DRACOREX HOGWARTSIA, N. GEN., N. SP., A SPIKED, FLAT-HEADED PACHYCEPHALOSAURID DINOSAUR FROM THE UPPER CRETACEOUS HELL CREEK FORMATION OF SOUTH DAKOTA

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Abstract—The pachycephalosaurid *Dracorex hogwartsia,* n. gen., n., sp.*,* is a new pachycephalosaurin based on a nearly complete, and excellently preserved, young-adult skull from the Upper Cretaceous Hell Creek Formation (Lancian) of South Dakota. *D. hogwartsia* shows an unexpected mix of truly very primitive and very advanced features: no dome; wide open supratemporal fenestrae; large, spiked nodes on the squamosals; nodes of various shapes and sizes covering the skull including the cheek and snout; and a very long snout and tooth row. The so-called "primitive" nature of the skull (i.e., the well-developed supratemporal fenestrae and discernable peripheral skull elements: anterior + posterior supraorbitals and postorbitals 1 + 2, suggest that these features are present as the result of paedomorphosis. Consequently, all previous phylogenetic analyses are considered inadequate. At least three pachycephalosaurins co-existed in the Lancian - *Dracorex*, *Pachycephalosaurus* and *Stygimoloch*. Strong sexual-social selection probably generated the morphological diversity in skull shapes of these Late Cretaceous pachycephalosaurids.

INTRODUCTION

The Pachycephalosauridae displays an extraordinary diversity of cranial nodes (osteoderms) that seem to be adapted for visual display and contact sexual-social interactions. The classic pachycephalosaurids of North America –such taxa as *Stegoceras validum* from the late Judithian age and *Pachycephalosaurus wyomingensis* from the Lancian age– are distinguished by solid bony domes composed of the co-joined parietal and frontal (frontoparietal). In addition, osteoderms modified as small spikes and rounded knobs were organized in lines and clusters around the orbits, down the snout, and around the margin of the dome. The domes most often have been interpreted as being analogous to moose antlers or water buffalo horns – massive devices useful for intimidation and for actual "head-banging." Head-to-head or head-to-body pushing, shoving and ramming has been suggested (Colbert, 1955; Galton, 1970, 1971; Carpenter, 1997), but Goodwin and Horner (2004) favor species recognition and possible sexual display behavior as a secondary function. *Stygimoloch,* from the same beds that produced *Pachycephalosaurus,* added an unexpected variation – the dome was small and narrow (consisting solely of the frontal and parietal bones) and the squamosals supported unusually massive, long, backwardly directed, potentially deadly horn-like spikes that conferred an oryx-like visage. Discoveries in Asia added what appeared to be a far more primitive stage. The taxa *Homalocephale calathocercos* (Maryañska and Osmólska, 1974), *Goyocephale lattimorei* (Perle et al., 1982) and *Wannanosaurus yansiensis* (Hou, 1977), which share with the American fully-domed pachycephalosaurids deep occiputs, had flat, knobby skull-roof bones and open supratemporal fenestrae. The North American pachycephalosaurid *Stegoceras validum* is somewhat intermediate between the flat-headed Asian taxa and the fully-domed taxa (Sereno, 2000; Sullivan 2003, 2006).

Here we report on a most surprising pachycephalosaurid, another Lancian age genus that co-existed with *Stygimoloch* and *Pachycephalosaurus.* This new pachycephalosaurin lacks the characteristic dome and has unusually large supratemporal fenestrae, much larger than in any other pachycephalosaurid genus. This apparently "primitive" condition is accompanied by advanced character states elsewhere in the skull. This suggests that the opened supratemporal fenestrae are juvenile features retained in the adult. The large *Stygimoloch*-style squamosal spikes, large cheek nodes ("hornlets") and a long snout, with prominent pyramidal nodes also seen in *Pachycephalosaurus,* are derived feautures. We

name the new pachycephalosaurid *Dracorex hogwartsia*, n. gen., n. sp., and give a brief discussion of the conceptual challenges presented by the incongruous combination of skull adaptations.

In this paper the institutional abbreviations are: AMNH = American Museum of Natural History, New York; GI SPS = Geological Institute, Section of Palaeontology and Stratigraphy, Academy of Sciences, Mongolian People's Republic, Ulaanbaatar; MPM = Milwaukee Public Museum, Milwaukee; TCMI = The Children's Museum of Indianapolis, Indianapolis; UALVP = University of Alberta Laboratory of Vertebrate Paleontology, Edmonton;YPM = Yale Peabody Museum (New Haven); and Z. Pal. = Palaeozoological Institute, Polish Academy of Sciences, Warsaw.

SYSTEMATIC PALEONTOLOGY

Pachycephalosauridae Sternberg, 1945

Pachycephalosaurini Sullivan, 2003

Dracorex, n. gen.

Type Species–-*Dracorex hogwartsia*, n. gen., n. sp.
Distribution—Late Cretaceous of North America.
Etymology—From the Latin words: *draco* (meaning dragon) + *rex* (meaning king). Translation: "dragon-king."
Diagnosis—same as for species.

Dracorex hogwartsia, n. sp.

Holotype—TCMI 2004.17.1, nearly complete skull, one lower tooth, plus first, third, eighth and ninth cervical vertebrae, nearly complete (Figs. 1-12).

Horizon/Stratum, Provenance and Age – middle part of the Hell Creek Formation, South Dakota (exact location reserved for qualified workers); Lancian.

Etymology–-After the fictional "Hogwarts Academy," invention of author J. K. Rowling, the species named in honor of her contribution to children's education and the joy of exploration.

Diagnosis–-Most similar to *Pachycephalosaurus* and *Stygimoloch,* particularly in the long snout, two half-rings of pyramidal spikes on the snout, and strong cheek node. Differs from *Pachycephalosaurus wyomingensis* and *Stygimoloch spinifer* in lacking a dome; differs from *S. spinifer* in possessing four smaller spikes, not three massive spikes, on the
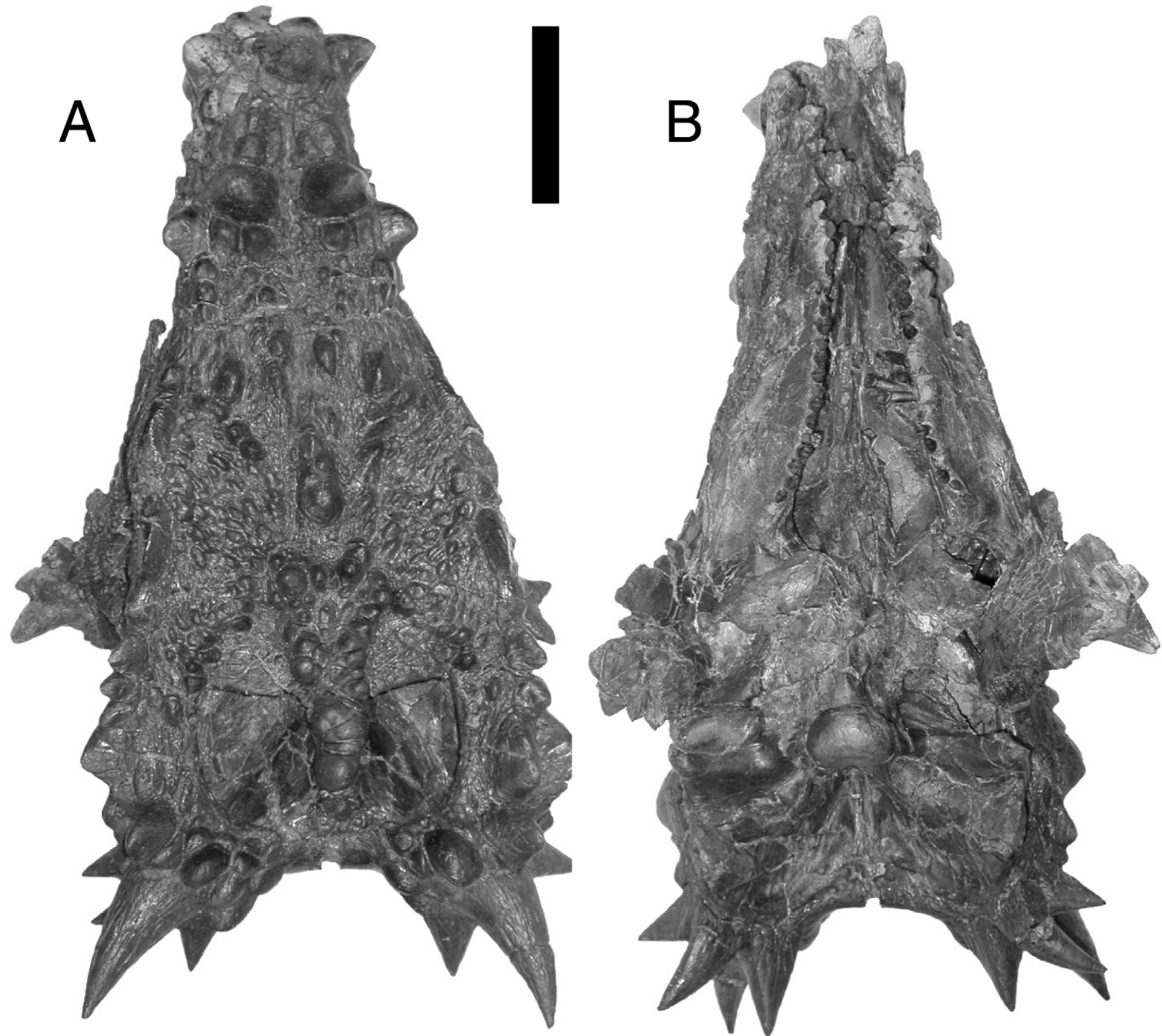
FIGURE 1. *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype), nearly complete skull. **A,** dorsal view; **B,** ventral (palatal) view. Bar scale = 10 cm (see Appendix for specific measurements for all figures).

squamosal, and lacking a dome. Differs from all other pachycephalosaurids in the extremely large supratemporal fenestrae, with the origin of the mandibular adductor muscles expanded anteriorly onto the dorsal surface of the parietal. Differs from the other monospecific genera (*Homalocephale, Goyocephale, Wannanosaurus,* and *Stegoceras*) with fenestrated skull tables, by having a long snout, two spike-half rings on the snout, parietal excluded from the posterior squamosal shelf, large cheek nodes, strong squamosal spike cluster on each side, generally strong accessory rugosities and longer snout.

DESCRIPTION

Skull

The skull (Figs. 1-2) is nearly complete and measures approximately 42 cm along the midline. The skull is slightly crushed, with the right maxilla folded in toward the midline. The tip of the snout is damaged around the external naris, but portions of the premaxillae are preserved. Node-like osteoderms, of different shapes and sizes, cover the entire skull roof and sides, including the snout. The left quadrate is detached from the skull.

Sutures of the skull-roofing bones are visible dorsally (Fig. 3) and laterally (Fig. 4).

Premaxilla—Most of the left and right premaxillae are preserved (Fig. 5). Right and left fragments of the premaxilla show nearly all the structure of the bone. Only the dorsal tip of the ascending narial process is missing. The subnarial-maxillary prong of the premaxilla is long and deep, far longer than that described for *Stegoceras* (Gilmore, 1924). The ventral edge of the prong has a rail-like shape, with two parallel ridges, for articulation with the underlying maxilla. The premaxillary bone here is surprisingly smooth with no indication of a tightly bound suture with the maxilla. The prong rises upward and backward more gently than in the holotype (Z. Pal. MgD-I/104) of *Prenocephale prenes* (Maryañska and Osmólska, 1974) because the muzzle is longer and lower. The ascending narial process tapers as it rises. The anterior half of the lateral surface is smooth with a sharply defined marginal thickening at the anterior edge. The posterior half of the lateral surface bears many oval scars and excavations, indicating that some sort of soft tissue from the narial capsule lay against the bone.

The alveolar-beak surface along the periphery of the premaxilla is of exceptional interest. There are no alveoli. Except for the tiny, vestigial
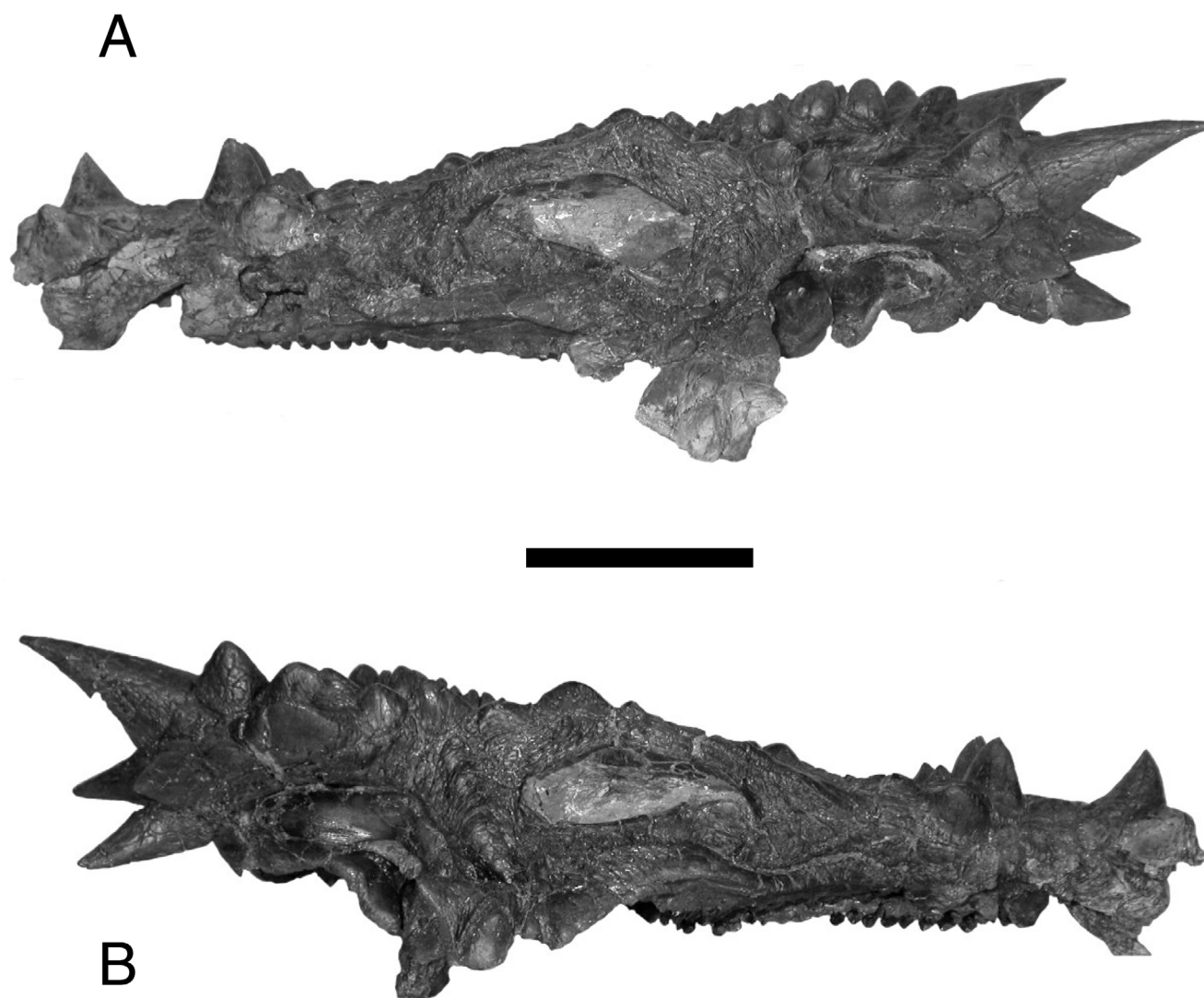
FIGURE 2. *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype), skull. **A,** left lateral view; **B,** right lateral view. Bar scale = 10 cm.

crown fragment mentioned below, there is no evidence that this individual possessed premaxillary teeth. There is no downwardly protruding beak at the anterior end of the premaxilla, of the sort usually present in ornithischians with premaxillary teeth. Instead, the entire periphery of the alveolar-beak bone is developed as one, continuous swollen zone of nearly constant depth, passing from the anterior midline symphysis backwards below the narial orifice and then terminating below the anterior part of the suture with the maxilla. This swollen zone is strongly convex, bulging upwards and downwards. The bone surface bears furrows and a fine pattern of pustules and small depressions, a pattern that resembles on a small scale that seen on the masticatory surface of the rostrum in the manatee (*Trichechus*). There is no cutting edge anywhere; no elevated, sharply defined ridge, unlike the condition in *Prenocephale, Stegoceras,* psittacosaurs and most other ornithischians. *Dracorex* may have possessed a thick, relatively soft pad on the premaxillary beak for the predentary beak to bite against. Above the swollen beak zone, on the lateral surface below the naris, the premaxilla has a longitudinal ridge that reinforces the swollen zone. The bone surface here is smooth and continues posteriorly onto the surface of the prong for the maxilla that is concave vertically. It does not appear that the premaxilla supported any of the thick, coarsely textured rugose prominences that cover

the sides and dorsal surfaces of the snout. The lowermost rugose prominence appears to be developed entirely on the maxilla. This prominence overhangs the maxillary prong of the premaxilla. On the dorsal surface of the premaxilla, lingual to the swollen beak zone, a vascular groove passes outward from a foramen near the base of the ascending narial process. The groove turns outward to run along the edge of the swollen zone. The groove probably housed an artery that fed the corial tissue that generated the dermal beak layer. The bone posterior and lingual to the groove is quite smooth, showing that the dermal beak did not extend here.

Nasals—The nasals are paired and long, measuring approximately 20 cm along the midline. They are covered with numerous osteoderms. Prominent half-rings with enlarged nodes characterize the anterior half (see below), which obscures their anterior extent (in dorsal view).

Prefrontals—Both prefrontals are preserved and are lateral to the posterior half of the nasals. They are also covered with osteoderms.

Frontals—The frontals are shorter anteroposteriorly than wide. The medial part of the frontals articulates with the nasals, and anterolaterally with supraorbital 1. Laterally the frontals articulate with supraorbital 2 and posteriorly with the parietal. As with the preceding elements, the dorsal surface is covered with numerous irregular osteoderms.
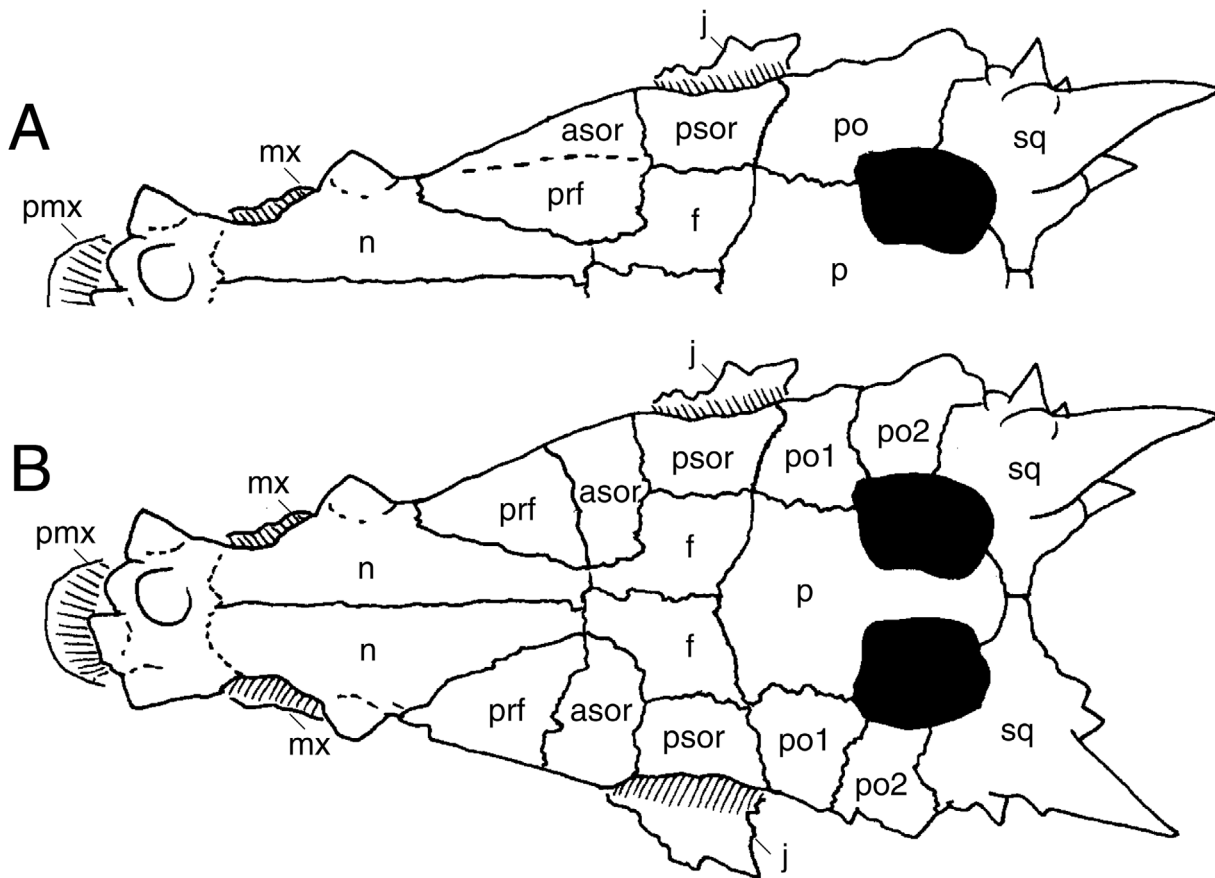
FIGURE 3. Line drawing of the skull roof of *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype), showing elements of the skull table. **A,** right side of skull showing the "normal" pachycephalosaurid condition, with coalesced prefrontal medial to the anterior supraorbital and single postorbital ossification; **B,** actual condition with extra transverse sutural divisions between anterior supraorbital and posterior supraorbital and the postorbital divided into an anterior half (po 1) and posterior half (po 2). **Abbreviations**: **asor** = anterior supraorbital; **f** = frontal; **j** = jugal; **mx** = maxilla; **n** = nasal; **p** = parietal; **po** = postorbital; **po 1** = postorbital 1; **po 2** = postorbital 2; **prf** = prefrontal; **prmx** = premaxilla; **psor** = posterior supraorbital; and **sq** = squamosal.

Parietal—The parietal is visible in both dorsal and ventral (occipital) views. The anterior half of the parietal is broad and has a wide contact with the paired frontals (anteriorly), strong contact with the supraorbitals 1 (laterally), and are bordered lateroposteriorly, in part, by the leading edge of the supratemporal fenestrae. The posterior half of the parietal forms the medial bar between the supratemporal fenestrae and is covered with large bulbous nodes (osteoderms). The supratemporal fenestrae are relatively gigantic; the origin of the jaw adductor muscles is expanded anteriorly beyond the limits of the fenestral rim and onto the parietal. Here the parietal surface is flat and depressed and free of the knobs that cover the surrounding parietal and postorbital. The posteriormost extension of the parietal (in dorsal view) fans out where it joins with the left and right squamosals. The posteriormost extension of the parietal does not participate in the formation of the squamosal (parietosquamosal) shelf (Fig. 3).

The exposed ventral surface of the posteriormost part of the parietal on the occiput is widest dorsally. The upper edge has a short tab that protrudes upward into the lower part of the squamosal midline commissure. This tab is the truncated remnant of the usual dorsal process. On either side of the parietal plate is a gentle concavity, bounded by a raised zone. Tendons of the m. rectus capitis posterior probably inserted here. There is no strong union, e.g., the median eminence that receives the insertion of the ligamentum nuchae. Instead, there is a very thin median crest, suggesting that the midline connective tissue was not strong.

Lacrimal—The left and right lacrimals are preserved. Anterolaterally, the lacrimal is expanded and contacts the posterodorsal surface of the maxilla. The lateral surface of the lacrimal is covered with minute dermal ossicles. Anterodorsally, the lacrimal is bordered by the prefrontal and anterior supraorbital. The posterior surface of the lacrimal is exposed in the orbit.

Jugal/quadratojugal—Both jugals are preserved. The left jugal is nearly complete, broken along its anterolateral edge. The jugal has a strong contact with the postorbital. The jugal forms a large triangular blade, the apex of which is directed posteroventrally. The surface of the jugal is largely covered with osteoderms, a large prominent spike-like node ("hornlet") is located on each jugal blade. The quadratojugal is partly exposed along the medial posterior margin of the ascending jugal process where it is laterally compressed. It is difficult to identify the suture between the jugal and quadratojugal.

Maxilla—Both maxillae are preserved and nearly complete. The right maxilla is folded in medially. Five labial foramina are present above the 3rd, 9th, 11th, 13th and 15th tooth positions (counted anterior to posterior) on the right maxilla. Two labial foramina are present from corresponding 11th and 15th tooth positions on the left. Other labial foramina cannot be verified due to damage along the anterior half of the left maxilla. Most of
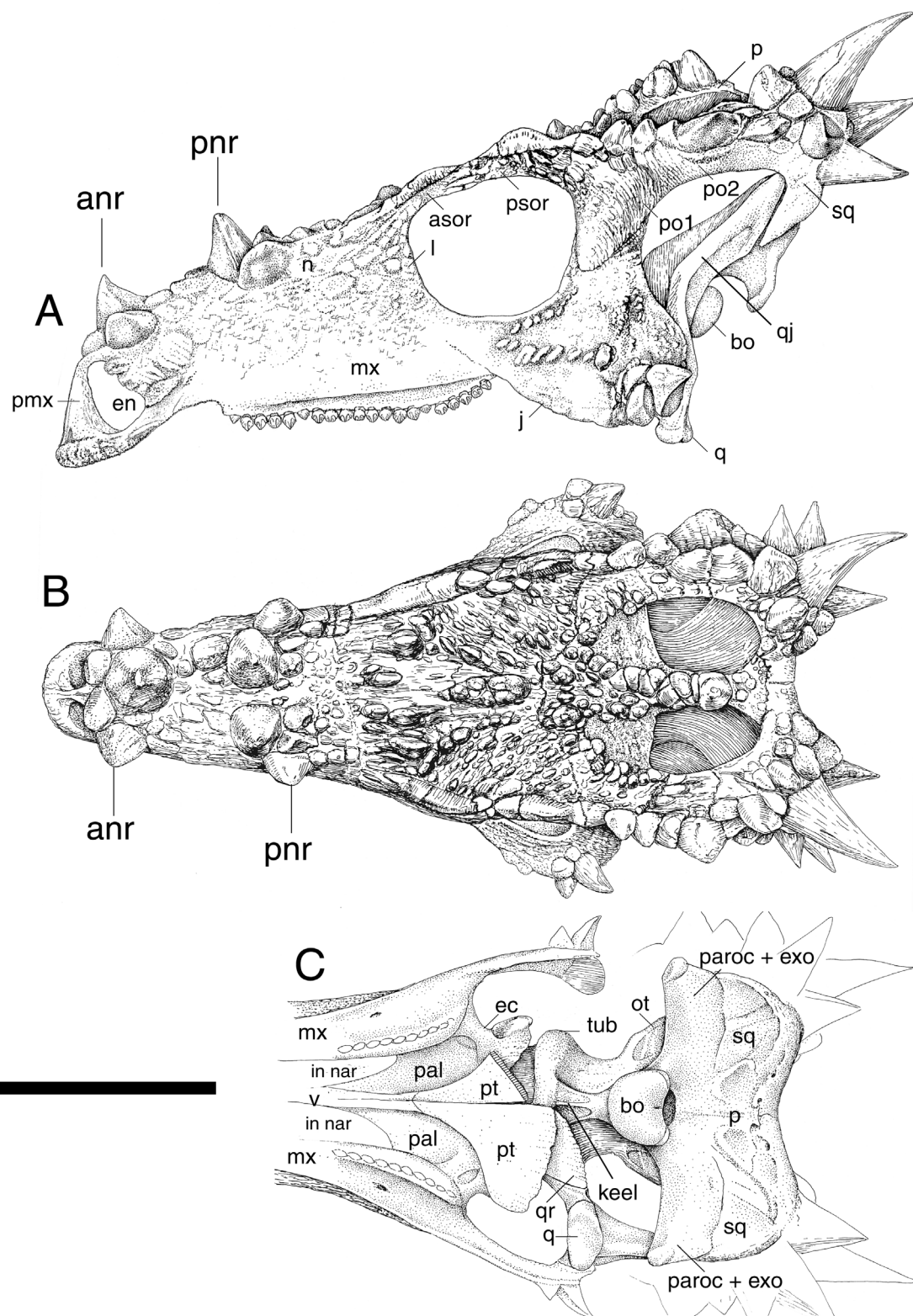
FIGURE 4. Reconstruction of the left lateral **(A),** dorsal **(B)** and posterior palatal view **(C)** of the holotype skull of *Dracorex hogwartsia,* TCMI 2004.17.1. **Abbreviations**: **anr** = anterior nasal ring**; asor** = anterior supra-orbital; **ec =** ectopterygoid; **en** = external naris; **in nar** = internal naris; **j** = jugal; **keel** = keel between muscle scars for ventro-flexors; **l** = lacrimal; **mx** = maxilla; n = nasal; **ot** = otosphenoid crest; **q** = quadrate; **qj** = quadratojugal, **qr** = quadrate ramus of pterygoid; **p =** parietal, **pal** = palatine; **paroc + exo** = paroccipital process + exocciptal; **pmx** = premaxilla; **pnr** = posterior nasal ring; **po** = postorbital; **po 1** = postorbital 1; **po 2** = postorbital 2; **posor** = posterior supra-orbital; **pt** = pteryogoid; **sq** = squamosal; **tub** = basitubera; and **v** = vomer. See Fig. 3 for key to dorsal skull elements (B). Bar scale = 10 cm. (The height of the skull structures have been restored using the undistorted left quadrate and by matching the facets on the quadrate and quadratojugal, and postorbital and jugal, as explained in the Appendix. The quadrate has been removed from the left side in the ventral view, to show the basitubera. The basitubera are badly crushed; they are restored after *Stegoceras*. (See the Appendix for details regarding reconstructions of figures 4 through 12.) (Copyright R.T. Bakker)
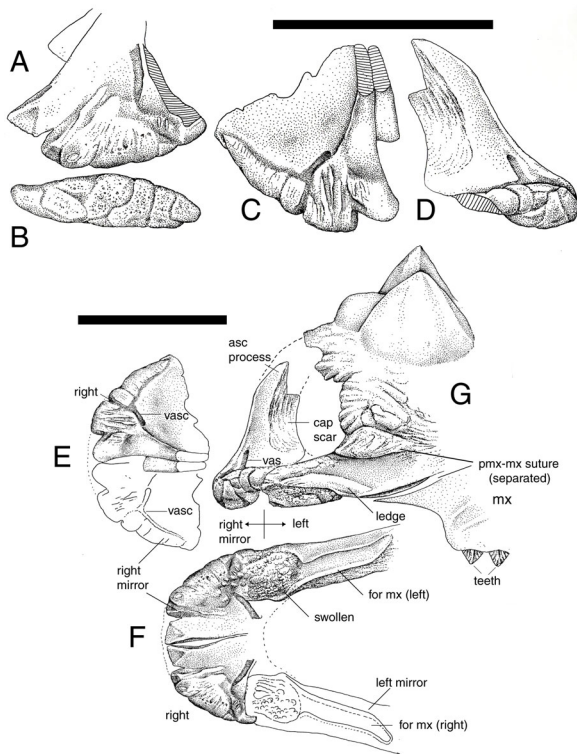
FIGURE 5. Left premaxilla and maxilla of *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype). Left premaxilla: **A,** ventral view of; **B,** anterior view; **C,** dorsal view; and **D,** lateral view. The right premaxilla is used to show the ascending narial process and the anterior half of the beak; **E,** dorsal-anterior view of the premaxillary beak (outline of right side drawn in mirror image to show full width of the beak; **F,** restored left side of anterior beak (note the rail-like attachment area for the maxilla); and **G,** left lateral view of premaxilla and anterior maxilla. The premaxilla is drawn slightly separated from the maxilla. Right and left fragments of the premaxilla show nearly all the structure of the bone. Missing are the dorsal tip of the ascending narial process, chips along the ventral edge and extreme anterior tip of the beak region, and the posterior part of the midline suture between right and left premaxillae. In the figure, the right side of the beak has been mirror-imaged (as indicated) to fit the posterior part of the premaxilla of the left side, and vice versa. The narial opening as seen in lateral view is restored as in *Stegoceras*. So restored, there is a short zone of overlap between the anterior tip of the left premaxilla and the posterior edge of the right premaxilla. It is possible that the overlap was greater and that the lower narial bar was longer than illustrated. Bar scale = 5 cm. (Copyright R.T. Bakker)

the teeth are well preserved, fully erupted and are still in their respective alveoli. On the right maxilla the 1st, 4th, 5th, 9th and 12th tooth are partially erupted. On the left maxilla the 15th and 18th tooth are partially erupted; four teeth have fallen out of their alveoli and are preserved resting, in part, on the ventral side of the left palatine.

Maxillary Teeth—The tooth crowns of the maxillary teeth share the same morphology for the entire maxilla. They are spade-shape and laterally compressed with a weakly developed basal cingulum on the labial side (Fig. 6). Each tooth has a central prominent cusp with smaller cusps on both the anterior and posterior edges in the same plane. The tooth root is long, measuring approximately 15 mm, based on the four dislodged teeth.

Peripheral skull/orbital elements— The peripheral skull and orbital elements are preserved, and the outlines are discernable. However, there is ambiguity and unusual possibilities among apparent sutures in the preorbital, surpaorbital and postorbital regions. In some well preserved pachycephalosaurid skulls, there is a large, triangular prefrontal situated medial to the anterior supraorbital (Fig. 3, right side, Fig. 4). The suture between the anterior supraorbital and the prefrontal aligned anterior-posteriorly. The prefrontal frequently coossified with the anterior supraorbital.

The posterior supraorbital typically has a transverse suture with the postorbital at the posterior corner of the orbital rim. On the skull table, the postorbital is very long, and sometimes it has been assumed that a postfrontal has coalesced with the postorbital (Fig. 4). In the holotype of *Dracorex hogwartsia* there is no trace of a prefrontal/anterior supraorbital suture of the usual longitudinal sort. Instead, there is a transverse suture. The two transverse sutures are equally well-developed on the left and right side and are symmetrical. These sutures do not appear to be post-mortem breaks.

In addition to the peculiar orientation of supraorbital series (noted above), there is a subdivision of the postorbital into two units that we identify as postorbital 1 and postorbital 2 (Fig. 3). This latter situation is unique, as all other pachycephalosaurids have only a single postorbital bone. A distinct suture divides the postorbital in half on both sides, near the anterior end of the infratemporal. Each of these elements is covered entirely with node-like osteoderms on their dorsal and lateral surfaces. The lateral edges of the anterior supraorbitals are characterized by enlarged, somewhat elongated osteoderms; those of the postorbitals 1 and 2 are larger and more node-like. A description of the supraorbitals and postorbitals immediately follows.

Supraorbitals (anterior supraorbital + posterior supraorbital)—The anterior and posterior supraorbitals largely occupy the region directly above the orbit. A distinct suture separates these elements from each other on both sides. The osteoderms along the lateral edges are elongated anteriorly and more keeled posteriorly.

Postorbitals 1 + 2— Laterally, both postorbital bars of postorbitals 1 are crushed dorso-ventrally. The facet on the descending process of the postorbital for the jugal is robust and has been displaced ventrally beyond the matching facet on the jugal for the postorbital. The jugal-quadratojugal suture is obscured by crushing. The descending process of the postorbital has an oval overlap onto the jugal, with a thin splint of jugal exposed anteriorly. The ascending portion of the postorbital has a strong contact with the squamosal.

Quadrate—The right quadrate is preserved in natural articulation with the squamosal socket and quadratojugal. Severe dorsal-ventral compression crushed the right quadrate, shortening the shaft. The left quadrate had become loose after death and had been displaced to lie in the plane of bedding below the basicranium. Consequently, the left quadrate is preserved almost without distortion. The left quadrate (Fig. 7) measures 16 cm from the distal to proximal end.

The distal quadrate is exceptionally well-preserved allowing for detailed description of the quadrate-articular joint. The inner and outer condyles are oblique, twisted so their long axes pass inwards and forwards. The outer condyle is more sharply keeled than the inner condyle and the keel is directly more strongly medially. Consequently, the axes of the condyles converge.

The shaft of the quadrate has a straight posterior margin in the upper and lower thirds; in between there is an embayment that in life would have been filled with the tympanic ligament sheet which would have contained the tympanum. The tympanic ligament sheet probably attached to the inner edge of the posterior quadrate surface, as in birds. The outer part of the tympanic notch then would function as a section of the external auditory meatus. The ligament sheet would have been attached to the descending outer corner of the paroccipital process and the connective tissue surrounding the m. depressor mandibulae passing from the paroccipital procsess to the retro-articular process of the lower jaw.

The quadrate head has a laterally compressed convex joint for the squamosal socket. In dorsal view the head is triangular, with apex facing posteriorly. The posterior descending process of the squamosal fits closely along the posterior edge of the quadrate; there is an anterior descending process that is applied to the anterior edge of the quadrate, but crushing has obscured the details of the process.

Squamosals—The squamosals are covered with nodes and spikes, with the central spike being the longest approximately 75 mm from base to tip. A cluster of 4-5 nodes ring the base of the central spike dorsally, while three shorter spikes are present ventrally, with the middle one offset ven-

trally. The tips of the central and ventral-most spikes are sharp, and slightly curved. Those of the other two are straight and more blunt. Anteriorly, the squamosals have a strong contact with the postorbitals 2, and medially they form the lateroposterior margins of the supratemporal fenestrae. There is on offset suture (opening) between the left and right squamosals, but it is clear that the two bones joined each other in life. Again, the posterior part of the parietal did not participate in the formation of the squamosal (parietosquamosal) shelf.

Viewed posteriorly, the occipital rim of the squamosal is thickened into a torus that extends around the upper margin of the bone (Fig. 8). It is broken at its lower end on both sides but more complete on the left and is thickest dorsally near the midline. A row of large foramina marks the lower limit of the torus. The row makes a very gentle V-shape, apex pointing downward. Above the foramina the texture of the bone is roughened by many narrow grooves, indicating the presence in life of a tough keratinized skin. Below the foramina the texture is smooth. The left squamosal is crushed downward onto the paroccipital process, decreasing the original depth.

The ventral surface of the squamosal bears a cluster of raised lines that pass downward and inward from the margin of the torus. These lines probably mark the attachment of ligament sheets within the fleshy head-neck muscles. The m. longissmus cervicis capitis should have attached lateral to the lines. The m. obliquus capitus should have attached medial to the lines.

Supraoccipital—The occiput is slightly crushed in the central area above the foramen magnum, so this region is more concave than in life, and the plane of the occiput is inclined more sharply relative to the long axis of the skull. The supraoccipital is cracked and buckled, and its true outline is obscured, and the foramen magnum has lost height top to bottom. The right side is uncrushed.

Paroccipital—The paraoccipital is an element that is almost as deep dorso-ventrally as the squamosals. The exit for the vena capitis is inscribed as a sharply-defined groove near the contact with the squamosal ventral plate. The outer-ventral corner is developed into a swollen apex that must mark the attachment of a major tendon–quite probably from the m. depressor mandibulae and/or the m. transversarius. Where the paroccipital meets the supraoccipital the adjacent bones are massively swollen, indicating that compressive forces were concentrated here.

Basioccipital/Occipital Condyle—The occipital condyle is composed of a large central bone, contributed by the basioccipital, and dorsal-lateral corners made of the exoccipitals have been displaced by crushing from the central basioccipital part of the condyle. The dorsal surface of the condyle is gently notched for the spinal cord. The overall shape of the condyle is swollen like a bloated kidney bean with a smooth surface. The condyle faces downward and backward relative to the occipital plane.

Ectopterygoids—The right ectopterygoid is a small bone that contacts the inner surface of the right maxilla. Its contact with the pterygoid is offset, pushed posteriorly. The anterior projection of the left ectopterygoid is preserved in contact with the inner surface of the left maxilla, and the distal part has been offset dorsoposteriorly above the left pterygoid wing.

Pterygoid—The pterygoid is nearly complete but has been crushed and fractured, especially along the midline. The posterior wings are nearly complete but are crushed, fractured and somewhat distorted.

Vomers—The vomers are long and are thin for most of their length. They are co-joined along the midline and unite with the pterygoids posteriorly, but the sutures between the vomers and the pterygoid are not readily discernable due to crushing.

Skull Dermal Armor

Dermal Spikes and Nodes—The holotype skull has an exceptionally well-developed system of accessory dermal armor that covers almost all of the outer cranial surfaces, from snout tip to the border of the lower temporal fenestrae and the entire skull table. Only the quadrate and cheek recess are free of such rugosities. Nodes are commonly grouped into clus-
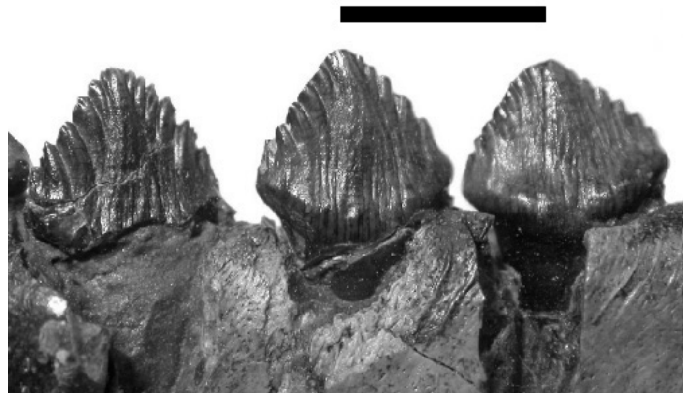

FIGURE 6. *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype), teeth. Photograph of right maxillary teeth (3, 4 and 5) in labial view (anterior to the right). Photograph taken with a medium-length telephoto lens to suppress distortion.

ters and lines that can be seen in many other pachycephalosaurids. The most prominent dermal ossifications are spikes that occur in clusters on the squamosals.

Nasal Half-rings—There are two transverse rings of large, pyramid-like spikes on the snout (Fig. 4B), the supra-narial (anterior nasal ring) row just behind the naris and the mid-snout (posterior nasal ring) row half way between the naris and orbit. In both rows the more lateral spikes are compressed laterally and have a narrow, crested apex. The medial spikes have bases that are more equi-dimensional and less compressed. Low knobs and rugosites are developed in front and behind the main spike-nodes; posterior to the medial spikes in the mid-snout row are several secondary nodes that have sharply-pointed apices. The two rows of spike-like nodes are developed in virtually identical fashion in the type of *Pachycephalosaurus wyomingensis* (AMNH 1696, Brown and Schlaikjer, 1943). The snout spike rings are not present in *Stegoceras, Prenocephale, Homalocephale,* or *Goyocephale.*

Supraorbital Node Row—The outer edge of the snout and skull table bears a line of prominent nodes. Anteriorly, this line is poorly expressed but becomes prominent and distinct above the orbit. The nodes here are developed as long, laterally compressed, low crests separated by shorter, rounded eminences. An especially high crest is situated above the posterior corner of the orbit. Most of the nodes have incised bases indicating a basal ring of vascular tissue that generated the keratinized dermis. Below the crest line is a zone where there are curved rugosities arranged in arcs passing upward and forward from the upper orbital margin and the postorbital bar and the postorbital-squamosal bar. Posteriorly, the supraorbital node row is distinguished by nodes that increase in size posteriorly, and on the postorbital-squamosal bar the crest line splits and generates two rows of compressed "hornlets" with sharp apices. The outer row produces a very large, compressed, sharply-pointed node that is directed outwards. The inner row is less prominent and shows strong asymmetry: the left side has a higher crest than the right side. The posteriormost node in the supraorbital row passes into the cluster of pyramid-shaped nodes that form a half ring around the dorsal root of the main dorsal-most spike of the squamosal cluster. The supraorbital node row in *Dracorex* is very close to that in *Stygimoloch* and some *Pachycephalosaurus* specimens; in the type of *Pachycephalosaurus wyomingensis* the nodes and apices are less prominent. The row is present but much less well-developed in *Stegoceras* and the Asian *Prenocephale prenes.*

Squamosal Spike Cluster—*Dracorex* bears a spike cluster on both squamosals. There are four prominent spikes. The anterior-lateral spike is at the posterior end of the supraorbital row. It is three sided and has a base with an equilateral-triangular cross section. The dorsal-posterior spike is the largest and has a more circular cross section. It is directed nearly di-
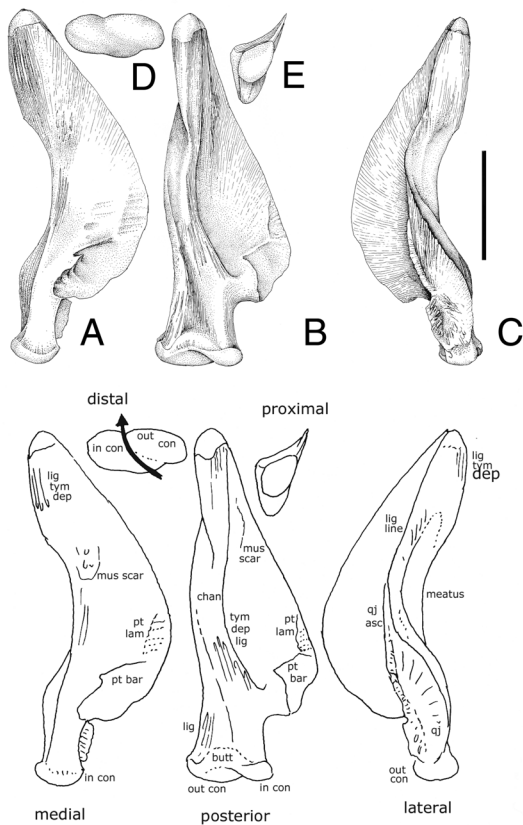
FIGURE 7. Left quadrate of *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype). Anterior edge of pterygoid process restored from right side. Otherwise, the bone is undistorted and complete. **A,** medial view; **B,** posterior view; **C,** lateral view; **D,** articular surface of distal condyle; and **E,** articular surface of proximal condyle. Below, map of features located on the left quadrate of *Dracorex hogwartsia*. **Abbreviations: in con** = inner distal condyle (arrow passes forward in divide between inner and outer condyles); **butt** = posterior swelling to reinforce distal joint; **chan** = channel for the chorda tympani nerve and associated artery; **dep** = origin of the m. depressor mandibulae; **lig** = attachment of ligament; **lig line** = attachment of ligament onto raised lines (probably part of the ligament sheet closing lateral temporal fenestra); **meatus** – external auditory meatus; **mus scar** = muscle attachment swelling, for ?m. protractor quadrati; **out con** = outer distal condyle; **pt bar** – attachment for the thick ventral bar of the pterygoid; **pt lam** = attachment for the thin dorsal lamina of the pterygoid; **qj** = attachment for main body of quadratojugal; **qj asc** = attachment for ascending process of quadratojugal; and **tym** = attachment for the tympanic ligament sheet. Bar scale = 5 cm. (Copyright R.T. Bakker)
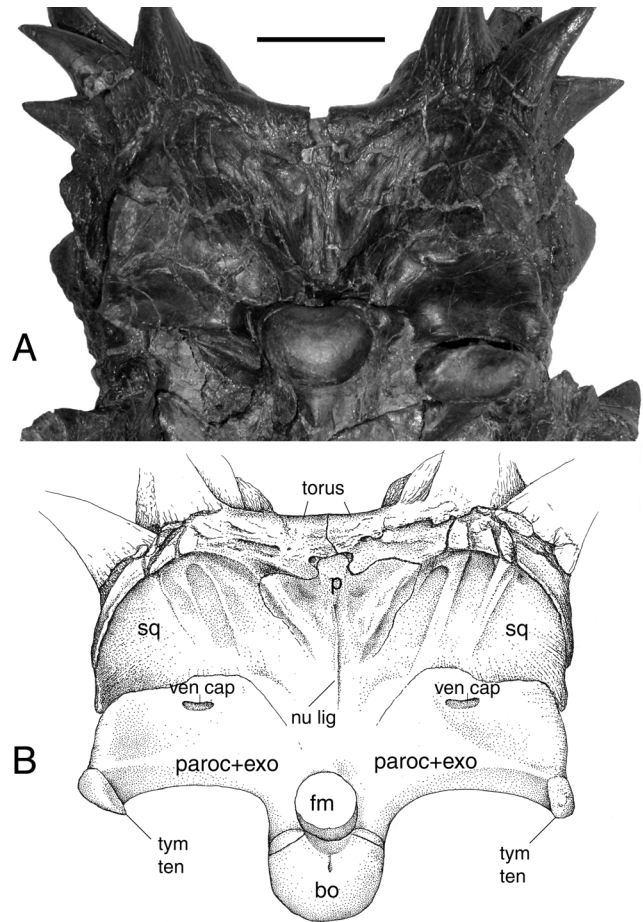

FIGURE 8. *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype), occiput. **A**, oblique posterior view (bar scale = 5 cm); **B**, reconstruction, with the occipital plane in the plane of the drawing. Right side used to restore the left. Outline shows inferred origin of muscles masses and tendon sheets. **Abbreviations**: **bo** = basioccipital; **fm** = foramen magnum; **nu lig** = nuchal ligament; **p** = parietal (posterior basal part); **paroc + exo** = paroccipital + exocciptal (fused); **sq** = squamosal; **ten** = tendon; **tym ten** = tympanic tendon; and **ven cap** = ?exit for head vein. (Copyright R.T. Bakker)

rectly posteriorly. The ventral-lateral spike is situated below the anterior-lateral horn and is of similar length; it is directed slightly outwards as well as posteriorly and ventrally; it has a more three-sided shape. The ventral-medial spike is of very similar size and shape and is directed inward as well as posteriorly. It is located medial to the dorsal-posterior spike and dorsal to the anterior-lateral spike. The four-spike cluster is nearly identical to that of an undescribed pachycephalosaurid in the Triebold collection (Triebold, 1997), where all the nodes along the occiput are low and lack sharp apices. *Stygimoloch spinifer* has a similar squamosal spike cluster with three greatly enlarged spikes; the anterior-lateral spike is not well developed, but the dorsal-posterior horn is huge. No other pachycephalosaurids have this prominent squamosal spike cluster.

Jugal (Cheek) Corner Node—A sharply pointed horn-like osteoderm with a triangular cross section is located at the posterior-ventral corner of the quadratojugal, just above the distal quadrate condyles. Two smaller "horn-like" nodes lie appressed against the main jugal node anteriorly, and there is a pavement of low nodes around this node cluster. Very similar "horn-like" cheek nodes occur in *Stygimoloch* and *Pachy-*

cephalosaurus. *Stegoceras* and the Asian genera have much weaker osteodermal nodes in this area.

Suborbital–Postorbital Row—Immediately below the lower orbital rim is a row of low, circular and oval nodes. The row passes upward into the center of the postorbital bar where the nodes die out and are replaced by a zone of rough arc-like dermal ridges. These "arcs" become thicker and are higher towards the posterodorsal corner of the orbit. Several "arcs" continue upwards and forwards and become elongated nodes that touch the base of the supraorbital osteoderms. *Stygimoloch* and *Pachycephalosaurus* have very similar suborbital rows. In *Stegoceras* and the Asian genera the row follows the same pattern, but the elements are less prominent.

Mid-cheek Row—A horizontal row of large but low nodes passes across the jugal, above the level of the large cheek horn. Low ridges and rows of nodes exist here in all the other well preserved skulls from the other genera.

Mid-temporal Row—A row of tall, conical nodes passes over the mid-temporal bar on the parietal and then divides, passing forward as two diverging rows of lower nodes. No other pachycephalosaurid species possesses this row of prominent knobs. In *Dracorex* the exceptionally tall knobs here would protect the bulging adductor mass protruding from the temporal fenestrae. However, both Milwaukee specimens of *Stygimoloch spinifer* (MPM 7111 and MPM 8111) have incipient bumps along the midline lo-
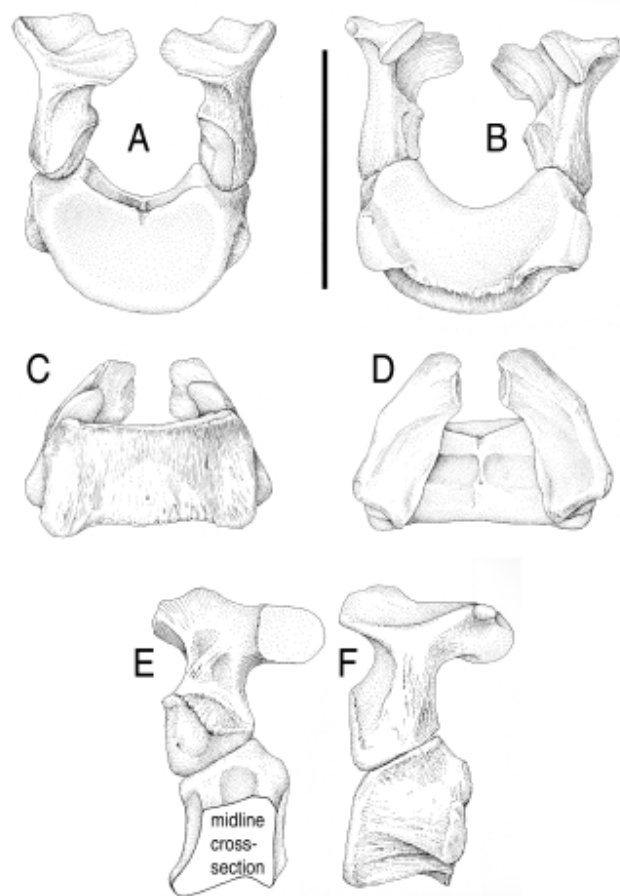
FIGURE 9. Atlas vertebra (reconstructed) of *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype). **A**, anterior view, **B**, posterior view; **C**, ventral view; **D**, dorsal view; **E**, medial view (with midline cross-section); and **F**, lateral view. Anterior direction is up in **C** and **D** and to the left in **E** and **F**. The atlas is nearly undistorted and perfect, missing only the left postzygapophyses. Right and left sides have been used for the restoration. Bar scale = 5 cm. (Copyright R.T. Bakker)

cated mostly on the posterior part of the dome. In *Goyocephale* and *Homalocephale* the mid-temporal surface carries faint depressions and knobs.

Postcrania

Four cervical vertebrae are preserved. These include: (1) atlas; (2) fourth (possibly fifth) cervical; and (3) ninth (last cervical), which are relatively complete. Another vertebra, the eighth (possibly seventh or sixth), lacks part of the centrum but has nearly complete zygapophyses on both sides.

Atlas—The atlas (Fig. 9) is nearly undistorted and perfect, missing only the posterior prong of the postzygapophysis. The centrum is rectangular in anterior or posterior view, with prominent posterolateral corners marking the attachment of cervical rib one. The cup for the occipital condyle is rectangular-oval; the posterior face of the centrum is almost flat, a condition that is most unusual among archosaurs and deserves comment (see below). The postzygapophyses are flat, oval-circular, and the posterior prongs – equivalent to the epipophyses of more posterior vertebrae – are long.

Fourth Cervical—The fourth (or fifth) is, in part, characterized by a centrum that is "reversed keystone" – e.g., beveled so the anterior face is tilted up and backward and the posterior face is tilted up and forward (Fig. 10). Such beveling in generalized dinosaurs is part of the design that produces the S-shaped curve in the column. The reversed keystone occurs posterior to the summit of the convex-up part of the S-shaped curve. Usu-
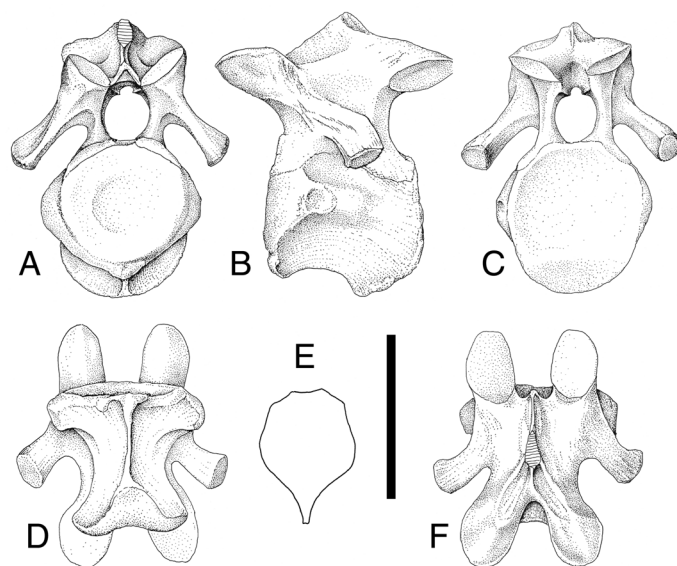

FIGURE 10. Cervical vertebra 4 (reconstructed) of *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype). **A**, anterior view, **B**, left lateral view; **C**, posterior view; **D**, ventral view; **E**, cross-section outline of centrum; and **F**, dorsal view. Except for the neural spine, nearly all the structure is preserved on right or left side; both sides have been used for the reconstruction. The vertebrae has suffered shear and lateral compression, which has reduced the width of the neural canal, the distance between right and left zygapophyses, and the width of the centrum. The width of all structures has been restored from the width of the anterior face, which appears undistorted. Anterior direction is up in **D** and **F**. Bar scale = 5 cm. (Copyright R.T. Bakker)

ally the fourth vertebra forms the anterior part of the concave-up section of the S-shaped curve. The beveling almost always shifts abruptly going from cervical three to cervical four. Cervical three is beveled in the other direction and makes a keystone for the convex-up arch. In the vertebrae preserved with the type, the zygapophyses project forward and aft equally, usually a feature of cervical four or five. More posteriorly, the posterior zygapophyses project farther than the anterior.

Except for the neural spine, nearly all the structure is preserved on the right or left side; both sides have been used for the reconstruction shown in Fig. 10. The fourth cervical vertebra has suffered shear and lateral compression, which has reduced the width of the neural canal, the distance between right and left zygapophyses, and the width of the centrum. In the reconstruction, the width of all structures has been restored from the width of the anterior face, which appears undistorted.

The anterior articular face is nearly perfectly circular and bordered by a recessed zone that separates the face from the lateral swellings for the rib attachment and from the ventral keel. The articular face is almost flat, with a slight depression in the center. The posterior-ventral corner of the centrum is rugose as preserved and appears to have been injured in life or broken after death, or both. The posterior articular face seems to be concave. The centrum is strongly pinched ventrally and makes a sharp keel where the m. longus colli et capitis would attach. The lower rib attachment (parapophysis) is developed into a large swollen area at mid height of the anterior centrum.

The neural canal is taller than wide; the reverse condition is the rule for generalized ornithopods. In the ceiling of the canal there is a sharp-edged ridge running longitudinally on each side, partly enclosing a small accessory canal. To our knowledge, the spinal cord never develops a separate cord strand here. More likely, the accessory canal housed a cylindrical ligament developed from the ligamentous sheath that surrounds the cord. The smooth wall of the accessory canal indicates that the ligament was free to move. This extra ligament may well have been associated with the locking zygapophyses, described below, as part of a complex design to pro-
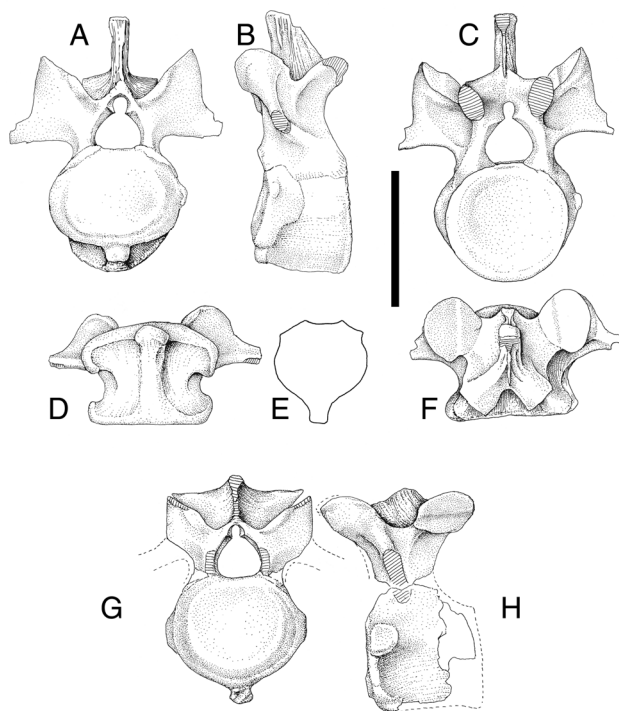
FIGURE 11. Cervical vertebra 9 (reconstructed) of *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype). **A**, anterior view, **B**, left lateral view; **C**, posterior view; **D**, ventral view; **E**, cross-section outline of centrum; and **F**, dorsal view. Anterior direction is up in **D** and **F**. The vertebra has suffered slight shear and slight anterior-posterior compression, resulting in dislocation at the anterior centrum-neural arch joint. Right and left sides allow reliable reconstruction of most features except for the tips of the postzygapophyses and extremity of the diapophyses. Cervical vertebra 8 (reconstructed): **G,** anterior view; and **H,** lateral view. The centrum has been crushed from behind and length is not known. The anterior centrum face is cracked but undistorted. Both post- and prezygapophyses are well preserved and required little restoration. Bar scale = 5 cm. (Copyright R.T. Bakker)

tect the spinal cord from injury when the neck was subjected to sudden, strong external forces.

Another alternative explanation for the accessory canal is that it housed a pinched-off vessel containing cerebrospinal fluid. Such a canal could, in theory, function to prevent damage to the brain induced by head-ramming. The pachycephalosaurid skull roof is composed of solid bones with no air chambers of the sort that cushion shock in sheep, goats, cattle and other mammals and birds, as well as in tyrannosaurids and other large theropods dinosaurs (Osborn, 1912). Therefore, a shock delivered on the frontal-parietal region could transmit violent shock waves into the fluid-filled space between braincase walls and the brain. Cerebrospinal fluid would transmit the shock into the brain tissue – if the fluid-filled space had little room for expansion. An accessory canal communicating with the endocranial space would allow the shock waves to pass posteriorly and dissipate. There is a rough analogue among extant mammals and birds in the ear: the fluid-filled canals of the inner ear carry waves from the fenestra ovalis to the fenestra rotunda; sensory hairs in the pathway of the waves carry information to the organs of hearing. The system is also shock absorbing - elastic membranes in each fenestra allow strong sound waves to be dissipated.

It is unlikely that a pneumatic vessel filled the accessory canal. Unlike theropods, pachycephalosaurids have no trace of pneumatic chambers or tubes invading the vertebrae elsewhere, or in the basicranium.

The zygapophyses are set at about a right angle to each other, viewed from in front. They are steeper and less widely separated than in generalized ornithopods. Both pre- and postzygapophyses are carried on projecting necks. There are no epipophyses. However, the dorsal midline of each postzygapophysis has deep sulci with sharp edges, marking the attachment

of the m. interarticularis muscles and ligaments; the innermost parts of the m. semispinalis may have attached here, too. The diapophyses are long, slender, and bear an oval attachment site for the rib. The outer surfaces of the diapophyses bear strongly incised muscle scars that pass upward and forward and continue onto the posterior root of the prezygapophyses. This incised scar marks the attachment of the ligament sheet between the short segmental muscles of the axial system. Slips of the m. semispinalis, m. inter-transversarius and the m. longissimus would attach here.

The neural spine is broken off but clearly was compressed laterally, wide anterior-posteriorly and tilted forward. The posterior edge is keeled and bears sharp ridges for the interspinous ligament and muscles.

Ninth Cervical— The final cervical (Fig. 11A-F) preserved is almost certainly the last; in a generalized ornithischian it would be the ninth. The centrum is 40% shorter than the vertebrae adjudged to be the fourth; the postzygapophyses project more than the prezygapophyses and the transverse process projects nearly directly laterally, as is the case usually in a last cervical. The centrum faces are beveled to participate in the concave-up part of the column where neck meets the torso. This vertebra has suffered slight shear and slight anterior-posterior compression, resulting in dislocation at the anterior centrum-neural arch joint. Right and left sides allow reliable reconstruction of most features except for the tips of the postzygapophyses and extremity of the diapophyses.

The anterior articular face of the centrum is wider than high and circumscribed by a depressed zone separating the face from the rib head and the ventral keel. The face is very slightly concave. The posterior face is slightly taller than wide and gently concave. There is no suggestion of the ball-in-socket design seen in hadrosaurs and iguanodontids and, in incipient form, in camptosaurids and thescelosaurs. The lower half of the centrum is pinched into a keel that is thicker than that of the fourth vertebra, and the constriction between anterior and posterior faces of the centrum is less extreme. The shortness of the centrum and sharp reverse-keystone beveling show that there was a marked concavity in the S-shaped curve here where the neck met the torso, a sharper curve than in most generalized ornithopods and ceratopsians.

The lower rib attachment is carried on a swollen zone located more dorsally on the centrum than in cervical four. The neural canal is turnip-shaped; the upper accessory canal is very well defined and marked off by strong longitudinal ridges. The transverse processes are deep dorsal-ventrally and carried slender diapophyses directed laterally. The zygapophyses are more widely spaced and less inclined than in the more anterior cervical. The incised ligament-muscle scars are less well developed and do not extend as far onto the postzygapophyses.

The articular facets on the prezygapophyses are oval-circular and show a "tongue-in-groove" structure. The joint surface is flat but subdivided by an abrupt break in slope that runs longitudinally. The flat surface outside the break in slope, projects farther upwards than the surface medial to the break in slope. The anterior rim of the zygapophysis is thickened along the edge of the more medial part of the facet. Such a break in slope would help lock the zygapophyses together when the neck musculature contracts and presses the prezygapophysis against the postzygapophysis of the next vertebra behind in the column. The locking mechanism would protect the column from damage induced by forces tending to twist the vertebrae about the long axis of the column but would not interfere with flexion-extension in a vertical plane.

The neural spine is almost complete, lacking the upper rear corner. It is thin, compressed side to side, with a weak swelling at the summit, and inclined forward. Strong vertical lines and grooves mark the attachment of the m. semispinalis.

A fourth cervical is represented by an arch with all four zyagapophyses and a centrum crushed from front to back (Fig. 11G-H). The shape indicates a position between what we identify as #4 and #9; we identify it as "cervical 8", but it could as easily be identified as number 6 or 7. The centrum was longer than in cervical 9 and the ventral keel was slightly thinner; otherwise the two centra are very close. The accessory canal is well developed. The zygapophyses are very much longer anterior-

posteriorly than in cervical 9. The tongue-in-groove articular surfaces are well developed for the full length of the joint surface, demonstrating that the anti-twisting articulation extended anteriorly into the neck.

DISCUSSION

Dracorex hogwartsia is most similar to *Stygimoloch spinifer* and to a lesser extent *Pachycephalosaurus wyomingensis*. It is considered to be a member of the Pachycephalosaurini as defined by Sullivan (2003). However, it is readily distinguishable from these two taxa based on a number of key features. *Stygimoloch spinifer* is characterized by a huge spike cluster, consisting of 3 enlarged (hypertrophied) spikes. This differs from the shorter 4 spike arrangement in *Dracorex hogwartsia*. Galton and Sues (1983) characterized *Stygimoloch spinifer* as having three-to-four spikes on the squamosal. This characterization allowed them to include a smaller, isolated squamosal with four spikes (YPM 335), a specimen we here consider to be referable to *Dracorex hogwartsia*. We have been able to determine, based on comparison with other documented specimens of *Stygimoloch spinifer* (MPM 7111 and MPM 8111), and two undescribed specimens in private collections, that *S. spinifer* consistently has these enlarged spikes coupled with an incipient, laterally compressed dome, made up of only the frontals and parietal. *S. spinifer* lacks open supratemporal fenestrae. Moreover, these skulls are of the same size as the holotype of *Dracorex hogwartsia*, so we conclude that these differences are not the result of ontogenetic development.

The skull of *Pachycephalosaurus wyomingensis* is largely characterized by a huge (broad) dome coupled with low rounded nodes clustered on the squamosals (Gilmore, 1931; 1936; Brown and Schlaikjer, 1943; Galton and Sues, 1983; Sues and Galton, 1987). The dome incorporates the peripheral elements (supraorbitals and postorbitals), whereas the dome of *Stygimoloch spinifer* does not (Goodwin et al., 1998).

The holotype of *Dracorex hogwartsia* displays a number of primitive features that call into question the conventional thinking of the polarity of characters that unite pachycephalosaurids. As a consequence, its discovery has profound implications concerning previous interpretations of their behavorial/social nature. These features are: (1) lack of the classic pachycephalosaurid dome; and (2) well–developed supratemporal fenestrae. Coupled with these two putative primitive features are the astounding number of osteoderms in the form of irregular osteodermal crust (covering), nodes, larger "hornlets," and spikes.

Flat-headed pachycephalosaurids include the Asian taxa *Homalocephale calathocercos*, *Goyocephale lattimorei*, and *Wannanosaurus yansiensis* (Sereno, 2000). Prior to this discovery of *Dracorex hogwartsia*, the only semi-flat headed pachycephalosaurid from North America was *Stegoceras validum* (which includes the flat-headed *Ornatotholus browni*), and the flat-headed nature of this taxon is only demonstrable in juveniles of the species (Sullivan 2003, 2005, 2006). Some specimens of *S. validum* retain a well-developed parietosquamosal shelf and moderate-sized supratemporal fenestrae (Sullivan, 2003, fig. 2). *D. hogwartsia*, however, has a skull that is totally flat, with no hint of doming. Although the specimen is considered to represent a young adult, we believe, based on the beginning of coosification of mid-cervical arch with centrum, that the animal was probably near maturity.

Aside from having a flat, node-covered skull, the most astonishing feature of *Dracorex hogwartsia* is the pair of huge and unrestricted superior temporal openings. The supratemporal fenestrae are very much larger front-to-back and side-to-side than in *Homalocephale calathocercos*, and larger than in *Goyocephale lattimorei*. Only the fragmentary skull of *Wannanosaurus yansiensis* shows fenestrae as large as those of *D. hogwartsia*. In *D. hogwartsia* the outer and anterior rims of the fenestrae are sharp-edged and overhang the interior of the supratemporal fenestrae; the inner edges descend downwards and outwards as the smooth surfaces of the braincase. As noted previously, there is no dome on the frontoparietal. Instead, there is a narrow median bar between right and left fenestrae. The origin of the jaw adductor muscles is expanded anteriorly beyond the limit of the fenestrae by a large depression on the dorsal surface of the parietal. Such an expansion of the adductor origin occurs to form a fossa in many archosaurs but has not been observed in any other pachycephalosaurid.

If unreduced superior fenestrae are primitive, and if one does not admit reversals, then *Dracorex hogwartsia* is more primitive in the temporal region than any other well known pachycephalosaurid. However, Sullivan (2003, 2006) has demonstrated that the oldest known pachycephalosaurids are, in fact, fully-domed, and that flat-headed morphs appear later in the fossil record. This suggests that doming may be primitive for pachycephalosaurids and that a reversal to the non-domed, flat-headed state is a secondary (derived) character reversal, coupled with the re-opening of the surpatemporal fenestrae. Indeed, while *Stegoceras validum* has been considered to be transitional between domed and flat-headed taxa, it may indicate the beginning of a character reversal to suppression of doming and opening of the supratemporal fenestrae in some taxa.

If we are correct about these being secondarily-derived features, then this destroys the concept of the Marginocephalia of Sereno (1986). Moreover, the principal character used to link ceratopsians to pachycephalosaurids is the "overhang of the occiput," meaning the posterior rim of the skull table is pulled backwards beyond the position of the foramen magnum. However, the conditions are not homologous. In primitive ceratopsians – psittacosaurs and protoceratopsids – the occiput overhangs the foramen magnum because the posterior part of the skull table is pulled backwards and the upper temporal fenestrae are elongated front-to-back. The lower temporal fenestra in psittacosaurs is large and unconstricted, as in primitive archosaurs generally, and not compressed front-to-back, and the jugal-quadratojugal bar is long. In psittacosaurs the quadrate is vertical. But, in pachycephalosaurids the lower temporal fenestra is compressed and the jugal-quadratojugal bar is abbreviated, so the quadrate slants downward and forward.

Postcranial differences are also worth noting. Many experienced Lancian field workers have noted that the isolated limb bones and vertebrae of thescelosaurs are difficult to tell from those of pachycephalosaurids. Not so with the cervicals – *Dracorex* displays features obviously distinct from that of any ornithopod. Since the pachycephalosaurid occiput is unusually tall and expanded in the outer-upper corners, it should be expected that the neck vertebrae would be tall, strongly keeled, and have well- developed muscle attachments. In these respects, *Dracorex* resembles protoceratopsids, which also carried a large head. However, pachycephalosaurids have a stronger S-curve in the column, stronger keels, longer anterior vertebrae, and more marked difference in centrum length between the anterior vertebrae and cervical nine (Fig. 12). The break in slope on the zygapophyses of the posterior cervicals ("tongue-in-groove" joints) is unique among ornithischians, to our knowledge. Small ankylosaurians (e.g. *Struthiosaurus? transilvanicus,* Nopsca, 1929) and small stegosaurians (*Huayangosaurus,* Zhou, 1984) have cervicals with more cylindrical centra, less well developed keels, and less beveling.

The cervical series of *Dracorex* actually has many features of primitive big-headed dinosaurs – e.g. ceratosaurs and megalosaurs – overlaid with adaptations to reinforce the column against twisting. The resemblance to protoceratopsids probably represents a common response to sporting a large head, not the result of homology.

PHYLOGENETIC AND BEHAVIORAL CONSIDERATIONS

Phylogenetics

It has become de rigueur to dissect skulls verbally, make long lists of characters and character states, and then grind the matrix through a computer program to generate the simplest branching pattern. Usually a version of PAUP (Phylogeny Analysis Using Parsimony) is employed. Such an exercise assumes that all potential character transformations are equiprobable. In our case, it would require assuming that evolving a long snout from a short snout, or vice versa, is as probable as evolving closed temporal fenestrae or secondarily opening the fenestrae via heterochrony. Or, that
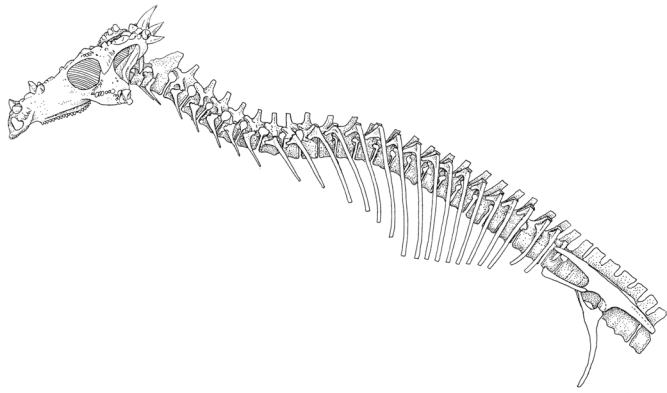
FIGURE 12. Reconstructed presacral column, hips and skull of *Dracorex hogwartsia*, n. gen., n. sp., TCMI 2004.17.1 (holotype). Cervicals 1, 4, 8, and 9 used to guide interpolation of missing vertebrae 2, 3, 5, 6, and 7. Pelvis, posterior dorsal vertebra, ribs restored from *Stegoceras validum* (UALVP-2) by equalizing the quadrate lengths of the two specimens. The sequence of dorsal vertebra centrum lengths is restored from that in the holotype of *Homalocephale calathocercos* (GI SPS 100/51), height taken from *Stegoceras validum* (UALVP-2). Estimated length as reconstructed from atlas to last sacral vertebra = 1426 mm. Estimated length reconstructed from tip of snout as shown to tip of ischium (= "snout-vent length") = 1625 mm. (Copyright, R.T. Bakker)

evolving spike half-rings on the snout are as probable as going from three to four occipital spikes. The assumption of equi-probable character transformation is wholly unwarranted. It is not like mixing apples and oranges – it's mixing apples and oranges, bowling balls and cannon balls, BB's and seeds from currants. Saying "Phylogeny A is preferred because it has 66 steps, while Phylogeny B has 70" is meaningless unless a rigorous and thorough evaluation is performed of the morphogenetic complexity and genetic control of the traits. Catalogues of the genetic basis for human skeletal traits show a wide range from simple multi-gene effects (e.g., shovel incisors; Hillson, 1996) to polygenic and pleiotropic traits, where contributions from many genes are expressed. Some skeletal features are tightly integrated into morphologic systems – for example, those regulated by HOX genes (Carrol, 2005; Coyne, 2005). Many scholars have noted this criticism before (Bowler, 1989; Van Valen, 1978), and we agree. Computer-generated "parsimony" analyses in most cases are not objective, quantitative hypotheses. They cannot test one another. They are scenarios. Much of the computer analyses of dinosaur phylogeny are so much PAUP Fiction.

A few complex characters seem to be expressed among pachycephalosaurid skulls. Prominent "horn-like" nodes and spikes arranged in snout half rings always co-occur with prominent cheek horns, and this condition co-occurs with the longest snouts. Prominent nodes and spikes are clearly derived. The nearest sister group of pachycephalosaurids is not known, so whether the long-snouted condition is primitive or advanced cannot be determined. Evidence comes from time-stratigraphy. The oldest skulls are all short-snouted and fully-domed. All the long-snouted skulls lack premaxillary teeth and are of Lancian age. Therefore, we favor the hypothesis that the long-snouted-spikey genera share a common ancestry separate from the Asian genera.

Most recently published phylogenies assume that the large dome evolved once and was never lost (Sereno, 1986, 2000). Such an assumption makes *Dracorex hogwartsia* difficult to interpret. The long snout and spikey condition would have to have evolved independently in two or more lineages that led to the Lancian long-snouted genera. *Stygimoloch spinifer* too is a problem. The dome is smaller, made up of only the frontal and parietal (peripheral bones are not incorporated into the sides of the dome as they are in most domed pachycephalosaurids), than in subadult-adult specimens of *Stegoceras validum*. Also, the spikes are huge, closest to the condition in *Dracorex hogwartsia*. All *Pachycephalosaurus* specimens have

no spikes. An undescribed large dome pachycephalosaurid (here referred to as the Triebold specimen; many mounted casts are on display in museums) has a four-spike cluster very close to that of *Dracorex*.

One of us (Sullivan, 2005) has suggested reversal through alteration of timing of sexual maturity and skeletal development. Both dome shape and spikes surely are controlled by sexual-social selection. There are good case histories of one type of display organ being replaced by another. For example, primitive rhinocerotids had large, sharp lower incisor tusks for fighting but very little development of the horn. *Subhyracodon* is an example. A few advanced genera combine a moderately long horn with incisor tusk – *Rhinoceros indicus*. Other advanced genera lose the tusk and substitute long nasal and frontal horns. *Diceros, Coelodonta* and *Ceratotherium* are examples. The distribution of cranial characters among pachycephalosaurids suggests that squamosal spike clusters were, in part, replacements for domes. We are persuaded that reconstruction of phylogeny should not proceed in a functional-behavioral vacuum. Any working hypothesis must weigh characters, using the criteria of sexual selection versus non-social adaptations. Display characters are known to evolve faster and produce more bizarre structures than do characters controlled by feeding and trophic position.

A flat-headed, spike-less, short-snouted species probably is primitive. The deep occiput is already well developed in the flat-headed *Homalocephale,* showing the presence of strong occipital muscles that did heavy work in dorsi-flexion of the head – or pushing upward. The contact display among flat-heads probably would have been executed by two individuals pressing the flat, slightly rugose skull tables against one another – and shoving. *Prenocephale* represents a departure, where the dome could inflict blunt trauma against the flank or shoulder or thigh. A long snout means a long tooth row, combined with loss of premaxillary teeth and transitional teeth and development of a diastema – a complex associated with a shift in feeding. Thus, the origin of the long-snouted taxa may be scored as a trophic shift. The *Pachycephalosaurus* specimens with large domes and four-spike clusters (e.g., Triebold's specimen) could be used as a starting point for long-snouted phylogeny. The *Pachycephalosaurus wyomingensis* type skull suppresses all spikes but has a wider, more massive dome. *Stygimoloch spinifer* can be interpreted as a case where very long spikes has permitted the partial suppression of the dome. Dorsi-flexion of the *Stygimoloch* head could produce fatal wounds in opponents and deter medium-sized predators. *Dracorex* could represent a further variant where lateral occipital spikes and mid-temporal conical horns replace the small dome. Butting with the highly rugose skull bearing many small and mid-sized horns produces a style of fighting different from that of *Stygimoloch*.

According to this scenario (we use the word carefully), sexual selection acted on the genes expressing the dome. The sequence *Pachycephalosaurus-Stygimoloch-Dracorex* is a reduction series, where dome growth is suppressed. Thus, the dome-less condition in *Dracorex* could be a secondary return to the flat-headed state. Whatever hypothesis of phylogeny is favored, it is clear that three distinct behavioral/morphological taxa co-existed in Lancian times, as sampled by the middle Hell Creek strata of Montana and South Dakota.

Lastly, there is this dilemma regarding the occurrence of these extra transverse sutures on the skull of *Dracorex*. We offer two other interpretations: that the sutures are neomorphs, not recognized before among ornithischians, or that they are pseudarthroses, joints that developed along fractures incurred during life. Pseudarthroses are common in ribs shafts, where a break in life has been stabilized by a slightly moveable joint. Some flat-headed ungulates today ram each other on the skull table – the Giant Forest Hog is the best exemple. Giant Forest Hog skulls often show fractures (d'Huart, 1993). If, as suggested strongly by the cervical vertebrae, *Dracorexes* rammed one another, they may have induced fractures that became assimilated into the sutural pattern of the skull. Such new joints would be adaptive in providing accessory zones of shock-absorption, where the ligaments stored some of the energy of impact.

Theories on Kinetic Cranial Behavior

Pachycephalosaurid heads have spawned theories of function since the first complete skull was found in the 1920's. Commenting on the endocast of *Pachycephalosaurus,* Colbert expressed befuddlement about why such a small brain would need ten inches of solid bone armor (Colbert, 1945). Museum labels offered "racial senescence" as a non-functional explanation of the bony dome in the fifties (R. T. Bakker, pers. ob., 1954). Galton invoked head-to-head ramming, a la Bighorn Sheep (Galton, 1971). Subsequent theories shifted the target site and envisioned head-to-flank collisions. Finally, recent variations have stressed the non-contact intimidation function and have posited visual display as the sole adaptive value (Goodwin et al., 2004). The new material of *Dracorex hogwartsia* offers some insight into how neck strength was linked to ramming adaptations.

In all known pachycephalosaurids, the suspensorium and occiput are modified to reinforce the posterior dorsal skull surfaces in ways not seen in any other dinosaurs. The forward inclination of the quadrate and the fore-to-aft compression of the lower temporal fenestra brings the occipital condyle forward, relative to the primitive ornithischian condition. The stronger ventral orientation of the condyle brings the neck more directly under the frontal-parietal area on the roof. Hence, a forced delivered perpendicularly onto the skull table would be transmitted almost directly downward through the head-neck muscles and neck joints. As Gilmore (1924) noted long ago, the occiput is deepened and widened more than in any other dinosaur, relative to skull size. Therefore the neck muscles attaching to the occiput achieved a thicker cross section.

Maryañska and Osmólska (1974) suggested that the thick neck muscles were for holding up the heavy head. However, merely supporting a static cranial load is not a sufficient explanation. The elastic ligaments within and between neck muscles do most of the work in supporting the head in humans, cows and horses. Active muscle contraction is needed to move the head from its stable default posture. Plus, the heaviness of the pachycephalosaurid skull has no correlation with the size of the occiput. *Dracorex hogwartsia* has a skull length and occipital dimensions almost identical to those of some *Pachycephalosaurus* skulls (e.g., Triebold's specimen), so the strength of the neck muscles must have been very close, even though *Pachycephalosaurus* carried a tall, heavy bone dome while *Dracorex* was dome-less. Likewise, the dome-less *Homalocephale* has an occiput as expanded as that of the big-domed *Prenocephale.* Indeed, the deep, square occiput is a definitive pachycephalosaurid feature that remained constant despite the vigorous diversification of domes, parietal-squamosal shelves, spikes, horns and knobs. The neck material of *Dracorex* demonstrates what should have been expected – the neck bones were long, bulky, and carried large processes for muscles. More of a surprise are the anti-twisting features, the tongue-in-groove zygapophyseal joints and flattening of the posterior face of the atlas intercentrum. In well-preserved dinosaur atlases known to us (e.g., hypsilophodontids, camarasaurids, allosaurids, tyrannosaurids) where the atlas is not coossified with the axis, the posterior face of the atlas intercentrum is strongly convex and forms a kidney-bean shaped surface that wraps around the odontoid and fits against the concave collar of the axis intercentrum. This condition permits a measure of ball-in-socket action between the atlas and axis. However, in *Dracorex* the posterior face of the atlas is almost flat; the ball-in-socket character is suppressed. This flat joint surface would be far superior in transmitting shock from the occiput through the neck without slipping and dislocation. The accessory canal above the neural canal too may well be part of neck reinforcement. The shock-absorbing reinforcement extended backwards through the lumbar region with the strong development of the tongue-in-groove joints, as shown by *Stegoceras* and *Homalocephale.* We now take it as proven beyond a reasonable doubt that pachycephalosaurids received unusually strong forces on their frontal-parietal regions and that these forces were transmitted through the vertebral column.

The forces need not have been high-speed ramming. The flat skull table of *Dracorex* would enable two individuals to press their heads together and push. The raised peripheral ridges and many small knobs could have worked as osteological "velcro," holding the skull tables and preventing slipping. Similar head-to-head kinetics can be observed between male
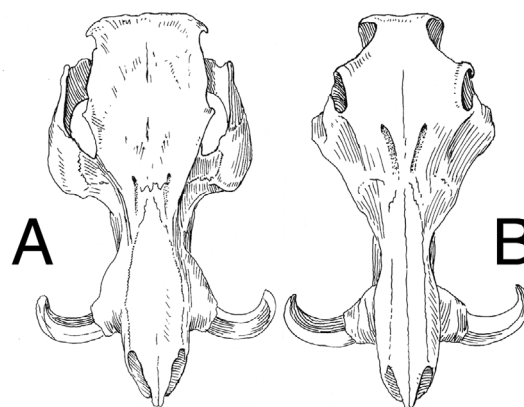

FIGURE 13. Functional similarity between the skulls of *Hylochoerus, Phacochoerus* and *Dracorex.* **A,** dorsal view of the skull of the Giant Forest Hog, *Hylochoerus meinertzhageni* (length 465 mm) and **B,** the warthog, *Phacochoerus aethipoics* (length 422 mm). Note the widening of the occiput in *Hylochoerus* and compare with Fig. 4. (Drawn from casts.)

and female polled cows, where flat zone between the horn cores are used as pushing platforms. The expansion of the pachycephalosaurid neck muscles is nearly entirely above the condyle and so would enlarge the power available for dorsi-flexing the head and neck. Head-to-head pushing would almost certainly involve massive upward thrusts aimed at forcing the opponent backwards. The strong backwardly directed spikes in several Lancian species could inflict fatal wounds on opponents if the head were dorsi-flexed when the horns were placed against the armpit or flank. Among modern day antelope, *Oryx* uses its backwardly directed horns to kill predators, and the horns in *Dracorex* and *Stygimoloch* should have functioned both as intra-specific weapons and anti-carnivore devices.

The modern day species that we have found to be closest to *Dracorex* in over all skull geometry and skull size is the Giant Forest Hog, *Hylochoerus meinertzhageni* (Fig. 13). Boar adults average about 450 mm total skull length, very close to that of *Dracorex* (d'Huart, 1993). The muzzle is long, low, tapered, and ends in a narrow premaxilla, as in the pachycephalosaurid. The frontal-parietal region of the skull table is wide and flat, with sharply defined lateral edges and a slight central concavity; again, strong similarities to the dome-headed dinosaur. Most unusual among suids, the Giant Forest Hog has an expanded occiput that is squared-off at its upper-outer corners. Compared to its close relative, the warthog, *Phacochoerus aethipoicus*, the Giant Forest Hog has an upper occipital rim that is 30% wider, for a given skull length (Fig. 13). Field observations provide a behavioral explanation for the wide skull table and expanded occiput. Among the closely related warthogs and Red River Hogs (*Potamochoerus porcus*), boars and sows perform frontal-pushing with the snout and forehead. Vigorous, quick dorsi-flexion at the head-neck joint contributes to the upward thrust of the skull. However, high-energy ramming is rare. In contrast, Giant Forest Hog boars engage in vigorous skull-to-skull shoving and ramming. Heads and necks are dorsi-flexed so powerfully that opponents are lifted off the ground. Plus – as aggression escalates, the boars begin to run at each other and ram their flat skull tables together. Some collisions are so violent they leave fractures in the bones (Estes, 1991; d'Huart, 1993).

Giant Forest Hogs have thin zones of sinuses between the dermal surface of the skull table and the endocranial wall, but the air spaces are far smaller than those in the base of the horns in horn-to-horn butters such as the Big Horn Sheep. The wide occiputs and flat skull tables of flat-headed pachycephalosaurids strongly suggests, in our opinion, that snout-shoving and forehead-ramming were employed.

Given the extraordinary adaptations to strengthen dorsi-flexion and reinforce the neck among pachycephalosaurids, we think it highly unlike

that the dome in big-domed species was solely a visual device. Solid bone domes would require a great investment in calcium phosphate, a material in short supply for most herbivores. Moose and elk today invest in heavy, solid-bone devices; their antlers certainly are visual display organs but also perform pushing and ramming functions. Giraffe domes are full of weight-saving air spaces and yet giraffes strike sideways blows with their domes. We favor the blow-to-the-flank scenario among dome-headed dinosaurs.

It is of exceptional interest that the largest pachycephalosaurid, *Pachycephalosaurus wyomingensis*, has only a blunt dome for offence and carried no sharp, dangerous spikes anywhere. We infer that sexual-social selection overpowered the selection for anti-predator spikes.

CONCLUSIONS

Dracorex hogwartsia n. gen., n. sp., is a new pachycephalosaurin that differs from its Lancian contemporaries *Pachycephalosaurus wyomingensis* and *Stygimoloch spinifer* in having a flat skull, four-spiked squamosals, enlarged supratemporal fenestrae and a skull covered entirely with dermal ossicles (knobs, rugosities, and spikes). The lack of a dome is considered not to be an ontogenetic feature, but rather it is phylogenetically derived, and may indicate a character reversal or be a paedomorphic feature. The loss of the dome and manifestation of the dermal ossifications may represent a shift in visual display structures or socio-behavorial strategies. Secondarily, these dermal knobs and spikes are interpreted to be defensive in nature and may also have served in agonistic behavior. The "overhang of the occiput" that has been used to unite the "Pachycephalosauria" and the Ceratopsia, is not homologous in these groups, therefore the "Marginocephalia" is not a natural group. The origin of the Pachycephalosauridae remains problematic.

REFERENCES

Bowler, P. J., 1989, Evolution: Berkeley, Univ. California Press, 432 p.

Brown, B. and Schlaikjer, E.M., 1943, A study of the troödont dinosaurs with the description of a new genus and four new species: Bulletin of the American Museum of Natural History, v. 82, p. 121-148.

Carrol, S. B., 2005, Endless Forms Most Beautiful: New York, W. W. Norton, 350 p.

Carpenter, K., 1997, Agnostic behavior in pachycephalosaurs (Ornithischia: Dinosauria): a new look at head-butting behavior: Contributions to Geology, University of Wyoming, v. 32, p.19-25.

Colbert, E. H., 1945, The dinosaur book: New York, McGraw-Hill Book Company, 156 p.

Colbert, E. H., 1955, Evolution of the vertebrates: New York, John Wiley, 479 p.

Coyne, J. A., 2005, Switching on Evolution: Nature, v. 435, p. 1029-1030.

D'Huart, J., 1993, The Forest Hog (*Hylochoerus meinertzhageni*); *in* Oliver, P., ed., Pigs Peccaries and Hippos. Gland (Switzerland), IUCN, p. 84-92.

Estes, R.D., 1991, The Behavior Guide to African Mammals: Berkeley, Univ. California Press, 610 p.

Galton, P. M., 1970, Pachycephalosaurids—dinosaurian battering rams: Discovery, Yale Peabody Museum, v. 6, p. 23-32.

Galton, P.M., 1971, A primitive dome-headed dinosaur (Ornithischia: Pachycephalosauridae) from the Lower Cretaceous of England and the function of the dome of pachycephalosaurids: Journal of Paleontology, v. 45, p. 40-47.

Galton, P.M. and Sues, H.-D., 1983, New data on pachycephalosaurid dinosaurs (Reptilia: Ornithischia) from North America: Canadian Journal of Earth Sciences, v. 20, p. 462-472.

Gilmore, C.W., 1931, A new species of troödont dinosaur from the Lance Formation of Wyoming: Proceedings of the United States National Museum, v. 79, p. 1-6.

Gilmore, C.W., 1936, Remarks on a skull cap of the genus *Troödon*. Proceedings of the United States National Museum, v. 79, p.1-4.

Goodwin, M.B., Buchholtz, E.A., and Johnson, R.E., 1998, Cranial anatomy and diagnosis of *Stygimoloch spinifer* (Ornithischia: Pachycephalosauria) with comments on cranial display structures in agonistic behavior: Journal of Vertebrate Paleontology, v. 18, p. 363-375.

Goodwin, M.B. and Horner, J.R., 2004, Cranial histology of pachycephalosaurs (Ornithischia: Marginocephalia) reveals transitory structures inconsistent with head-butting behavior: Paleobiology, v. 30, p. 253-267.

Hillson, S., 1996, Dental Anthropology: New York, Cambridge Univ. Press, 411 p.

Hou, L., 1977, A new primitive Pachycephalosauria from Anhui, China: Vertebrata PalAsiatica, v. 15, p. 198-202.

Maryañska, T. and Osmólska, H., 1974, Pachycephalosauria, a new suborder of ornithischian dinosaurs: Palaeontologia Polonica, v. 30, p. 45-102.

Nopsca, F., 1929, Dinosaurierreste aus Siebenburgen V: Geologica Hungarica Series Palaeobiologica, v. 4, p.1-76.

Osborn, H. F., 1912, The crania of *Tyrannosaurus* and *Allosaurus*: Memoirs of the American Museum Natural History, v. 1, 1-30.

Perle, A., Maryañska, T., and Osmólska, H., 1982, *Goyocephale lattimorei* gen. et sp. n., a new flat-headed pachycephalosaur (Ornithischia, Dinosauria) from the Upper Cretaceous of Mongolia: Acta Palaeontologia Polonica, v. 27, p.115-127.

Sereno, P., 1986, Phylogeny of the bird-hipped dinosaurs (order Ornithischia): National Geographic Research, v. 2, p. 234-256.

Sereno, P., 2000, The fossil record, systematics and evolution of pachycephalosaurs and ceratopsians from Asia; *in* Benton, M.J., Shiskin, M.A., Unwin, D.M., and Kurochkin, E.N., eds., The age of dinosaurs in Russia and Mongolia: Cambridge, Cambridge University Press, p. 480-516.

Sues, H.-D. and Galton, P.M., 1987, Anatomy and classification of the North American Pachycephalosauria (Dinosauria: Ornithischia). Palaeontographica Abt., v. 198, p. 1-40.

Sullivan, R.M., 2003, Revision of the dinosaur *Stegoceras* Lambe (Ornithischia, Pachycephalosauridae): Journal of Vertebrate Paleontology, v. 23, p.167-193.

Sullivan, R.M., 2005, Pachycephalosaurs from Dinosaur Provincial Park, Alberta: taxonomy, biostratigraphy, and paleobiogeographic implications; *in* Braman, D.R., Therrien, F., Koppelhus, E.B., and Taylor, W., eds., Dinosaur Park Symposium—Short Papers, Abstracts, and Program. Drumheller, Special Publication of the Royal Tyrrell Museum, p. 121-126.

Sullivan, R.M., 2006, A taxonomic review of the Pachycephalosauridae (Dinosauria: Ornithischia): New Mexico Museum of Natural History and Science Bulletin (this volume).

Triebold, M., 1997, The Sandy site: Small dinosaurs from the Hell Creek Formation of South Dakota; *in* Wolberg, D.L., Stump, E., and Rosenberg, G.D., eds., Dinofest International: Proceedings of a symposium sponsored by Arizona State University: Philadelphia, Academy of Natural Sciences, p. 245-248.

Van Valen, L., 1978, Why not to be a cladist: Evolutionary Theory, v. 11, 11-34.

Zhou, S., 1984. The Middle Jurassic dinosaurian fauna from Dashanpu, Zigong, Sichuan: Chonking, Sichuan Scientific and Technical Publications, v. 2, p. 1-51.

APPENDIX

Notes on distortion and reconstruction— All drawings, cranial and postcranial, are ortho-projections, made from CT-scans and proportional dividers; none are drawn from photographs. All the reconstructions are guided by the following observations: Right and left squamosals have separated slightly along the occipital rim and are restored in contact. The occiput is slightly crushed in the central area above the foramen magnum, so this region is more concave than in life, and the plane of the occiput is inclined more sharply relative to the long axis of the skull. The supraoccipital is cracked and buckled and its true outline is obscured, and the foramen magnum has lost height top to bottom. The left squamosal plate is crushed downward onto the paroccipital process, decreasing the original depth here. The right side is uncrushed and used it to restore the left. The exoccipitals have been displaced by crushing from the central basioccipital part of the condyle. The right quadrate is preserved in natural articulation with the squamosal socket and quadratojugal. Severe dorsal-ventral compression crushed the quadrate, shortening the shaft. The left quadrate had become loose after death and had been displaced to lie in the plane of bedding below the basicranium. Consequently, the left quadrate is preserved almost without distortion and is used to restore the left side of the skull to its original height. The quadratojugal and quadrate have matching large, sharply marked, lenticular scars for their mutual contact. Placing the undeformed quadrate in the squamosal socket demonstrates how much dorso-ventral deformation has occurred in the lateral temporal fenestra. The side view

has been restored so the contacts between the quadrate-quadratojugal match. On both sides the postorbital bar is crushed dorso-ventrally. The degree of crushing is shown by the imbrication of the postorbital and jugal. The facet on the descending process of the postorbital for the jugal has been displaced ventrally beyond the matching facet on the jugal for the postorbital. The height of the postorbital bar has been restored by correcting all the imbrications. Length restored from premaxilla to upper occipital rim, excluding spikes, 422 mm.

Measurements— **Figs. 1, 2, 3,** maximum skull length (along midline) = 412 mm; **Fig. 5**, height from outer condyle to head = 155 mm; height from inner condyle to head = 160 mm; and distal width = 37.5 mm. **Fig. 9**, maximum width of intercentrum (undistorted) = 55 mm; maximum length of intercentrum (undistorted) = 27 mm; and height from ventral midline of intercentrum to upper edge of postzygapophysis (undistorted) = 57 mm. **Fig. 10**, anterior width of centrum as preserved = 49 mm; anterior height of centrum as preserved = 44 mm; centrum length as preserved = 49 mm; and width across prezygapophyses as preserved (crushed) = 34 mm. **Fig. 11A-F**, anterior width of centrum as preserved = 52 mm; anterior height of centrum as preserved = 46 mm; total height as preserved = 90 mm; width across prezygapophyses as preserved = 55 mm; **G-H**, anterior width of centrum as preserved = 51 mm; anterior height of centrum as preserved = 50 mm; width across prezygapophyses as preserved = 48 mm; and length from postzygapophysis to prezygapophysis as preserved = 114 mm.