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The fossil record, systematics and evolution of pachycephalosaurs and ceratopsians from Asia

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Introduction

Although little is known of the first half of their evolutionary history, margin-headed ornithischians (Marginocephalia) are represented by a remarkable array of small- and large-bodied species during the last 20 million years of the Mesozoic. Marginocephalians comprise two distinctive subgroups, pachycephalosaurs and ceratopsians, both characterized by a bony shelf that projects from the posterior skull margin. Pachycephalosaurs, as their group name suggests, have thickened the skull roof, the margins of which are ornamented with distinctive tubercles. Ceratopsians, by contrast, have extended the posterior shelf as a thin bony frill, which is often accompanied by one or more cranial horns.

Abundant in late Early and Late Cretaceous deposits in central Asia and western North America, marginocephalians are exceptionally rare earlier in the Cretaceous (Neocomian) and have never been found in deposits that are regarded with confidence as Jurassic in age. Marginocephalian origins, however, surely date back at least to the Early Jurassic, when they diverged from their sister group, the ornithopods.

In this chapter, the best-known Asian pachycephalosaurs and ceratopsians are reviewed and a general account of their osteology is presented. The phylogenetic relationships of all marginocephalians are considered. The biogeographic history of marginocephalians is particularly interesting, as it clearly involves a polar dispersal route across Beringia – a well-trodden passage that played a major role in the evolution of dinosaurs in the Northern Hemisphere during the Late Cretaceous (Sereno, 1997, 1999a).

Institutional abbreviations

AMNH, American Museum of Natural History, New York; GI, Geological Institute, Ulaanbaatar; GPI, Geologische-Paläontologisches Institut, Göttingen; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MIWG, Museum of the Isle of Wight (Geology), Sandown; MNHN, Muséum National d'Histoire Naturelle, Paris; MOR, Museum of the Rockies, Bozeman; NMC, National Museum of Canada, Ottawa; PAL, Institute of Paleobiology, Warsaw; PIN, Paleontological Institute, Moscow; TF, Department of Mineral Resources, Bangkok; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller; UA, University of Alberta, Edmonton; USNM, National Museum of Natural History, Washington; YPM, Yale Peabody Museum, New Haven.

History of discovery

Excluding large-bodied ceratopsids from North America and *Psittacosaurus* and *Protoceratops* from Asia, marginocephalian fossils are generally rare and incomplete. The first relatively complete skeletal remains were discovered in Alberta and pertain to the pachycephalosaur *Stegoceras validus* (Gilmore, 1924; Sues and Galton, 1987) and the ceratopsian *Leptoceratops gracilis* (Brown, 1914). The type skull and skeleton of *Stegoceras* (UA 2), still the most complete pachycephalosaur skeleton from North America, revealed the peculiar anatomy of these bipedal ornithischians, known previously from isolated teeth and thickened skull caps. Shortly after the discovery of the first skeleton of *Leptoceratops* (AMNH 5205), three additional skeletons were discovered (Sternberg,

Table 25.1. *Age and known geographic range of pachycephalosaurs and ceratopsians*

Taxa	Age	Known geographic range
Pachycephalosauria		
Stenopelix valdensis	Barremian	central Europe
Wannanosaurus yansiensis	Campanian	eastern China
Goyocephale lattimorei	Campanian	southern Mongolia
Homalocephale calathocercos	Maastrichtian	southern Mongolia
Ornatotholus browni	Campanian	western North America
Yaverlandia bitholus	Barremian	western Europe
Stegoceras validus	Campanian	western North America
Prenocephale prenes	Maastrichtian	southern Mongolia
Tylocephale gilmorei	Campanian	southern Mongolia
Stygimoloch spinifer	Maastrichtian	western United States
Pachycephalosaurus wyomingensis	Maastrichtian	western United States
Ceratopsia		
Psittacosaurus	Barremian–early Aptian	China, Mongolia
Chaoyangsaurus youngi	latest Jurassic/Neocomian	northern China
Archaeoceratops oshimai	Neocomian	northern China
Leptoceratops gracilis	Maastrichtian	western Canada
Udanoceratops tschizhovi	Campanian	southern Mongolia
Bagaceratops rhozhdestvenskyi	Campanian	southern Mongolia
Protoceratops andrewsi	Campanian	southern Mongolia
Graciliceratops mongoliensis	Campanian	southern Mongolia
Montanoceratops cerorhynchus	Maastrichtian	western North America
Turanoceratops tardabilis	Cenomanian or Turonian	Uzbekistan
Ceratopsidae	Campanian–Maastrichtian	western North America

1951) that, likewise, constitute the most complete basal ceratopsian to date from North America.

Expeditions to the Gobi Desert in the 1920s by the American Museum in New York (see Chapter 12) and to northern China in the 1930s by the Palaeontological Institute in Uppsala brought to light much of what we currently know about marginocephalian diversity during the Late Cretaceous (Table 25.1). Numerous skulls and skeletons and the first well documented growth series were recovered for the basal ceratopsians *Psittacosaurus mongoliensis* (Osborn, 1923, 1924; Coombs, 1982; Sereno 1987, 1990a, b) and *Protoceratops andrewsi* (Granger and Gregory, 1923; Brown and Schlaikjer, 1940; Dong and Currie, 1993). Several new genera of pachycephalosaurs and basal ceratopsians were discovered by subsequent expeditions to Mongolia and northern China (Maryańska and

Osmólska, 1974, 1975; Perle *et al.*, 1982; Kurzanov, 1992; Dong and Azuma, 1997; see also Chapters 12 and 13).

Systematics of Asian marginocephalians

Taxonomic definitions

The utility of taxon names based on phylogenetic definitions has been explored by de Queiroz and Gauthier (1990, 1992). Node-based or stem-based phylogenetic definitions were applied to groups with living members to differentiate crown groups (node-based) from more inclusive groups (stem-based) that incorporate intervening extinct taxa.

Recently, this approach has been generalized to stabilize the phylogenetic meaning of widely used names

Table 25.2. *Unranked classification for marginocephalians. Taxa with node-based definitions are shown in bold, and those with stem-based definitions are shown in regular type (Sereno, 1997, 1998). This configuration of phylogenetic definitions specifies four node-stem triplets*

Marginocephalia
Pachycephalosauria
Pachycephalosauridae
Stegoceras
Pachycephalosaurinae
Ceratopsia
Neoceratopsia
Coronosauria
Protoceratopsidae
Ceratopsoidea
Ceratopsidae
Centrosaurinae
Ceratopsinae

for living or extinct clades (Sereno, 1997, 1998, 1999b). Taxa are defined with respect to one another using the same reference taxa to create stable node-stem triplets. The unranked classification used in this review is based on four node-stem triplets (Table 25.2).

Pachycephalosauria Maryańska and Osmólska, 1974
Definition. All marginocephalians closer to *Pachycephalosaurus* than *Triceratops* (Sereno, 1998)

Wannanosaurus yansiensis. *Wannanosaurus* is based on a partial skull (Figure 25.1) and several postcranial bones of one immature individual (IVPP V4447) with additional vertebrae and limb bones of a second individual found nearby (Hou, 1977). Like *Yaverlandia*, *Wannanosaurus* is a small pachycephalosaur, although the open sutures in the holotype cranium suggest that at maturity it may have reached a somewhat larger body size (contrary to Maryańska, 1990, p. 574, who remarked that the cranial sutures were obliterated). *Wannanosaurus* has a flat dorsal skull table with relatively large supratemporal fossae. The associated postcranial bones share several features with *Homalocephale* and *Stegoceras*, such as the short forelimb (humerus less than one-half femoral length), sigmoid-shaped humerus, and slender distal fibula. Diagnostic

features of *Wannanosaurus* include the low, fan-shaped dentary crowns with a marked median eminence on the lateral crown surface and the extreme flexure of the humerus (proximal and distal ends set at approximately 30° to one another).

Goyocephale lattimorei. *Goyocephale* is based on a relatively complete skeleton with a partial skull (GI SPS 100/1501) and is the best known of basal pachycephalosaurs (Perle *et al.*, 1982). It falls in the middle of the range of body size for pachycephalosaurs, similar to that of *Homalocephale*, *Stegoceras* and *Prenocephale*. Although Perle *et al.* (1982, p. 117) presented a lengthy diagnosis for *Goyocephale*, most of the listed features characterize other pachycephalosaurs as well. There are only a few features that are peculiar to *Goyocephale*, and these include the sinuous lateral margin of the skull as seen in dorsal view. The lateral margin is particularly prominent above the orbit where the two supraorbitals meet, resulting in an S-shaped edge as seen in dorsal view. In addition, the sternals in *Goyocephale* (Perle *et al.*, 1982, pl. 41) are more slender and gently curved than those in *Stegoceras* (UA 2).

Homalocephale calathocercos. *Homalocephale*, known from a partial skeleton and flat-headed skull (GI SPS 100/1201; previously listed as GI SPS 100/51, Maryańska and Osmólska, 1974), can be distinguished from other pachycephalosaurs by the crescent-shaped, ventrally deflected postacetabular process of the ilium. Other features, such as the sacral attachments to the ischium, may eventually prove to be diagnostic, but these are not preserved in any other pachycephalosaur.

Pachycephalosauridae Sternberg, 1945
Definition. *Stegoceras*, *Pachycephalosaurus*, their most recent common ancestor and all descendants (Sereno, 1998).

Prenocephale prenes. Based on a beautifully preserved cranium and partial postcranial skeleton (PAL MgD I/104; Figure 25.2), *Prenocephale* is currently the best known fully domed pachycephalosaur (Maryańska and Osmólska, 1974). The straight dorsal margin of the snout, which resembles that in *Goyocephale* (Perle *et*
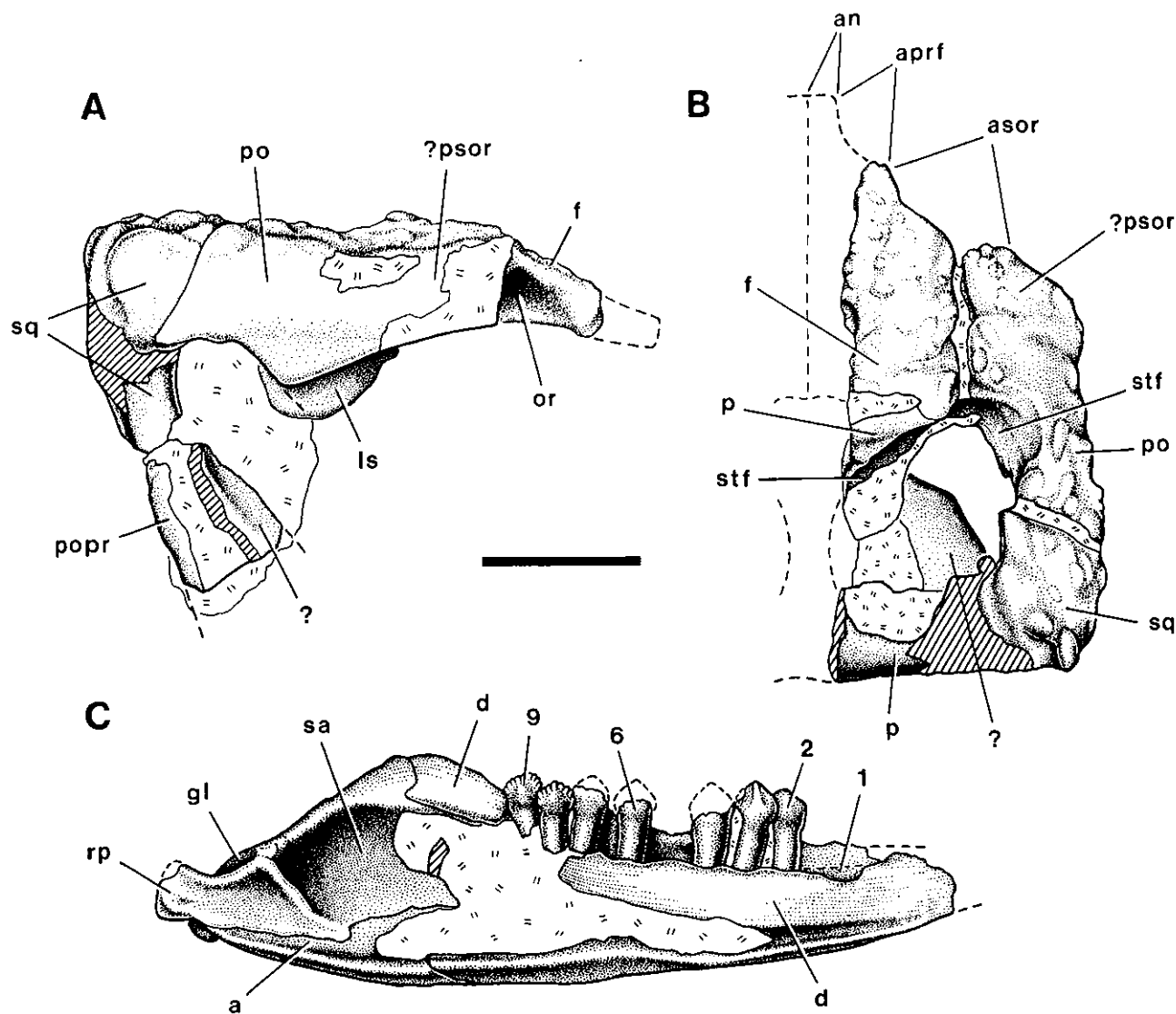
Figure 25.1. *Wannanosaurus yansiensis* (IVPP V4447), partial cranium in right lateral (A) and dorsal (B) views and left lower jaw in (C) medial view. Abbreviations: a, angular; an, articular surface for the nasal; aprf, articular surface for the prefrontal; asor, articulation for anterior supraorbital; d, dentary; f, frontal; gl, glenoid; ls, laterosphenoid; p, parietal; po, postorbital; popr, paroccipital process; psor, posterior supraorbital; rp, retroarticular process; sa, surangular; sq, squamosal; stf, supratemporal fossa; 1–9, position in tooth row. Scale bar equals 10 mm.

al., 1982), differs from the gently arched margin and shorter premaxilla in *Stegoceras* (Figure 25.3). In *Prenocephale*, the proximal end of the quadrate is tongue-shaped, and there is an unusual bulbous knob on the free dorsal margin of the quadratojugal (preserved on both sides). Aspects of cranial ornamentation, such as the unbroken line of tubercles that connect those on the postorbital with those on the jugal, may also be diagnostic for *Prenocephale*.

Tylocephale gilmorei. *Tylocephale*, known from a single weathered cranium and the posterior portion of the lower jaws (PAL MgD I/105; Figure 25.4), is a fully domed pachycephalosaur (Maryańska and Osmólska, 1974). As these authors noted, it differs in several details from *Prenocephale*, which it otherwise resembles quite closely. The dome and occiput are narrower, and the postorbital bar and quadrate are more slender (Maryańska and Osmólska, 1974, p. 51). The orbit was described as more elongate, but this may be the result
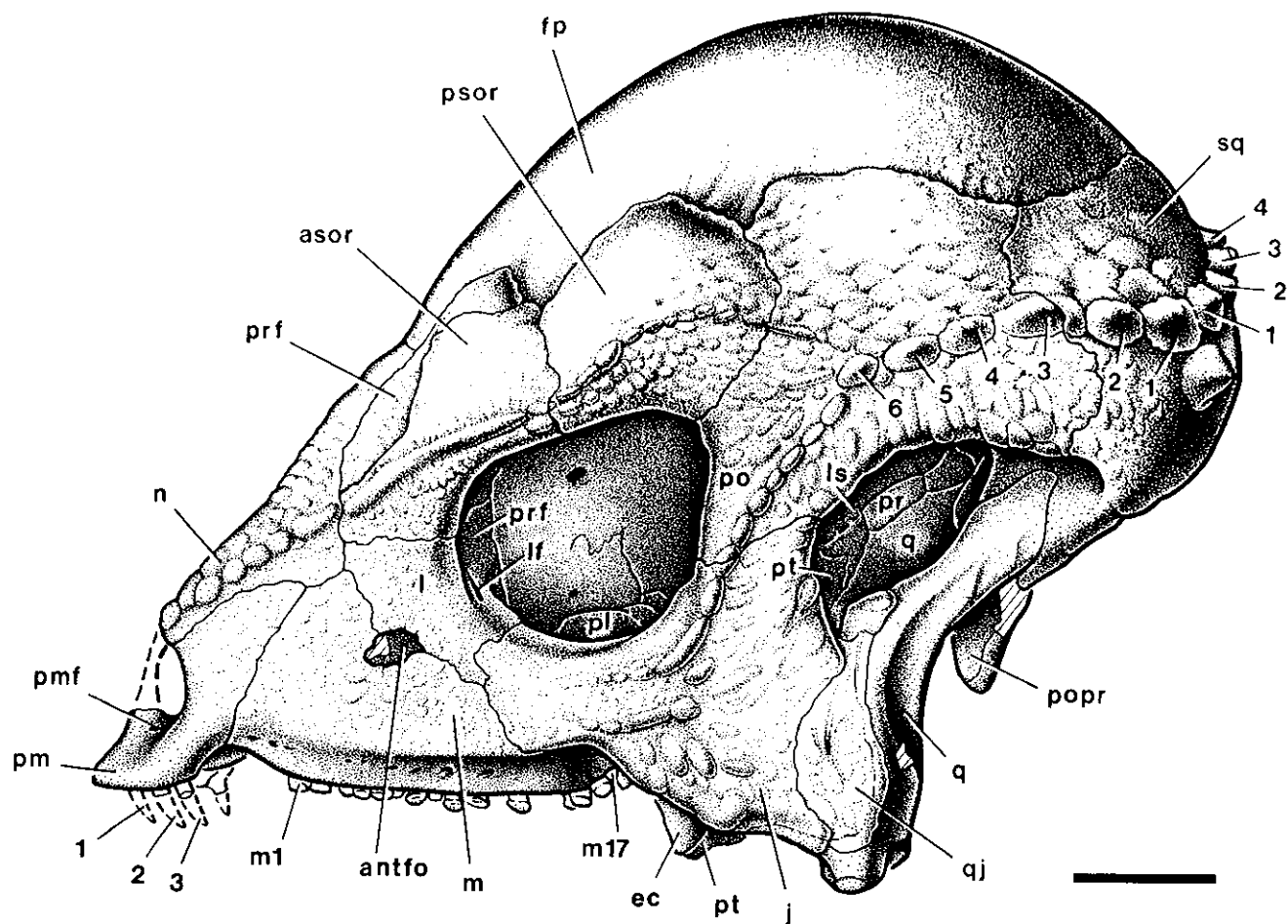
Figure 25.2. *Prenocephale prenes* (PAL MgD I/104), cranium in left lateral view. Abbreviations: as in Figures 25.1 and 25.3 and antfo, antorbital fossa; lf, lacrimal foramen; pmf, premaxillary foramen; pr, prootic; pt, pterygoid. Scale bar equals 30 mm.

of dorsoventral crushing of the cranium. The nodular ornamentation that characterizes the margins of the dome also differs from that in *Prenocephale*. *Tylocephale* has a dorsally upturned corner tubercle on the squamosal as in *Prenocephale*, but there are fewer tubercles medial to the corner tubercle in *Tylocephale*, probably only four on the right side and three on the left (contrary to Maryańska and Osmólska, 1974, fig. 1B4). In *Tylocephale* the ornamental tubercles on the postorbital bar are reduced compared to those in *Prenocephale*, but there are tubercles on the supraorbitals above the orbital margin that are absent in *Prenocephale*. A large oval depression, centred on the quadratojugal and preserved on both sides of the skull, may constitute a diagnostic feature of this pachycephalosaur. *Prenocephale* has a similar, although much smaller,

quadratojugal depression. In the lower jaw, the angular is ornamented with tubercles (contrary to Maryańska and Osmólska, 1974, p. 52), and the jaw articulation is positioned somewhat below the maxillary tooth row, as in other pachycephalosaurs. The dentary teeth, which are the best preserved, are characterized by a primary ridge and secondary ridges that extend down much of the crown surface. These crowns are easily distinguished from those of *Stegoceras*, in which the medial side of the crowns are dorsoventrally concave.

In summary, the skull and dentition of *Tylocephale* clearly indicate that it is a distinct, fully-domed pachycephalosaur that is similar, and quite possibly closely related, to *Prenocephale*. Diagnostic features include a narrow, deep skull and large fossa on the quadratojugal.
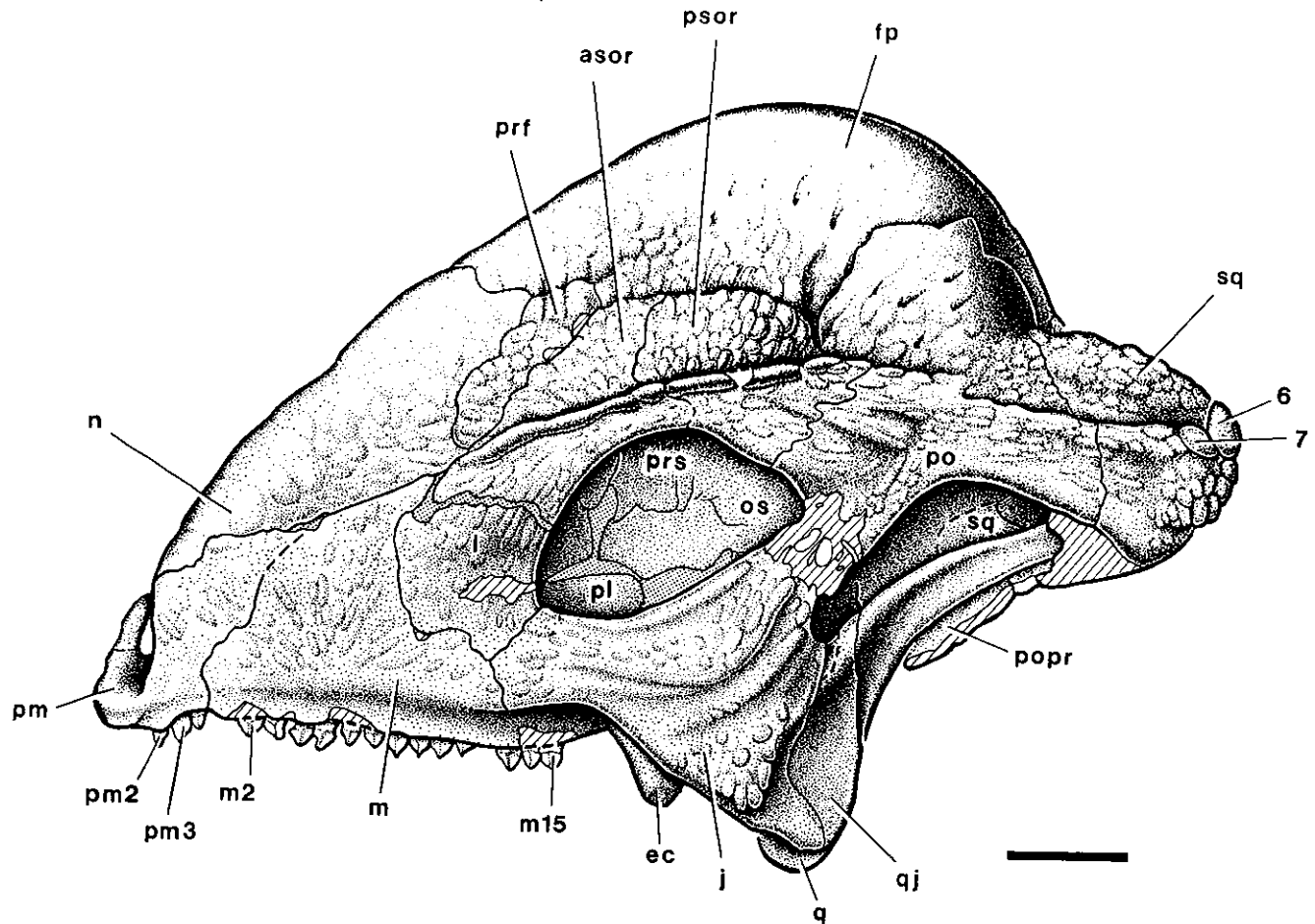
Figure 25.3. *Stegoceras validus* (UA 2), cranium in left lateral view. Abbreviations: as in Figure 25.1 and asor, anterior supraorbital; ec, ectopterygoid; fp, frontoparietal; j, jugal; l, lacrimal; m, maxilla; m1–17, maxillary tooth positions; n, nasal; os, orbitosphenoid; pl, palatine; pm, premaxilla; pm1–3, premaxillary tooth positions; prf, prefrontal; q, quadrate; qj, quadratojugal; 1–7, postorbital or squamosal tubercles. Scale bar equals 30 mm.

Ceratopsia Marsh, 1890

Definition. All marginocephalians closer to *Triceratops* than to *Pachycephalosaurus* (Sereno, 1998).

Psittacosaurus. Psittacosaurids, or 'parrot-beaked' dinosaurs, constitute a tightly knit group of species in the single genus *Psittacosaurus* (Figure 25.5), known only from Lower Cretaceous beds in China, Mongolia and Siberia (Sereno, 1987, 1990a, b; Eberth *et al.*, 1993). *P. mongoliensis* and *P. sinensis*, the former the larger and less derived of the two, are known from many skeletons, some with complete skulls. Two additional species, *P. xinjiangensis* and *P. meileyingensis* (Sereno and Chao, 1988; Sereno *et al.*, 1988), based on less complete material, have been described from China. The

former has a characteristic pyramidal jugal horn, and the latter has an extremely short skull that is nearly round in profile. Recently, two additional species have been described from Inner Mongolia, *P. neimongoliensis* and *P. ordosensis* (Russell and Zhao, 1996), which are extremely close to *P. mongoliensis* and *P. sinensis*, respectively. Finally, additional species have been described from China and Thailand (*P. mazongshanensis*, *P. sattayataki*), but their taxonomic status is questioned below.

The genus *Psittacosaurus* and the six species recognized here are diagnosed almost entirely on the basis of cranial characters. The deep and very short psittacosaurid snout, which constitutes less than 40% of skull length, most closely resembles that in the aberrant
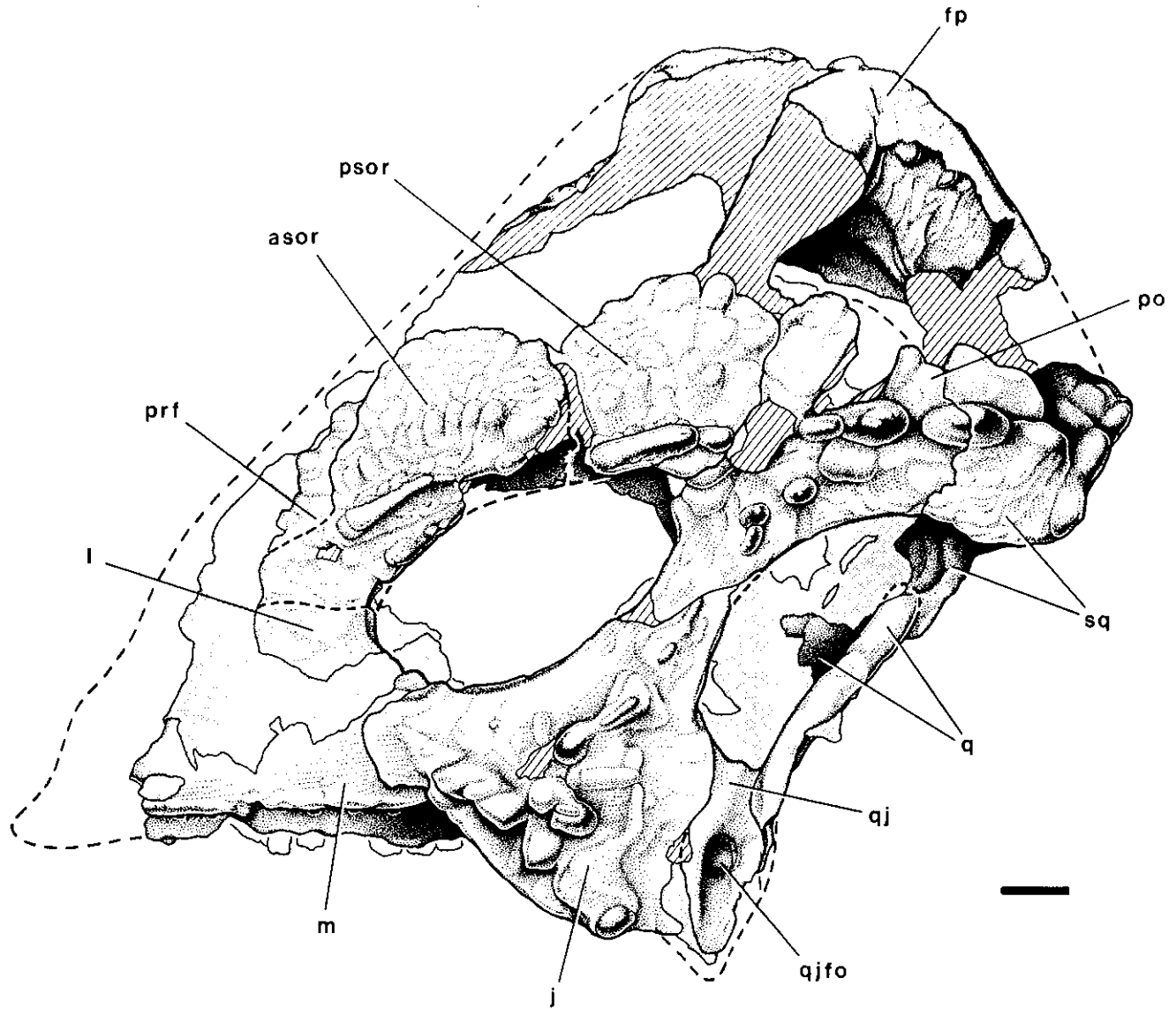
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Figure 25.4. *Tylocephale gilmorei* (PAL MgD I/105), cranium in left lateral view. Abbreviations: as in Figures 25.1–25.3. Scale bar equals 10 mm.

theropod subgroup Oviraptoridae. The external naris is positioned very high on the snout, which is composed of the ceratopsian rostral bone and the broadly expanded premaxilla (Figure 25.5). The antorbital fenestra is closed and the antorbital fossa is absent. A small lateral depression is present on the maxilla in several species of *Psittacosaurus* and has been identified as a reduced antorbital fossa (Sereno, 1987; Sereno and Chao, 1988; Sereno *et al.*, 1988). This structure, however, is regarded here as a neomorphic depression unrelated to diverticulae of the cranial sinus system. Unlike any other dinosaurs, a section of the lateral wall of the lacrimal canal remains unossified in psittacosaurs; a foramen of variable size between the premaxilla and lacrimal exposes a section of the canal. Species differences are based primarily on cranial features, such as the shape of the jugal horn and length of the parietosquamosal frill.

The psittacosaurid postcranial skeleton is remarkably primitive compared to most other Cretaceous
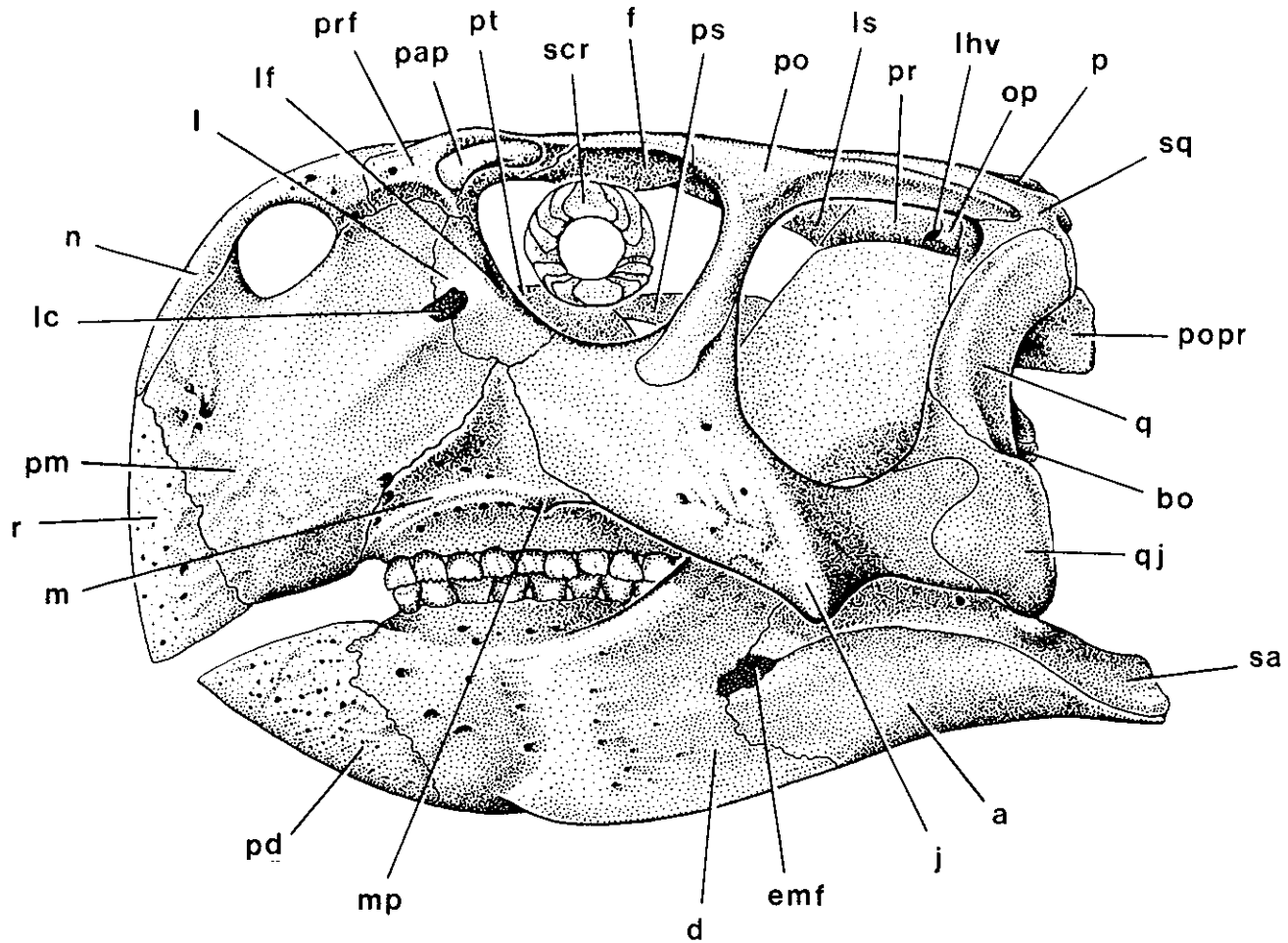
Figure 25.5. *Psittacosaurus mongoliensis*, skull reconstruction in left lateral view. Abbreviations: as in Figures 25.1–25.3 and bo, basioccipital; emf, external mandibular fenestra; lc, lacrimal canal; lhv, lateral head vein; mp, maxillary process; pap, palpebral; pd, predentary; ps, parasphenoid; r, rostral; sc, sclerotic ring. (From Sereno *et al.*, 1988.)

ornithischians. The relatively long and strongly built forelimb and the flattened manual unguals suggest that psittacosaurids may have been facultatively quadrupedal. Unlike later quadrupedal ceratopsians, however, the external digits of the manus are reduced or eliminated such that only digits I-III are functional.

Neoceratopsia Sereno, 1986

Definition. All ceratopsians closer to *Triceratops* than to *Psittacosaurus* (Sereno, 1998).

Chaoyangsaurus youngi. Described briefly by Zhao (1983, 1986), and in more detail by Zhao *et al.* (1999) from possible Jurassic beds in northern China,

Chaoyangsaurus is an intriguing basal ceratopsian intermediate in form between psittacosaurs and other neoceratopsians. Similar to a large psittacosaur in body size, *Chaoyangsaurus* is known only from the holotype specimen (IVPP V11527), which consists of a partial skull with lower jaws, several cervical vertebrae and a partial scapula and humerus. The rostral bone clearly establishes *Chaoyangsaurus* as a ceratopsian, and several features clearly link this early form with later neoceratopsians, including the narrow snout, strongly flared jugal arch, and pair of reduced, subconical premaxillary teeth (Zhao, 1983; Zhao *et al.*, 1999). As in other neoceratopsians, but unlike psittacosaurs and other outgroups, the skull appears to be quite large

relative to girdle and appendicular bones, although more complete postcrania are needed for confirmation of this. The low, subtriangular maxillary and dentary crowns are primitive and resemble the condition in psittacosaurs. Likewise, the relatively broad proportions of the laterotemporal fenestra, absence of an epijugal ossification, substantial length of the postdentary elements of the lower jaw, and unfused condition of the anterior cervical vertebrae are plesiomorphic relative to other neoceratopsians. Unfortunately, the posterior portion of the dorsal skull roof and occiput are not preserved, so the presence and development of the parietosquamosal shelf is not known.

Archaeoceratops oshimai. Described recently from Early Cretaceous beds in Gansu Province, China, *Archaeoceratops* is known from two partial skeletons of relatively small size that include a relatively complete skull with lower jaws (Dong and Azuma, 1996, 1997; IVPP V11114, V11115). *Archaeoceratops* is clearly more advanced than *Chaoyangsaurus* on the basis of many features of the skull that closely resemble the condition in *Protoceratops* and other neoceratopsians, including the strong lateral crest on the jugal and the marked anteroposterior shortening of the laterotemporal region and postdentary elements of the lower jaw (Dong and Azuma, 1997, fig. 2). The antorbital fossa has a sharp rim and oval shape as in *Leptoceratops* and *Protoceratops* (contra Dong and Azuma, 1997, fig. 2A). The short parietosquamosal frill, low number of sacral vertebrae, and relatively long tapered tail establish *Archaeoceratops* as a very primitive neoceratopsian. Although reconstructed as a biped (Dong and Azuma, 1997, figs. 11 and 12), the pectoral girdle and forelimb are unknown, and the habitual posture of this early neoceratopsian cannot be reliably determined. Diagnostic features for the genus and species have yet to be identified, but may involve the dentition.

Udanoceratops tschizhovi. Recently described on the basis of a partial skull from Mongolia (Kurzanov, 1992), *Udanoceratops* has a skull length of approximately 0.6 m, which equals that of the largest specimens of *Protoceratops* (Brown and Schlaikjer, 1940, fig.

13). Distinguishing cranial features include an enlarged, oval external naris that, unlike other basal neoceratopsians, exceeds the orbit in maximum diameter. A depression on the posterolateral process of the premaxilla and an extremely deep and strongly arched lower jaw also distinguish this new neoceratopsian. *Udanoceratops* shares with *Leptoceratops* the strongly arched lower jaw and absence of premaxillary teeth, but differs from the latter in having straight tooth rows (Kurzanov, 1992, fig. 2b). The teeth are very similar to *Leptoceratops* and have enamel on both sides of the dentary crowns.

Coronosauria Sereno, 1986

Definition. *Protoceratops*, *Triceratops*, their most recent common ancestor and all descendants (Sereno, 1998).

Bagaceratops rozhdestvenskyi. Known from many specimens from the Hermiin Tsav red beds of the Baruungoyot Formation in Mongolia, *Bagaceratops* is second only to *Protoceratops* in the quantity of known remains, although the postcranial material has not been described in detail (Maryańska and Osmólska, 1975; Osmólska, 1986). As discussed below (see Problematic taxa), *Breviceratops* (Kurzanov, 1990) is regarded here as a junior synonym of *Bagaceratops*, and it is very likely that *?P. kozlowskii* and *Bagaceratops rozhdestvenskyi* represent the same species.

Cranially and postcranially, *Bagaceratops* is similar to *Protoceratops* in nearly all details. The most outstanding differences in the cranium of *Bagaceratops* are an oval accessory fenestra between the premaxilla and maxilla and a coossified median nasal horn. The premaxillary–maxillary fenestra appears to decrease in size with maturity (Maryańska and Osmólska, 1975, fig. 9). The median nasal horn, which fuses early in growth and migrates posteriorly (Kurzanov, 1990), preserves traces of a median suture on its posterior aspect in immature individuals (PIN 3142/1; PAL MgD-I/125). Thus, the horn is composed of coossified processes of the nasals, as in centrosaurines (Gilmore, 1917), rather than a separate median ossification, as in some chasmosaurines.

Several other aspects of *Bagaceratops* appear to be

artefacts of preservation. The skull has been recon-structed with a short, unfenestrated frill, an antorbital fossa floored in part by the nasal, and a jugal without the accessory epijugal ossification (Maryańska and Osmólska, 1975, fig. 6). The frill in mature individuals, however, is fenestrated, as shown in additional speci-mens (Kurzanov, 1990, fig. 2; H. Osmólska, pers. comm.). The participation of the nasal in the antorbi-tal fossa, a configuration not found in any ceratopsian, was reconstructed from a specimen that does not pre-serve this portion of the fossa (Maryańska and Osmólska, 1975, pls. 42 and 43). Attachment scars on the jugal and quadratojugal (PAL MgD-I/125) indi-cate that an epijugal, as large and prominent as in *Protoceratops*, is present in *Bagaceratops* (contrary to Dodson and Currie, 1990, p. 613). The squamo-sal–jugal contact occurs above the laterotemporal fenestra (contrary to Dodson and Currie, 1990, p. 613), but this contact is exposed only on the medial side of the postorbital (Maryańska and Osmólska, 1975, p. 158; Kurzanov, 1990, fig. 1). The reduction of this contact (and the posterior arching of the ascending ramus of the jugal) may characterize *Bagaceratops*.

Other features previously considered diagnostic for *Bagaceratops* – such as the low number of maxillary teeth (10) and straight margin of the lower jaw – are probably due to the immaturity of even the largest available specimens. All of these features occur in immature individuals of *Protoceratops* (Brown and Schlaikjer, 1940; Kurzanov, 1992). In addition, the absence of premaxillary teeth in *Bagaceratops* requires further documentation, given the poor preservation of the critical posterior margin of the premaxilla in all available specimens and the presence of premaxillary teeth in juvenile individuals (Dong and Currie, 1993).

Protoceratops andrewsi. Based on a splendid series of skeletons from hatchlings to adults, *Protoceratops* is the best known neoceratopsian (Brown and Schlaikjer, 1940). Generic and specific diagnoses for *Protoceratops*, nevertheless, do not include any derived features (e.g., Steel, 1969) because the skeleton is plesiomorphic in nearly all regards at the level of Neoceratopsia. Possible autapomorphies include the short lateral pro-

cesses on the rostral, low tab-shaped processes on the frill margin (three on the squamosal and four or five on the parietal), parasagittal nasal prominences, and hoof-shaped pedal unguals (Figure 25.6).

Graciliceratops mongoliensis, n. gen., n. sp. Bohlin (1953) erected a new genus, *Microceratops*, with two new species on the basis of teeth, fragmentary jaws and assorted postcrania, much of which he believed to be from immature individuals. This fragmentary material came from two localities in different horizons in Gansu Province, China, the ages of which remain uncertain (Dong and Azuma, 1997). Bohlin (1953, p. 35) observed that the primary ridge in the dentary teeth in *Microceratops gobiensis* may be less prominent than in the closely related genus *Protoceratops*. No other diagnostic features were given, and it can be seen that the primary ridge varies in strength in the dentary crowns figured by Bohlin. Furthermore, the holotype dentary (Bohlin, 1953, fig. 14c) does not have any com-plete crowns and is now apparently lost (Z. Dong, pers. comm.). Young (1958, fig. 1B) referred an isolated maxilla and other small neoceratopsian material from Shansi Province, China to *M. gobiensis* on the basis of its small size. There appears to be no other basis for this referral. The second species, *Microceratops sulcid-ens*, is based on two isolated teeth, vertebrae and bones of the manus and pes (Bohlin, 1953, figs. 36–38, pl. II). The small size of this material is usually the only feature mentioned in taxonomic diagnoses (e.g., Steel, 1969). Dodson and Currie (1990, tab. 29.1) listed *M. sulcidens* as a junior synonym of *M. gobiensis*, but gave no reasons for this synonymy. Given the absence of any diagnostic features of the holotype material and the abundance of immature individuals at many Asian localities that have yielded ceratopsian remains, the genus *Microceratops* and the species *M. gobiensis* and *M. sulcidens* are regarded here as *nomina dubia*.

Maryańska and Osmólska (1975) referred an articu-lated skeleton (PAL MgD-I/156) from Shireegiin Gashuun in Mongolia to *Microceratops gobiensis*, osten-sibly because of its small size relative to other basal neoceratopsians. Although no other reason was given, this referral has never been questioned. The primary
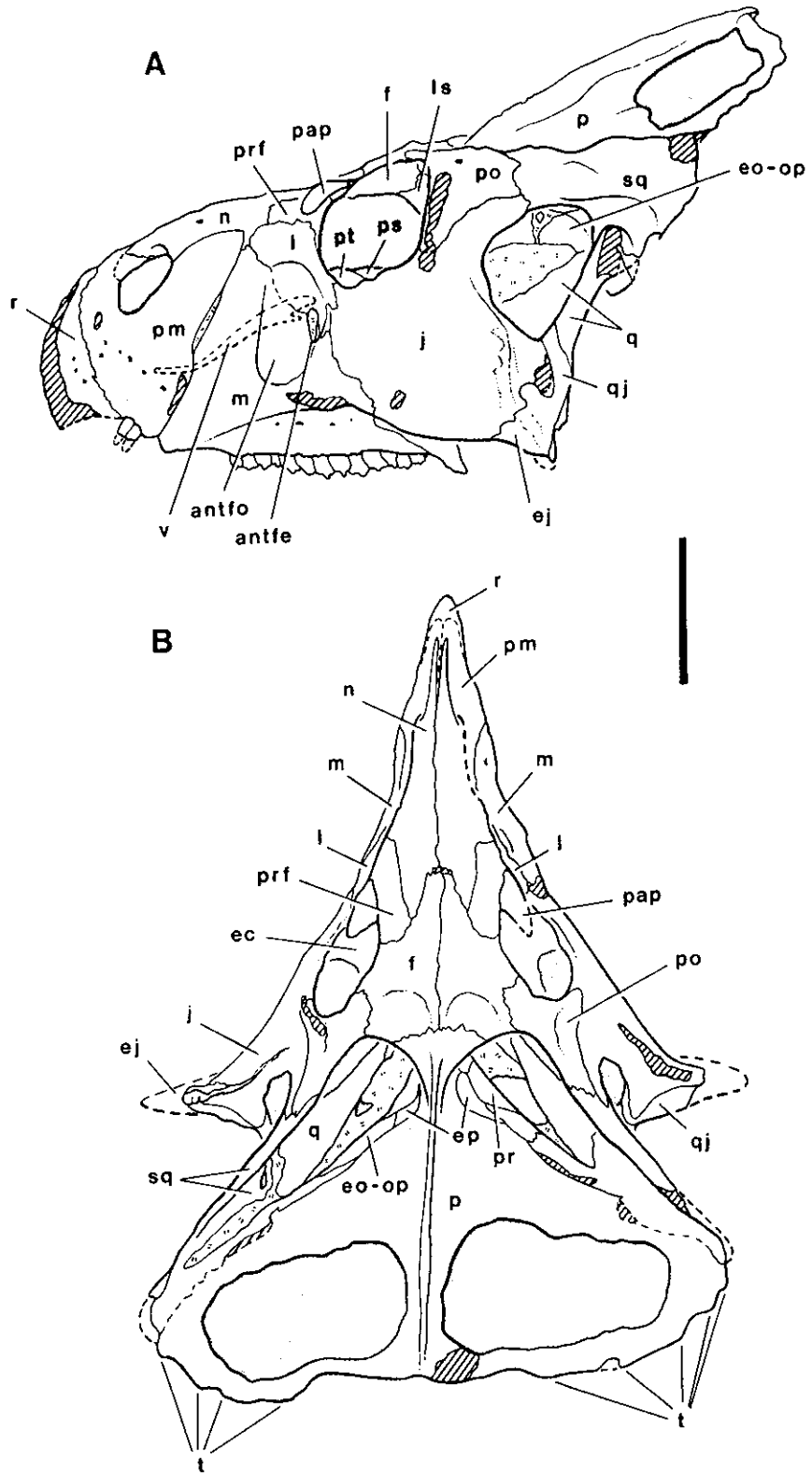
Figure 25.6. *Protoceratops andrewsi* (AMNH 6408), cranium in left lateral (A) and dorsal (B) views. Dashed outline shows position of vomer. Abbreviations: as in Figures 25.1–25.5 and antfe, antorbital fenestra; ej, epijugal; eo-op, exoccipital-opisthotic (fused); ep, epiotic; t, tab-shaped flange; v, vomer. Scale bar equals 50 mm.
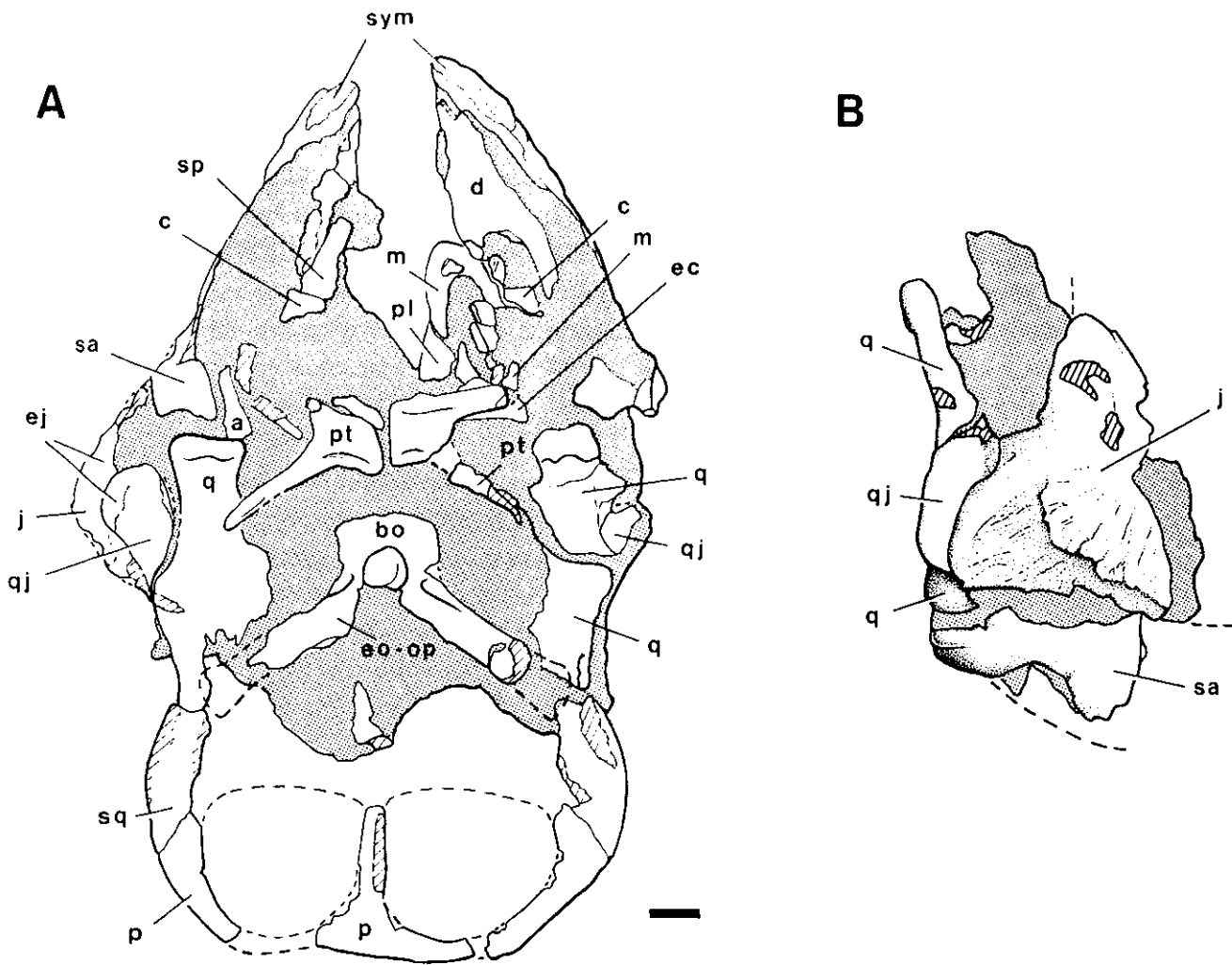
Figure 25.7. *Graciliceratops mongoliensis*, gen. nov., sp. nov. (A) Partial skull in ventral view and (B) posterior portion of skull in right lateral view showing inset articular surface for the epijugal. Abbreviations: as in Figures 25.1–25.6. Scale bar equals 10 mm.

ridge in the dentary crowns of this specimen, however, is as prominent as in other neoceratopsians. There is no basis, therefore, for referral of this specimen to *Microceratops* or to the species *M. gobiensis*. Because this skeleton is also from an immature individual (as shown by the disarticulated presacral neural arches and unfused sacral centra), its body size at maturity remains unknown and may well have equalled that of *Protoceratops*.

This skeleton is placed here in a new genus and species, *Graciliceratops mongoliensis* (*gracilis*, L. slender; *cerato-*, Gr. horn; *mongolia*, Mongolia; *-ensis*, L. place), characterized by the very slender median and poste-

rior parietal frill margins (Figure 25.7A) and high tibiofemoral ratio (1.2:1). The slender frill margins are very distinctive and much more delicate than reconstructed by Maryańska and Osmólska (1975, fig. 1). The frill extends quite far posterior to the occiput, and its lateral margins are formed by a well developed posterior process of the squamosal. Like *Bagaceratops*, the jugal and squamosal do not overlap extensively, as shown by well marked articular scars on the postorbital. A well demarcated scar on the jugal and quadratojugal indicates that a large epijugal was present (Figure 25.7B). The quadratojugal would have been exposed primarily in posterior view on the posterior aspect of

the prominent jugal–epijugal horn, as in most other basal neoceratopsians.

Ceratopsoidea Hay, 1902

Definition. All coronosaurs closer to *Triceratops* than to *Protoceratops* (Sereno, 1998).

Turanoceratops tardabilis. Based on isolated teeth and cranial fragments of unknown association (Nesov *et al.*, 1989), *Turanoceratops* provides important evidence that two-rooted maxillary and dentary teeth, previously known only in North American ceratopsids, appeared first in much smaller Asian ceratopsians during the Cenomanian or Turonian. Broken horn cores (presumably from the postorbital), a maxilla, and predentary were described along with the two-rooted teeth (Nesov *et al.*, 1989, pl. 1, figs. 16–21). The two-rooted cheek teeth probably indicate an increase in packing along the tooth row, and a primitive tooth battery may already have evolved. *Turanoceratops* appears to be a small-bodied neoceratopsian. Further study is required to adequately characterize the genus and species.

Problematic marginocephalians

Five problematic marginocephalians from Asia are considered first and set aside. *Micropachycephalosaurus hongtuyanensis* (Dong, 1978; IVPP V5542) is based on fragmentary postcrania of discordant size. Much of the ilium (Dong, 1978, fig. 2) exists only as an impression in rock. Although this taxon has survived recent systematic review (Maryańska, 1990), no pachycephalosaurian features or autapomorphies are apparent in this material. *Micropachycephalosaurus* is here considered a *nomen dubium*.

Psittacosaurus sattayaraki, recently described on the basis of a partial dentary and possibly a fragment of the maxilla (TF 2449) from Cretaceous beds in Thailand, is regarded by the authors as 'clearly referable to the genus *Psittacosaurus*' (Buffetaut *et al.*, 1989, p. 370). The justification given by Buffetaut and Suteethorn (1992, pp. 803, 805) for the generic reference ('relatively deep and short dentary' and 'bulbous primary ridge and secondary denticles') and erection

of a new species ('small incipient ventral flange,' 'strongly convex' alveolar region of the dentary and 'five denticles on both sides of the primary ridge') is questionable. The association between the dentary and maxillary fragment, described as 'possibly belonging to the same individual' (Buffetaut and Suteethorn, 1992, p. 801), must be regarded with suspicion as no supporting evidence for association of these specimens, collected years apart, was presented.

All basal ceratopsians have short, deep dentary rami, and the primary ridge on the dentary tooth of the Thai ornithischian, such as it is preserved (Buffetaut and Suteethorn, 1992, fig. 2C), is not bulbous as in *Psittacosaurus* (Osborn, 1923, figs. 4 and 5; Sereno and Chao, 1988, fig. 5C; Sereno *et al.*, 1988, fig. 7D). A dentary flange is developed only in some psittacosaurs (*P. mongoliensis* and *P. meileyingensis*) and extends vertically as a ridge across the posterior portion of the ramus (Sereno, 1990a, b), unlike the dentary from Thailand. The unusual features of this dentary are the low position of the predentary attachment surface relative to the tooth row and the abrupt medial arching of the symphysial region of the dentary. The anterior end of the dentary appears unfinished and weathered (Buffetaut and Suteethorn, 1992, fig. 2E), bringing into question its interpretation as a broad attachment area for the predentary. Given the poor preservation of the dentary and its dubious association with the supposed maxillary fragment, assignment to a new genus of uncertain phylogenetic affinity is not warranted. '*Psittacosaurus' sattayaraki* is tentatively referred here to Ceratopsia, incertae sedis.

Psittacosaurus mazongshanensis, described recently from a skull and partial skeleton from Gansu Province, China (Xu, 1997; IVPP V12165), may represent a distinct species. The available description, however, does not establish that fact convincingly, as there are no clear diagnostic features that are absent in other psittacosaur species. Until the basis for this species is clarified, the partial skeleton is here referred to *Psittacosaurus*, incertae sedis, and the species *P. mazongshanensis* is regarded as a *nomen dubium*.

Asiaceratops salsopaludalis, described from disarticulated, fragmentary remains from Cenomanian or early

Turonian beds in Uzbekistan, is a small basal ceratopsian (Nesov *et al.*, 1989). If properly assigned to *Asiaceratops*, the unguals are pointed as in most basal ceratopsians and unlike the broader unguals in *Protoceratops*. The maxillary tooth rows in at least two individuals have nine teeth, which is fewer than in subadult specimens of *Protoceratops*. The dentition is indistinguishable from that in several other basal ceratopsians, and no other autapomorphies are apparent in the holotype (a left maxilla) or referred material. *Asiaceratops* therefore is regarded here as a *nomen dubium*.

Finally, Kurzanov (1990) recently transferred *Protoceratops kozlowskii* to a new genus, *Breviceratops*. Maryańska and Osmólska (1975) originally tentatively referred an immature holotype skull (PAL MgD 1/117) from the locality Khulsan to *Protoceratops* as a new species, *?P. kozlowskii*. The new referred material consists of five partial skulls of immature individuals (PIN 3142/1–5; Kurzanov, 1990, figs. 1 and 2) from a different locality (Hermiin Tsav) in the same formation (Baruungoyot). The taxonomic status of *?P. kozlowskii* and *Bagaceratops rozhdestvenskyi*, the latter based on material also collected at Hermiin Tsav, is complicated by the immaturity and incompleteness of many of the specimens.

The diagnostic features originally listed for *?P. kozlowskii* (Maryańska and Osmólska, 1975, pp. 143–144) are either present in juveniles or adults of other species or are difficult to assess. The position of the nasal–frontal suture above the orbit, for example, is not unique to *?P. kozlowskii* but rather characterizes *Protoceratops andrewsi* and juveniles of *Bagaceratops*. The supposed advanced characters in the postcranium, such as the stronger lateral flare of the iliac preacetabular process, are based on the very immature holotype skeleton and were not figured or photographed in a manner allowing comparison. There are no unique features linking *?P. kozlowskii* to the genus *Protoceratops*. The presence of a nasal horn, which occurs in specimens referred to this species (Kurzanov, 1990) and in *Bagaceratops*, cannot be determined in the material upon which the species was based. There is some indication that an accessory premaxilla–maxilla fenestra

may have been present in the holotype skull of *?P. kozlowskii* (Maryańska and Osmólska, 1975, pl. 50, fig. 1a), as also occurs in specimens later referred to this species (Kurzanov, 1990) and in *Bagaceratops*. The characters Kurzanov (1990) invoked to distinguish this species from *Bagaceratops* (larger size, higher and wider skull, and parietal fenestrae) are not valid given the better preserved material now known for *Bagaceratops*. The only apparent difference between *?P. kozlowskii* and *Bagaceratops* is the presence of premaxillary teeth in the former, but this can no longer be considered significant given the presence of premaxillary teeth in immature individuals of *Bagaceratops* (Dong and Currie, 1993, fig. 3). The subcylindrical premaxillary teeth in these juveniles appear to have been lost during growth in *Bagaceratops*, although the one adult skull with an intact ventral margin of the premaxilla is not complete posteriorly (PAL MgD-I/127; Maryańska and Osmólska, 1975, pl. 45, 1c). In summary, it seems very likely that all of the basal ceratopsian specimens from the Baruungoyot Formation pertain to a single species. The most appropriate name for that taxon is *Bagaceratops rozhdestvenskyi*, the holotype of which exhibits several diagnostic features. *Breviceratops* is regarded here as a junior synonym of *Bagaceratops*.

Phylogeny

In the following sections, previous work on the phylogeny of marginocephalians is reviewed, marginocephalian synapomorphies are re-examined, and the branching pattern within Pachycephalosauria and Ceratopsia is analyzed. The central phylogenetic issues to resolve are the affinities of two enigmatic early marginocephalians, *Stenopelix* (Schmidt, 1969; Sues and Galton, 1982; Sereno, 1987) and *Chaoyangsaurus* (Zhao, 1983; Zhao *et al.*, 1999), and the phylogenetic reality of the basal subgroups Homalocephalidae and Protoceratopsidae.

Marginocephalia

Traditional classification. After the description of the first relatively complete skull and skeleton (*Stegoceras*

validus, Figure 25.3) by Gilmore (1924), early opinion presented two possibilities regarding the affinities of pachycephalosaurs (then termed 'troödonts'). Gilmore (1924) and others (Russell, 1932; Sternberg, 1933) regarded pachycephalosaurs as divergent ornithopods, and the Family Pachycephalosauridae was erected within Ornithopoda (Sternberg, 1945). Others linked pachycephalosaurs with ankylosaurs and were influenced by the downwardly curved shaft of the ischium and posterior extension of the palate (Romer, 1927, 1968) or by the armoured, akinetic condition of the skull (Nopcsa, 1929). Brown and Schlaikjer (1943, p. 146) sided with ornithopod origins, concluding that pachycephalosaurs shared 'a closer relationship to the Ceratopsia–Ornithopoda line than to the Stegosauria–Nodosauria group.' Besides noting similarities that are now clearly understood as plesiomorphic, they mentioned derived similarities shared with *Protoceratops*, such as grooved zygapophyseal articulations in the dorsal vertebrae and the downward curve of the ischial shaft. The former, now known in several pachycephalosaurs, is not present in *Protoceratops* or any other ceratopsian; the latter constitutes a potential synapomorphy as discussed below.

In summary, pre-cladistic notions of pachycephalosaurian ancestry were based as much on overall similarity as on the presence of shared derived characters. Bipedal ornithischians, such as pachycephalosaurs and psittacosaurs, were presumed to have evolved from a persistently primitive ornithopod stock (e.g., Romer, 1968; Steel, 1969; Galton, 1972; Thulborn, 1974) and were generally classified within Ornithopoda. More recently, pachycephalosaurs were removed from the Suborder Ornithopoda and accorded subordinal rank as Pachycephalosauria (Maryańska and Osmólska, 1975). Removal from Ornithopoda was not initiated on phylogenetic grounds, but rather was predicated upon the degree to which pachycephalosaurs were judged to have diverged from mainline ornithopods. Raising rank on the basis of morphologic distance, however, is an arbitrary phenetic decision (Sereno, 1990c), as arguments opposing such revision attest (Wall and Galton, 1979, p. 1185).

Pre-cladistic discussion of ceratopsian ancestry followed a similar pattern – an ambivalent relationship with Ornithopoda, the group believed to encompass the ancestral mainline of ornithischian evolution. Initially described as a 'pre-ceratopsian', *Protoceratops* was heralded as the bridge between ceratopsids and 'such primitive Jurassic Ornithopoda as *Hypsilophodon*' (Granger and Gregory, 1923, p. 4). The Family Protoceratopsidae, comprising *Protoceratops* and *Leptoceratops*, was later allied with Ceratopsidae within Ceratopsia (Gregory and Mook, 1925). Psittacosaurs, likewise, were originally described and classified as ornithopods (Osborn, 1923). Although Gregory (1927) outlined several ceratopsian features in the skull of psittacosaurs shortly after their initial discovery, many years elapsed before psittacosaurs were placed within Ceratopsia. The identification of the ceratopsian rostral bone, which was initially regarded as the premaxilla by Osborn (1923), played a key role in the recognition of psittacosaurs as basal ceratopsians (Romer, 1968; Maryańska and Osmólska, 1975).

Recent studies. Coombs (1979, p. 679) mentioned several features that unite pachycephalosaurs and ankylosaurids including the everted dorsal margin of the preacetabular process, ossification of an interorbital septum, 'tendency to close the supratemporal fenestra,' and 'armour-like texturing of the dorsal skull roof.' As discussed by Sues and Galton (1987, p. 36), these features fail to unite these groups because of problems of definition, homology, and distribution. One feature mentioned by Coombs (1979) – contact between the ilium and ischium on the anterior side of the acetabulum (i.e., exclusion of the pubis from the acetabular margin) – is a potential pachycephalosaur–ankylosaur synapomorphy. It is clearly manifest in both ankylosaurs (*Sauropelta*, YPM 541) and pachycephalosaurs (Maryańska and Osmólska, 1974) and is absent in all other ornithischians. This apomorphy, however, may not be present in the most primitive pachycephalosaur (see *Stenopelix* below) and is absent in thyreophoran outgroups to Ankylosauria as well. Thus, although character support for Marginocephalia is not overwhelming (as discussed below), opposing data is extraordinarily weak in the context of ornithischian phylogeny.

Sereno (1984, 1986) and Maryańska and Osmólska (1985) provided the first character evidence to establish a phylogenetic link between pachycephalosaurs and ceratopsians. Coining the name Marginocephalia for the combined clade, Sereno (1986) narrowed an initial list of nine proposed synapomorphies to four, which are further tailored here to three: (1) posterior extension of a parietosquamosal shelf that obscures the occiput in dorsal view of the skull; (2) median contact between the maxillae that excludes the premaxillae from the anterior margin of the internal nares; and (3) a short postpubic process that lacks the distal pubic symphysis.

The first two synapomorphies are unique among ornithischians. Sues and Galton (1987, p. 36) criticized the first synapomorphy because 'the parietosquamosal shelf of pachycephalosaurs shows no close resemblance to the frill of ceratopsians, which is characterized by transverse expansion of the parietal overhang.' The synapomorphy in question, however, concerns only the presence of a parietosquamosal shelf, not the relative composition of the shelf. The predominance of the parietal in forming the shelf was listed separately as a ceratopsian synapomorphy (Sereno, 1986), because the parietal in pachycephalosaurs and other ornithischians usually forms only a small proportion of the posterior margin of the skull roof. Dodson (1990, p. 562) remarked that the second synapomorphy is 'plesiomorphic for the group [Marginocephalia],' although no supporting evidence was cited. Marginocephalian outgroups, nevertheless, exhibit the plesiomorphic condition, in which the premaxillae form the anterior rim of the internal nares (e.g., *Hypsilophodon, Lesothosaurus*, Sereno, 1991). Sues and Galton (1987, p. 36) rejected the third synapomorphy because it is also present in Ankylosauria. The primitive condition (long postpubic process with distal symphysis), however, clearly obtains in more primitive armoured dinosaurs (thyreophorans), basal ornithopods, and the basal ornithischian *Lesothosaurus* and must be considered the outgroup condition for Marginocephalia. Other features, such as the ventral curvature of the ischial shaft, may eventually support Marginocephalia in a higher-level quantitative analysis. These features,

however, are particularly homoplastic – i.e., they are not uniformly present among marginocephalians and absent in outgroups.

Pachycephalosauria

Traditional classification. The only pre-cladistic phylogenetic tree of pachycephalosaurs shows an ancestral relationship between *Stegoceras* (*Troödon*) and *Pachycephalosaurus* (Brown and Schlaikjer, 1943, p. 148) – not surprising given that all other pachycephalosaurian genera have been described in the past 25 years.

Recent studies. The description of several new pachycephalosaurs from Mongolia (Maryańska and Osmólska, 1974; Perle et al., 1982), China (Hou, 1977) and western North America (Giffen et al., 1987) has opened the door to phylogenetic analysis. In the first cladogram of pachycephalosaurs, Sereno (1986) arranged five of the best known genera as a series of sister taxa to the large, fully domed, long-snouted genus *Pachycephalosaurus.* Three genera (*Wannanosaurus, Goyocephale, Homalocephale*) were positioned at basal nodes and comprise the so-called 'flat-headed' pachycephalosaurs. The domed genus *Stegoceras* occupied an intermediate position as sister taxon to two fully domed genera, *Prenocephale* and *Pachycephalosaurus.* Two familial names (Tholocephalidae, Domocephalinae) were proposed for subgroups in the analysis, but these are invalid because they are not based on existing genera. Although the phylogeny was based on 37 characters, only 13 apply to internal nodes on the cladogram, which reflects the very incomplete comparative information available for most pachycephalosaurs.

Sues and Galton (1987) presented an alternative phylogenetic arrangement, which divides pachycephalosaurs into 'flat-headed' (Homalocephalidae) and 'dome-headed' (Pachycephalosauridae) clades, following an earlier suggestion by Dong (1978). Maryańska (1990, fig. 27.5) followed Sues and Galton (1987), but (without explanation) altered the position of *Tylocephale* among pachycephalosaurids.

The character evidence listed by Sues and Galton (1987, p. 35) overlaps broadly with that in Sereno

(1986, pp. 243–244) with some notable exceptions. Thickening of the skull table characterizes all pachycephalosaurs known from cranial remains (Sereno, 1986). The only character evidence supporting the monophyly of 'flat-headed' pachycephalosaurs (Homalocephalidae) is the flat condition of the dorsal skull roof (as in Maryańska, 1990, p. 574). The growth series available for *Stegoceras* shows, however, that during growth the dome rises at the centre of an already thickened skull table (e.g., NMC 138; Lambe, 1918, pls. 1 and 2). The dome is surrounded by a broad, thickened, marginal shelf that is indistinguishable from that in 'flat-headed' forms. This strongly suggests that the 'flat-headed' condition is plesiomorphic within Pachycephalosauria (because it is also present early in growth in domed forms).

Within the 'flat-headed' group, Sues and Galton (1987) unite *Goyocephale* and *Homalocephale* (to the exclusion of *Wannanosaurus*) on the basis of the small size of the supratemporal fenestrae and the presence of squamosal tubercles. But these derived features are also present in all of the domed genera in their analysis (*Stegoceras, Tylocephale, Prenocephale, Pachycephalosaurus*) and characterize a more inclusive group of pachycephalosaurs (Sereno, 1986).

Much of the branching pattern in the domed clade outlined by Sues and Galton (1987) is based on an elaborate scenario for the evolution of the fully domed condition. A 'structural sequence from *Yaverlandia* to *Pachycephalosaurus*' is hypothesized, beginning with parasagittal frontal doming and followed by median frontal doming, frontal versus parietal doming, and ultimately frontoparietal doming (Sues and Galton, 1987; Maryańska, 1990). That *Majungatholus* – based on a thickened frontoparietal and braincase (MNHN MAJ4; Sues and Taquet, 1979; Sues, 1980) that pertains to an abelisaurid theropod – has been incorporated effortlessly into this sequence is telling. This scenario could be justified in a quantitative cladistic analysis only if it were coded as a single, ordered multistate character. Moreover, because this doming scenario is the only character evidence listed for several nodes within the domed clade (Sues and Galton, 1987), the implied *a priori* ordering of this character also specifies the structure of their cladogram.

As far as I can discern, several of the inferred stages in the development of the fully domed condition – such as the paired frontal thickenings in *Yaverlandia* (Galton, 1971) – do not occur in more than one taxon at any growth stage and therefore constitute autapomorphies. Other synapomorphies mentioned by Sues and Galton are based on incorrect information. *Tylocephale*, for example, has a distinct row of tubercles on the postorbital and a pair of supraorbital elements; there is no available character evidence to link *Tylocephale* and *Stegoceras* as closest relatives. Frontoparietal fusion, a synapomorphy used to link *Stegoceras* and fully domed pachycephalosaurs (Sues and Galton, 1987), is an informative synapomorphy, but is also present in *Yaverlandia*. In summary, no character evidence has been discovered to date that will support the monophyly of 'flat-headed' pachycephalosaurs. Domed pachycephalosaurs, on the other hand, have been viewed as a monophyletic subgroup (Sereno, 1986; Sues and Galton, 1987), in which the partially domed *Stegoceras* is the sister taxon to fully domed genera.

Stenopelix valdensis, based on the natural mold of a single postcranial skeleton (GPI 741–2) from the Early Cretaceous (Barremian) of Europe (inadvertently listed as Berriasian in age by Dodson, 1990, p. 563), has been regarded in recent studies as a basal pachycephalosaur (Maryańska and Osmólska, 1974; Sereno, 1987), a basal ceratopsian (Sues and Galton, 1982), and, most recently, the sister group to Pachycephalosauria plus Ceratopsia (Dodson, 1990, p. 563). Regarding the latter hypothesis, no supporting evidence was mentioned and it will not be considered further. Sues and Galton (1982, p. 188) also did not specify synapomorphies for their referral of *Stenopelix* to the Ceratopsia, stating only that such reference was based on the 'structure of the pelvic girdle, especially the form of the ilium and the reduced pubis.' However, I am not aware of any derived characters in the pelvic girdle shared by *Stenopelix* and ceratopsians or, for that matter, by ceratopsians alone. The downwardly curved preacetabular process of the ilium in *Stenopelix* occurs in several ornithischian subgroups (e.g., pachycephalosaurs), and the short prepubic process figured by Sues and Galton (1982, fig. 1A) for *Stenopelix* is half

the length of the process as preserved in the natural mould (Schmidt, 1969, fig. 1).

The hypothesis of Maryańska and Osmólska (1974, pp. 48, 101), that *Stenopelix* shares a close relationship with pachycephalosaurs, deserves closer scrutiny. Two of the three characters listed to support this connection – tibia shorter than femur, and pubis excluded from the acetabulum – are not valid. Regarding the first, the tibia and femur are equal in length in *Stegoceras*, the only pachycephalosaur in which this can be measured. Other marginocephalians and a variety of marginocephalian outgroups, moreover, have very similar tibiofemoral ratios. Regarding the second feature, the pubis in *Stenopelix* clearly forms a significant portion of the acetabular margin, as observed by Sues and Galton (1987). The third feature mentioned by Maryańska and Osmólska (1974) – elongate anterior caudal ribs – is based, apparently, on the elongate posterior sacral ribs in the holotype skeleton (Sereno, 1987). This unusual feature, also present in pachycephalosaurs, is discussed below.

Present results. The following summary of pachycephalosaur phylogeny is based on an analysis of 41 characters in 12 species (Table 25.3; Figure 25.8; Appendix, Sereno, 1999a). The character data is derived for the most part from 37 synapomorphies listed in Sereno (1986, pp. 243–4). Some of these were omitted upon review; others were combined in the process of character coding; and several new characters have been added. One character, the position of a neomorphic process on the iliac blade (character 28), is not phylogenetically informative (because it cannot be polarized). Using Ceratopsia and Ornithopoda as successive outgroups, the analysis resulted in 15 most parsimonious trees (42 steps; consistency index, 0.95; retention index, 0.97; Fig. 25.8). These trees differ only in the position of two taxa that are based on frontoparietals – *Ornatotholus* and an undescribed dwarf pachycephalosaur from Alberta. *Ornatotholus* forms an unresolved trichotomy with *Homalocephale* and a group consisting of *Yaverlandia* and more derived, domed forms. The dwarf form belongs among fully domed pachycephalosaurs, but its more precise relations cannot be determined without additional information. Removal of *Ornatotholus* and the dwarf pachycephalo-

saur from the analysis results in a single tree involving nine pachycephalosaurs and that lacks any homoplasy (41 steps; consistency and retention indices, 1.0).

There is no available character evidence supporting the monophyly of flat-headed pachycephalosaurs. Using the framework phylogeny of nine pachycephalosaur genera mentioned above, six additional steps are required to maintain a clade of flat-headed pachycephalosaurs. Most of the additional homoplasy is introduced by *Wannanosaurus*, which is distinctly more primitive than other pachycephalosaurs. As discussed below, however, some of this apparent plesiomorphy may be attributable to the immaturity of the holotype.

Although the present analysis is nearly free of homoplasy and does not support the monophyly of flat-headed pachycephalosaurs, the most parsimonious arrangement is not particularly robust. Accepting trees two steps longer than the most parsimonious tree (42 steps) for the nine most complete taxa yields five trees, the strict consensus of which collapses the more advanced position of *Goyocephale* relative to *Homalocephale* and collapses most relationships among domed genera. The loss of structure is caused by the significant amount of missing data for most available taxa (approximately 50% or more in two-thirds of included genera).

In the following discussion, character numbers correspond to those tabulated in the Appendix, and synapomorphies are described at their least inclusive node (i.e., under delayed-transformation optimization).

Basal pachycephalosaurs. *Stenopelix* is positioned in this analysis as the most basal pachycephalosaur on the basis of three synapomorphies: (1) elongate posterior sacral ribs; (2) strap-shaped distal end of the scapular blade; and (3) distal expansion of the preacetabular process of the ilium. The peculiar elongate posterior sacral ribs (fourth to sixth) in *Stenopelix* and other pachycephalosaurs broaden by about 30% the transverse width of the posterior end of the sacrum (Maryańska and Osmólska, 1974). The strap-shaped scapular blade, preserved, but not yet described, in *Stenopelix* (Sereno, 1987) is very similar to that in *Stegoceras*, the only other pachycephalosaur in which
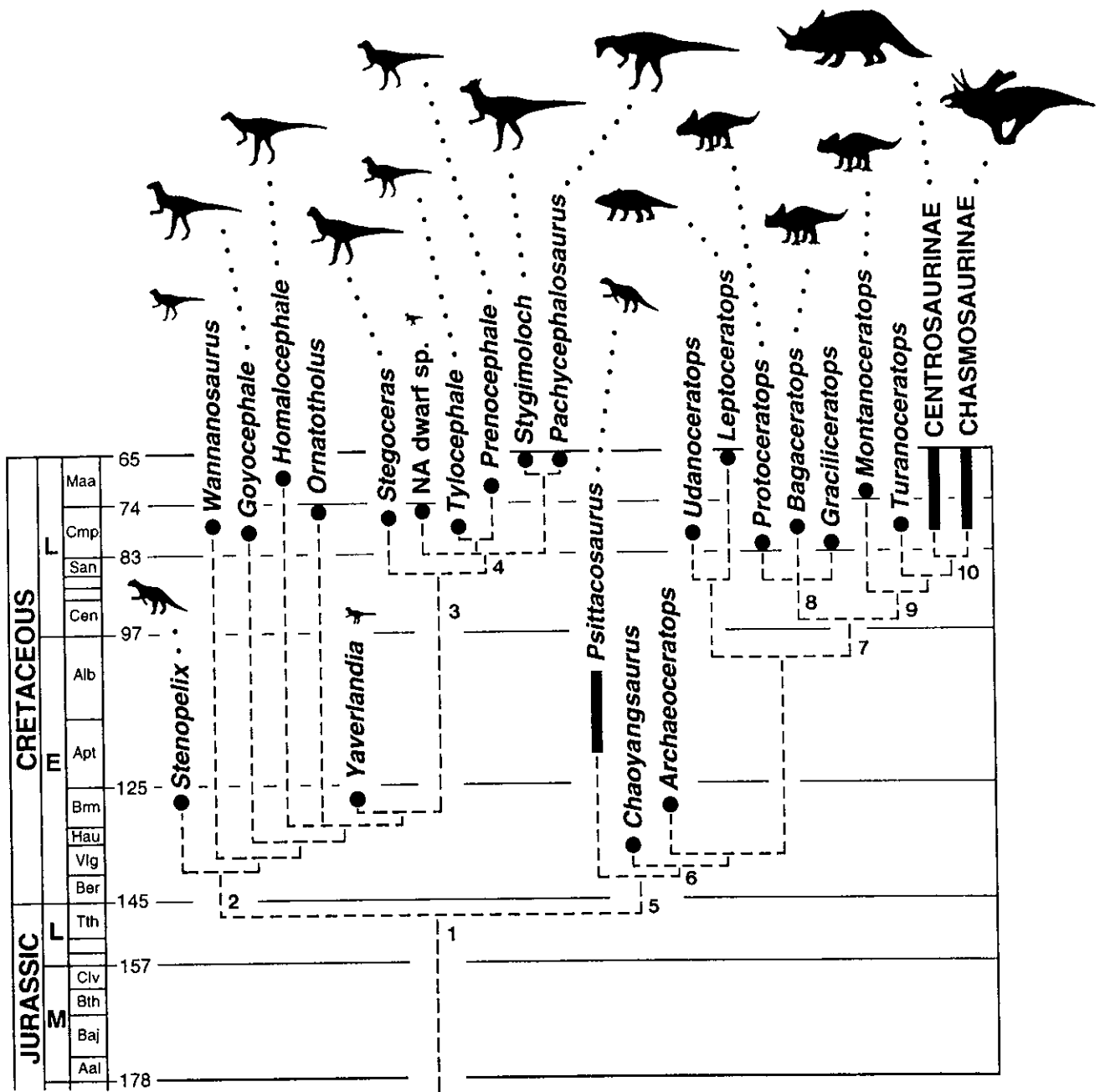
Figure 25.8. Calibrated phylogeny for marginocephalians based on cladistic relationships established in this analysis and recorded temporal ranges. The ages of *Chaoyangsaurus* and *Archaeoceratops* are uncertain, but probably lie somewhere between the latest Jurassic and the end of the Neocomian. Abbreviations: 1, Marginocephalia; 2, Pachycephalosauria; 3, Pachycephalosauridae; 4, Pachycephalosaurinae; 5, Ceratopsia; 6, Neoceratopsia; 7, Coronosauria; 8, Protoceratopsidae; 9, Ceratopsoidea; 10, Ceratopsidae.

this bone is known (Sues and Galton, 1987, fig. 10). A strap-shaped scapular blade also occurs in a few basal neoceratopsians (*Protoceratops*; Brown and Schlaikjer, 1940, fig. 26) and in heterodontosaurids (Santa Luca, 1980). The lobe-shaped expansion of the distal end of the preacetabular process of the ilium in *Stenopelix* is broader than the base of the process by about 30%. This is very similar to the shape of the process in several pachycephalosaurs. Distal expansion of the preacetabular process occurs only rarely in other

Table 25.3. *Character-taxon matrix for Pachycephalosauria. (See Appendix for characters and character states.)*

		10		20		30		40	
ORNITHOPODA	00000	00000	00000	00000	00000	00X00	00000	000?0	0
CERATOPSIA	00000	00000	00000	00000	00000	00X00	00000	000?0	0
Stenopelix	111??	????0	0?0??	????0	?00??	??X00	0????	?????	?
Wannanosaurus	???11	11111	11100	0?0??	????0?	?????	?0000	0??00	?
Goyocephale	1?111	11111	11?11	11111	1110?	??00?	?0000	0??00	?
Homalocephale	1?11?	1111?	??111	11?11	11111	11111	10000	00000	0
Ornatotholus	???1?	??1??	???1?	?????	???1?	?????	?00?0	0????	?
Yaverlandia	???1?	1?0??	???1?	?????	?????	?????	?10?0	0????	?
Stegoceras	?1111	11111	11111	11111	11111	11111	11111	00000	0
NA dwarf sp.	???1?	??0??	???1?	?????	???1?	?????	?11?1	1????	?
Tylocephale	???1?	1111?	???11	1?1??	???11	?????	?1111	11100	0
Prenocephale	1?111	1111?	???11	11??1	?1111	11111	11111	11100	0
Stygimoloch	???1?	111??	???1?	1????	???1?	?????	?1111	1??11	1
Pachycephalosaurus	???1?	1111?	???11	11???	???11	?????	?1111	11011	1

ornithischians (e.g., *Centrosaurus*, Lull, 1933; *Kentrosaurus*, Galton, 1982).

All remaining pachycephalosaurs, including the diminutive *Wannanosaurus* (Figure 25.1), are united by a suite of cranial and postcranial synapomorphies. The classic cranial features of pachycephalosaurs are already evident and include a thickened frontal and parietal portion of the skull roof (4), broadened and flattened postorbital–squamosal bar (6), broad exposure of the squamosals on the occiput (7), two supraorbital elements forming the roof of the orbit lateral to the frontal (8), and an arched premaxillary–maxillary diastema (5) that very likely accommodated a dentary canine (Hou, 1977, fig. 1). Postcranial synapomorphies include the shortened forelimb (humerus less than 50% of femur) (10), bowed humeral shaft (11) with reduced deltopectoral crest (12), and slender midshaft of the fibula (13). Most of these postcranial synapomorphies can be verified as absent in *Stenopelix*.

Several synapomorphies link other 'flat-headed' pachycephalosaurs, in particular *Goyocephale* and *Homalocephale*, with more advanced forms. The supratemporal openings are reduced in size and the frontals are excluded from their margins (14). The skull is less kinetic, as evidenced by the broad postorbital–jugal bar (15) and the plate-shaped basal tubera (17).

Classic pachycephalosaur ornamentation is present with a linear row of at least five prominent tubercles on the posterior rim of the squamosal (16) and a smaller row of tubercles on the angular (18). Only rarely are the squamosal tubercles suppressed (Goodwin, 1990, fig. 14.5). In the most advanced pachycephalosaurs, such as *Pachycephalosaurus*, the squamosal tubercles are clumped. Diagnostic features in the girdles include shafted sternals (21), which resemble those in ankylosaurs and in advanced iguanodontians, and the presence of an unusual subtriangular process that projects medially from the dorsal margin of the iliac blade (23).

Several of these synapomorphies cannot be scored in *Wannanosaurus* because of the incompleteness of available material (IVPP V4447, V4447.1). The apparent immaturity of these remains (as suggested by the open sutures), moreover, may cast doubt on the interpretation of other features, such as the tubercle row on the angular, that may appear with age. Therefore, the position of *Wannanosaurus*, as the sister taxon to other pachycephalosaurs, is regarded here as tenuous.

Homalocephale appears to be more advanced than *Goyocephale* in two regards. In *Goyocephale* the parietal roof between the supratemporal fossae is smooth and transversely arched as in basal ceratopsians and

ornithopods. In *Homalocephale* the parietal is flattened, broadened transversely, and textured (24), similar to other thickened portions of the skull roof, and the size of the supratemporal fossae is reduced (Perle *et al.*, 1982). Other cranial synapomorphies uniting *Homalocephale* and more advanced pachycephalosaurs include the highly derived pterygoquadrate processes, which project posteriorly above the palate (26), and the complete separation of subtemporal and occipital spaces by a flange of the prootic and basisphenoid (27) (the condition in *Goyocephale* remains unknown). In the postcranium, the medial process on the iliac blade, which is positioned above the acetabulum in *Goyocephale*, is located more posteriorly on the postacetabular process (28) and continues to the distal end of the process as a tapering flange (29).

In *Yaverlandia* and all other pachycephalosaurs, the frontals fuse early in ontogeny, completely obliterating the interfrontal suture internally and externally (32). The frontals also fuse to the parietal, although this suture is often visible on the roof of the braincase (common in *Stegoceras*). The holotype and only specimen of *Yaverlandia* (MIWG 1530) follows this pattern, with both the interfrontal and frontoparietal sutures fused externally, though the latter are still visible on the internal surface of the roof of the braincase.

Pachycephalosauridae, domed forms. *Stegoceras* bridges a morphological gap between flat-headed forms and those with a fully developed dome (Figure 25.3). In *Stegoceras* the coossified frontoparietal is strongly domed by upgrowth of vertical columns of bone (33), most of which occurs long after hatching. Doming of the frontoparietal on this scale appears to have evolved only once among pachycephalosaurs. In *Stegoceras* the dome never fully incorporates surrounding elements of the dorsal skull roof, which have deep columnar bone along their sutural contact with the frontoparietal, but which always maintain at least a narrow external shelf. This is true even in the oldest, most prominently domed individuals (see Goodwin, 1990, figs. 14.4 and 14.5). Other features that unite *Stegoceras* and fully domed forms include the closure, or near closure, of the supratemporal fossa (35) and the strong posterior displacement of the

parietal and squamosal over the occiput (34), as is best visualized in side view. Significant doming of the frontoparietal and closure of the supratemporal fossa may constitute correlated characters, yet they occur at different times during growth in *Stegoceras* (doming first, with closure of the fossa occurring very late in growth).

Pachycephalosaurinae, fully domed forms. In fully domed pachycephalosaurs, the bones that are sutured to the lateral and posterior aspects of the frontoparietal are fully incorporated into the vault of the dome (36). In the side view of the skull, tubercles occur only on the portion of the squamosal that projects away from the curve of the dome (Figure 25.2). The primitive parietosquamosal shelf, such as that in *Stegoceras*, extends posteriorly and laterally from the junction of the parietal, postorbital and squamosal – the remnant of the supratemporal fossa. No such shelf is present in fully domed pachycephalosaurs. In the top view of the skull, the posterior margin of the dome is vertical, or near vertical, and lacks any development of a posterior shelf.

This structural aspect of fully domed pachycephalosaurs has been confused by reference to the cluster of nodules on the squamosal in *Pachycephalosaurus* and *Stygimoloch* as a 'parietosquamosal' or 'squamosal' shelf (Galton and Sues, 1983; Maryańska, 1990). These nodules are attached to the back end of a fully domed skull that lacks any remnant of the original parietosquamosal shelf. This can be verified in specimens that lack the squamosals, as in the case of the disarticulated frontoparietal of *Stygimoloch* (Giffen *et al.*, 1987, fig. 3). In this specimen, the steep, shelfless profile of the dome is exposed even in this subadult individual. The ornamentation of the squamosal should not be confused with the primitive shelf that extends posteriorly from the supratemporal fossa.

The only other synapomorphy known to be shared by at least three fully domed forms (*Tylocephale*, *Prenocephale* and *Pachycephalosaurus*) is the establishment of a contact between the jugal and quadrate (37) (Figure 25.4). Although these bones approach each other in *Stegoceras* (Figure 25.3), they do not establish sutural contact. *Tylocephale* and *Prenocephale* share a

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unique oval fossa on the quadratojugal (38) that may indicate a close relationship (Figures 25.2 and 25.4).

Stygimoloch + Pachycephalosaurus, hypernoded forms. The large Maastrichtian pachycephalosaurs from western North America, *Pachycephalosaurus* and *Stygimoloch*, appear to be closely related. Both forms have a cluster of enlarged nodes on the squamosal (39), pronounced development of snout tubercles (41), and proportionately long snouts (40). A proportionately long, noded snout is preserved in *Pachycephalosaurus* and inferred for *Stygimoloch* on the basis of the low angle of the anterior end of the frontals and the presence of enlarged frontal nodes (Giffin et al., 1987, p. 405, figs. 2, 3). The clumped configuration of nodes on the squamosal in these forms is also unique among pachycephalosaurs. Although it is difficult to establish a one-to-one correspondence, there are at least six or seven main nodes whose bases are in mutual contact in both *Pachycephalosaurus* and *Stygimoloch* (Sues and Galton, 1987). In the latter genus, three are extended as horn cores.

Ceratopsia

Traditional classification. Psittacosaurs, like pachycephalosaurs, were believed to have evolved from a central ornithopod stock and were originally classified within Ornithopoda (Osborn, 1923). Once the median, bill-supporting bone that capped the anterior end of the psittacosaur snout was properly identified as the ceratopsian rostral bone (Romer, 1956, 1968), psittacosaurs were allied with ceratopsians (Maryańska and Osmólska, 1975). Other small-bodied ceratopsians have been placed in the Family Protoceratopsidae, which was originally erected for *Protoceratops* (Granger and Gregory, 1923), but has served over the years as a repository for all small-bodied ceratopsians except psittacosaurs. The monophyly of the large-bodied forms within the Family Ceratopsidae has never been questioned.

Recent studies. The first cladistic analysis of basal ceratopsians not surprisingly placed *Psittacosaurus* as the outgroup to other ceratopsians, which were placed in Neoceratopsia (Sereno, 1986). The arrangement of basal neoceratopsians, formerly classified within Protoceratopsidae, has been more controversial. Sereno (1986) argued that some protoceratopsids are more closely related to ceratopsids that others. In particular, *Leptoceratops* was regarded as more primitive, and *Montanoceratops* as more derived, than other protoceratopsids. Dodson and Currie (1990, p. 610, fig. 29.9), by contrast, favoured protoceratopsid monophyly, and presented a cladogram showing a fully resolved pectinate protoceratopsid clade. Although no evidence was given to support the branching sequence within the clade, three synapomorphies were mentioned to support the monophyly of the traditional Protoceratopsidae: a circular antorbital fossa, inclined parasagittal process of the palatine, and maxillary sinus.

A distinctly oval (rather than circular) antorbital fossa characterizes *Leptoceratops*, *Protoceratops*, *Bagaceratops*, and probably *Montanoceratops* (MOR 542). *Chaoyangsaurus* may also have an oval antorbital fossa, but only a portion of its margin is preserved. The principal difficulty with this synapomorphy is that available outgroups are difficult or impossible to score because the fossa is strongly reduced or absent. In *Psittacosaurus*, for example, there is no antorbital fenestra or fossa. The external depression on the maxilla (formerly identified as the antorbital fossa; Sereno et al., 1988, fig. 5) does not communicate with the nasal cavity and is not homologous with the oval fossa in basal neoceratopsians. Among ceratopsids, chasmosaurines often retain at least a small antorbital fossa (Forster et al., 1993, fig. 3). The dorsal margin of the fossa forms an arc across the maxilla and lacrimal and is not that different in shape, although less incised, from that in basal neoceratopsians. The posteroventral margin of the fossa, however, is straight. To conclude, the oval antorbital fossa may link basal neoceratopsians, but it is an ineffective character in a cladistic analysis because the plesiomorphic ceratopsian condition remains unclear.

The two remaining characters mentioned by Dodson and Currie (1990) to support protoceratopsid monophyly are difficult to justify. Osmólska (1986, p. 152) mentioned that the snout in both psittacosaurids and basal neoceratopsians was particularly deep and

the angle of the palatine very steep. This is also true of ceratopsids, in which the palatine assumes a parasagittal orientation (Hatcher et al., 1907, fig. 26). If Dodson and Currie (1990) meant to refer to the 'vertical transverse wing of the palatine,' this process appears to be fully developed in this manner only in *Protoceratops*, *Bagaceratops*, and ceratopsids; it is absent in *Leptoceratops* and *Psittacosaurus*, as noted by Osmólska (1986, p. 152). The distribution of the 'maxillary sinus' described by Osmólska is poorly known. Developed as a space above the tooth row, it communicates with the antorbital fossa, which communicates with the nasal cavity via the antorbital fenestra, suggesting that the 'maxillary sinus' may be a ramification of the nasal cavity (contrary to Osmólska, 1986, p. 154; Witmer, 1995). The distribution of this cavity among ceratopsians is poorly known.

Other evidence, such as the prominence of the wedge-shaped epijugal (24), may eventually be shown to support the traditional assemblage of protoceratopsids as a monophyletic clade. The jugal/epijugal crest is low in *Psittacosaurus*, *Chaoyangsaurus* and ceratopsids. A plate-shaped sagittal crest on the parietal (60) also links several basal neoceratopsians (*Leptoceratops*, *Protoceratops*, *Bagaceratops*) but is lacking in others (*Graciliceratops*, *Montanoceratops*).

Present results. The following summary of ceratopsian phylogeny is based on analysis of 72 characters in 10 ceratopsian genera (those reviewed above) and Ceratopsidae (see Appendix; Figure 25.8; Table 25.4). The character data are a modification and extension of synapomorphies listed in Sereno (1986, p. 244; 1990b, pp. 587–588). Using Pachycephalosauria and Ornithopoda as successive outgroups, the analysis yielded three most parsimonious trees differing only in the resolution of a trichotomy between *Protoceratops*, *Bagaceratops*, and *Graciliceratops* (consistency index, 0.86; retention index, 0.92). Accepting trees one step longer breaks the tenuous link between *Leptoceratops* and *Udanoceratops* and creates a trichotomy between these genera and Coronosauria. Protoceratopsidae *sensu stricto* (*Protoceratops, Bagaceratops, Graciliceratops*) collapses when trees two steps longer than the minimum are accepted.

Reconstituting the traditional Protoceratopsidae requires four extra steps; and eight are required if *Turanoceratops* is included in the family. Thus, these data show a decided preference for a paraphyletic arrangement of small-bodied neoceratopsians. Here, Protoceratopsidae is tentatively restricted to include only *Protoceratops*, *Bagaceratops*, and *Graciliceratops*, as discussed below. In the following discussion, character numbers correspond to those tabulated in the Appendix. When synapomorphies have an ambiguous location on the cladogram due to missing data or homoplasy, they are described under the least inclusive group that they could characterize (i.e. delayed-transformation optimization).

Ceratopsia. The monophyly of Ceratopsia is based exclusively on cranial synapomorphies, the most striking of which is the neomorphic rostral bone (1), a median, bill-supporting element sutured firmly to the tall and narrow anterior end of the snout (Figure 25.5). Other cranial features include broad, pointed jugals (3, 4), which give the skull a distinctly subtriangular shape in dorsal view (Gregory, 1927; Maryańska and Osmólska, 1975). The vaulted premaxillary palate (6) is deeply arched in psittacosaurs and narrower and more bird-like in neoceratopsians in contrast to the flat secondary palate that is present in *Lesothosaurus* (Sereno, 1991) and other ornithischians. The ventral process of the predentary has an unusually broad base (7) supporting the dentary symphysis.

The absence of ceratopsian postcranial synapomorphies reflects the conservative form of the postcranium in basal ceratopsians rather than missing information. In psittacosaurs the postcranium is remarkably primitive, differing only in minor ways from that in hypsilophodontids (Sereno, 1987). Basal neoceratopsians, likewise, exhibit few modifications in the postcranium. Except for some modification of the axial column, there is no major alteration of the postcranial skeleton among nonceratopsid ceratopsians.

Neoceratopsia. The discovery of *Chaoyangsaurus* (Zhao, 1983; Zhao et al., 1999), the oldest known ceratopsian, has begun to bridge the substantial morphologic gap between psittacosaurs and neoceratopsians. Its linkage

Table 25.4. *Character–taxon matrix for Ceratopsia (see Appendix for characters and character states).*

	10	20	30	40	50	60	70	
ORNITHOPODA	00000 00000	XX000 00000	000X0 000X0	00000 00000	00000 00000	00000 0000X	0X000	00
PACHYCEPHALOSAURIA	00000 00000	XX?00 0?000	X10X0 00100	0000? 0?000	00000 00000	00000 00?0X	0X?00	00
Psittacosaurus	11111 11XX0	00000 X0000	00000 00000	00000 02000	10000 00000	00000 0000X	0X000	00
Chaoyangsaurus	11111 ?1111	11111 ??00?	00??? ??200	00??? ??200	0000? ?????	????? ??20?	0?000	0?
Archaeoceratops	11111 ??111	1?111 11111	11??0 00???	??20? ??200	00020 00010	2000? ??00X	02000	0?
Leptoceratops	11111 11XX1	11111 11111	11211 11111	11111 11111	11100 00010	00001 ??00X	02?00	00
Udanoceratops	11111 1?XX?	11111 11111	?211? ?11??	?21?? ?????	11100 00010	00001 0000X	0X000	00
Graciliceratops	??11? ????1	?11?? 11211	1?21? ?11??	?211? ?????	11100 ?????	????? ??20X	02?00	0?
Bagaceratops	11111 11X11	11111 ?1111	11211 ?21??	?211? ?????	?201? ?1121	?1?11 11?11	0??0?	0?
Protoceratops	11111 11111	01111 ?1111	11211 11211	11111 11111	01011 11121	11111 11100	11100	00
Montanoceratops	11111 11111	01111 ?1111	11211 11211	11111 11111	01011 11121	11111 11100	11100	00
Turanoceratops	????? ?1???	?11?? ?????	1?21? 1?21?	1???? ?????	????? ?????	????? ??21?	??211	11
CERATOPSIDAE	1011? 11XX1	?1112 X2101	11211 11211	11101 11100	10011 11121	11110 00011	12111	11

with later neoceratopsians is based on cranial synapo-morphies alone. The subcylindrical, procumbent form of the premaxillary teeth in *Chaoyangsaurus* establishes this unusual tooth form as the plesiomorphic condition within Neoceratopsia. Similar premaxillary teeth are now known in *Archaeoceratops* (Dong and Azuma, 1997), *Protoceratops*, (Brown and Schlaikjer, 1940), at least one specimen of *Bagaceratops* (Dong and Currie, 1993), and a basal neoceratopsian from the Two Medicine Formation (Gilmore, 1939; USNM 13863).

The marked increase in the relative size of the skull (10), which measures (without the frill) as much as 20–30% of the length of the postcranial skeleton, characterizes neoceratopsians. *Chaoyangsaurus* appears to have a large skull relative to the preserved portions of the scapula. The keeled, pointed predentary (13), distally tapered ventral process of the predentary (14), and lack of a significant retroarticular process (15) constitute further links between *Chaoyangsaurus* and other neoceratopsians which can be scored as primitive in neoceratopsian outgroups. Other features, such as the keeled, pointed shape of the rostral bone (12), are less decisive because the rostral is a neomorphic bone; neoceratopsian outgroups that lack the rostral cannot be used to polarize characters involving this bone. Thus, potential neoceratopsian synapomorphies involving the rostral (11, 12) may also be regarded as plesiomorphic, with the condition in *Psittacosaurus* interpreted as derived.

Archaeoceratops + Leptoceratops + Udanoceratops + Coronosauria. Major modification of the ceratopsian skull is apparent in all neoceratopsians more advanced than *Chaoyangsaurus* (Zhao, 1983; Zhao *et al.*, 1999). The postorbital and supratemporal bars are broadened into strap-shaped struts (22), and the dorsal and particularly the ventral margins of the laterotemporal fenestra are shortened (23). Although the jugal is prominent in all ceratopsians, it forms a wedge-shaped process capped by the horn-covered epijugal (24) in neoceratopsians more advanced than *Chaoyangsaurus*. An epijugal was not described by Dong and Azuma (1997) in *Archaeoceratops*, but this bone is commonly disarticulated and lost in subadult individuals and was probably present in this early neoceratopsian. The

supratemporal region is reconfigured by the confluence of the supratemporal fossae in the midline (32) and the upward tilt of the posterior margin of the parietal (31). Modifications in the lower jaw include a cropping surface on the predentary (34), the participation of the splenial in the median symphysis (39), and major expansion of the coronoid process (37). The more closely packed dentition (20) in these neoceratopsians is characterized by the inset margin at the base of the maxillary and dentary crowns on their lateral and medial surfaces, respectively (17).

Leptoceratops + Udanoceratops + Coronosauria. Several cranial features unite *Leptoceratops*, *Udanoceratops* and coronosaurs, but nearly all of these have an ambiguous distribution because of missing data for *Archaeoceratops*. The most significant postcranial modifications among basal neoceratopsians involve the cervical and caudal vertebrae. The anterior three cervical vertebrae coalesce in *Leptoceratops* (NMC 1889) and more advanced neoceratopsians (41), and the neural spines of the mid-cervicals (third and fourth) are as tall as the axis (42). The distalmost caudal vertebrae have proportionately short centra, rudimentary neural arches and articulate with small chevrons (44). In *Psittacosaurus* and *Archaeoceratops*, by contrast, the distalmost caudals have cylindrical centra that lack neural arches and do not have associated chevrons. In *Leptoceratops* and Coronosauria, the mid-caudal vertebrae have particularly long neural spines and long chevrons, resulting in a 'leaf-shaped' tail in lateral view (45). *Psittacosaurus* (Sereno, 1987) and *Archaeoceratops* (Dong and Azuma, 1997, fig. 5) clearly lack these modifications, although the latter genus has been reconstructed with a leaf-shaped tail (Dong and Azuma, 1997, fig. 11).

Leptoceratops + Udanoceratops. A single synapomorphy suggests that *Leptoceratops* and *Udanoceratops* constitute a subgroup within Neoceratopsia. In several genera of basal neoceratopsians, the lower margin of the jaw is arched (*Leptoceratops, Udanoceratops, Bagaceratops, Protoceratops*), but in *Leptoceratops* and *Udanoceratops* the downward arching of the ventral margin (47) is pronounced and begins under the retroarticular process (48) rather than under the coronoid region. However,

the material for *Udanoceratops* is very limited and the close relationship to *Leptoceratops* is supported only by this single feature.

Coronosauria. The synapomorphies that diagnose Coronosauria are located principally in the cranium. At least a rudimentary nasal horn is present (50), though least developed in *Protoceratops* (Brown and Schlaikjer, 1940, fig. 13B), and the supratemporal fossae are distinctly triangular (51) with long axes diverging posteriorly (52). In coronosaurs, enamel is present only on the lateral side of the maxillary crowns and medial side of the dentary crowns. In *Leptoceratops, Udanoceratops* (Kurzanov, 1992), and more basal ceratopsians, by contrast, enamel is present on both sides of the crowns.

The frill is particularly well developed (Figure 25.6). The parietal portion extends far posterior to the quadrate head (54), the distal portion of which has a sizable pair of fenestrae (55), one on each side of the midline. The fenestrae weaken the frill, which is frequently broken away along the anterior margin of these openings (as in the initial specimens of *Bagaceratops*, Maryańska and Osmólska, 1975). A distinct posterodorsal process of the squamosal, the frill process (59), forms much of the lateral margin of the frill. Except in chasmosaurines, the squamosal does not extend as far posteriorly as the parietal, and the posterolateral corners of the frill are rounded. In the anterior view of the skull (that encountered in display; Brown and Schlaikjer, 1940, pl. 6C), the frill forms a semicircular corona, from which the group name was derived. In *Montanoceratops* (TMP 82.11.1) the posterior extension of the parietal is less extreme, although the presence of sizable parietal fenestrae suggest that the parietal frill was longer than that in *Archaeoceratops* and *Leptoceratops*. The absence of a discrete frill process on the squamosal (AMNH 5464; TMP 82.11.1), however, introduces homoplasy. If coronosaurs split into protoceratopsid (*sensu stricto*) and ceratopsoid clades, as the data suggest as a whole, the frill process on the squamosal either was reduced in *Montanoceratops* or evolved independently in protoceratopsids (*sensu stricto*) and Ceratopsidae. I regard the former optimization (accelerated transformation with

loss) as the more likely, given the derived form of the parietal (somewhat lengthened and fenestrated) in *Montanoceratops*.

Postcranial synapomorphies for Coronosauria are limited to the axial column and include the presence of a neomorphic element anterior to the atlas, the hypocentrum (56), and an increase to eight sacral vertebrae (57) with neural spines in mutual contact (58).

Protoceratopsidae (sensu stricto). Three synapomorphies suggest that *Graciliceratops, Protoceratops*, and *Bagaceratops* may constitute a monophyletic subgroup within Coronosauria. This subgroup, here referred to as Protoceratopsidae (*sensu stricto*), is characterized by a narrow strap-shaped paroccipital process (61), very small occipital condyle (62), and upturned dorsal margin of the predentary (63). Two of the three (*Protoceratops* and *Bagaceratops*) share a blade-shaped parietal sagittal crest (63) (Figure 25.6), but this is absent in *Graciliceratops* and present in at least one genus outside this subgroup (*Leptoceratops*).

Ceratopsoidea. Montanoceratops and ceratopsids share five synapomorphies, two of which are present in the poorly known central Asian species *Turanoceratops* (Nesov et al., 1989). The anterior ramus of the squamosal is particularly deep in *Montanoceratops* (AMNH 5464; twice as long as deep) and plate-shaped in Ceratopsidae (22), which continues a trend in ceratopsians toward reduction of the laterotemporal fenestra. The nasal horn, which is quite well developed in *Montanoceratops* (AMNH 5464), is positioned over the external naris (65) rather than more posteriorly as in *Bagaceratops* and *Protoceratops*. Given that the nasal horn is a neomorph, however, the primitive position of the horn cannot be determined. It may be that the posteriorly positioned horn in protoceratopsids (*sensu stricto*) is derived, as suggested by its posterior migration during growth (Kurzanov, 1990). Two more decisive characters are present in the lower jaw in *Montanoceratops* and ceratopsids – the dentary ramus increases in depth toward its anterior end (66), a unique proportion among ornithischians, and the dentary teeth have very prominent primary ridges

(64). The latter can also be observed in *Turanoceratops* (Nesov *et al.*, 1989, pl. 1, fig. 16).

Turanoceratops + *Ceratopsidae*. The unique two-rooted cheek teeth (69) of ceratopsids, which lock together successive teeth in a vertical column, are also present in the recently discovered ceratopsoid *Turanoceratops* (Nesov, 1989, pl. 1, figs. 16 and 19). Despite the presence of two roots, there appears to be only two teeth in a vertical column in this ceratopsoid, as opposed to four or five in the much larger-bodied ceratopsids. Other aspects of the teeth in *Turanoceratops* are also advanced, including the sharp angle of the crown to the axis of the roots (70) and the reduction in height of the secondary ridges relative to the primary ridge (71). Broken horn cores (Nesov *et al.*, 1989, pl. 1, fig. 18) suggest that *Turanoceratops* had postorbital horns (72) as in ceratopsids. Postorbital horns have also recently been reported in an even more primitive neoceratopsian with single-rooted cheek teeth from approximately coeval deposits in western North America (Moreno Hill Formation; Childress, 1997). More complete and associated remains of these Cenomanian–Turonian forms will shed light on the initial stages of the evolution of the derived dental and cranial adaptations of ceratopsids.

Evolutionary trends

Body size

Both pachycephalosaurs and ceratopsians exhibit trends toward increasing body size, with maximum recorded body size (length) in each group appearing in the Maastrichtian (latest Cretaceous). The body size of the ancestral marginocephalian probably did not exceed 2 m, because known basal marginocephalians (*Stenopelix*, *Psittacosaurus*, *Chaoyangsaurus*) and basal members of marginocephalian outgroups (Ornithopoda, Thyreophora) have never exceeded this length.

Among pachycephalosaurs, moderate body size (2–3 m) probably evolved by the Early Cretaceous, when many pachycephalosaurs in this body size range

must have diverged. Large body size (6–8 m) was attained only among Maastrichtian pachycephalosaurs (*Stygimoloch*, *Pachycephalosaurus*) and presumably evolved some time in the Late Cretaceous. At least twice during the evolution of pachycephalosaurs, marked decrease in body size yielded some of the smallest ornithischians on record: *Yaverlandia* and an as yet undescribed North American species of similar size. These pachycephalosaurian dwarfs, represented by fully coossified skull caps of mature individuals, do not appear to form a clade, but rather seem to have evolved independently from ancestors of moderate body size. Not included here among dwarf pachycephalosaurians is the basal pachycephalosaur *Wannanosaurus*, the materials of which may be immature.

The trends described above are asymmetrical (McKinney, 1990). The range of body size increased over time, from a minimum skeletal length of about two metres in the Early Cretaceous to skeletons four or five times that length toward the end of the Late Cretaceous. In pachycephalosaurs, the body size range appears to have extended to smaller values as well, to skeletal lengths no greater than one metre. In both pachycephalosaurs and ceratopsians, the asymmetrical trend toward increase in body size is accretive, because species of moderate body size persisted alongside their larger cousins in the latest Cretaceous (Maastrichtian). In ceratopsians, increase in body size was also accretive, but unlike pachycephalosaurs, large-bodied species greatly outnumbered smaller species in the Maastrichtian. Mean body size for ceratopsians, therefore, increased more dramatically toward the end of the Cretaceous.

Doming of the skull roof

The extraordinary thickening of the skull roof in pachycephalosaurs occurred in several stages, according to the best estimate of the phylogenetic history of this group. First, the entire skull table was thickened; later, in one clade (Pachycephalosauridae), a dome arose composed principally of the frontal and parietal; finally, in one subgroup of that clade (Pachycephalosaurinae), the dome expanded to incorporate other

bones of the skull table fully (Figures 25. 2 and 25.3). Excluded here are relatively minor proportional changes in the dome that characterize some genera.

The most remarkable fact about this trend in cranial thickening is that, despite body size evolution over more than an order of magnitude (*Yaverlandia* to *Pachycephalosaurus*), doming of the skull cap apparently occurred only once and was never reduced or eliminated. In this regard, the predominance in the data of characters pertaining to the skull roof is cause for concern, because of the potential to create an artificial transformation series. Nonetheless, there is no indication in available character evidence that a vaulted dome evolved more than once, that such a dome was ever later substantially reduced, or that it was ever subject to marked sexual dimorphism (contrary to Chapman *et al.*, 1981).

Extension of the frill

The evolution of the frill among ceratopsians followed a somewhat more complex course than the thickening of the skull roof among pachycephalosaurs. In psittacosaurs the short parietosquamosal shelf projects horizontally over the occiput (Figure 25.5). In the basal neoceratopsians *Archaeoceratops* and *Leptoceratops*, a posterodorsally inclined, transversely broadened frill has evolved, composed almost entirely of the parietal. The frill incorporates the squamosal laterally and becomes progressively more hyperextended in Late Cretaceous protoceratopsids (Figure 25.6) and ceratopsids, with the longest frills (relative to skull length) occurring among chasmosaurines.

The trend outlined above toward longer and broader frills is complicated by the presence in *Montanoceratops* of a short frill, composed almost entirely of the parietal. Other features of *Montanoceratops* clearly justify its derived position among neoceratopsians (such as the parietal fenestrae in the frill). Either the frill was shortened in *Montanoceratops*, with concomitant reduction in the participation of the squamosal, or the frill was lengthened independently in protoceratopsids (*sensu stricto*) and ceratopsids. Only the discovery of additional taxa can resolve this question.

Pachycephalosaurian jaw morphology and tooth form appears to have undergone only superficial modification. The structure of the lower jaw remains primitive with the dentary forming no more than half of the lower jaw; the tooth row remains relatively loosely packed with spaces between adjacent crowns; tooth form remains primitive with triangular crowns and simple roots; and the dentary canine and associated diastema between the premaxillary and maxillary teeth – a derived condition present in basal pachycephalosaurs such as *Goyocephale* – is clearly maintained in fully domed forms such as *Prenocephale*.

The ceratopsian snout, jaws and teeth, by contrast, had undergone considerable transformation by the Late Cretaceous. Marked change in the form of the snout is present as early as the latest Jurassic or Early Cretaceous and clearly predates the angiosperm radiation (Figure 25.9). Moreover, the bird-like neoceratopsian snout, formed by a very narrow rostrum and pointed, upturned predentary, had also evolved by the earliest Cretaceous, as evidenced by *Chaoyangsaurus* (Figure 25.9). Other neoceratopsians show a more advanced condition of the lower jaw and tooth rows. The postdentary elements are reduced, a bevelled cropping edge is present on the predentary, the cheek teeth are more tightly packed, and the rate of tooth replacement is increased. The crowns of the cheek teeth, in addition, are taller than in psittacosaurs with enamel restricted to a single side. The discovery of *Archaeoceratops* in the Early Cretaceous of Asia demonstrates that many of these adaptations were established during the Early Cretaceous, when psittacosaurs with simple jaws and dentitions were more abundant. Most of these changes, likewise, significantly predate the rise of angiosperms toward the end of the Early Cretaceous (Figure 25.9).

Two-rooted cheek teeth must also have evolved before the end of the Early Cretaceous, given the presence of two-rooted teeth in the Cenomanian ceratopsian *Turanoceratops* (Figure 25.9). Dentary batteries are known only among ceratopsids from the Campanian and Maastrichtian of western North America and
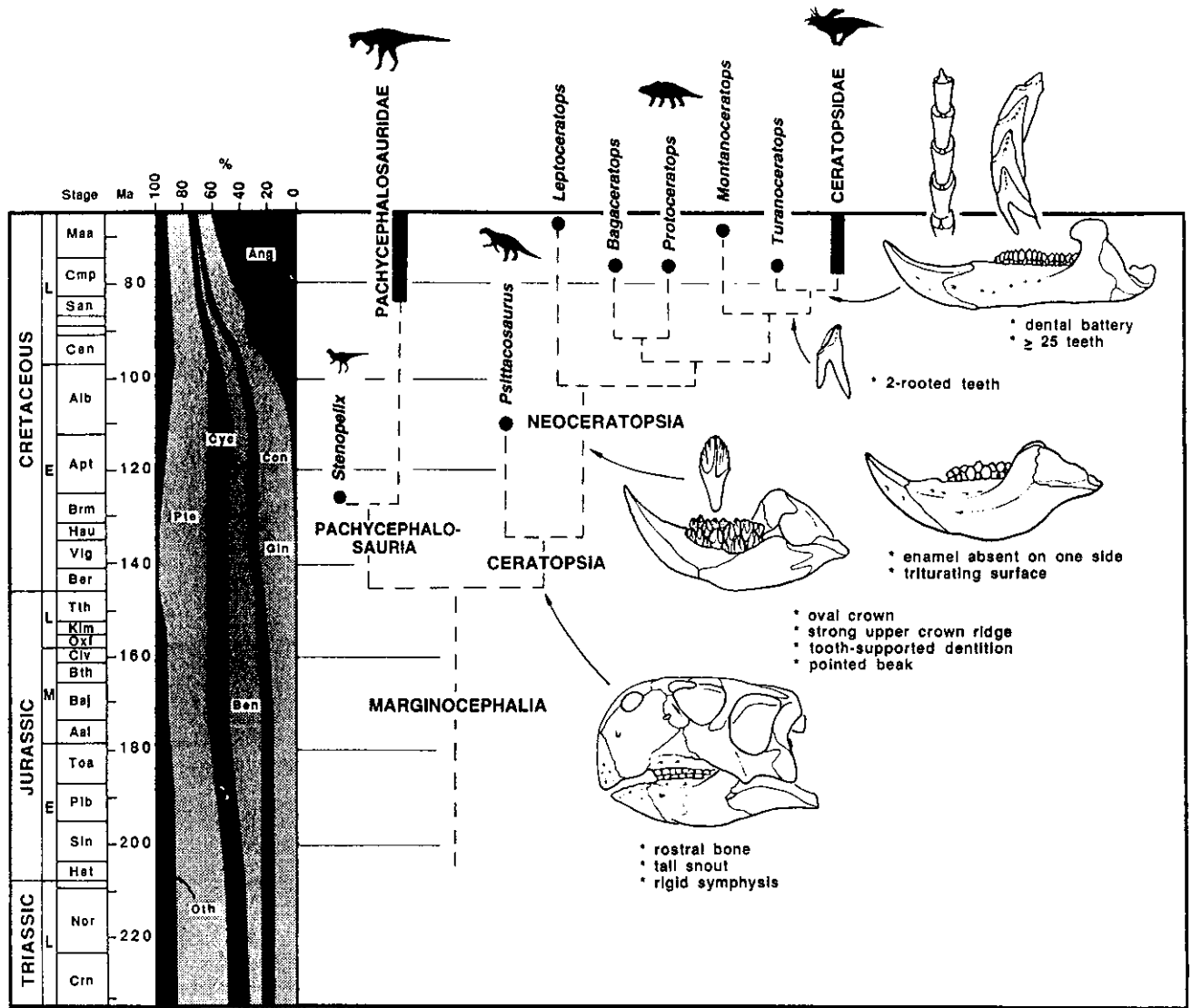
Figure 25.9. Calibrated phylogeny showing the temporal and phylogenetic origin of major cranial and dental features associated with herbivory in ceratopsians. Relative change in diversity (percent) in major plant clades is shown at left (based on Niklas, 1986). Abbreviations: ang, angiosperms; cyc, cycads; con, conifers; gin, ginkgophytes; oth, other; pte, pteridophytes.

might well be correlated with an increase in body size. Thus, there is a trend toward increased packing and replacement in the dentition which culminates in the tooth-supported dental batteries of ceratopsids. Almost identical trends occurred somewhat earlier in ornithopods, including the dominance of the dentary in the lower jaw, increased relative height of the tooth crowns and asymmetry of the enamel, and increased compaction and replacement of cheek teeth (Sereno, 1997).

Biochronology

Temporal calibration of the phylogeny provides insight into (1) major missing lineages that have left no fossil record and (2) the timing of cladogenic events. Three major missing lineages are apparent in the calibrated phylogeny of marginocephalians, the longest occurring before the earliest known marginocephalian. A missing lineage, possibly as long as 100 million years – one of the longest among major groups of

dinosaurs – precedes the oldest marginocephalian (arguably *Chaoyangsaurus*), as evidenced by the appearance of the sister taxon to Marginocephalia (Ornithopoda) during the Early Jurassic (Figure 25.8). Given the relatively small body size of known basal marginocephalians, their predecessors may have been as small, or smaller, and less likely to have entered the fossil record. Other factors, such as habitat preference, may also may have contributed to the absence of fossil evidence for the early appearance of marginocephalians, because several small-bodied ornithopods are recorded during the early Jurassic. The origin of pachycephalosaurian and ceratopsian lineages may date back to the Early Jurassic, given the low number of derived features shared by both subgroups.

Other missing lineages, 40–50 million years in duration, are predicted for Late Cretaceous pachycephalosaurs and neoceratopsians. The discovery of the Early Cretaceous pachycephalosaur *Yaverlandia* and the neoceratopsians *Chaoyangsaurus* and *Archaeoceratops* identify major missing lineages preceding closely related genera (Figure 25.8). With the exception of *Stenopelix*, the most primitive pachycephalosaurs are Late Cretaceous in age, but must be the descendants of lineages that diverged early in the Cretaceous. Likewise, a long missing lineage precedes domed pachycephalosaurs (pachycephalosaurids). Among ceratopsians, a long missing lineage precedes all Late Cretaceous neoceratopsians, as established by the Early Cretaceous genus *Archaeoceratops* (Figure 25.8).

Not one of these missing lineages is associated with major structural modification. Among pachycephalosaurs, nearly all of the many unusual postcranial features (such as the ossified caudal tendons) are present in *Goyocephale*, and therefore must have evolved no later than the earliest Cretaceous (Figure 25.8). Likewise, among early ceratopsians, most structural change seems to have occurred after the divergence of *Chaoyangsaurus*. From available remains, *Archaeoceratops* appears to be very similar to primitive Late Cretaceous neoceratopsians such as *Protoceratops*, suggesting that the majority of the cranial modifications that characterize Late Cretaceous neoceratopsians had already evolved by the earliest Cretaceous,

though several of these features currently have an ambiguous temporal origin because of missing data for *Archaeoceratops*.

Biogeography

Except for two Early Cretaceous pachycephalosaurs, *Stenopelix* and *Yaverlandia*, and one ceratopsian, *Chaoyangsaurus*, marginocephalians are known exclusively from late Early and Late Cretaceous deposits in central Asia and western North America. Their phylogeny has direct bearing on their biogeographic history. Their limited biogeographic distribution, and the fact that no species has ever been found distributed across both areas, suggests a possible phylogenetic solution.

Previous hypotheses proposed a central Asian origin for the group in the Early Cretaceous, followed by a one-way dispersal event from Asia, across Beringia, to western North America in the Late Cretaceous for ceratopsians (Maryańska and Osmólska, 1975) and for other groups as well (Russell, 1993). This hypothesis predicts that, for each group distributed across these two areas, Asian taxa will compose a basal paraphyletic subgroup that, via a single, one-way dispersal event, gave rise to a monophyletic subgroup in western North America. Alternative biogeographic scenarios would be consistent with different phylogenetic patterns. If a given group were distributed initially across both central Asia and western North America and later divided by a Cretaceous vicariance event, for example, group members on each land mass would compose monophyletic sister clades. Or, if a given group had a more complicated biogeographic history, with multiple, bidirectional dispersal events across Beringia, an alternating pattern of Asian and western North American taxa would obtain.

The marginocephalian phylogeny presented here clearly favours the latter biogeographic scenario (Figure 25.10; Sereno, 1997, 1999a). Although Asian pachycephalosaurs and ceratopsians predominate at the basal end of their respective phylogenies, the alternating areal relationships among marginocephalians
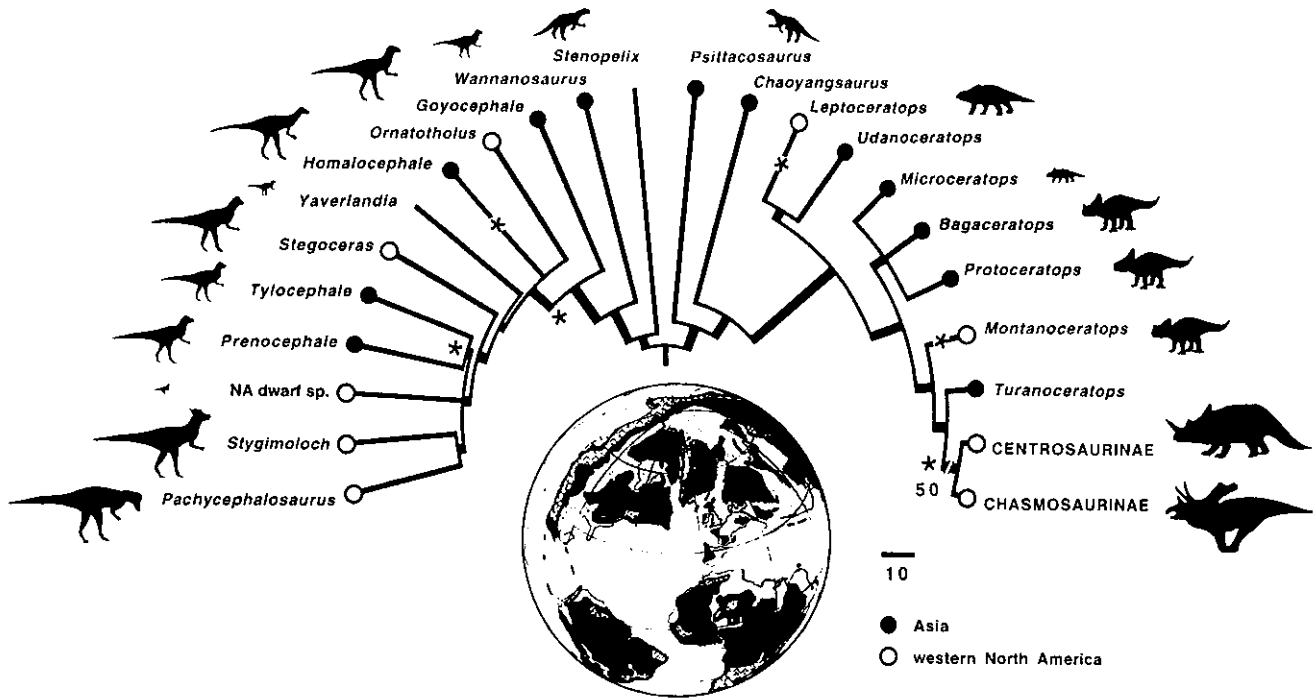
Figure 25.10. Polar sweepstakes dispersal by marginocephalians during the Cretaceous. Globe shows Maastrichtian (70 Ma) palaeogeography divided into orogenic belts (inverted Vs), lowlands (black), and shallow (grey) and deep seas (white). Cladogram for marginocephalians shows relative support for relationships based on the present analysis. Internal branch lengths are scaled to the number of synapomorphies under delayed character-state optimization (scale bar equals 10 synapomorphies; 50-synapomorphy ceratopsid branch shortened). Internal branch segments are filled (black) according to the number of unambiguous synapomorphies; open segments indicate ambiguous synapomorphies. Palaeogeographic distributions for marginocephalian genera are shown at branch tips (solid circles, Asia; open circles, western North America; blank, Europe). Six dispersal events (asterisks) across Beringia (in both directions) must be invoked to account for the palaeogeographic distributions shown by the cladogram (alternative positions for some of the dispersal events are possible). Increase in body size in pachycephalosaurs and ceratopsians is shown by body silhouettes (palaeogeographic projection courtesy of the Paleogeographic Atlas Project, University of Chicago).

requires a minimum of three dispersal events in two directions across Beringia in each group. Phylogenetic patterns suggesting bi-directional dispersal also occur in other Cretaceous dinosaurian groups with a similar bimodal distribution during the Late Cretaceous (hadrosaurids, ornithomimids, tyrannosaurids; Sereno, unpublished data).

The tectonic and palaeogeographic history of the north polar region during the Cretaceous is consistent with the emergence during the late Early–early Late Cretaceous of a high-latitude dispersal route. That route formed when the North Slope block collided with the East Siberian block, joining it with the western North American land mass (Worrall, 1991, fig.

8). Following the shoreline along a continuous, active trench, that route would have passed within five degrees of the paleopole during the Late Cretaceous. This polar passage, hidden from direct sunlight for six months of the year, may have functioned as a sweepstakes dispersal route (McKenna, 1973), periodically allowing passage of animals from one side to the other.

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APPENDIX

Character coding and distribution of character states are shown below for 41 characters in 12 pachycephalosaurian genera and 72 characters in 10 ceratopsian genera and Ceratopsidae. All characters in the pachycephalosaurian data set are binary; 6 of the 72 characters in the ceratopsian data set are three-state characters and the remainder are binary. One character in the pachycephalosaurian data set (character 28) and three characters in the ceratopsian data set (characters 12, 21, 67) are uninformative because the structures involved are neomorphic (i.e. impossible to polarize with outgroups). Character-state abbreviations: 0 = plesiomorphic state; 1, 2 = derived states; ? = not preserved or unknown; X = unknown as a result of transformation.

Pachycephalosauria

Characters and character states

Pachycephalosauria

1. Sacral rib length: subrectangular (0); strap-shaped (1).
2. Scapular blade, distal width: broad (0); narrow (1).
3. Preacetabular process, shape of distal end: tapered (0); expanded (1).

Hannanosaurus + other pachycephalosaurs

4. Frontal and parietal thickness: thin (0); thick (1).
5. Arched premaxilla–maxilla diastema, dentary canine: absent (0); present (1).
6. Postorbital–squamosal bar, form: bar-shaped (0); broad, flattened (1).

7. Squamosal exposure on occiput: restricted (0); broad (1).
8. Anterior and posterior supraorbital bones: absent (0); present (1).
9. Postorbital–squamosal tubercle row: absent (0); present (1).
10. Humeral length: more (0), or less than (1), 50% of femoral length.
11. Humeral shaft form: straight (0); bowed (1).
12. Deltopectoral crest development: strong (0); rudimentary (1).
13. Fibular mid-shaft diameter: 1/4 or more (0), or 1/5 or less (1), mid-shaft diameter of tibia.

Goyocephale + more derived pachycephalosaurs

14. Postorbital–parietal contact: absent (0); present (1).
15. Postorbital–jugal bar, shape: narrow (0); broad (1).
16. Squamosal tubercle row (5 to 7): absent (0); present (1).
17. Angular tubercle row: absent (0); present (1).
18. Basal tubera, shape: knob-shaped (0); plate-shaped (1).
19. Zygapophyseal articulations, form: flat (0); grooved (1).
20. Ossified interwoven tendons: absent (0); present (1).
21. Sternal shape: plate-shaped (0); shafted (1).
22. Iliac blade, lateral deflection of preacetabular process: weak (0); marked (1).
23. Iliac blade, medial tab: absent (0); present (1).

Homalocephale + more derived pachycephalosaurs

24. Parietal septum, form: narrow and smooth (0); broad and rugose (1).
25. Quadratojugal ventral margin, length: moderate (0); very short (1).
26. Pterygoquadrate rami, posterior projection of ventral margin: weak (0); pronounced (1).
27. Prootic-basisphenoid plate: absent (0); present (1).
28. Iliac blade, position of medial tab: above acetabulum (0); on postacetabular process (1).
29. Iliac blade, medial flange on postacetabular process: absent (0); present (1).
30. Ischial pubic peduncle, shape: transversely (0), or dorsoventrally (1), flattened.
31. Pubic body: substantial (0); reduced (1).

Yaverlandia + Pachycephalosauridae

32. Interfrontal and frontoparietal sutures: open (0); closed (1).

Pachycephalosauridae

33. Frontoparietal doming: absent (0); present (1).

34. Parietal–squamosal position relative to occiput: dorsal (0); posterodorsal (1).

35. Supratemporal opening: open (0); closed (1).

Pachycephalosaurinae

36. Frontoparietal doming, extent: incomplete (0), or complete (1), posteriorly and laterally.

37. Jugal–quadrate contact: absent (0); present (1).

Tylocephale + Prenocephale

38. Quadratojugal fossa: absent (0); present (1).

Stygimoloch + Pachycephalosaurus

39. Preorbital skull length: much less than (0), or subequal to (1), length from anterior orbital margin to posterior aspect of quadrate head.

40. Squamosal node cluster: absent (0); present (1).

41. Anterior snout nodes: absent (0); present (1).

Ceratopsia

Characters and character states

Ceratopsia

1. Rostral bone: absent (0); present (1).

2. Narial fossa, position: adjacent to (0), or separated by a flat margin from (1), the ventral margin of the premaxilla.

3. Jugal, lateral projection: chord from frontal orbital margin to extremity of jugal is less (0), or more (1), than minimum interorbital width.

4. Jugal (or jugal–epijugal) crest: absent (0); present (1).

5. Jugal infraorbital ramus, relative dorsoventral width: less (0), or subequal to or greater (1), than the width of the infratemporal ramus.

6. Premaxillary palate, form: flat (0); vaulted (1).

7. Predentary ventral process, width of base: less (0), or equal to or more (1), than half the maximum transverse width of the predentary.

Neoceratopsia

8. Premaxillary tooth number: 3 or more (0); 2 (1).

9. Premaxillary teeth, crown shape: recurved, transversely flattened (0); straight, subcylindrical (1).

10. Skull length (rostral–quadrate): 15% or less (0), or 20–30% (1), of length of postcranial skeleton.

11. Rostral anterior margin: rounded (0); keeled with point (1).

12. Rostral lateral processes: rudimentary (0); well developed (1).

13. Predentary anterior margin: rounded (0); keeled with point (1).

14. Predentary posteroventral process, shape: broader distally (0); narrower distally (1).

15. Retroarticular process length: long (0); very short or absent (1).

Archaeoceratops + Leptoceratops + Udanoceratops + Coronosauria

16. Edentulous maxillary/dentary margin, length: 2 (0), or 4 or 5 (1), tooth spaces.

17. Maxillary teeth, primary ridge development: low (0); prominent (1).

18. Maxillary/dentary primary ridge, position: near midline (0); offset posteriorly/anteriorly, respectively (1).

19. Maxillary/dentary teeth, packing: space between roots in adjacent teeth (0); no space between roots in adjacent tooth columns (1); no space between crowns within a tooth column (2).

20. Dentary tooth row, position of last tooth: anterior to (0), coincident with (1), or posterior to (2), the apex of the coronoid process.

21. Antorbital fossa shape: subtriangular (0); oval (1).

22. Postorbital and supratemporal bars, maximum width: narrow, bar-shaped (0); broad, strap-shaped (1); very broad, plate-shaped (2).

23. Infratemporal bar length: long, subequal to supratemporal bar (0); short, less than one-half supratemporal bar (1).

24. Jugal/epijugal crest: low (0); pronounced (1).

25. Quadrate shaft, anteroposterior width: broad (0); or narrow (1).

26. Predentary dorsal margin, form: sharp edge (0); bevelled cropping surface (1).

27. Dentary coronoid process, width and depth: narrow dentary process, low coronoid process (0); broad dentary process, moderately deep coronoid process (1); broad dentary process with distal expansion, very deep coronoid process (2).

Leptoceratops + Udanoceratops + Coronosauria

28. Maxillary/dentary crown, height: subequal to (0), or 1.5 times (1), maximum crown width.

29. Lateral maxillary/medial dentary crown base, form: convex (0), or inset (1), from root.

30. Jugal–squamosal contact above laterotemporal fenestra: absent (0); present (1).

31. Epijugal: absent (0); present (1).
32. Supratemporal fossae, relation: separated (0); joined in midline (1).
33. Posterior shelf composition: squamosal and parietal equal (0); squamosal dominant (1); parietal dominant (2).
34. Parietal shelf, inclination: horizontal (0); inclined posterodorsally (1).
35. Exoccipital–exoccipital contact below foramen magnum: absent (0); present (1).
36. Predentary surface between dentaries: absent (0); present (1).
37. Coronoid shape: strap-shaped (0); lobe-shaped (1).
38. Surangular eminence: absent (0); present (1).
39. Splenial symphysis: absent (0); present (1).
40. Axial neural spine, posterior margin: subtriangular (0); blade-shaped (1).
41. Cervicals 1–3, vertebral articulations: free (0); fused (1).
42. Cervicals 3–4, neural spine height: much shorter than (0), or subequal to (1), the axial neural spine.
43. Posteriormost caudals, neural spines and chevrons: absent (0); present (1).
44. Mid and posterior caudals, neural spine cross-section: subrectangular (0); oval (1).
45. Tail shape: tapering (0); leaf-shaped (1).

Leptoceratops + *Udanoceratops*
46. Premaxillary teeth: present (0); absent (1).
47. Dentary ventral margin, form: straight (0); curved (1).
48. Angular ventral margin, form: anterior portion (0), or nearly all of ventral margin (1), convex.

Coronosauria
49. Enamel distribution, maxillary/dentary teeth: both sides of crown (0); restricted to lateral/medial sides in maxillary/dentary teeth (1).
50. Nasal horn: absent (0); present (1).
51. Supratemporal fenestra, shape: oval (0); subtriangular (1).
52. Supratemporal fenestra, orientation of long axis: parasagittal (0); posterolaterally divergent (1).
53. Parietal width: subequal to (0), or much wider than (1), the dorsal skull roof.

54. Parietal posterior extension: as far posteriorly as (0), just posterior to (1), or far posterior to (2), the quadrate head.
55. Paired parietal fenestrae: absent (0); present (1).
56. Hypocentrum: absent (0); present (1).
57. Sacral number: 5 or 6 (0); 8 (1 dorsal, 1 caudal added) (1).
58. Sacral neural spines, mutual contact: absent (0); present (1).

Protoceratopsidae
59. Squamosal frill process: absent (0); present (1).
60. Sagittal crest, height: low and rounded (0); blade-shaped (1).
61. Paroccipital process, proportions: length is 2 (0), or 3 (1), times maximum depth of distal end.
62. Occipital condyle, size: large (0); small (1).
63. Predentary dorsal margin, inclination: horizontal (0); anterodorsally inclined (1).

Ceratopsoidea
64. Dentary teeth, primary ridge development: low (0); prominent (1).
65. Nasal horn position: posterior (0), or dorsal (1), to posterior margin of external nares.
66. Dentary ramus, position of maximum dorsoventral width: posterior (0); anterior (1).
67. Hypocentrum shape: wedge-shaped (0); U-shaped (1); ring-shaped (hemispherical occipital condyle) (2).
68. Mid cervical (C5–C7) neural spines, height: low (0); as high as dorsal neural spines (1).

Turanoceratops + Ceratopsidae
69. Maxillary/dentary teeth, root form: single (0); double (1).
70. Maxillary/dentary crowns, apical plane orientation: less (0), or more (1), than 45 degrees from the primary axis of the root.
71. Lateral maxillary/medial dentary crowns, secondary ridges: present (0); rudimentary or absent (1).
72. Postorbital horn: absent (0); present (1).