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ON ORNITHISCHIAN PHYLOGENY

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The ornithischian dinosaurs are analysed using the cladistic methodology. The preferred hypothesis (see fig. 1) is that: 1. Ornithischia are monophyletic, 2. Ankylosauria are sister group of all other ornithischians, 3. Pachycephalosauria + Ceratopsia are monophyletic unit sharing common characters not found in other ornithischians. Quadrupedality is considered as primitive ornithischian condition.

Key words: dinosaurs, Ornithischia, cladistics.

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INTRODUCTION

The mutual relationships of different ornithischian groups have often been discussed. It has been suggested that Ornithopoda are the central group (e.g. Galton 1978) from which most other ornithischians derived, although recently (e.g. Santa Luca 1984; Sereno 1984) ornithopods have been removed from the ornithischian ancestry. We (Maryńska and Osmólska 1974) excluded pachycephalosaurs from ornithopods, establishing for them a new suborder — the Pachycephalosauria, deriving, however, that suborder traditionally from an ornithopod family — the Hysilophodontidae. In our other paper (Maryńska and Osmólska 1975) we also followed the traditional opinion that the Ceratopsia evolved from the Ornithopoda. We removed, however, the Psittacosauridae from the Ornithopoda and considered them as true representatives of the Ceratopsia, at the same time arguing against psittacosaur ancestry to the remaining Ceratopsia.

More recent papers (Coombs 1979; Santa Luca 1980, 1984; Norman 1984a) drew attention to the fact that the ornithopod ischium is unique in possessing an obturator process and this derived character may

discredit the idea of ornithopod ancestry to Pachycephalosauria and Certopsia, the representatives of which have an ischium without the process. In this situation, a question of origins of these two groups remains still open. In fact, the origin of Ankylosauria, and their relationship with other ornithischians, are also still unclear (comp. Maryańska 1977; Coombs 1978a, 1979).

For the above reasons, we try in the present paper to test the relationships among ornithischian taxa by means of cladistic methodology. Accordingly, we present below our preferred hypothesis (fig. 1) which in our opinion is more parsimonious than others. The present hypothesis is very close to the one which we have outlined earlier (Maryańska and Osmólska 1984a); some minor differences are discussed here in the respective chapters.

PHYLOGENETIC HYPOTHESIS

Ornithischia. — Using as the outgroup the archosaurs traditionally called Thecodontia¹⁾ we state that ornithischians (Group A) share a large number of derived characters, among which we discuss five of those most commonly recognized. They are: predentary (1), quadratojugal with long axis vertical (2), palpebral bones (3), pelvis with caudally directed pubis and anterior prepubic process (4), ossified tendons associated with the vertebral column (5). These synapomorphies support the opinion that Ornithischia are monophyletic, a view which has never been seriously questioned. Some authors quoted additional characters, Sereno (1984) for instance, listed 15 ornithischian synapomorphies, many of which are acceptable. Two of these characters cannot be considered synapomorphies: “premaxilla extended posterodorsally on the lateral aspect of the face, excluding the maxilla from the border of the external nares” and “pes digit V loses last phalanx” (Sereno 1984: 222). The first of the two is also quoted as a synapomorphy by Charig (1982), and the second by Norman (1984b). Although it is generally true that premaxilla extends laterally backwards in most ornithischians, resulting in the exclusion of maxilla from the external naris, the character is already present in many thecodonts (e.g., *Chasmatosaurus*, *Euparkeria*) and some other archosaurs (e.g. in some prosauropods), and may be a plesiomorphy in ornithischians. The second character, the reduction of fifth digit, is often observed as a derived condition in representatives of every dinosaur group.

¹⁾ The discussion whether Dinosauria are monophyletic is out of the scope of this paper. Some evidence was presented (Bakker and Galton 1974; Sereno 1984) in favor of the close relationships between Ornithischia and Prosauropoda and dinosaur monophyly. We considered this hypothesis as premature.

Norman (1984b) considers absence of the anterior pubic process as an ornithischian synapomorphy. However, the process (=prepubis) is present in all known ornithischians, although in some it is very short. It should be thus accepted that the process was already present in a common ornithischian ancestor.

First dichotomy — Ankylosauria. — Within the Ornithischia, the ankylosaurs differ from all other groups by having the following synapomorphies: closing of supratemporal fenestra (6), closing of antorbital fenestra (7), development of postocular shelf on the postorbital (8), very short olfactory stalks (9), laterally twisted iliac blade with very long preacetabular process (10), acetabulum situated mainly on the ventral surface of ilium (11), extensive armor (12).

We consider the imperforate acetabulum, an outstanding ankylosaur character, a plesiomorphy, in which we follow Maryńska (1977) and Coombs (1979). It is possible that ankylosaurs realized the vertical posture of their hind limbs independently from other ornithischians without developing of the inturned, set-off femoral head and without perforation of the acetabulum, simply by the lateral twist of the ilium (10). It caused a change in the position of the acetabulum which became placed primarily on the ventral surface of ilium. One can suppose that this way to achieve the vertical (or near-vertical) posture of the femur in ankylosaurs parallels a similar development in raiisuchid thecodonts (Bonaparte 1981, 1984).

The closed supratemporal and antorbital fenestrae (6, 7) are considered by us as ankylosaur synapomorphies. These characters are found sporadically among other ornithischians, often as individual features or in the progressive representatives of a given group. For that reason one can consider that these characters appeared convergently in some non-ankylosaur ornithischians.

Contrary to our earlier hypothesis (Maryńska and Osmólska 1984a), we do not consider now that the system of cranial sinuses is synapomorphic for Ankylosauria, as it is lacking in the Nodosauridae.

According to our preferred hypothesis (fig. 1), the Ankylosauria constitute a sister-group to all other Ornithischia (Group B); the latest common ancestor of the latter had at least one derived character — a perforated acetabulum (13). However, if the hypothesis of the dinosaur monophyly is corroborated (comp. foot-note on p. 138) our hypothesis would be falsified in this point.

Stegosauria. — Two of most widely known synapomorphies of Stegosauria, the unit which we include in the Group B. are: the double row of plates, or spikes, along the backbone (14) and the very broad and short ischium (15). If, as it appears, stegosaurs were devoid of the ossified tendons associated with the vertebral column, the lack of ossification might be also considered as a derived character of that group.

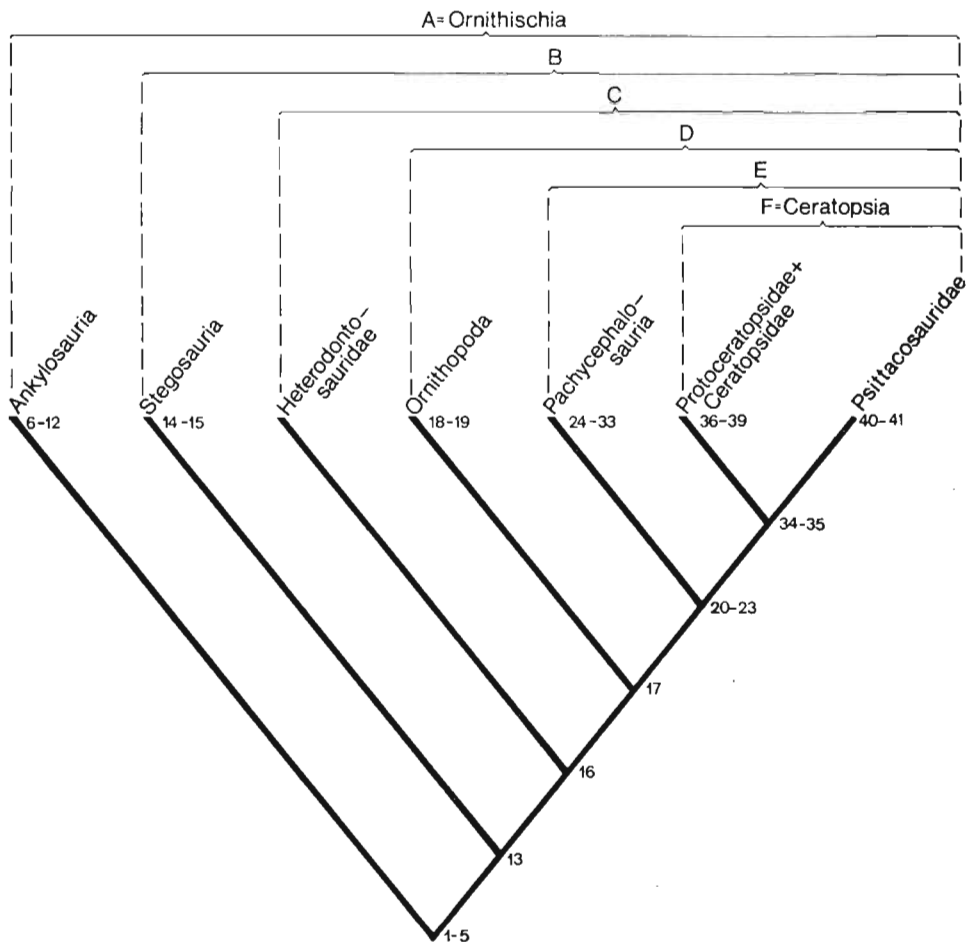


Fig. 1. Cladogram showing preferred hypothesis of phylogenetic relationships within Ornithischia. Numbers refer to synapomorphic or autapomorphic characters. 1—predeontary, 2—quadratojugal with the long axis vertical, 3—palpebral bones, 4—pubis directed caudally, prepubis developed, 5—ossified tendons associated with vertebral column, 6—closure of supratemporal fenestra, 7—closure of antorbital fenestra, 8—postocular shelf on postorbital, 9—very short olfactory stalks, 10—ilium twisted laterally with long preacetabular process, 11—acetabulum placed on ventral surface of ilium, 12—extensive armor, 13—perforate acetabulum, 14—double row of plates or spikes along backbone, 15—broad and short ischium, 16—medially turned femoral head, 17—greater trochanter expanded anteroposteriorly, separated from femoral head, lesser trochanter separated from the greater, 18—obturator process on ischium, 19—more than twenty-three presacral vertebrae, 20—parietals and squamosals extended posteriorly overhanging occiput, 21—vomera in palatal aspect contacting maxillae anteriorly, 22—reduced, short and slender pubis, 23—acetabular portions of opposing ilia more distant than the dorsal ones, 24—thickened skull roof bones, 25—surface of skull roof bones textured, 26—ossification of anteromedial orbital wall, orbit separated from nasal cavity, 27—high occiput, 28—basicranium separated from palatal and suborbital regions by extended quadrate and pterygoid and by junction of basisphenoid and prootic with quadrate wing of pterygoid, 29— anterior portion of preacetabular process of ilium horizontal, medial flange on ilium, 30—pubis peduncle of ischium long, contacting pubis peduncle of ilium, 31—forelimb about a fourth of hind limb length, 32—tongue-and-groove articulation between trunk vertebrae zygapophyses, 33—basket-like structure around caudals formed of S-shaped ossified tendons, 34—rostral bone, 35—widening of skull across jugals, 36—nasal horn core, 37—parietosquamosal frill, 38—sharply pointed and compressed predeontary, 39—three anterior cervicals coossified, 40—small, highly placed naris, 41—external manus digits reduced: fifth entirely lost, fourth with but one phalanx.

The Scelidosauridae have been traditionally assigned to the Stegosauria, although Romer (1968) considered them as ankylosaurs and Thulborn (1977) as ornithopods. According to our opinion, scelidosaurids are neither ankylosaurs (they have, among other characters, the perforated acetabulum) nor ornithopods (they lack the ornithopod synapomorphy — the obturator process to the ischium). Whether they are stegosaurs is difficult to decide as long as the entire scelidosaurid material is not re-examined.

Our conclusion concerning phylogenetic position of stegosaurs is similar to that proposed by Norman (1984b) although we would not accept all his synapomorphies. We consider the presence of palpebrals as an ornithischian synapomorphy, and their incorporation in the orbital margin is found in such non-ankylosaurian and non-stegosaurian ornithischians as most pachycephalosaurs and some ornithopods. Norman proposes a common ancestor to ankylosaurs, stegosaurs, and scelidosaurids; our conclusion in that matter is more reserved (see above) although Norman's view may be acceptable.

We do not agree with Sereno's (1984) phylogenetic hypothesis suggesting a common ancestry to ankylosaurs, stegosaurs and pachycephalosaurs + ceratopsians. We consider the synapomorphies quoted by this author in his point 11 as doubtful. The reduction of the interpterygoid vacuity, caused by medial extension of pterygoids is a common trend within archosaurs (as well as generally in many reptiles); in pachycephalosaurs this character is also very variable: from a narrow, long vacuity in *Stegoceras* through vacuity separated into two portions (the anterior and the posterior) in *Homalocephale*, to medially connected pterygoids with very restricted vacuity visible only in posterior view in *Prenocephale*. A very similar pattern of development of the pterygoids is observed in ceratopsians which is completely different from that found in the ankylosaurs. The vomera do not extend to the posterior margin of the tooth row in *Bagaceratops* and in any pachycephalosaur in which the region is known. The degree of reduction of the retroarticular process in the three pachycephalosaurs in which the mandible is known (*Stegoceras*, *Goyocephale* and *Wannanosaurus*) is about the same as in some ornithopods (e.g., *Hypsilophodon*, *Thescelosaurus*), which makes it probable that reduction of retroarticular process was realized independently several times in ornithischian groups. The another character in the point 11 of Sereno (1984) — reduction of distal carpals to two — cannot be investigated in pachycephalosaurs, because the manus is unknown in these dinosaurs. In our opinion, the number of distal carpals does not constitute a good character for considering phylogeny of dinosaur groups, because these small bones are very often missing and there is often doubt about how many ossified carpals were, in fact, present in a given species.

Heterodontosauridae. — A femur with a distinctly medially turned head and very prominent 4-th trochanter (16) is a synapomorphy of Group C (the sister-group of Stegosauria). Within that group, the Heterodontosauridae constitute, according to our hypothesis, a sister-group to the remaining ornithischians (Group D), the latter sharing as a synapomorphy the greater trochanter anteroposteriorly expanded, clearly separated from the femoral head, and the lesser trochanter well separated from the greater (17). Only one completely preserved heterodontosaurid is presently known — *Heterodontosaurus tucki*. However, only its post-cranial skeleton has been described (Santa Luca 1980); its skull is so far preliminarily characterized (Crompton and Charig 1962; Charig and Crompton 1974). In this situation it is difficult to recognize cranial synapomorphies of that family (for the derived characters of *H. tucki* see Santa Luca 1980).

Heterodontosauridae were earlier considered by us (Maryańska and Osmólska 1984a) as a sister-group of Pachycephalosauria + Ceratopsia, the opinion which we regard now untenable.

Sereno (1984) included the Heterodontosauridae to Ornithopoda on the basis, among others, of the “asymmetrical enamel thickness” occurring in the representatives of these dinosaur groups. Consequently, he had to exclude *Lesothosaurus* from the ornithopods. We consider *Lesothosaurus* rather a “good” ornithopod. To us, it seems probable that such a character as the asymmetric enamel might be quite often developed convergently several times (and it was at least twice: in the Ceratopsidae and Ornithopoda). The convergent development of the obturator process on the ischium should be hypothesized in *Lesothosaurus* and ornithopods in the case if the assymetry of enamel is considered a synapomorphy of heterodontosaurids and ornithopods. In our opinion, this is less probable taking into account that, aside of the presence of the obturator process, the entire structure of pelvis is very similar in *Lesothosaurus* and the ornithopods.

Ornithopoda. — In Group D, the Ornithopoda (including *Lesothosaurus*) share the obturator process to the ischium (18) and a variable number of presacral vertebrae but greater than twenty three (19). As Santa Luca (1980) has noted, the common ornithischian ancestor either had, or had not, an obturator process. Assuming the first possibility, reduction of the process in all non-ornithopod ornithischians should be regarded as a derived state, accepting the second possibility it should be considered a primitive one. However, hypothesis considering presence of the obturator process an ornithopod synapomorphy, which appeared after the basal ornithischian divergence had taken place, is more parsimonious. More than 23 presacral vertebrae is found also in stegosaurids; we assume here that this character might appear convergently in the latter group.

Pachycephalosauria + Ceratopsia. — Ornithopods constitute a sister group to the Group E, formed of the Pachycephalosauria and Ceratopsia. In agreement with Sereno (1984), we hypothesize the Pachycephalosauria as the sister-group of the Ceratopsia. According to our hypothesis, the shared derived characters of the Group E are: posterior expansion of the parietals and squamosals, all of which overhang the occiput (20), the vomer anteriorly contacting the maxillae within palate (21), reduced, short and narrow pubis (22), distance between acetabular portions of the ilia much larger than that between the dorsal portions (23). Reduction of the pubis, even complete, is found also in the ankylosaurs. The pelvic structure is, however, so entirely different in these groups that the atrophy of the pubis has to be a convergent character. The bending out of the acetabular iliac portions (23) enlarges the effect of a generally broad spacing of the ilia within the entire group E, and consequently of the hind limbs.

Sereno (1984) mentions nine synapomorphies for pachycephalosaurs and ceratopsians. Two of the above listed derived characters (21, 22) are the same as those of Sereno. His two other characters, these concerning configuration of the jugal are acceptable to us. We cannot agree, however, with Sereno's opinion that "long, slender postacetabular process on the ilium" is a synapomorphy of that group: the process is by no means slender in pachycephalosaurs having a broad medial horizontal extension in form of a medial flange. The tooth characters considered by Sereno as synapomorphies are either plesiomorphy or homoplasy.

Unique pachycephalosaur characters include: thickening of the skull roof bones (24), their textured nature (25), complete ossification of the anterior and medial wall of orbit forming a bony separation between the orbit and the nasal cavity (26), high occiput (27), separation of the basicranium from the palatal and suborbital regions by an extension of the quadrate and pterygoid and by junction of the basisphenoid and prootic with quadrate wing of the pterygoid (28), broad, horizontal anterior portion of preacetabular process of the ilium and the medial flange of ilium (29), pubic peduncle of the ischium long, contacting pubic peduncle of the ilium (30), forelimb reduction to about a fourth of the hind limb length (31), tongue-and-groove articulation between the zygapophyses of trunk vertebrae (32), basket-like structure formed of the S-shaped ossified tendons around caudal vertebrae (33).

The tongue-and-groove articulation between zygapophyses (32) was mentioned by Brown and Schlaikjer (1943) also in *Protoceratops andrewsi* Granger et Gregory; the character is evidently absent in all other ceratopsians, and its presence in *Protoceratops andrewsi* is highly doubtful.

The Ceratopsia (Group F) share as derived characters: the rostral

bone (34) and widening of the skull across the jugals (35). Testing the three units constituting the Ceratopsia — Psittacosauridae, Protoceratopsidae and Ceratopsidae — we found that the two latter share several derived characters not found in the Psittacosauridae which indicates that the Protoceratopsidae and Ceratopsidae share a common ancestor, which neither had in common with the Psittacosauridae. These synapomorphies are: nasal horn core (36), extensive parietosquamosal frill (37), sharply pointed and compressed prementary (38), three anterior cervicals coossified (39). These of the Psittacosauridae are: external nares small and highly placed (40), reduction of external digits in the manus, the fifth being completely lost, while the fourth having but one vestigial phalanx (41). Formerly, we (Maryańska and Osmólska 1975) reported the presence of the nasal horn core also in the psittacosaurids. Lately, we were able to state that this is not true and there is no horn core in any psittacosaurid known.

Conclusions. Our preferred hypothesis maintains our former separation of the Pachycephalosauria and the Psittacosauridae from the Ornithopoda, as well as the assignment of the Psittacosauridae to the Ceratopsia as the sister-group to the Protoceratopsidae plus Ceratopsidae. These opinions are now almost generally accepted (Santa Luca 1980, Coombs 1982, Sues and Galton 1982). However, our earlier hypothesis concerning the hypsilophodontid ancestry to the Pachycephalosauria and to the Ceratopsia has been here falsified. The Ornithopoda constitute the sister-group to the Pachycephalosauria plus Ceratopsia, the two latter sharing an ancestor in common which neither has in common with the Ornithopoda.

We do not create in this paper new categorical ranks or new names for taxa which would result from our cladogram (fig. 1). We believe that proliferation of ranks and names would lead to a confusion. So the more that to our knowledge, ours is the third hypothesis (comp.: Norman 1984; Sereno 1984) concerning ornithischian inter-relationships published within two last years (1984—1985). For the same reason, we do not follow Zhao (1983) who united Ceratopsia (*sensu* Maryańska and Osmólska 1975) and Pachycephalosauria in one suborder Pachycephalosauria, although we arrived to a similar conclusion that both groups are more closely related to each other than to the remaining ones.

REMARKS ON ORNITHISCHIAN EVOLUTION

The first ornithischian radiation took place towards the end of the Triassic, because in the Lower Jurassic deposits representatives of heterodontosaurids, fabrosaurids and scelidosaurids are already known. According to the hypothesis here proposed, it started with the first major dichotomy, separating the Ankylosauria from an ancestor of all other

ornithischians. This opinion is supported by a great morphological distance between ankylosaurs and the remaining ornithischians. Among the most peculiar characters emphasizing that distance should be mentioned: universal absence of supratemporal and antorbital fenestrae, which are present, at least primitively, in all other ornithischian groups, as well as the occurrence of the "tabulars" in the posterior portion of the skull roof, bones which are never found in any advanced archosaur (comp. Maryńska 1971: 48). Lately Toumanova (1981) has also drawn the attention to the morphological uniqueness of the Ankylosauria. We should, however, admit that at the moment paleontological record does not confirm such an early separation of the ankylosaurs: their first known presence is from the Callovian of the Northern Hemisphere (Laurasia). From the Southern Hemisphere (Gondwana) ankylosaurs are reported (Molnar 1980) still later, their only unquestionable representative, *Minmi* Molnar, being known from the Aptian; assignment of *Lametasaurus* Matley and *Brachypodosaurus* Chakravarti to the Ankylosauria is doubtful (comp. Galton 1981).

Similarly as for ankylosaurs, the paleontological record of Stegosauria is non-existing in the Triassic; their first occurrence is from the Bathonian of the Northern Hemisphere, where they survived until Neocomian. In Gondwana, however, stegosaurs have their latest record still in the Coniacian, and may be even in the Maastrichtian (Galton 1981). Early divergence of Stegosauria from the line leading to other non-ankylosaur ornithischians is supported, in our opinion, by still not fully open acetabulum. Presence of several primitive characters in that group (see: Galton 1980: 832) also speaks in favor of early separation.

Dong *et al.* (1983: 145) considered stegosaurs and ankylosaurs as the descendants of a late Triassic heterodontosaurid. We think that the present knowledge of heterodontosaurids does not corroborate the hypothesis of the close relationships between these dinosaurs.

The unquestionable Heterodontosauridae are known only from the Early Jurassic of the Southern Hemisphere (Elliot and Clarendon formations, southern Africa: Olsen and Galton 1984; Kitching and Raath 1984). In the Northern Hemisphere, *Tatisaurus* Simmons and *Dianchungosaurus* Young are reported from Lufeng in China (Young 1982); the assignment of these genera to Heterodontosauridae is doubtful. Although the only well known representative of that family, the Early Jurassic *Heterodontosaurus tucki* Crompton *et* Charig, was already specialized in some respects (Santa Luca 1980), it still displays several primitive ornithischian characters, which may, in our opinion, indicate that it was close to a common ancestor of all other ornithischians, excluding ankylosaurs and stegosaurs. Such characters include: the long forelimbs with a large pentadactyl manus, the continuous lesser and greater trochanters on femur (comp. Santa Luca 1980).

The ornithischians which are most differentiated and have the most extensive stratigraphic and geographic record are the Ornithopoda, which range from the Lower Jurassic to the end of Cretaceous; the representatives of almost all ornithopod families are present on both hemispheres. They derived very early: their earliest well known representative, Early Jurassic *Lesothosaurus diagnosticus* Galton, may not necessarily be close to the ancestor of the later ornithopods (see below). The ornithopods were evidently the most successful ornithischians.

The Pachycephalosauria and Ceratopsia have their earliest records in the Lower Cretaceous, thus their divergence might have taken place in the Late Jurassic. Also still in the Late Jurassic, the Psittacosauridae probably separated from the line ancestral to the remaining ceratopsians: the Protoceratopsidae and Ceratopsidae. These two latter families have their records in the Upper Cretaceous, the earliest protoceratopsids somewhat preceding ceratopsids. It seems reasonable to accept that their divergence started in the Early Cretaceous. Ceratopsia so far seem restricted to the Laurasia (the only ceratopsian recorded from Gondwana *Notoceratops* Tapia has been questioned by some authors), while within the Pachycephalosauria one representative (*Majungatholus atopus* Sues et Taquet 1979) is known from the Campanian of Gondwana (Madagascar).

In our earlier papers (Maryańska and Osmólska 1974, 1975) we derived both Pachycephalosauria and Ceratopsia from the Hypsilophodontidae. Galton (1978) considered the Fabrosauridae as a basal ornithischian family. Presently, we agree with Santa Luca (1980), that no ornithopod can be considered a possible ancestor to any other ornithischian group. Galton (1978) suggested that an archetypal ornithischian was close to bipedal *Lesothosaurus*. In contrast, we argue that the first ornithischian was rather a quadruped, or at best only a facultativ biped (we agree in this respect with Coomb's opinion expressed in 1979), with: somewhat shortened forelimbs, a presacral count of vertebrae lower than 24, ossified tendons, closed acetabulum, short prepubis, rather long, posteriorly directed pubis, straight ischium without obturator process, small predentary, unspecialized, leaf-like cheek tooth crowns and canine-like premaxillary dentition, slender mandible with low coronoid process and retroarticular process well developed.

During a subsequent evolution, one observes gradual improvements of the hip joint preventing the instability of the erect limb during parasagittal motion (characters **13**, **16**) and establishing the capability for the transverse adjustment of the footfall (character **17**; comp. Hotton 1980). It is evident that efficient ornithischian bipedality could be achieved only after the hip joint had been adequately modified.

The obligatory bipedality within Ornithischia occurred unquestiona-

bly only in two groups: in some (at least) fabrosaurids (*Lesothosaurus*) and in all known pachycephalosaurs in which the weakness and shortness of the forelimbs excluded any possibility of quadrupedal progression. In all other ornithischians for which the obligatory bipedality was traditionally postulated, it was not unequivocally proved, and often the evidence quoted in favor of bipedality speaks rather for the cursoriality (comp. Coombs 1978b). Recently some authors rejected the idea of obligatory bipedality in many ornithischians. For instance: it was suggested by Santa Luca (1980: 200) that "heterodontosaurids... have quadrupedal as well as bipedal capabilities"; Norman (1980) considered *Iguanodon* Mantell and *Tenontosaurus* Ostrom as capable of quadrupedal locomotion; we (Maryńska and Osmólska 1983, 1984b) considered that in some circumstances hadrosaurs might be quadrupeds, although we share the traditional opinion that they were habitual bipeds because the structure of their manus was unsuited for progression on a hard ground. Our recent inspection of new psittacosaur material in Ulan Bator (presently under elaboration by Dr. A. Perle) has convinced us that the structure of the forelimb, particularly an exceptionally strong deltopectoral crest, as well as the natural curvature of the vertebral column, speak in favor of the quadrupedal abilities of the psittacosaur. *Microceratops* Bohlin was once considered by us (Maryńska and Osmólska 1975) as secondarily adapted to quadrupedal progression. It seems, however, equally possible that quadrupedality in that protoceratopsid was the retained, primitive condition and that *Microceratops* (as the only protoceratopsid) was bipedal during fast progression.

If one excludes ornithopods from the ornithischian ancestry, as we propose in the present paper, it is no longer necessary to assume that bipedality was primitive for ornithischians. Accordingly, we presume that such ornithischians as: ankylosaurs, stegosaurs and ceratopsians were not secondary, but primary quadrupeds, while pachycephalosaurs were secondary bipeds. Heterodontosaurids may be regarded as quadrupeds which achieved a certain degree of bipedal faculty. The strong curvature of the vertebral column in the naturally (?) arranged skeleton of *H. tucki* (Santa Luca 1980: fig. 3) agrees well with the suggested quadrupedality of that animal. What concerns the ornithopod lineage, a tendency to quadrupedality observed in some forms may be explained either as a retention of primitive ornithischian faculties, or as a secondary condition. If the former is true, as we suppose, fabrosaurids would be the ornithopods which achieved very early a high degree of bipedality and thus could not give rise to any other ornithopod family. Lastly, it should be mentioned here that ornithopods were the only ornithischians which attained large sizes being still able to progress bipedally. One may suppose that it was possible only due to the presence of obturator process which in a way preadapted the pelvis to support the increasing weights.

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O FILOGENEZIE DINOZAUROW PTASIOMIEDNICZYCH (ORNITHISCHIA)

Streszczenie

Dokonano kladystycznej analizy pokrewieństw między różnymi grupami dinozaurów ptasiomiedniczych (Ornithischia). Preferowana hipoteza (fig. 1) postuluje, że: dinozaury ptasiomiednicze są grupą monofiletyczną; dinozaury pancerne (Ankylosauria) są grupą siostrzaną wszystkich pozostałych ptasiomiedniczych; dinozaury grubogłowe (Pachycephalosauria) + dinozaury rogate (Ceratopsia) są jednostką monofiletyczną. Zdaniem autorek, nie ma dotychczas dostatecznych dowodów pozwalających utrzymywać pogląd, że pierwotną cechą dinozaurów ptasiomiedniczych jest dwunożność. W chwili obecnej bardziej prawdopodobne wydaje się, że przodek ptasiomiedniczych był czworonożny.

Praca została wykonana w ramach problemu MR II 6.
