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PHYLOGENY AND EVOLUTIONARY STAGES OF DINOSAURIA

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New suggestions are offered concerning the phylogeny of the dinosaurs, based on the Chinese materials as well as those from other parts of the world. The two dinosaur orders, Saurischia and Ornithischia, differed in tempo of evolution. The Saurischia include four evolutionary branches (Plateosauria, Sauropoda, Coelurosauria, Carnosauria) originating from different pseudosuchians in the Late Triassic, most of which extend to the Late Cretaceous. Ornithischia also evolved from different pseudosuchians in the Late Triassic and include three evolutionary branches: Ornithopoda, Pachycephalosauria and Armatosauria n. suborder. Four main stages can be distinguished in the evolution of all dinosaurs. Within Ornithischia one new suborder Armatosauria is erected and eight new superfamilies: Tianchungosauroidea, Chaoyoungosauroidea, Psittacosauroidea, Pachycephalosauroidea, Scelidosauroidea, Stegosauroidea, Oligosacralosauroidea and Polysacralosauroidea are introduced.

Key words: Dinosauria, evolution, phylogeny.

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INTRODUCTION

Dinosaurs are very abundant in China and many important dinosaur specimens have been found there in recent years. Based on materials available in this country, as well as on the references from other parts of the world, some new suggestions are offered below concerning the taxonomy, phylogeny and evolutionary stages of the Dinosauria.

PHYLOGENY OF DINOSAURIA

The division of Dinosauria into Saurischia and Ornithischia by means of structural characteristics of pelvic girdles is here considered as suitable. These two groups differ in the tempo of evolution and formerly different

views were expressed on this question, causing difficulty for the study of dinosaurs. A study of new materials (Chao 1983) has helped the present author to form the following opinions on the phylogeny of these orders (Table 1). The taxonomic approach here adopted should be considered as tentative until all new materials are fully investigated. This especially concerns the rank of new groupings here suggested.

I. ORDER SAURISCHIA

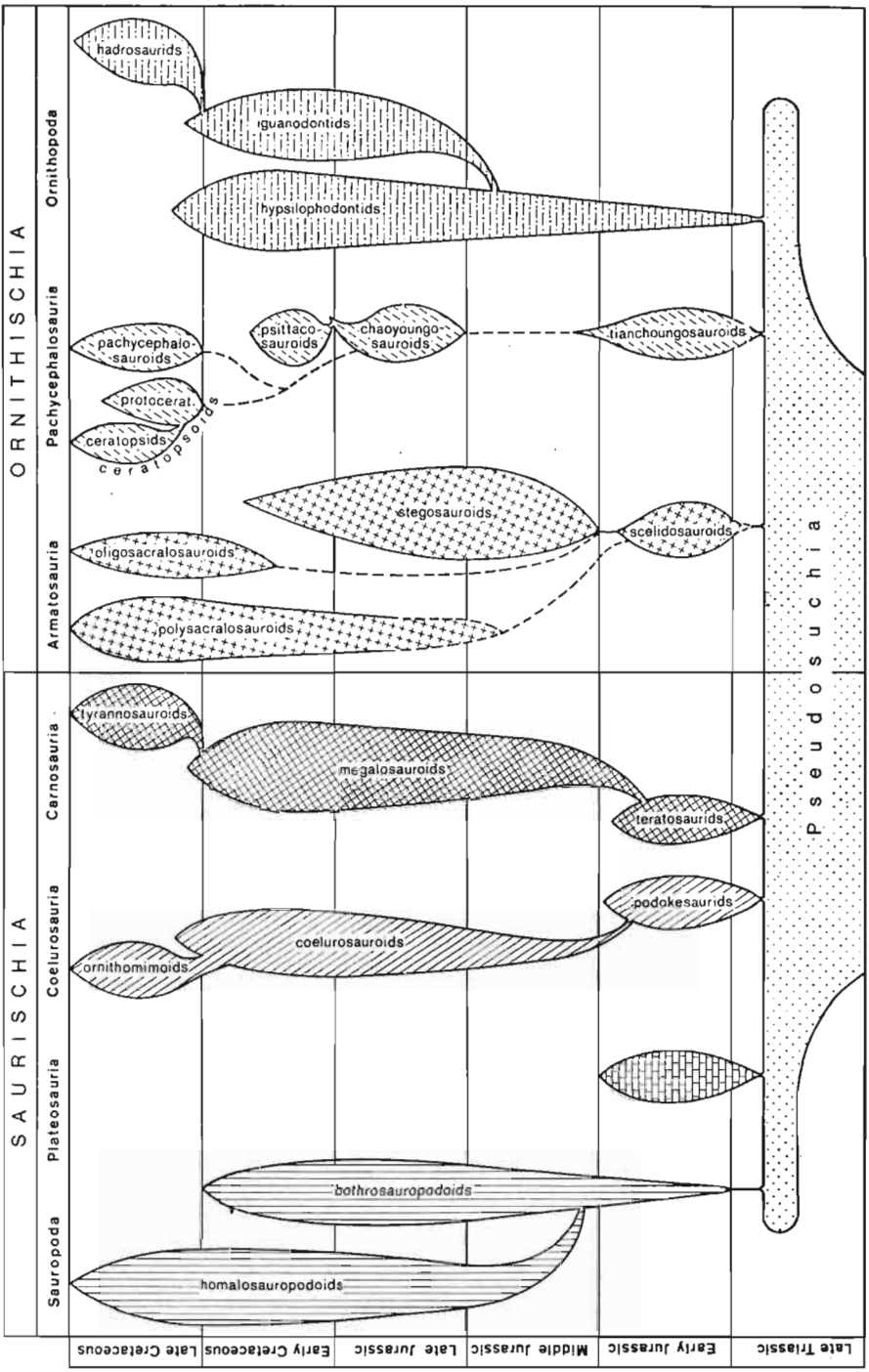
Saurischia include four evolutionary branches originating from different pseudosuchians in the Late Triassic and most of them extend to the Late Cretaceous. These four branches range as follows: Plateosauria Colbert, 1964 — Upper Triassic to Lower Jurassic; Sauropoda Marsh, 1878 — Lower Jurassic to Upper Cretaceous (Bothrosauropodoidea Kuhn, 1961 — Lower Jurassic to Lower Cretaceous; Homalosauropodoidea Kuhn, 1966 — Middle Jurassic to Upper Cretaceous); Coelurosauria Huene, 1914 — Upper Triassic to Upper Cretaceous (Podokesauridae Huene, 1914 — Upper Triassic, Coeluridae Marsh, 1881 — Middle Jurassic to Lower Cretaceous, Ornithomimoidea n. superfam. — Upper Cretaceous); Carnosauria Huene, 1920 — Upper Triassic to Upper Cretaceous (Megalosauroidea Nopcsa, 1928 — Upper Triassic to Lower Cretaceous, Tyrannosauroidea Walker, 1964 — Upper Cretaceous).

1. Plateosauria

At present many paleontologists consider that Plateosauria (= Prosauropoda) evolved from a pseudosuchian ancestor in the Late Triassic, then in the Early Jurassic evolved directly into Sauropoda. Fossil materials accumulated so far show that this view does not tally with the facts. In several localities of China (Tibet, Yunan) "prosauropods" and sauropods appear in the same horizon; thus they form two parallel, and not successive evolutionary branches (Chao 1983). In fact, primitive "prosauropods" were derived from a pseudosuchian ancestor in the Late Triassic. According to the morphological characteristics of the Chinese "prosauropods" (*Lufengosaurus*), this suborder is similar to the pseudosuchian ancestor, but still acquiring many new features, namely: its skull smaller, orbit and narial opening situated upward, teeth transitional from carnivorous to herbivorous, forelimb greatly increased in length, cervical vertebrae longer, the structure of vertebrae cavernous. In short, "prosauropods" evolved step by step from a carnivorous to an omnivorous feeding habit. Whether it was because of their tooth development or their level of skeletal evolution, "prosauropods" were not very successful dinosaurs, because they did not produce any descendant branch. At the end of the Early Jurassic all prosauropods disappeared rapidly. Since sauropods are not descendants of "prosauropods", the latter name is misleading and

Table 1

Phylogeny of dinosaurs



should be abandoned; the name Plateosauria introduced by Colbert (1964) is here retained.

2. Sauropoda

Within the Saurischia, sauropods form a more progressive suborder, originating from pseudosuchians in the Early Jurassic. According to the new materials from China, the evolution of sauropods may be divided into two phases, primitive and progressive, and two branches (superfamilies): the Bothrosauropodoidea (J_1—Cr_1) and the Homalosauropodoidea (J_2—Cr_2).

A. The primitive sauropods are provided with weak, spatulate teeth, rather low crowns with sharp, serrate anterior and posterior edges, longer root, middle ridge of crown easily recognized. The boundary between the crown and root is distinct. The crown is rather round and lacks a central point. The cavernous structure of all vertebrae shows its primitiveness. The ischium is rather massive but very curved. The pubic peduncle of the ilium is strong and is directed anteriorly more obviously than in other progressive forms. The femur is very massive. The fibula is only slightly longer than the tibia. The astragalus is rather thick. The terminal phalanx of the first digit is massive, sharply pointed and moderately curved. At the end of the Middle Jurassic, the primitive bothrosauropodoids gave rise to the homalosauropodoids.

B. Progressive sauropods. In Late Jurassic and Cretaceous, the bothrosauropodoids and homalosauropodoids evolved into a new phase — the progressive phase of sauropods.

a. The bothrosauropodoids are characterized by typical spatulate teeth. The external surface of the crown is convex while the internal surface is concave. The middle ridge of the crown is reduced. The serration of the crown increased. The postcranial skeleton is strongly built and very massive. The cavernous structure of vertebrae is distinctly progressive. The limb girdles and limb bones obviously lengthened. The pubic peduncle of the ilium is strong and massive. The fourth trochanter of femur is poorly developed and situated proximally. The femur is a straight, massive structure, imperfectly ossified at its articular surfaces and at the greater trochanter — the surfaces which were obviously furnished with cartilage in life. The lesser trochanter is absent, but may be represented by a scar on the shaft margin. At the end of the Early Cretaceous the bothrosauropodids suddenly disappeared.

b. The homalosauropodoids are characterized by peg-like teeth. The crowns of the teeth are long and thin, without serration. On the crown surface the ridge is rather developed. The root is cylindrical. The postcranial skeleton is progressive. The cavernous structure of vertebrae is well developed. The anterior dorsal and posterior cervical vertebrae show divided neural spines. The centra of all sacrals are firmly coossified,

with the anterior and posterior ends conspicuously projecting. The ilium is very massive, the pubic foramen is very large and the distal end of ischium is obviously expanded.

In the Late Cretaceous the homalosauropodoids evolved into a new specialized stage. Late Cretaceous sauropods have characteristic teeth: the crown and root are typically cylindrical, the boundary between the crown and root has vanished. The serrate structure of tooth crown has also disappeared. The length and width of postcranial skeleton, especially of cervical and dorsal vertebrae, rapidly increase. At the end of the Late Cretaceous these gigantic homalosauropodoids all died out.

3. Coelurosauria

In the Late Triassic two parallel branches evolved from certain pseudosuchian ancestors: Coelurosauria and Carnosauria. The evolutionary trend in coelurosaurs is the decrease in size, i.e. the smaller the more evolved. The evolutionary trend is in decrease in number of teeth; five stages of tooth evolution may be distinguished. They are: 1 — Late Triassic, when the tooth is very massive and crown serrated; 2 — Early Jurassic, when the crown becomes thinner and serration less marked; 3 — Middle Jurassic, when the crown becomes thinner with serrated anterior edge only; 4 — Late Jurassic-Early Cretaceous, when the tooth is thinnest and no serration occurs; 5 — Late Cretaceous, when coelurosaurs become toothless.

At the end of the Cretaceous coelurosaurs disappear all together.

4. Carnosauria

Carnosaurs evolved from pseudosuchians in the Late Triassic and may be divided into two stages: the primitive stage (Late Triassic-Early Cretaceous) and the progressive stage (Late Cretaceous). At the end of the Cretaceous carnosaurs vanished. The evolutionary trend in carnosaurs is increase in size, i.e. the larger the more evolved. The evolution of the carnosaur tooth is shown in two aspects. 1. The flat tooth: the crown becomes gradually thicker and curved backward, and the degree of serration of edges gradually increases; 2. the cylindrical tooth: the crown becomes gradually cylindrical, the serration of edges stretches gradually to the root, the middle ridge of the crown surface inclines gradually forward or backward.

II. ORDER ORNITHISCHIA

Ornithischia, though initially relatively rare, also evolved from different pseudosuchians in the Late Triassic, but their suborders differ greatly in their age of origin and their geological ranges. They include: Ornithopoda Marsh, 1871 — Upper Triassic to Upper Cretaceous, Pachy-

cephalosauria Maryańska et Osmólska, 1974 — Lower Jurassic to Upper Cretaceous, Armatosauria n. suborder — Lower Jurassic to Upper Cretaceous.

1. Ornithopoda

According to the traditional ideas, the iguanodontids were derived from primitive ornithopods (primitive hypsilophodontids) in the Early or Middle Jurassic, and early in the Cretaceous large iguanodontids evolved into the largest ornithopods — hadrosaurids. The detailed analysis of ornithopod phylogeny is omitted here, as the author will not put forward any new ideas about the subject.

2. Pachycephalosauria

The pachycephalosaurs may be divided into five groups differentiated in varying degrees by the following features: skull with a rugose, often dome-like thickening of the frontoparietal region or thickening of the jugal region, further thickening of other external dermal elements and accessory lateral dermal nodules. These five groups are characterized below, in evolutionary order.

A. **Tianchungosauroidea** new superfamily

The tianchungosauroids (J_1—J_2) are primitive small ornithischians characterized by massive skull, weak jugal process, slightly trilobed teeth with low crowns, arranged in a single row in maxilla and dentary; canine-like teeth present in premaxilla (and in the anteriormost part of dentary). *Heterodontosaurus* is referred to this superfamily.

B. **Chaoyoungosauroidea** new superfamily

The chaoyoungosauroids (J_3), known thus far only from North China (Chao, in press), evolved from the tianchungosauroids. They are small transitional ornithischians characterized by massive and strongly developed jugal arch and trilobed teeth with low crowns, weak canine-like teeth on the premaxilla. *Chaoyoungosaurus* [1] Chao is here referred.

C. **Psittacosauroidea** new superfamily

The psittacosauroids (Cr_1) derived from the chaoyoungosauroids and are limited to the beginning of the Early Cretaceous. They are characterized by a rugose skull and a long beak apparently formed by a separate rostral bone, remarkable jugal process and marked trilobed teeth with low crowns.

D. **Ceratopsoidea** Hay, 1902

They include protoceratopsids and ceratopsids. The protoceratopsids derived also from the chaoyoungosauroids and are limited to the early

and middle stages of the Late Cretaceous. They are primitive forms not too distant from the more primitive chaoyoungosauroids in many features, such as: the presence of premaxillary canine-like teeth, and of the comparatively weakly developed jugal process. The ceratopsids derived directly from the protoceratopsids and are limited to the late stage of the Late Cretaceous. They are characterized by rugose skull, with horn cores and posterior frill.

E. **Pachycephalosauroidea** new superfamily

The pachycephalosauroids include the pachycephalosaurids and homalocephalids; they are limited to the Late Cretaceous and are the descendants of the chaoyoungosauroids. They are characterized by canine-like premaxillary teeth, dome-like or strongly thickened frontoparietals, nodose skull ornamentation.

3. Armatosauria new suborder

All armatosaurs commonly have the skull and trunk nearly completely, or partly, covered by superficial dermal ossifications. From the evolutionary point of view, the change in the number of sacrals from few to many is an important development for the same evolutionary branch. The armatosaurs are divided into a series of superfamilies according to the number of sacral vertebrae.

A. **Scelidosauroidea** new superfamily

The scelidosauroids of the Lias are the earliest forms of the armatosaurs. They were derived from the pseudosuchians. Unfortunately, the exact number and shape of their sacrals remain unknown. Judging by the skeletal features, the scelidosauroids might be the direct ancestral branch of the armatosaurs.

B. **Stegosauroidea** new superfamily

The stegosauroids (J_2—Cr_1) are protected with a principal armor consisting of the paired row of dorsal plates inherited from the scelidosauroids. They have about 27 presacral vertebrae including 17 dorsals and 4 sacrals.

C. **Oligosacralosauroidea** new superfamily

The oligosacralosauroids (Cr_1—Cr_2) include *Monkonosaurus* [1] Chao. They probably derived from the primitive scelidosauroids at the end of the Early Jurassic or at the beginning of the Middle Jurassic. The number of sacrals is 3—5 and the skull is completely covered by superficial dermal ossifications; armor present on the back of trunk and neck; the

[1] Chao, 1983.

armor is more or less flat and of simple shape. The degree of fusion of the sacral vertebrae is fairly good. The oligosacralosauroids were discovered in China and in other regions of Asia. The climax of their evolution is in the Early Cretaceous, but they disappeared in the Late Cretaceous.

D. **Polysacralosauroidea** new superfamily

The polysacralosuaroids (J_2—K_2) include *Sangonghesaurus* [1] Chao. They probably also derived from the primitive scelidosauroids in the Middle Jurassic. Their skulls are completely or nearly completely covered by dermal ossifications, hence there is no antorbital opening and the supratemporal fenestra is closed; the infratemporal fenestra is a small slit or covered by an armor. The number of sacrals is 6—9, and the armor is well developed on the back of neck and trunk and around the tail; the dorsal armor typically includes rows of large keeled plates, projecting lateral spines and smaller intermediate ossicles. The polysacralosauroids attained their greatest development in the Late Cretaceous.

EVOLUTIONARY STAGES OF DINOSAURIA

All above dinosaurs passed through four important evolutionary stages, i.e. from primitive to progressive and from the lower to the higher stages (Table 2).

I. The initial stage of dinosaur evolution — Late Triassic (or Middle--Late Triassic) — was very short, with a very limited number of taxa preserved, all of which are marked with primitive characteristics. This stage includes also a pre-dinosaurian pseudosuchian phase. The major dinosaur groups include primitive plateosaurs, primitive theropods and ornithopods.

II. The developing stage of dinosaur evolution — Early-Middle Jurassic — spanning a longer range, and divisible into early and late phases.

1. Early phase (J_1). In this phase, all dinosaurs show primitive features. Ornithischians are very rare including scelidosauroids (*Scelidosaurus* Owen), pachycephalosaurs (*Tianchungosaurus* [1] Chao) and ornithopods (*Tatisaurus* Simmons), but saurischians are rich, e.g. plateosaurs (*Lufengosaurus* Young), primitive carnosaurs (*Megalosaurus* Buckland), primitive coelurosaurs (*Lukousaurus* Young), primitive sauropods (*Damalosaurus* [1] Chao).

2. Late phase (J_2). This phase, being transitional from stages II to III of dinosaur evolution, is characterized by the appearance of intermediate forms of stegosauroids (*Changtusaurus* [1] Chao), polysacralosauroids (*Sangonghesaurus* [1] Chao), iguanodontids (*Sanpasaurus* Young), carnosaurs (*Megalosaurus*), coelurosaurs (*Ngexisaurus* Chao), bothrosauropodoids (*Lancanjiangosaurus* [1] Chao).

Table 2

Major features of dinosaur evolution

Evolutionary stage/phase		Geological age	Characteristic events	Main dinosaur groups
IV Specialized and wanning stage		Late Cretaceous	Rapid morphological changes, high levels of specialization, strong development of dental apparatus, appearance of "grotesque" structures on skull and/or trunk, sudden extinction;	homalosauropodoids tyrannosauroids ornithomimoids polysacralosauroids ceratopsoids pachycephalosauroids hadrosaurids oligosacralosauroids
III Climax stage	Late phase	Early Cretaceous	increase in number of ornithischians, extinction of stegosauroids and bothrosauropodoids, appearance and extinction of psittacosauroids:,	megalosauroids coelurosaurs bothrosauropodoids homalosauropodoids stegosauroids psittacosauroids iguanodontids hypsilophodontids
	Early phase	Late Jurassic	development of progressive sauropods, appearance of chaoyoungosauroids;	homalosauropodoids bothrosauropodoids coelurosaurs megalosauroids iguanodontids stegosauroids chaoyoungosauroids
II Developping stage	Late phase	Middle Jurassic	appearance of homalosauropodoids, wane of plateosaurs, appearance of primitive stegosauroids;	bothrosauropodoids megalosauroids coelurosauroids stegosauroids polysacralosauroids iguanodontids
	Early phase	Early Jurassic	appearance of sauropods, climax of plateosaurs, appearance of pachycephalosaurus and armatosaurs;	plateosaurs bothrosauropodoids teratosaurids scelidosauroids tianchungosauroids ornithopods podokesaurids
I Initial stage		Late Triassic	emergence of dinosaurs, small size of forms.	plateosaurs primitive coelurosaurs primitive carnosaurs primitive ornithopods

In the late phase following the disappearance of the plateosaurs, the primitive homalosauropodoids (*Microdontosaurus* [1] Chao) came in succession. To sum up, all dinosaurs of the Late phase set a solid foundation for stage III.

III. Climax-stage of dinosaur evolution — Late Jurassic-Early Cretaceous — the range is also divisible into early and late phases. The dinosaurs are widespread, and all genera belong to the realm of progressive dinosaurs.

1. Early phase (J_3). This phase marking a transitional period has two major characters: the sauropods developed rapidly and the ornithischians started to become important. The groups are: progressive homalosauropodoids (*Mamenchisaurus* Young), coelurosaurus (*Sinocoelurus* Young), progressive carnosaurs (*Szechuanosaurus* Young), iguanodontids (*Yandusaurus* He, 1975), stegosauroids (*Tuojiangosaurus* Dong, Li, Zhou Chang), pachycephalosaurs (*Chaoyoungosaurus* [1] Chao). Overall, in this phase some forms of more progressive dinosaurs already entered into the realm of advanced dinosaurs, still appearing in the transitional period of dinosaur evolution.

2. Late phase (K_1). The phase is a prelude to the specialized and wanning stage. In this phase the evolution of Saurischia is distinctive. The bothrosauropodoids (*Asiatosaurus* Osborn) began to decline and by the end of the phase they completely disappeared, while homalosauropodoids grew very large and abundant. The teeth of coelurosaurids (*Microvenator* Ostrom) gradually decreased and became few in number. The carnosaurs (*Prodeinodon* Osborn) began to specialize. The stegosauroids (*Wuerhosaurus* Dong) disappeared at the end of the stage. The psittacosauroids appeared in the phase. Another ornithischian groups, e.g. oligosacralosauroids (*Monkonosaurus* [1] Chao), iguanodontids (*Iguanodon* Mantell), hypsilophodontids (*Hypsilophodon* Huxley) also developed rapidly. Overall, the evolution of the Ornithischia created favourable conditions for eruptive specialization of ornithischians in the next stage.

IV. Specialized and wanning stage of dinosaur evolution. In the Late Cretaceous, all dinosaurs entered into the period of specialization. The evolutionary characters of the stage may be summarized as follows: 1. rapid change; 2. a high level of specialization; 3. "grotesque" shape of teeth and trunk; 4. lack of adaptation to the environment; 5. rapid disappearance. The stage is represented by such major groups as homalosauropodoids (*Megacervixosaurus* [1] Chao), tyrannosauroids (*Tyrannosaurus* Osborn), ornithomimids (*Ornithomimus* Marsh), polysacralosauroids (*Pinacosaurus* Young), ceratopsoids (*Protoceratops* Granger & Gregory), pachycephalosauroids (*Stegoceras*) and hadrosaurids (*Tsintaosaurus* Young). The psittacosauroids and stegosauroids did not enter the stage, but in the beginning of the stage iguanodontids also became extinct.

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