, but *Saichania* is characterized by a very massive skeleton. The oldest well known Upper Cretaceous ankylosaurid (*Talarurus*) occupies an intermediate position with regard to massiveness of the skeleton. A comparison of the postcranial skeleton shows that no essential change occurred in pelvic structure from *Talarurus* to "*Dyoplosaurus*". The pectoral girdle has been subjected to much greater changes. The sternum has changed considerably.

A comparison of Asiatic Ankylosauridae with North American genera, generally younger stratigraphically, suggests that forms similar to *Talarurus* and *Pinacosaurus* may have migrated from Asia to North America. These genera could not have been more advanced than *Pinacosaurus*. North American ankylosaurids (*Euoplocephalus* and *Ankylosaurus*) have more progressive ossification of the palate and further shortening of the skull in relation to its width.

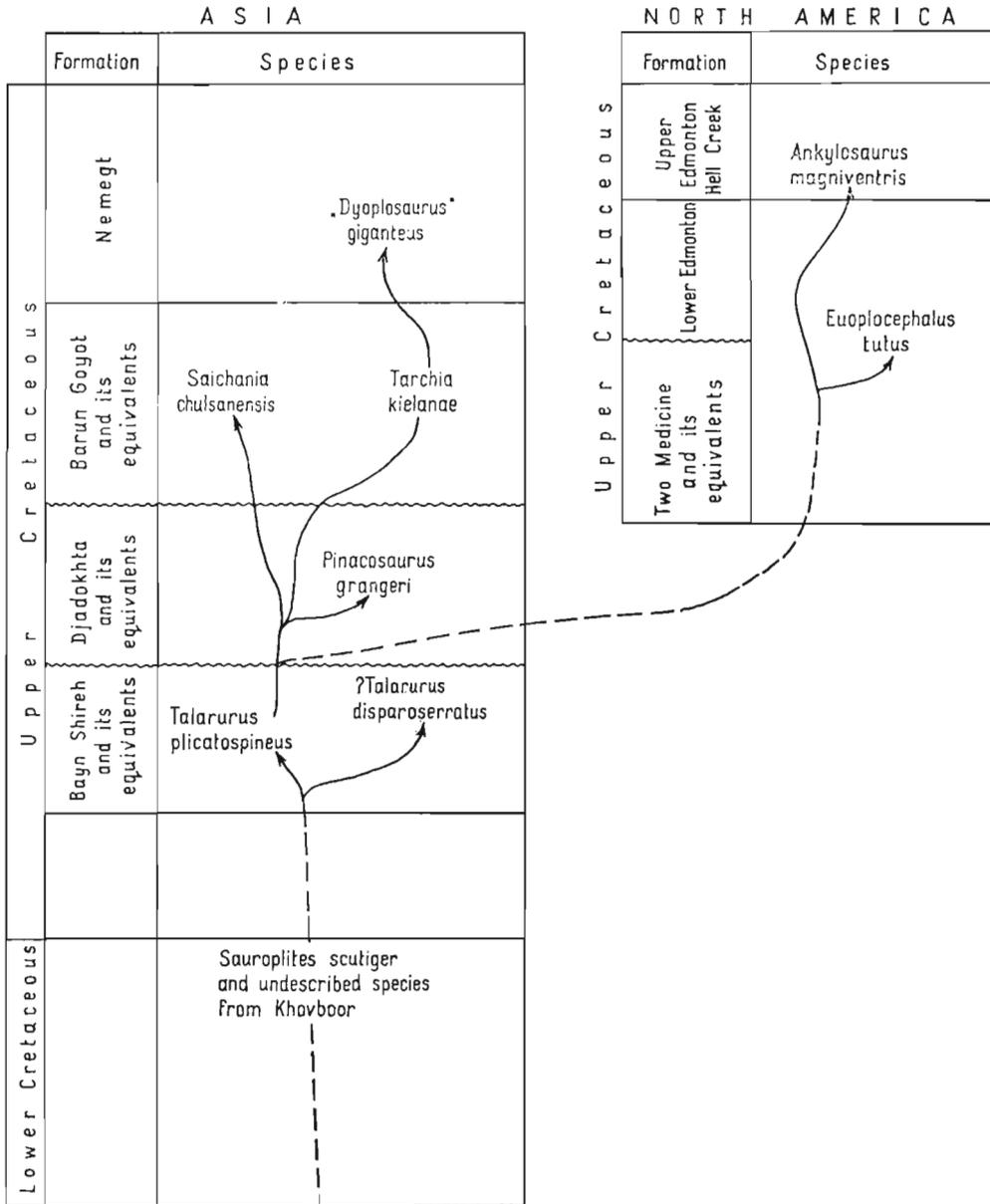


Fig. 12
Distribution of the Ankylosauridae in Asia.

But, they show some new tendencies such as a different structure of the nasal region and body size increase. COOMBS (MS) suggested that *Euoplocephalus*, *Talarurus* and Asian “*Dyoplosaurus*” are congeneric. A detailed comparison of these forms shows that they represent separate genera, presumably of common origin. There is no basis for the suggestion that the same ankylosaurid genera are present in Asia and North America as e.g. “intercontinental” distribution of *Dyoplosaurus* (CHARIG, 1973) and *Euoplocephalus* (COOMBS, MS).

The present study of the Asiatic Ankylosauridae, similar to that for North America made by COOMBS (*l.c.*), does not elucidate the relationships between the Nodosauridae and the Ankylosauridae. One of the oldest Mongolian ankylosaurids — *Talarurus*, is a typical member of the Ankylosauridae. It shows some similarities to the Nodosauridae, such as a relatively long skull, subspherical occipital condyle, incomplete coossification of distal caudal vertebrae. Also, some of these are probably primitive characters, retained in Nodosauridae but lost in Ankylosauridae, for example with development of tail club. All these characters, probably

primitive in *Talarurus*, are, however, insufficient to prove an origin of the Ankylosauridae directly from the Nodosauridae. New data on the origin of the Ankylosauridae will be supplied by a study of an Early Cretaceous specimen of a primitive ankylosaur from Khovboor.

POSITION OF ANKYLOSAURIA WITHIN ORNITHISCHIA

The origin of the Ankylosauria and their relation to other Ornithischia are still an open question; MARSH (1895), LAPPARENT and LAVOCAT (1955), HUENE (1956), SWINTON (1970) and others, classified ankylosaurs with stegosaurs (Stegosauria, Thyreophora, Orthopoda), whereas ROMER (1927, 1968) put them into a separate suborder, Ankylosauria. The basis for uniting ankylosaurs and stegosaurs, were common characters such as quadrupedality, the presence of armour, and tooth morphology. ROMER (1968), who was skeptical about a possibility of a common origin of the Ankylosauria and Stegosauria stated (*l.c.*, p. 143): "It is possible that there may have been an early armoured common ancestor of stegosaurs and ankylosaurs, but there is no reason to believe that there was, and no evidence for it". COOMBS (MS) pointed some common features of both groups such as: presence of armour; lack of an obturator process; lack of a premaxilla-lacrima contact; tooth morphology; limb proportions; phalangeal formula; structure of the metapodia; as well as the morphology of the palpebral bones. According to COOMBS (MS) some characters that are common to the Ceratopsia and the Pachycephalosauria suggest a derivation of those groups from quadrupedal ancestors and are not a basis to unite the Ankylosauria and Stegosauria into one natural group. The Ankylosauria and Stegosauria are the only ornithischian groups in which we cannot show that their quadrupedality is secondary. There is evidence that the Ceratopsia derive from an ornithopod line and are secondarily quadrupedal (ROMER, 1968; MARYAŃSKA & OSMÓLSKA 1975). ROMER'S (1968) conviction about secondary quadrupedality of Stegosauria resulted from the considerable differences in length of fore and hind limbs. However, the relative length of hind limbs increased in the group with time (STEEL, 1969). CHARIG'S (1964, 1972) hypothesis of archosaur locomotion and evolution of archosaur pelvis and hind limbs also supports the theory of primary quadrupedality for Stegosauria and Ankylosauria.

In light of the data about the Mongolian ankylosaurs, one cannot dismiss the possibility of a common derivation of the Stegosauria and Ankylosauria separate from the ornithopod line. This seems to be supported by the following common characters: lack of a premaxilla-lacrima contact; primitive tooth structure; convergence in general skull structure; presence of two palpebral bones incorporated in the skull roof; presence of a postfrontal; lack of the obturator process; completely (Ankylosauria) or partly (Stegosauria) closed acetabulum; presence of armour; and a primary quadrupedalism. According to ROMER (1956) the postfrontal does not occur in the Ornithischia. In fact, this bone does not occur in the representatives of broadly termed ornithopod line, but as evidenced by *Stegosaurus* (GILMORE, 1914) and *Pinacosaurus* (MARYAŃSKA, 1971), one must accept its existence in the Stegosauria and Ankylosauria. According to OSTROM (1970) and COOMBS (MS) the pelvis of all the Ankylosauria has a closed acetabulum, no anterior pubic process (weakly developed in *Sauropelta*), and the pubis is significantly or completely reduced. The ilium differs from that of other Ornithischia. No pelvis so far known among Triassic and Jurassic Ornithischia is a suitable predecessor to that of the Ankylosauria. The oldest Ornithischia (e.g. *Fabrosaurus*) have a fenestrated acetabulum. CHARIG (1972) assumes that the acetabulum of ankylosaurs is secondarily closed. However, there is no proof of this in known ankylosaur material. It seems probable that the closed acetabulum is a primary character of ankylosaurs. According to CHARIG (1972) the vertical limb posture in dinosaurs is always accompanied by fenestration of the acetabulum,

by development of a very distinct and strong, inwardly turned femoral head, and by development of digitigrady. The limb posture of the ankylosaurs is different from that of quadrupedal ceratopsian and sauropods. The femoral head of ankylosaurs is less developed than that of other Ornithischia and is only very slightly turned inwards. The fore limbs are flexed, in some ankylosaurids very strongly (*Saichania*), with an almost horizontal and laterally directed humerus. The stance and gait of ankylosaurs did not necessitate fenestration of the acetabulum. Primary primitiveness of some pelvic characters in ankylosaurs may be an additional argument against connections between the Ankylosauria and the ornithopod line of the Ornithischia. If the characters shared by ankylosaurs and stegosaurs argue for their common origin, the difference in the structure of pelvis must be considered. Both Stegosauria and Ankylosauria are characterized by greater development of the anterior process of the ilium compared to the posterior process. Differences in morphology of the anterior process of the ilium probably originated

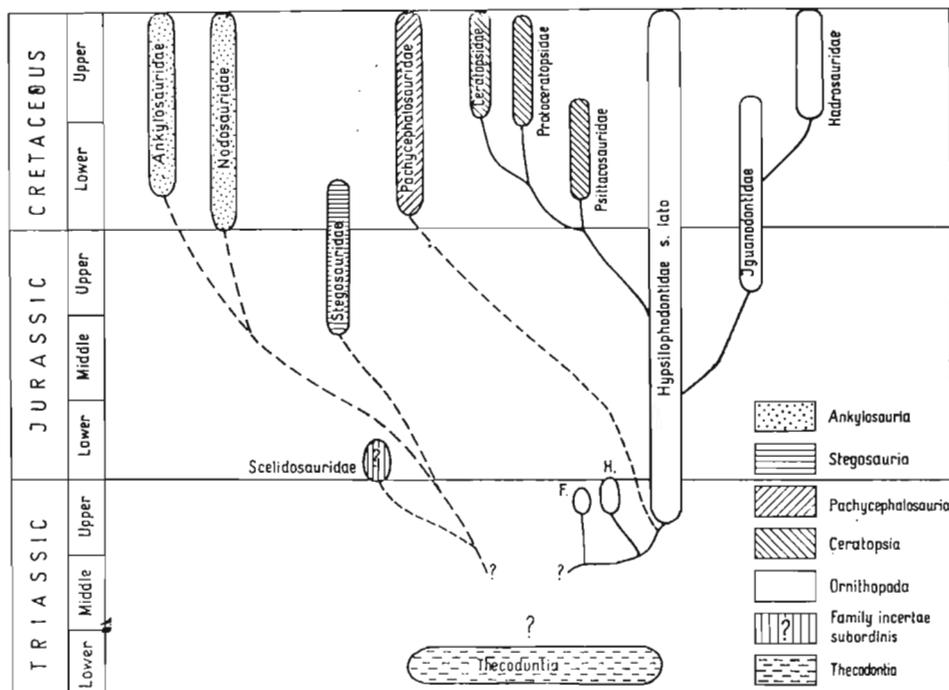


Fig. 13

Supposed phylogenetical relationships of the ornithischian dinosaurs.

after the definitive separation of the two groups and are correlated with the structure of the pubis. The anterior process of the pubis in stegosaurs might have developed in connection with large body size and a different mode of locomotion than in ankylosaurs. Stegosaurian vertical limb posture resulted in partial perforation of the acetabulum. It follows from studies of the Ceratopsia that the anterior process of the pubis changed relatively quickly in various protoceratopsids and ceratopsids, being extensive in some groups and weakly developed in others. Pelvic changes in stegosaur evolution were directed differently than in ankylosaurs.

One may presume that the closed acetabulum of the Ankylosauria is primary and that partial closure of acetabulum in e.g. *Omosaurus*, *Stegosaurus* (GILMORE, 1914) or *Wuerhosaurus* (DONG-ZHI-MING, 1973) is primary as well. It follows that stegosaurs did not reach complete fenestration of the acetabulum. Closure of the acetabulum in some Ceratopsia is similar to that in Stegosauria, and should be considered as a result of secondary adaptation to quadrupedality.

It is difficult to decide whether the Ornithischia are diphyletic or whether their subdivision into two branches took place immediately after their monophyletic origin from a thecodont

ancestor. THULBORN who accepts monophyletic origin of the Ornithischia wrote (1971, p. 77): "This hypsilophodont plexus is fundamental to the whole of ornithischian phylogeny; it represents the ancestry, ultimately at least, of such groups as the iguanodonts, hadrosaurs, and ceratopsians". Only the origin of the iguanodonts, hadrosaurs and ceratopsians from the hypsilophodont line can be proved. Lack of evidence on derivation of the ankylosaurs and stegosaurs from hypsilophodontids does not preclude diphyletic origin of the Ornithischia. GALTON (1974) assumed that the Upper Triassic *Fabrosaurus* stands close "to the archetypical ornithischian from which all other ornithischian originally derived". If, however, all known Triassic Ornithischia (e.g. *Pisanosaurus*, *Fabrosaurus*, *Heterodontosaurus*) are not only bipedal but also cursorial (GALTON, 1974), then derivation of the early Jurassic, quadrupedal *Scelidosaurus* from forms related to *Fabrosaurus* seems doubtful. Secondary quadrupedality had appeared in Ornithischia not earlier than the Late Cretaceous. Ancestors of the ankylosaurid line are expected among quadrupedal Pseudosuchia which might have produced two lines of ornithischians. Acceptance of primary bipedality for all primitive Ornithischia (GALTON, 1973) also seems impossible because of reasons similar to those given above.

Suggestions of WALKER (1961) about similarities between Aetosauria and Ornithischia seem to be supported by the following characters of the Ankylosauria: lack of contact between maxilla with lacrimal; presence of the postfrontal and epipterygoid; (?) retention of the so called „tabular” in the posterior margin of skull roof; enormously large external nasal openings reaching far over the skull roof, secondary covering of skull roof by dermal elements; loss of teeth in front of the maxilla and dentary; and extensive armour. Critical remarks of THULBORN (1972) concerning the similarities suggested by WALKER (1961) refer only to ornithopod ornithischians and do not argue against an aetosaurian ancestry for ankylosaurs. Diversity of pelvic structure in Actosauria (e.g. the small pubis in *Aetosaurus crassicauda*, strongly prolonged anterior process of the ilium and short posterior one in *Typhothorax meadei*) as well as the variability of the position and dimensions of temporal fenestrae support the possibility of a connection with ankylosaurs. This does not mean that known aetosaur might be an ancestor of the ankylosaur line, but an aetosaurian origin for ankylosaurs is no less acceptable than an ornithopod origin.

The concept of a monophyletic origin of ornithischians (e.g. THULBORN, 1971, 1975), or extreme hypotheses of monophyly of all the Dinosauria (BAKKER & GALTON, 1974) are not convincing. The statement by THULBORN (1975, p. 251) "The lack of fossil evidence makes it impossible to maintain that any one theory of Ornithischia ancestry is more acceptable than another", is appropriate. His statement (*l.c.*) saying that several lines of thecodonts during the Triassic period approached the dinosaurian level of organization and that the observed similarities between various dinosaurian groups are a result of parallel evolution within those lines, seems to be most convincing.

The Scelidosauridae (*Scelidosaurus* and *Sarcolestes*) might also be assigned to the ankylosaurid line of Ornithischia (see fig. 13). Lack of detailed description of *Scelidosaurus* (specimens BM(NH)R. 1111 and BM(NH)R. 6704, CHARIG, 1972) prevents determination of the systematic position of the Scelidosauridae. Suggestions that *Scelidosaurus* is a primitive representative of the Ankylosauria (ROMER, 1968) is, at this moment, groundless, as lack of an anterior pubic process has been stated for all early Ornithischia. It follows that the lack of this process in *Scelidosaurus* does not speak for its assignment to the Ankylosauria. Reduction of digits in *Scelidosaurus* is more advanced than in known early Cretaceous ankylosaurs, making such assignment even more difficult. Similarly unsatisfactory are arguments claiming assignment of *Scelidosaurus* to the Stegosauria. Assignment of *Scelidosaurus* to the suborder Ornithopoda, grade Brachypoda by THULBORN (1975) is also unacceptable. His opinion (1975): "In practically every part of its skeletal anatomy *S. harrisoni* appears to be a perfectly acceptable ornithopod dinosaur" lack sufficient grounds.

HABITS OF ANKYLOSAURIDAE

Keenly developed olfaction in ankylosaurids is probably connected with relative sluggishness of these animals. They were the slowest and clumsiest of all the Ornithischia. Not only the presence of armour, but also forelimb structure and conformation of the pectoral girdle as well as development of limb musculature indicate lack of adaptations to quick movements (COOMBS, MS). The position of articular surfaces on humerus, radius, and ulna indicates a strongly flexed attitude for the forelimb of *Saichania*, with the humerus oriented outward, strongly horizontally, and slightly backward and the ulna and radius strongly oblique in a medial direction. Fusion of the coracoid with the scapula and an additional connection of the coracoid with the vertebral column indicate lack of mobility in the pectoral girdle. A relatively extensive range of phalangeal movements both relative to the metacarpals and to one another is characteristic of *Saichania* and other Mongolian ankylosaurids. Extension movements prevailed over flexion. Because of the strongly flexed position of the fore limbs, the anterior part of the trunk in *Saichania* was slightly raised off of the ground. The distance from the glenoid cavity of *Saichania chulsanensis* (ZPAL MgD-I/112) to the ground is about 35 cm. The strong ventral armour of the body indicates a low position for the abdomen.

Differences in the structure of the humerus and the scapulocoracoid in *Saichania*, *Tarchia* and *Pinacosaurus* indicate that the humerus was most vertical in *Pinacosaurus*. The structure and curvature of the pectoral girdle and ribs and the position of limbs suggest that the whole trunk of *Saichania* was flattened dorso-ventrally. In *Pinacosaurus* the anterior part of the trunk was similarly flattened, whereas in *Talarurus plicatospineus* the trunk is slightly compressed laterally. The pelvic region was distinctly raised over the pectoral girdle in all specimens as in all ankylosaurs, and the hind limb was more vertical than fore limb.

The structure of the occipital condyle indicates that the atlas of *Pinacosaurus* and *Talarurus* embraces the condyle ventro-posteriorly which gave good vertical and horizontal mobility to the head. Strong oblique displacement of anterior articular surfaces of the cervical vertebrae in *Pinacosaurus* and posterior surfaces in *Talarurus* offer a considerable range of vertical movements to the neck. In *Saichania* the articular surface of the occipital condyle is developed only ventrally. Much smaller displacement of the articular surface of vertebrae than in *Pinacosaurus*, together with a ventral occipital condyle, prove lesser vertical mobility of the head and neck in *Saichania*. The range of horizontal movements was much greater than that of vertical ones. Coossification of the ribs of the first dorsal vertebra with the pectoral girdle, the character of zygapophysal connections and coossification of distal dorsal vertebrae indicate little mobility in the back. The structure of the caudal vertebrae in *Pinacosaurus*, *Talarurus* and "*Dyoplosaurus*" indicates that both lateral and vertical mobility of the tail was possible only in the proximal part between the third to fourteenth caudals. In *Pinacosaurus*, because of very high neural spines in that region, the vertical movements were also limited. Coossification of neural and hemal arches distally in the tail, and fusion between distal vertebral centra, indicate that the posterior portion of the tail forming the tail-club was immovable.

In connection with limited general mobility, olfaction probably played a great role in the life of ankylosaurs, especially in searching for food, finding a mate, and detecting an enemy. Presence of the Jacobson's organ proves a necessity to expand the anterior olfactory area of the snout, in association with procurement of a particular food. A well developed hyoid apparatus and a strongly developed entoglossal process may indicate the existence of a long, thin, and movable tongue, similar to some recent Squamata.

It is a common belief that ankylosaurs were entirely herbivorous (see COOMBS, MS). It seems highly probable, however, that they may have taken animal food as well, such e.g. as insects and their larvae (NOPCSA, 1928), which could have been dug out with the long tongue. Occasional feeding on carrion cannot be excluded either. Taking such a food is not denied

by such features of the dentition as: small dimensions of teeth, weak development of enamel, and lack of possibilities of propalinar movements of the mandibles. The presence of a long tongue and vomeronasal organ are arguments against only herbivorous diet of ankylosaurids.

MALEEV (1954) suggested that *Syrmosaurus* (= *Pinacosaurus*) may have dug itself in the sand by means of anteroposterior body movements. The body shape of *Saichania*, which is strongly dorso-ventrally flattened, armoured on the ventral side, and provided with sharp keeled plates on the lateral sides seems to support this hypothesis. The bony eyelid of *Euoplocephalus* described by COOMBS (1972) may have protected the eyes when the animal dug in the sand. The structure of the manus and pes, which are terminated with nail or hoof-like phalanges, contradicts this view to some extent. These were not fossorial limbs. Hence some ankylosaurs may have dug by body movements as proposed by MALEEV (1954).

Modification of the scapulocoracoid observed in *Hyleosaurus* by COOMBS (MS) suggests fossorial habits for the Nodosauridae and may also point to similar fossorial tendencies in all Ankylosauria. In my opinion the habits and food of the ancestors of ankylosaurs were similar to those of the present-day *Ornithorhynchus*. They should be looked for among the Triassic Reptilia with a terrestrial-aquatic mode of life, and not among Triassic Ornithischia which were not only bipedal but also cursorial animals.

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EXPLANATION OF PLATES

PLATE 19

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Pinacosaurus grangeri GILMORE, 1933 101

(see also pls 20—25)

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgD-II/1

- 1a. Skull of a young individual, lateral view.
 1b. The same specimen, occipital view.
 1c. The same specimen, palatal view.

All \times ca 0.5

Photo: M. Malachowska-Kleiber

PLATE 20

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<i>Pinacosaurus grangeri</i> GILMORE, 1933	101
(see also pls 19 and 21—25)	

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgD-II/1

- 1a. Skull of a young individual, anterior view, \times ca 0.5.
- 1b. The same specimen, dorsal view, \times ca 0.5.
2. Left premaxilla in lateral view, three nasal openings are visible, \times ca 1.
3. Ventral part of the endocranial cavity, dorsum sellae and pituitary fossa are visible, \times ca 1.
4. Right basicranial region in oblique latero-dorsal view, the right stapes and opisthotic not in natural position are visible, \times ca 2.

Photo: M. Malachowska-Kleiber

PLATE 21

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<i>Pinacosaurus grangeri</i> GILMORE, 1933	101
(see also pls 19—20 and 22—25)	

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgD-II/1

- 1a. Right maxilla in lateral view, \times ca 1.5.
- 1b. The same specimen, medial view of the maxillary teeth, \times ca 1.5.
- 2a. Maxillary teeth, labial surface, \times 4.
- 2b. The same specimen, lingual surface, \times 1.
3. Posterior part of palatal region, the palatines and contact of the vomer with the pterygoid are visible, \times ca 2.

Photo: M. Malachowska-Kleiber

PLATE 22

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<i>Pinacosaurus grangeri</i> GILMORE, 1933	101
(see also pls 19—21 and 23—25)	

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgD-I/1

1. and 5. Middle dorsal vertebrae.
- 2a. The neural arch of the middle dorsal vertebra, lateral view.
- 2b. The same specimen, posterior view.
- 2c. The same specimen, anterior view.
3. The isolated cervical vertebra, posterior view.
4. The neural spine of the posterior dorsal vertebra, lateral view.
5. Three dorsal vertebrae from the presacral rod; lateral view.

- 6a. Mandibular teeth, labial side, $\times 3$.
 6b. The same specimen, lingual side, $\times 3$.
 7a. Left mandible with symphyseal portion and predentary, lateral view.
 7b. The same specimen, ventral view.

All $\times 0.5$, except fig. 6

Photo: M. Malachowska-Kleibe

PLATE 23

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<i>Pinacosaurus grangeri</i> GILMORE, 1933	101

(see also pls 19—22 and 24—25)

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgD-II/1

- 1a. Right humerus, dorsal view, $\times 0.5$.
 1b. The same specimen, ventral view, $\times 0.3$.
 1c. The same specimen, posterior view, $\times 0.3$.
 2a. Proximal portion of the right ulna, postero-medial view, $\times ca 0.3$.
 3a. Proximal portion of the right radius, antero-medial view, $\times 0.3$.
 3b. The same specimen, posterior view, $\times ca 0.3$.
 4a. Left scapula, ventral view, $\times ca 0.5$.
 4b. The same specimen, dorsal view.
 4c. The same specimen, internal view.
 4d. The same specimen, external view.
 5a. Right coracoid, internal view, $\times ca 0.5$.
 5b. The same specimen, external view.
 6a. Lateral portion of the cervical dermal half-ring, external view, $\times ca 0.3$.
 6b. The same specimen, internal view.

Photo: M. Malachowska-Kleibe

PLATE 24

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<i>Pinacosaurus grangeri</i> GILMORE, 1933	101

(see also pls 19—23 and 25)

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia; ZPAL MgD-II/1

- 1a. Left femur, posterior view, $\times ca 0.3$.
 1b. The same specimen, anterior view.
 1c. The same specimen, internal view.
 2a. Left tibia, posterior view, $\times ca 0.5$.
 2b. The same specimen, anterior view.
 3a. Left fibula, lateral view, $\times ca 0.3$.
 3b. The same specimen, medial view.
 4a. Two sacral vertebrae, dorsal view, $\times ca 0.3$.
 4b. The same specimen, ventral view.
 5a. Right metacarpalia I—IV and proximal articular surface of metacarpal V in articulation with preserved phalanges; anterior view; ZPAL MgD-II/9, $\times ca 0.7$.

- 5b. The same specimen; posterior view.
 6. Damaged left metatarsalia I—IV with preserved phalanges, anterior view; ZPAL MgD-II/9, \times ca 0.5.
 7. Terminal phalanx of the left metatarsal III, ventral view; ZPAL MgD-II/9, \times ca 0.5.

Photo: M. Malachowska-Kleiber and L. Dwornik

PLATE 25

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Pinacosaurus grangeri GILMORE, 1933 101

(see also pls 19—24)

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia

- 1a. Left ilium, dorso-lateral view; ZPAL MgD-II/1, \times ca 0.5.
 1b. The same specimen, internal view.
 1c. The same specimen, ventro-lateral view.
 2a. Left ischium, external view; ZPAL MgD-II/1, \times ca 0.3.
 2b. The same specimen, internal view.
 3. Left cervical rib, lateral view; ZPAL MgD-II/1, \times ca 0.4.
 4a. The chevron of the middle caudal, posterior view; ZPAL MgD-II/1, \times ca 0.5.
 4b. The same specimen, lateral view.
 5. Anterior portion of the tail-club, dorsal view; ZPAL MgD-II/9, \times ca 0.3.

Photo: M. Malachowska-Kleiber

PLATE 26

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Talarurus disparoserratus (MALEEV), 1952 100

Upper Cretaceous, Bayn Shireh svita, Sheeregeen Gashoon, Gobi Desert, Mongolia

- 1a. Left maxilla with preserved teeth, internal view; Holotype, PIN 554/1—1, \times ca 0.8.
 1b. The same specimen, lateral view.

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Talarurus plicatospineus MALEEV, 1952 100

Upper Cretaceous, Bayn Shireh svita, Bayn Shireh, Gobi Desert, Mongolia

2. Left ulna, antero-lateral view; PIN 557—80/1, \times ca 0.3.

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Pinacosaurus grangeri GILMORE, 1933 101

(see also pls 19—25)

Upper Cretaceous, Djadokhta Formation, Bayn Dzak, Gobi Desert, Mongolia

4. Left humerus, dorsal view; PIN 614-1/24, \times ca 0.3.
 3. Left ulna, antero-dorsal view; PIN 614-1/10, \times ca 0.3.
 5a. Right scapulocoracoid, internal view; PIN 614-1/7, \times ca 0.3.
 5b. The same specimen, dorsal view.

Courtesy of PIN, photo W. Skarżyński

PLATE 27

Past

Tarchia kielanae gen.n., sp.n..... 105

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype ZPAL MgD-I/111
 Id. Damaged posterior portion of the skull, occipital view, x 0.3.

lb. The same specimen, dorsal view.

le. The same specimen, ventral view.

2. The same specimen, antero-ventral view of the brain case, the exits of olfactory nerves are visible, x0.5.

3. The same specimen, stereo-photograph of right lateral side of brain case, the exits of cranial nerves and arteries are visible, x0.5.

Photo: U. Malachowtho-Kleiber

PLATE 28

Put

Saichania chulsanensis gen.n., sp.n..... 103

(see also pls 29—36)

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype GI SPS 100/151

Id. Stereo-photograph of the skull, dorsal view, x ca 0.2.

It. The same specimen, stereo-photograph, palatal view, x ca 0.2.

le. The same specimen, occipital view, x 0.25.

Photo: L. Dwornik

PLATE 29

Past

Saichania chulsanensis gen.n., sp.n..... 103

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype GI SPS 100/151

la. Right mandible, lateral view, x ca 0.3.

lb. The same specimen, medial view.

2 . The predentary of the same specimen, dorsal view, x ca 0.3.

3 a. The skull of the same specimen, lateral view, x ca 0.2.

3b. The same specimen, anterior view, x ca 0.3.

4a. Anterior maxillary tooth, labial surface, x ca 1.5.

4t. The same specimen, lingual surface.

5a. Left ulna, posterior view, x ca 0.3.

5 *b.* The same specimen, antero-medial view.

5 *c.* The same specimen, antero-lateral view.

6 . Proximal part of the left ceratobranchial I, x0.5.

7 . Corpus of hyoid apparatus with entoglossal process and fragments of ceratohyal, x0.5.

Photo- L. Dwornik

PLATE 30

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<i>Saichania chulsanensis</i> gen.n., sp.n.....	103
(see also pls 28—29 and 31—36)	

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype GI SPS 100/151

1. Anterior part of the palatal region, ossified conchae are visible through palatal vacuities, xl.
2. Posterior part of palatal region, the structure of the palatine and contact of the pterygoid with vomer and ectopterygoid are visible, xl.

Photo: L. Dwonrik

PLATE 31

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<i>Saichania chulsanensis</i> gen.n., sp.n.....	103
(see also pls 28—30 and 32—36)	

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype, GI SPS 100/151

1. Right wall of the brain case, the exits of cranial nerves II—VII are visible, xl.
2. The basicranial region of the skull; ventral view, almost fiat and ventrally placed articular surface of the occipital condyle and left epipterygoid are visible, xl.

Photo: L. Dwonrik

PLATE 32

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<i>Saichania chulsanensis</i> gen.n., sp.n.....	103
(see also pls 28—31 and 33—36)	

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype, GI SPS 100/151

- 1a. Fused atlas and axis, anterior view, x ca 0.4.
- 1b. The same specimen, posterior view.
- 1c. The same specimen, ventral view.
- 1d. The same specimen, lateral view.
- 2 a. The last cervical vertebra, anterior view, x ca 0.2.
- 2b. The same specimen, posterior view.
3. Posterior part of left sternal plate, x ca 0.2.
4. Anterior part of left sternal plate, x ca 0.2.

Photo: t. Dvornik

PLATE 33

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<i>Saichania chulsanensis</i> gen.n., sp.n.....	103
(see also pls 28—32 and 34—36)	

Upper Cretaceous, Banin Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype, GI SPS 100/151

1. Anterior dorsal vertebrae and damaged sternal plates, ventral view, x 0.25.
2. Distal part of IV left dorsal rib, x ca 0.3.
3. Part of VI left dorsal rib with damaged plate-like intercostal process, x ca 0.2.
4. Ventro-lateral portion of VI right dorsal rib with partly preserved plate-like intercostal process, internal view, X ca 0.3.
5. Fragment of ventral portion of dorsal ribs with plate-like intercostal processes in natural arrangement, x ca 0.3.

Photo: L. Dwornik

PLATE 34

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<i>Saichania chulsanensis</i> gen.n., sp.n.....	103
(see also pls 28—33 and 35—36)	

Upper Cretaceous, Batun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype, GI SPS 100/151

1. Left lateral view of the skeleton before the preparation. The photograph shows anterior dorsal ribs in natural arrangement and the first dorsal rib coossified with the coracoid, x ca 0.15.
2. The same specimen, right lateral view.

Photo' W. Skariyhski

PLATE 35

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<i>Saichania chulsanensis</i> gen.n., sp.n.....	103
(see also pls 28—34 and 36)	

Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype, GI SPS 100/151

- 1a. Left humerus, dorsal view, x ca 0.24.
16. The same specimen, ventral view.
- 2 a. Left radius, posterior view, ca 0.25.
26. The same specimen, anterior view.
- 3 a. Right scapula, dorsal view, x ca 0.3.
36. The same specimen, internal view.

Photo: L. Dwornik

PLATE 36

Page

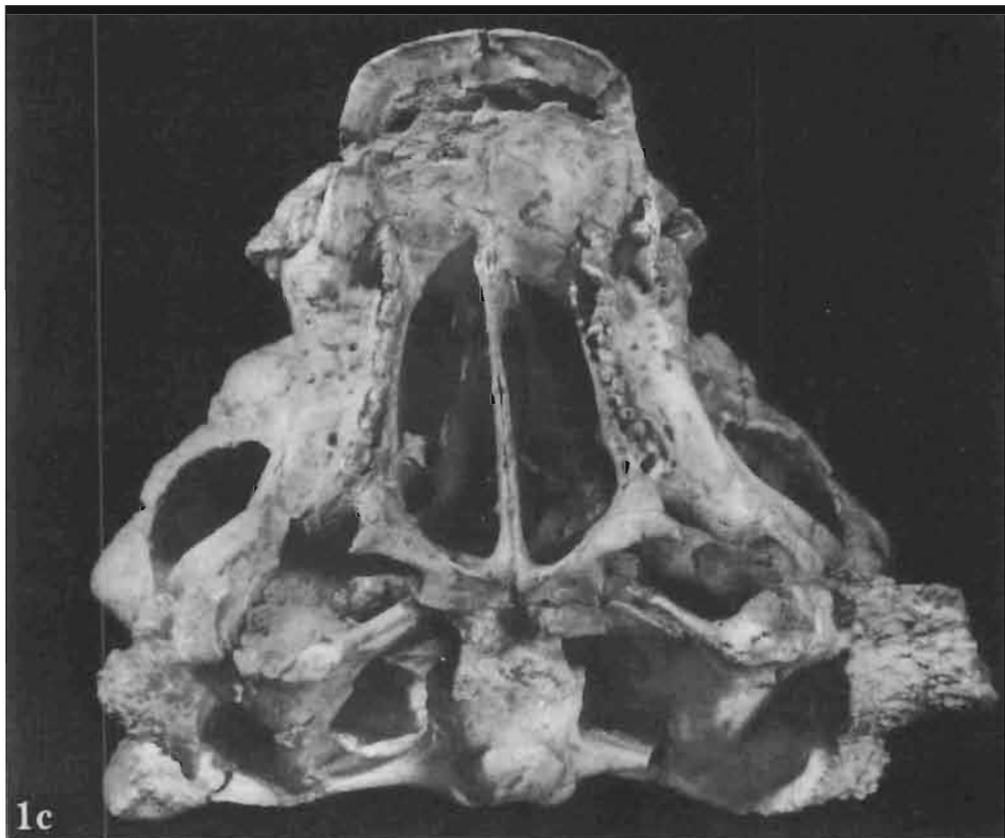
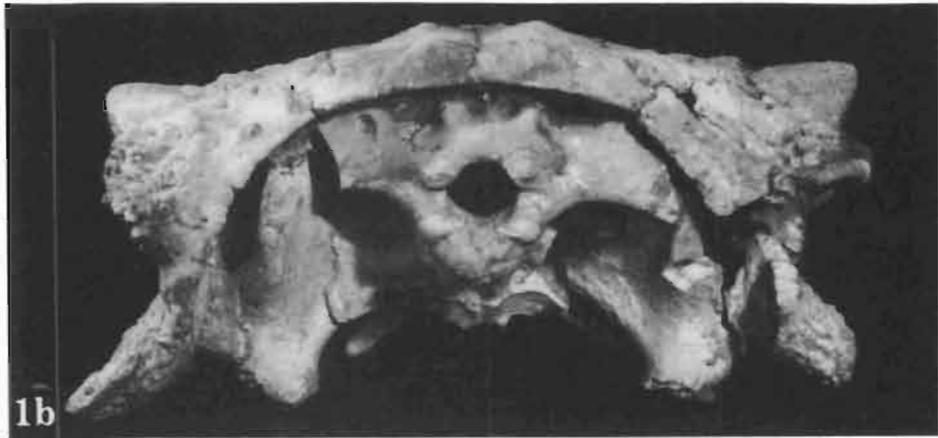
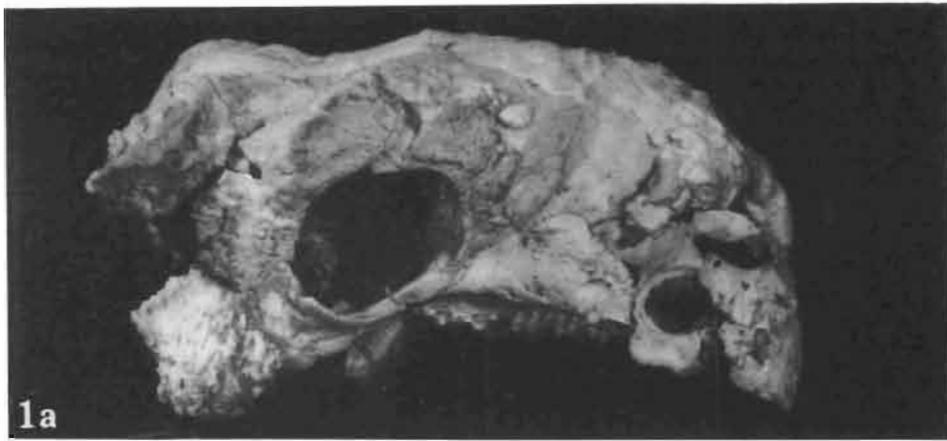
Saichania chulsanensis gen.n., sp.n..... 103

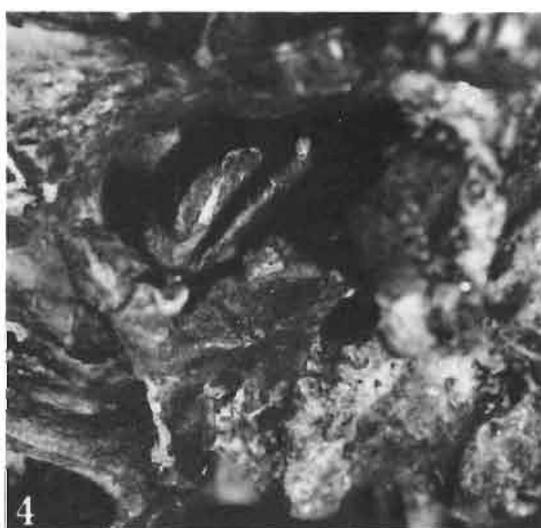
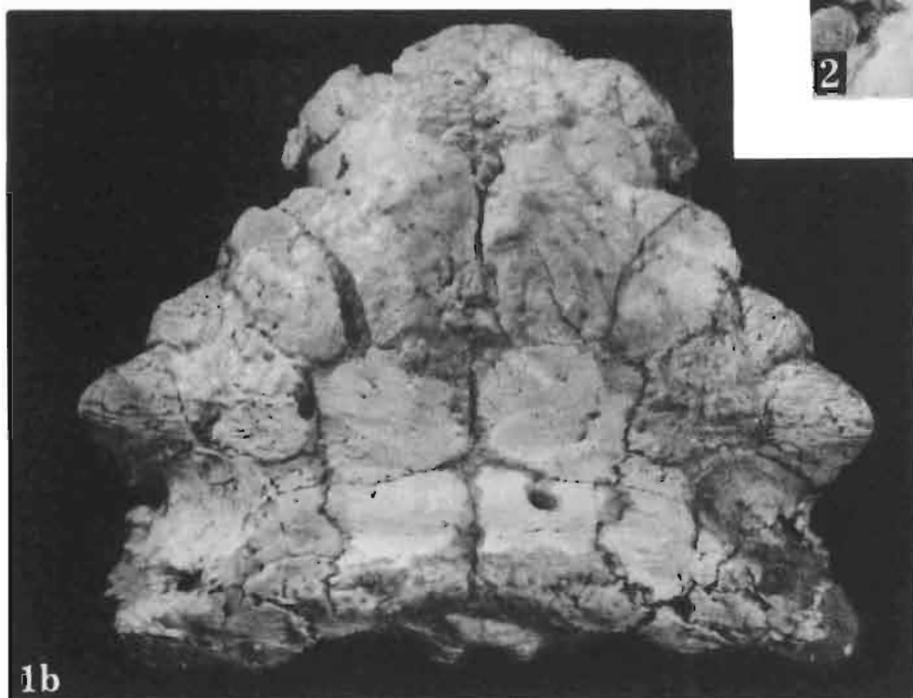
(see also pls 28—35)

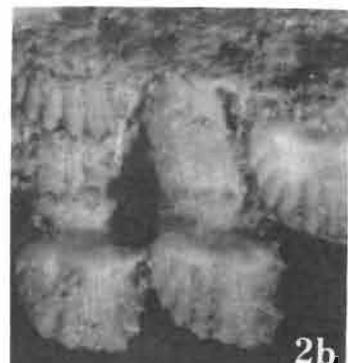
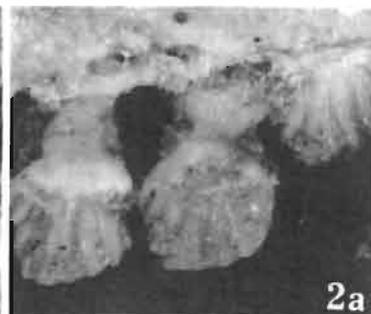
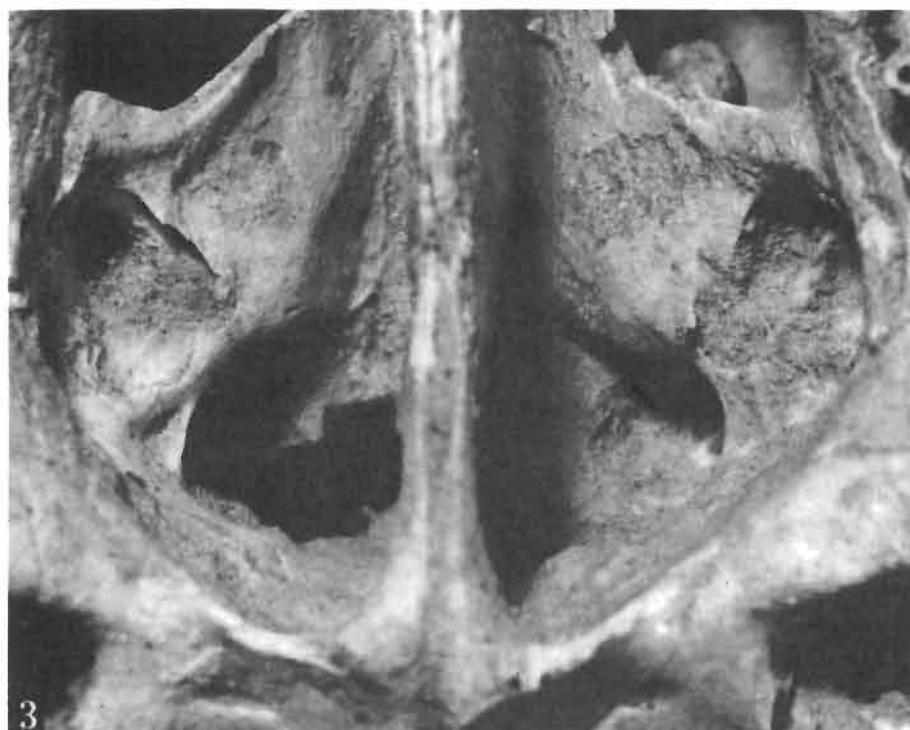
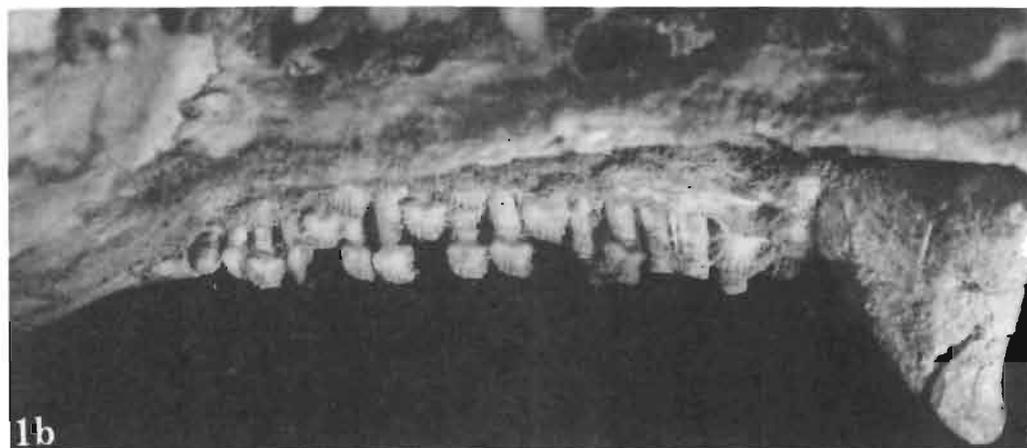
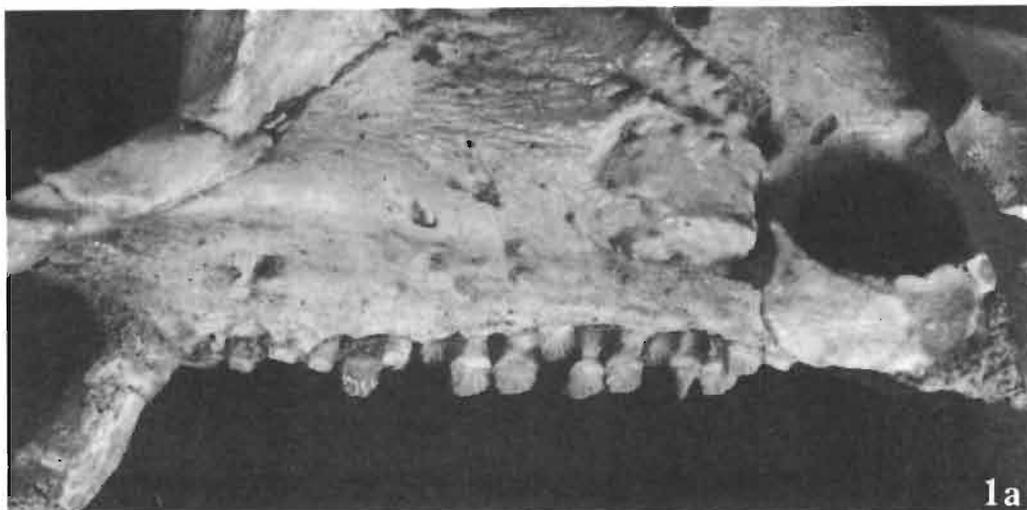
Upper Cretaceous, Barun Goyot Formation, Khulsan, Gobi Desert, Mongolia; holotype, GI SPS 100/151

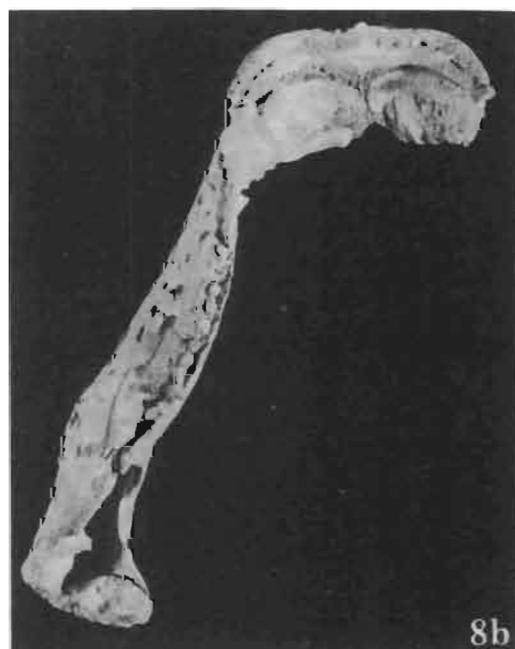
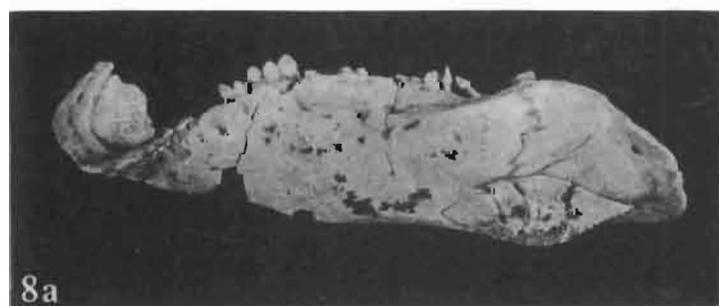
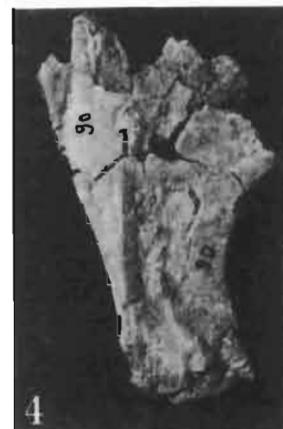
- 1a. Cervical dermal half-ring, anterior view, x ca 0.13.
- 1b. The same specimen, posterior view.
- 2 a. Right metacarpalia I—V, posterior view, x ca 0.4.
- 2b. The same specimen, anterior view, x ca 0.5.
- 3. Terminal phalanx of the right digit II (?), x ca 0.5.
- 4. The sesamoid of right metacarpal II, x ca 0.5.
- 5. Phalanx 1 of the right digit III, x ca 0.5.
- 6- 11. Different types of dermal scutes, x ca 0.4.

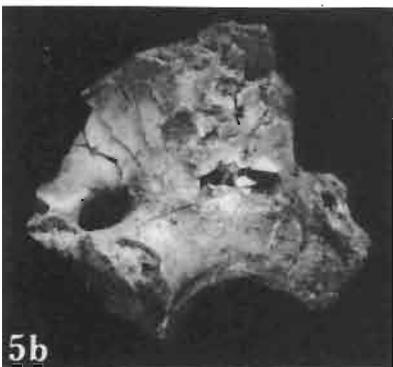
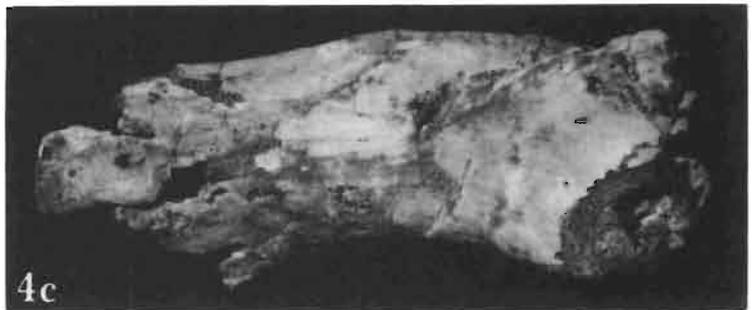
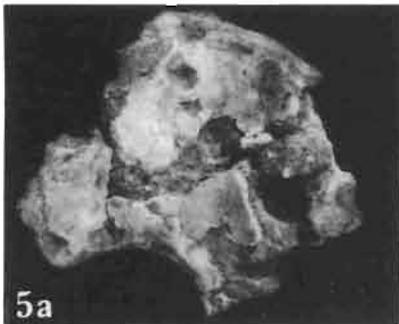
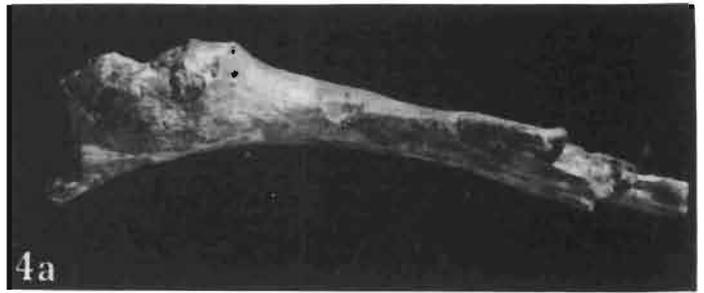
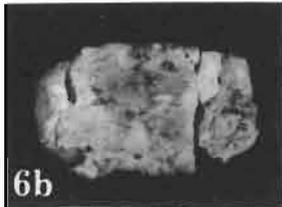
Photo: L. Dwornik

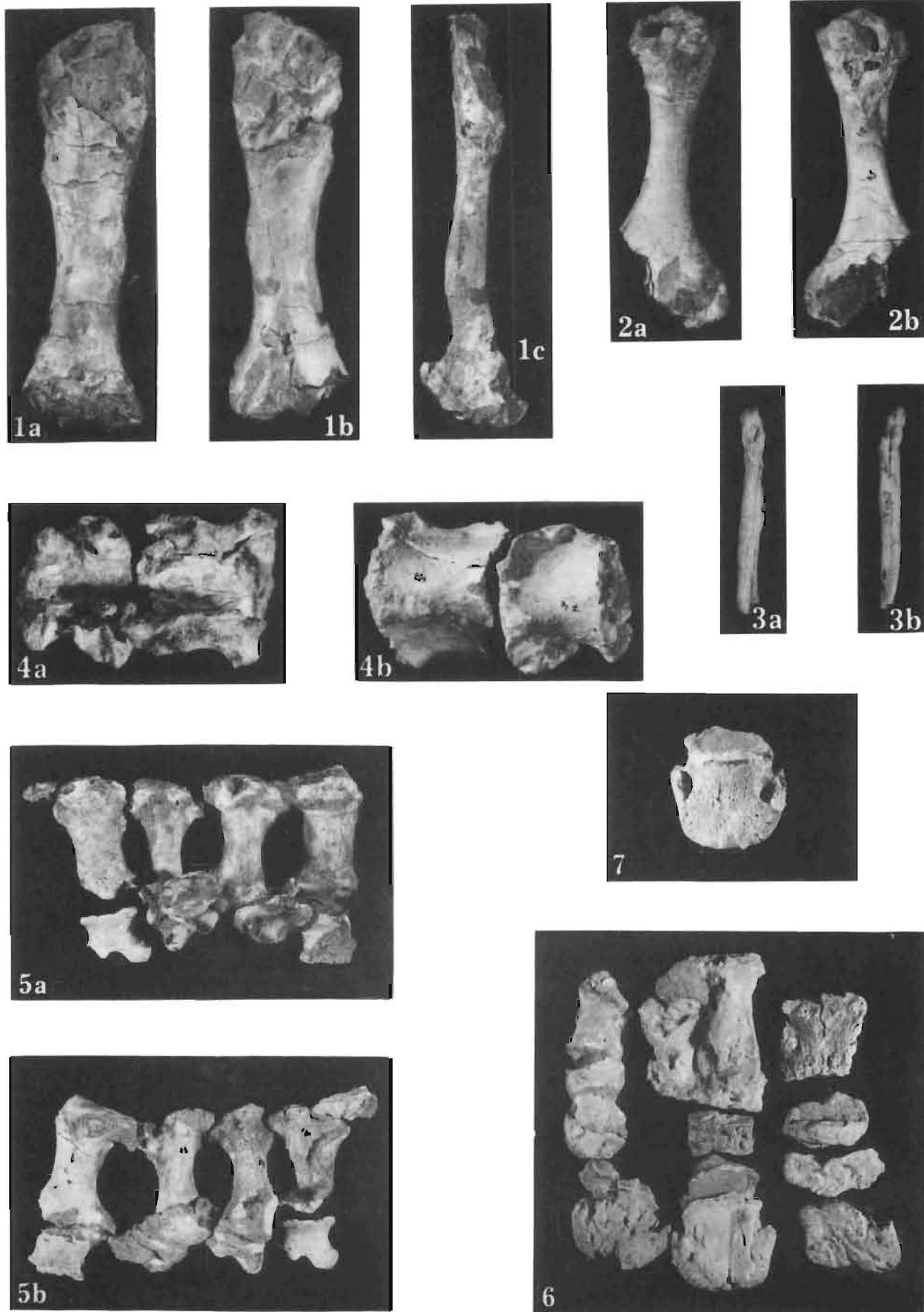


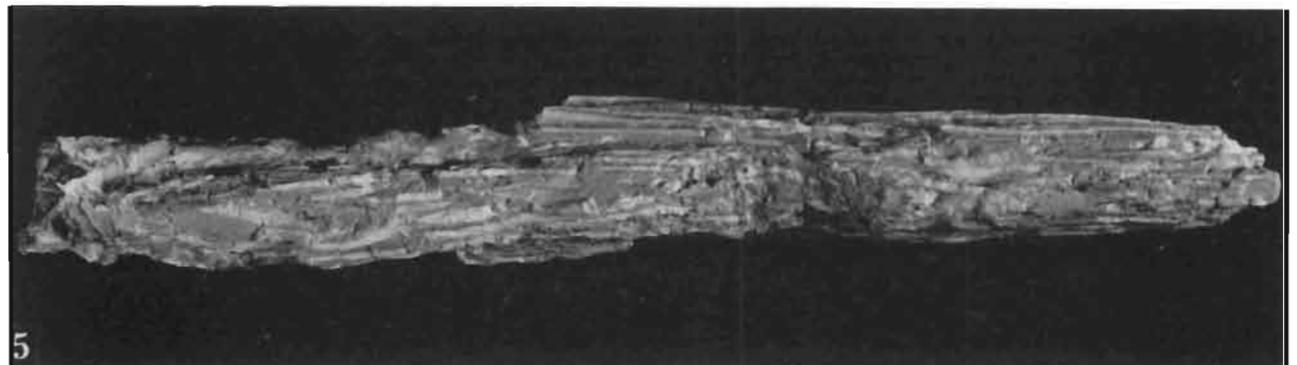
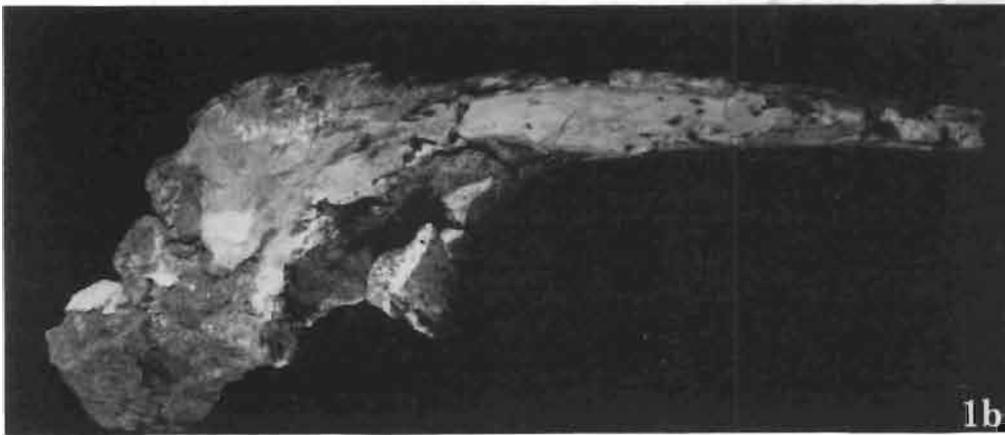
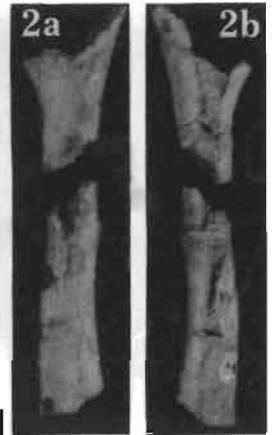














1a



1b



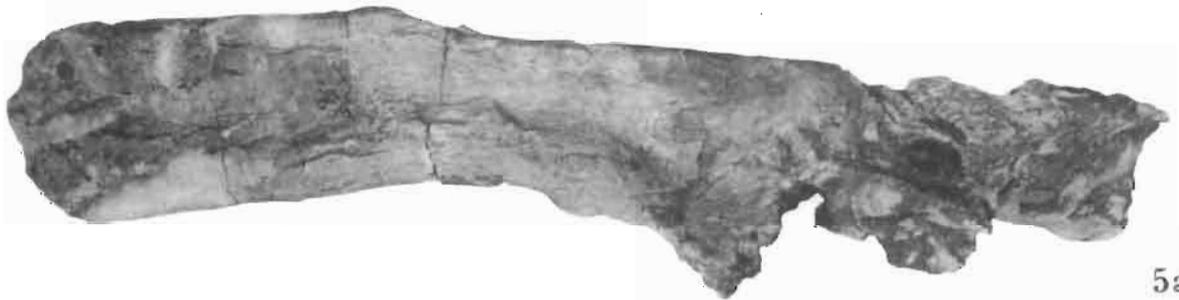
2



3



4



5a



5b

