

DELTAHERPETON HIEMSTRAE, A NEW COLOSTEID TETRAPOD FROM THE MISSISSIPPIAN OF IOWA

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ABSTRACT—A new colosteid, *Deltaherpeton hiemstrae* gen. et sp. nov., is described from the Mississippian Upper Viséan site at Delta, Iowa. *Deltaherpeton* is represented by a skull roof and both jaws. The new taxon is unique among colosteids in having an internasal and single midline postparietal. An additional midline pair of cf. ‘interfrontonasals’ may be present. Characters previously used to define the colosteids are reviewed and a refined diagnosis for the family Colosteidae is presented. Synapomorphies which unite *Deltaherpeton*, *Colosteus*, *Greererpeton*, and *Pholidogaster* as Colosteidae are: premaxilla with fang pair; dentary with notch for receipt of premaxillary fang; mandible with single elongate exomeckelian fenestra; pre-narial infraorbital lateral line terminating at ventral margin of premaxilla just anterior to external naris; and post-narial infraorbital lateral line terminating at the ventral margin of the maxilla just posterior to the external naris. Our review of dermal bones in the colosteid snout concludes that no specimen is sufficiently free of distortions or breakage to indicate clearly whether or not the prefrontal borders the external naris, or that an anterior tectal is present. The morphology of *Deltaherpeton* and the revised data presented for colosteids do not clarify the relationship of colosteids to other early tetrapods.

INTRODUCTION

IN THIS paper, we update and revise the definition of the Colosteidae and describe a new member, *Deltaherpeton hiemstrae* gen. et sp. nov., from the Upper Viséan locality at Delta, Iowa (Bolt et al., 1988). This new taxon adds to the tetrapod diversity from that locality, which also includes *Whatcheeria deltae* Lombard and Bolt, 1995, and *Sigournea multidentata* Bolt and Lombard, 2006. Colosteids are morphologically coherent and found in low north latitude Carboniferous sediments of Euramerica. They presently are known to range from the Asbian (Upper Viséan) through the Upper Moscovian (Westphalian D), thus spanning the Mississippian-Pennsylvanian boundary. For such an early group they are remarkably well known thanks to descriptions of the numerous well-preserved specimens of *Greererpeton burkemorani* (e.g., Smithson, 1982; Godfrey, 1989a, 1989b; Schultze and Bolt, 1996; Bolt and Lombard, 2001).

The first two described colosteids were found in sediments associated with coal mining in the mid-nineteenth century. *Colosteus scutellatus* Newberry 1856 is represented by numerous specimens, all as impressions in an Upper Moscovian (Westphalian D) cannel coal from the famous Linton locality in southeastern Ohio. The most significant of these were figured and described by Hook (1983) as part of a thorough review of the complex taxonomic history of *Colosteus*. The holotype of *Pholidogaster pisciformis* Huxley 1862, the second described taxon, was unearthed from the Brigantian (uppermost Viséan) Gilmerton Ironstone in a coalfield near Edinburgh, UK. It was “...first acquired by Sir Philip Egerton and the Earl of Enniskillen, but as, on mature consideration, it appeared to them not to be a fish, it was handed over to the British Museum” (Huxley, 1862, p. 294). Described briefly by Huxley, it was restudied by Watson (1929) who considered it to be one of the “Embolomers” but did not further explore its relationships. The postcranium was prepared further and described by Romer (1964), who did not then recognize it as a colosteid. Subsequently, the entire specimen was re-prepared and described by Panchen (1975). In that study Panchen synonymized the somewhat older holotype of *Otocratia modesta* Watson 1929

from the Asbian (Upper Viséan) with *Pholidogaster*. *Pholidogaster* is thus represented only by the type specimen consisting of skull, jaws, and partial postcranium, and the unique “*Otocratia*” skull. The specimens of both are fragmentary, indifferently preserved, and difficult to prepare.

The most recent addition to the family, *Greererpeton burkemorani* Romer 1969, was first found in a shale layer in the wall of an Upper Viséan–Lower Serpukovian (?) limestone quarry in West Virginia during the 1950s (Romer, 1969, 1972), and additional specimens have been found in a limestone quarry of similar age in southern Illinois (Schultze and Bolt, 1996). *Greererpeton* is represented by several relatively well-preserved and well-prepared specimens that include both cranial and postcranial skeletal remains, those from West Virginia being somewhat flattened and those from Illinois relatively undistorted but less complete. The West Virginia specimens, in addition to Romer’s initial descriptions, were subsequently described and illustrated by Smithson (1982), Godfrey (1989a, 1989b), and Bolt and Lombard (2001). Many of the specimens from southern Illinois have been figured by Schultze and Bolt (1996), Bolt and Lombard (2001), and Clack (2003a).

Recently, a new but as yet undescribed colosteid has been identified in the late Chesterian Elvirian (Serpukhovian, Arnsbergian) Buffalo Wallow Formation of Kentucky (Storrs and Garcia, 2002; Garcia, 2003; Garcia, Storrs and Greb, 2006). Assorted fragments identified as colosteid but not assigned to one of the recognized genera have also been reported from various Carboniferous localities (Carroll et al., 1972; Milner, 1980; Smithson, 1982; Holmes et al., 1995; Bolt and Lombard, 2001). Fragments from the Viséan (Holkierian) Australian Middle Paddock locality first identified as colosteid (Thulborn et al., 1996) have since been referred to *Ossinodus*, a whatcheeriid (Warren and Turner, 2004; Warren, 2007; Ruta and Bolt, 2006).

MATERIAL AND METHODS

Preparation.—The only specimen recovered was found in a thin shale layer draped on the surface of a limestone slab. The

slab was reduced in the field using a rock saw. Preparation of the specimen was carried out with pin vise and needle and involved both complete dorsal exposure and also some undercutting to expose the full dentition of the right maxilla and some aspects of the occipital region.

Abbreviations used in paper.—AMNH, American Museum of Natural History; BMNH, British Museum of Natural History; FMNH, Field Museum of Natural History; KMNH, University of Kansas Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

Superclass TETRAPODA Goodrich, 1930

Family COLOSTEIDAE Cope, 1875

Diagnosis.—Premaxilla with a fang. Pre-narial segment of the infraorbital lateral line terminates posteriorly at ventral margin of premaxilla just anterior to the external naris. Post-narial segment of the infraorbital lateral line terminates anteriorly at the ventral margin of the maxilla just posterior to the external naris. Mandible with single elongate (length $> 4 \times$ width) exomeckelian fenestra, with smooth (not notched) border. Dentary with a notch on lateral surface for receipt of premaxillary fang.

Remarks.—As with many older taxa, Colosteidae has had a complex history since it was erected by Cope in 1875, and not surprisingly, with each revision the contained taxa and defining characteristics have varied. Sunk by Hay (1902), the family was resurrected by Romer (1930) to be subsequently considered by Panchen (1975), Smithson (1982), Hook (1983), and Godfrey (1989a). Smithson (1982) was the first to formally list defining characteristics and Hook (1983) to recognize *Colosteus scutellatus* Newberry 1856, *Pholidogaster pisciformis* Huxley 1862, and *Greererpeton burkemorani* Romer 1969 as the presently accepted contents of the family. We list in the Appendix the 43 features that are used with some variation by Smithson (1982, p. 31), Hook (1983, p. 6, Godfrey, 1989a, p. 82, and the present paper in considering a diagnosis for colosteids. Our diagnosis above uses only those five characters that with current knowledge appear to be synapomorphic for colosteids.

A single (apparently alternately-replacing) premaxillary fang is present in all named colosteids and no other taxa. The fang has a basal diameter and height $>200\%$ that of adjacent marginal teeth. The only other tetrapod of similar age with fangs in the premaxilla, the poorly-known Linton genus *Erpetosaurus*, was indeed at one time placed in the colosteids (Romer, 1930) but is now informally suggested as a trimerorhachoid temnospondyl (Hook, 1983, p. 31; Hook and Baird, 1986). *Erpetosaurus* differs from colosteids in several derived characters, including the presence of two fangs on the premaxilla (Hook, 1983). In *Greererpeton* and *Colosteus*, the premaxillary fang has been described as seated on a flange of the premaxilla that is directed medially between the anterior palatal fenestra and the internal choana (Smithson, 1982; Hook, 1983). The “flange” appears to us to be better described as a local swelling of the premaxilla to seat the large base of the fang and replacement pit.

For colosteids the pattern of the infraorbital lateral line at the external naris has been clearly illustrated for *Colosteus* (Romer, 1930; Hook, 1983) and *Greererpeton* (Smithson, 1982; Godfrey, 1989a, 1989b) and noted in the text of the first three authors, as well. None, however, indicated this morphology as unusual or unique among tetrapods. The lateral line is discussed further in the Description and Discussion. *Deltaherpeton* has the same lateral-line morphology as *Colosteus* and *Greererpeton*. The condition of *Pholidogaster* is unknown.

The morphology of the exomeckelian fenestra is unknown in *Pholidogaster*. There is some suggestive, though not definitive, evidence of an elongate exomeckelian fenestra in *Deltaherpeton* (Bolt and Lombard, 2001). Nevertheless, we list this condition as a possible synapomorphy since no other early tetrapods are known to have it, and it occurs in all colosteids in which the appropriate area can be described. This character state may be part of a transformation series between the single, exomeckelian slit that is open posteriorly (and found in some very early primitive tetrapods) and the small single or multiple exomeckelian fenestra(e) that occur in more derived early tetrapods such as anthracosaurs and temnospondyls (Bolt and Lombard, 2001).

The dentary notch, found in all described colosteids and no other Paleozoic taxa, is illustrated for AMNH 6927, identified as *Erpetosaurus* by Romer (1930, fig. 15) and in his reconstruction of the genus (fig. 16). Subsequent work by others does not mention this specimen and we have not seen it.

Readers who would expect to find features of the prefrontal bone, maxillary vs. dentary tooth size, etc. as part of the diagnosis will discover them with comments in the Appendix.

DELTAHERPETON, n. gen.

Type species.—*Deltaherpeton hiemstrae*, n. gen. and sp.

Etymology.—After Delta, Iowa, the town nearest to the quarry locality. *Herpeton* (Greek) —crawling animal or reptile, now used for both amphibians and reptiles.

Diagnosis.—As for type and only species.

DELTAHERPETON HIEMSTRAE, n. gen. and sp.

(Bolt, 1990, fig. 7; Bolt and Lombard, 2001, fig. 7; figs. 1–3)

Holotype.—FMNH PR 1637, skull in association with mandibles preserved in shale on the surface of a limestone slab. Skull prepared in dorsal view, left mandible in medial view and right mandible in lateral.

Horizon and Locality.—Fill within a collapse structure formed in the Waugh and Verdi Members of the Iowa “St. Louis” Limestone, Mississippian, Lower Chesterian; correlative with the Lower Carboniferous upper Viséan. Quarry on land owned at the time by Mr. Jasper Hiemstra, SW1/4, SW1/4, section 15, T75N, R13W, Keokuk County, Iowa, USA. For detailed descriptions refer to Bolt et al. 1988 and Witzke et al., 1990. For the most recent analysis of the age of the locality see Snyder, 2006.

Etymology.—After the late Mr. Jasper Hiemstra, for his interest and generosity, who owned the land that includes the Delta quarry at the time *Deltaherpeton hiemstrae* was discovered.

Diagnosis.—Colosteid tetrapod with the following additional character states: unpaired postparietal; midline unpaired internasal. A paired interfrontonasal is possibly present.

Remarks.—A midline unpaired postparietal is a derived state for tetrapods. Among Devonian and Mississippian tetrapods it occurs only in *Ichthyostega* (Jarvik, 1996). The state also occurs in some Permian diadectomorphs and the Pennsylvanian microsaurs *Odonterpeton* (Carroll and Gaskill, 1978). Presence of an internasal (paired midline bones or an unpaired midline bone bounded by both the premaxillae and nasals) appears to be a primitive state for tetrapods. Among Devonian and Early Carboniferous tetrapods internasals are present in *Acanthostega* (Clack, 1994), *Ichthyostega* (Jarvik, 1996), and baphetids (Beaumont, 1977). A (fused) single midline internasal appears to be derived and is otherwise found only in *Ichthyostega* (Jarvik, 1996).

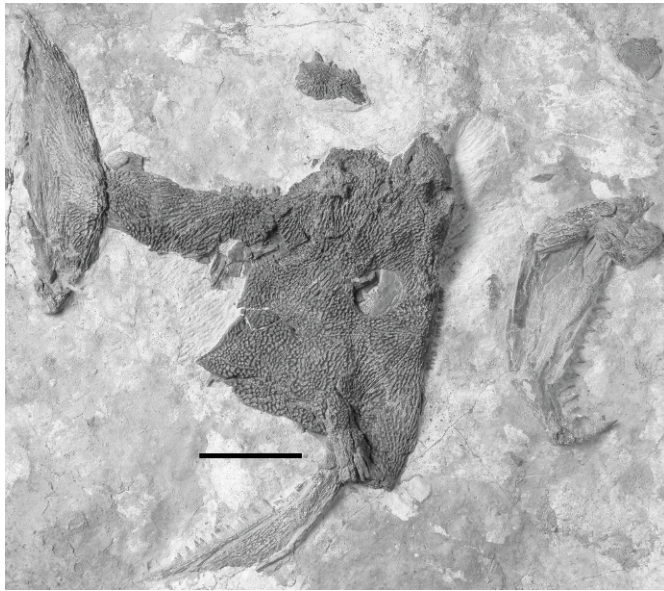


FIGURE 1—FM PR 1637, type specimen of *Deltaherpeton hiemstrae*, gen. et sp. nov. skull and jaws as preserved on limestone surface. Scale bar equals 5 cm.

Presence of an interfrontonasal (paired or unpaired bone(s) bounded by both the frontals and nasals) is of uncertain polarity for tetrapods and does not seem to characterize any other colosteid. Though illustrated (as “internasal”) for *Greererpeton* by Romer, 1969, subsequent workers have not supported this interpretation (Smithson, 1982; Godfrey, 1989b). This topic is covered in the section on roofing bones of the snout in the Discussion. It is also described in eryopoids (Sawin, 1941; Gubin, 1983), the capitosaurid *Kestrosaurus* (as “interfrontal” Haughton, 1925), and some microsaurids (as “interfrontal;” Carroll and Gaskill, 1978).

DESCRIPTION

The following description is organized in two sections. The first is a general description of the specimen. The second is a detailed description of individual dermal bones, considered in alphabetical order. The descriptions are supported by Figures 1–3. The mandible was described and illustrated by Bolt and Lombard, 2001.

General.—The skull as preserved is dorsoventrally compressed and has been prepared in dorsal view (Fig. 1). Most of the elements of the dorsal skull surface from both sides are present, though the left cheek region has been partly separated and rotated clockwise around its anterior end, and the left premaxilla together with the single internasal are separated from the rest of the skull by about 2.5 cm. The skull exhibits three major subparallel transverse complex fractures (Fig. 2). The posteriormost passes through the postparietal and its suture with the tabular on the left, and between the supratemporal and its suture with the tabular on the right. The middle fracture passes through the postorbitals and parietals including the parietal foramen, and the anterior fracture runs between the orbits through the prefrontal (?) and frontals. In addition, a major subparasagittal fracture is present on the right running from the prefrontal (?) through the lacrimal and into the jugal. Smaller fractures are present between the orbits and in the region of the supratemporals and squamosals. Fragments of the palate and perhaps braincase are visible through the right orbit but are not identifiable in detail. No part of the occiput is visible. Both jaws are

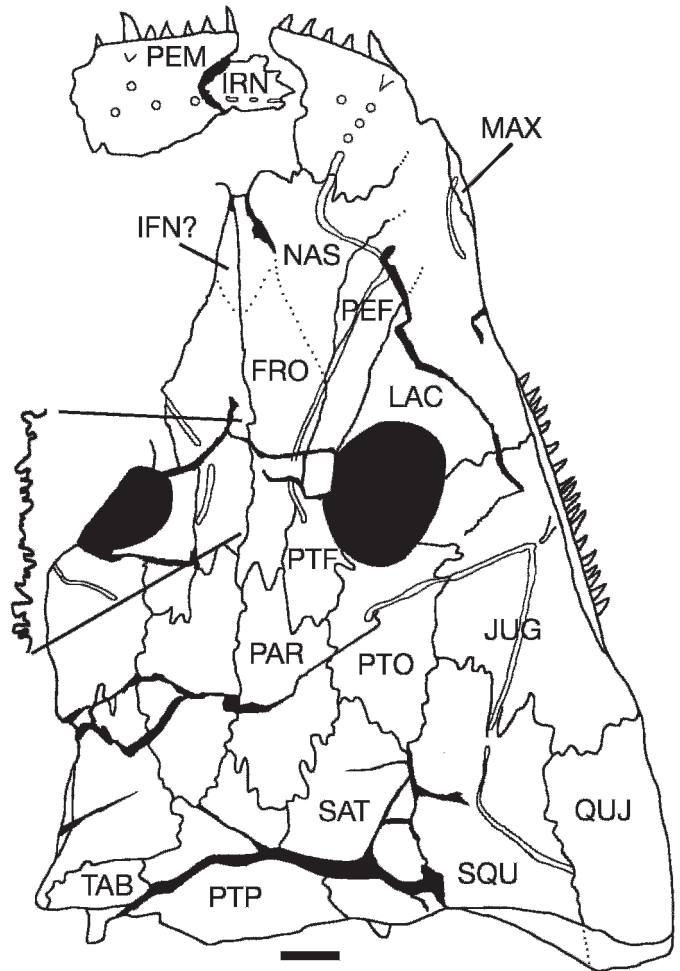


FIGURE 2—Interpretation of the suture pattern in FM PR 1637, *Deltaherpeton hiemstrae*, gen. et sp. nov. The fragment containing the left premaxilla and the internasal has been moved into closer association with the skull than found in specimen and the left cheek fragment has been omitted. Major breaks in the specimen are indicated. A highly folded stretch of the interfrontal suture is drawn to a higher magnification on the left. Sutures that are readily detected are solid lines, uncertain sutures are dotted. FRO, frontal; IFN?, interfrontonasal; IRN, internasal; JUG, jugal; LAC, lacrimal; MAX, maxilla; NAS, nasal; PAR, parietal; PEF, prefrontal; PEM, premaxilla; PTF, postfrontal; PTO, postorbital; PTP, postparietal; QUJ, quadratojugal; SAT, supratemporal; SQU, squamosal; TAB, tabular. Scale bar equals 1 cm.

preserved and are separated from the skull (Fig. 1). The *Deltaherpeton* jaw was fully described and illustrated by Bolt and Lombard (2001). Briefly, the right is in two pieces and is exposed in lateral view; the left is crumpled lengthwise and exposed in medial view. The anterior tip of the right jaw is out of view under the right quadrate region of the skull. The posterior portion of the left jaw is folded on itself lingually and crumpled. The anterior part is sharply broken from the rest and rotated dorsally.

Although the skull as preserved is somewhat distorted, its shape in dorsal view appears not to differ significantly from that of other colosteids. There are no squamosal embayments and the quadrates lie slightly behind the posterior border of the skull table. There is a beveled joint between the supratemporal and squamosal, visible because the left cheek has separated from the skull at that joint. A short “horn” with blunt termination projects from the occipital surface of the tabular. A modest pineal opening occurs in the posterior 1/3 of

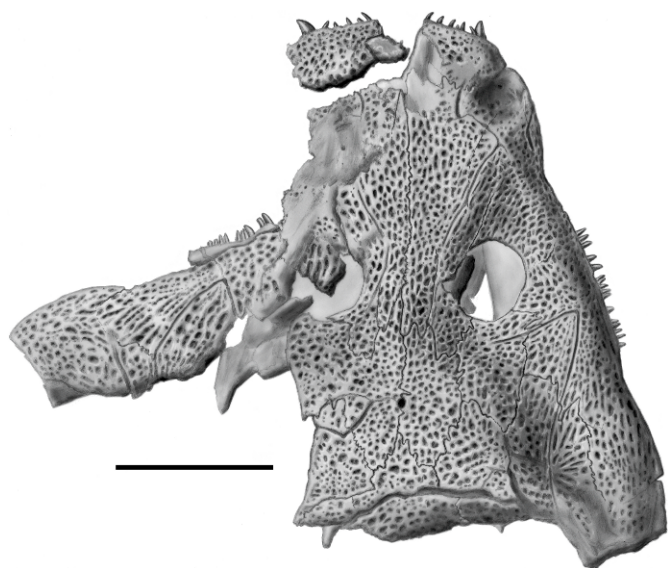


FIGURE 3—Interpretation of the skull dorsal surface of FM PR 1637, *Deltaherpeton hiemstrae* gen. et sp. nov. The fragment containing the left premaxilla and the internasal has been moved into closer association with the skull then found in specimen. Most major breaks are not shown though significant undulated distortions are indicated. No attempt has been made to estimate skull shape in life. The jaws are not shown. Sutures readily detected on the specimen are solid lines. Scale bar equals 5 cm.

the interparietal joint. The subcircular orbits, as in other colosteids save *Colosteus*, have their centers at about 47% of the skull length as measured on the midline from the premaxillae to the postparietals. The orbits are definitely bordered by the lacrimals, jugals, postorbitals, and postfrontals. They may be bordered by the prefrontals, as well, depending on the location of the postfrontal–prefrontal suture. The frontal–parietal suture is in roughly the same transverse plane as the posterior borders of the orbits. In the snout, the external naris is low on the side of the skull and the maxilla and premaxilla meet below the opening with no sign of beveling or interdigitation. Rather, the apposed surfaces have the appearance of finished periosteal bone. The maxilla and premaxilla form the smooth, finished edges of the narial opening from anterodorsal to posteroventral. The bone(s) bordering the remaining dorsal and posterior margins are uncertain but may include one or more of the nasal, prefrontal, or septomaxilla (see Discussion section on roofing bones of the snout).

Sutural outlines of individual bones are readily interpreted everywhere but on the snout between the orbit and the external naris (Figs. 2, 3). Joints between bones may have large-scale interdigitations such as between the parietal and supratemporal. Interdigitations in some areas may be on a very fine scale, readily seen with low power on a dissecting microscope. Examples occur at the medial half of the suture between the supratemporal and the tabular and the interfrontal suture between the orbits as illustrated in Figure 2.

Posterior to the orbits, the skull roof comprises paired parietals and an unpaired postparietal along the midline, bounded laterally by a temporal series of postfrontals, supratemporals, and tabulars. Intertemporals are absent. The supratemporal completely separates the tabular from the squamosal and in so doing, reaches the posterior border of the skull roof. The cheeks are formed by postorbital, squamosal, jugal, and quadratojugal. There is no preopercu-

lar. The snout is composed of paired prefrontals, lacrimals, nasals, premaxillae and maxillae and a midline internasal. There may have been an interfrontonasal. Neither an anterior tectal nor a septomaxilla are discernible though their presence cannot be ruled out and the relationships of nasal, prefrontal, and lacrimal to each other and to the external naris are not clear (see Discussion section on roofing bones of the snout).

The mandible preserves evidence of all bones present in primitive tetrapods and, for those parts preserved, does not differ in any way from that described for *Greerpeton* (for details, see Bolt and Lombard, 2001).

Premaxillary and maxillary marginal teeth are less than 50% the length and basal diameter of marginal dentary teeth. Each premaxilla bears 11 teeth + tooth spaces as well as a fang (plus fang replacement space) that in life fit into the notch in the dentary. The only maxilla preserved bears 44 teeth plus tooth spaces. In contrast, the dentary has about 28–29 teeth plus tooth spaces as well as a large fang and replacement space at its anterior extreme. The skull is pushed up in three paired, localized areas near its lateral margins—the first anterior to the external naris, the second, and greater, between the naris and orbit, and the last at the anterolateral margin of the orbit. We interpret these as providing indirect evidence of fangs on the vomer, palatine, and ectopterygoid respectively.

The surface sculpture is very well preserved over most of the skull roof and mandibles, with a pronounced “pit and ridge” texture (Figs. 1, 3). Individual pits contain one or two small openings which appear to extend deep into the bone. Posterior to the orbits, each individual dermal bone displays a unique pattern of ridges that assist in identifying its boundaries.

The skull and jaws preserve evidence of a well-developed lateral line system (Figs. 1–3). Where it is openly exposed, the lateral line may be characterized as deeply incised into the bone, the sulcus being somewhat deeper than broad. In other places, such as in the premaxilla and internasal, the lateral line is completely enclosed in bone and opens to the surface periodically via a series of foramina. Finally, in a few places, it exhibits an intermediate condition in which the incised canal is spanned by occasional bony bridges, e.g., between the orbits and at the junction of the infraorbital and jugal sulci within the jugal.

The unusual pattern of the infraorbital lateral line at the naris in *Deltaherpeton* and other colosteids requires some terminology for clarity. There is no evidence that the infraorbital line is continuous through or beneath the naris as it appears to be in all other non-colosteid early tetrapods that preserve evidence of a lateral line. We term the two discontinuous segments as pre-narial and post-narial. From its opening at the ventral margin of the maxilla the post-narial segment extends posterodorsally arching into the lacrimal where it then is placed close to or within the lacrimal–maxilla suture and further posteriorly the jugal–maxilla suture. In the jugal, the line turns dorsally to pass posterior to the orbit and (apparently) terminates in the postorbital. While in the jugal it is joined by/gives rise to the jugal canal which curves high on the cheek in the squamosal and then turns ventrally towards the jaw joint but cannot be traced into the quadratojugal. From its beginning in the ventral margin of the premaxilla anterior to the external naris and close to the base of the premaxillary fang the pre-narial segment of the infraorbital canal runs dorsally then anteriorly to the junction of the ethmoid commissure and supraorbital lines. The supraorbital line extends posteriorly from the junction of the ethmoid commissure and pre-narial segment of the infraorbital and after making an “S” curve through the nasal and prefrontal bones,

passes along the lateral part of the frontal to then curve laterally and end in the prefrontals or anterior part of postfrontals between the orbits (sutures are unclear). There is no evidence of a temporal sulcus as described in *Colosteus* (Hook, 1983). The ethmoid commissure connecting the junction of the supraorbital sulci with the pre-narial infraorbital segment passes through the internasal bone and is represented by a series of openings along its course.

Anterior tectal.—We have been unable to determine whether this bone is present or absent. The region that it might have occupied is distorted and broken on the right and missing on the left. Some aspects of the morphology of the snout remain uncertain in *Deltaherpeton*, as in other colosteids—see Discussion section on roofing bones of the snout.

Frontal.—This is the longest bone in the skull midline and, depending on how it is interpreted, may be 1½ to 2 times as long as any other midline roofing bone. As in other colosteids the frontals are quite long relative to the length of the nasals. The interfrontal suture is highly interdigitated on a small scale between the orbits but appears relatively straight posterior to that region (Fig. 2). Anteriorly, crushing and some displacement make it virtually impossible to trace the midline suture. The sutures with the postfrontal and possibly the prefrontal are relatively straight. Whereas the sutures with the parietal and postfrontal are evident, the path of the joints with the nasal, prefrontal, and the possible interfrontonasal is less certain. If the possible interfrontonasals are actually the anterior continuation of the frontals, then the frontals terminate anteriorly at the internasal or very near to it. The midline suture between the nasals would then be absent or short. The ornament of the frontal does not appear to differ from the general appearance common to other roofing bones. The supraorbital lateral line appears in two segments, one that continues into the prefrontal anteriorly and one that continues posteriorly into the postfrontal.

Internasal.—The unpaired, roughly oval internasal is the smallest bone in the skull roof. It clearly sutures to the premaxillae anteriorly and laterally (Figs. 2, 3). Posteriorly, it is joined to the nasal and if the nasal is indeed excluded from the midline, to either the possible interfrontonasal or to the frontal if the interfrontonasal does not actually exist. Internasals are not widespread in early tetrapods, having been observed only in *Acanthostega* (Clack, 2003b), *Ichthyostega*, (Jarvik, 1996), and baphetids (Beaumont, 1977). There is also some evidence of an internasal in *Ventastega* (Ahlberg et al, 1994). In all these taxa, the internasals are bounded by the premaxillae and nasals only. The unpaired nature of this element in *Deltaherpeton* is shared only with *Ichthyostega*. Compared to all other skull roofing bones, the internasal lacks pronounced ornamentation. The path of the ethmoid commissure of the lateral line system in *Deltaherpeton* is marked by a transverse line of foramina which can be traced laterally into the premaxillae.

Interfrontonasal.—An internasal is generally defined as bounded by the premaxillae and nasals. An interfrontonasal is defined here as bounded by the frontals and nasals. In *Deltaherpeton*, an area of bone in that position is present on the left side of the midline and a broken area of bone, of approximately the same shape and mostly devoid of superficial ornamentation, is present on the right (Fig. 2). If these areas do not represent interfrontonasals, then they are anterior continuations of the frontals. As interfrontonasals they would be rare indeed, shared only with some eryopoids (Sawin, 1941, where it is called “internasofrontal”; Gubin, 1983), and some “microsaurs” (Anderson, 2007) as “interfrontal” (Carroll and

Gaskill, 1978). An unpaired midline bone with the sutural relationships of both an internasal and an interfrontonasal (sutures with the premaxillae, nasals, and frontals) was illustrated in the species description of the colosteid *Greerherpeton* by Romer, 1969 as an “internasal” (Fig. 5.1, 5.2). Smithson (1982, p. 41), said of this: “Close examination of a cast of the dorsal surface of the holotype revealed that the suture which Romer identified between the left nasal and the internasal is a crack along the anteroposterior axis of the left nasal.” What Romer actually said was, “However, the sculpture pattern of this area shows no relation to that adjacent to it on either nasal, and I think it likely that what we have here is an internasal, a median unpaired element such as is found occasionally in other labyrinthodonts.” In other words, Romer based the possible existence of this bone on sculpture pattern rather than sutures, which lessens the strength of Smithson’s observation. On the *Deltaherpeton* specimen, the midline and lateral sutures of the left element are without interdigitation and very clear. Identification as an interfrontonasal rather than as a continuation of the frontal hinges on identification of a posterior suture separating the element from the frontal. Presence of such a suture is reasonably interpreted but not certain. The surface ornament on the left element is not remarkably different from that on surrounding bones in the *Deltaherpeton* specimen and so does not confirm the sutural evidence. There is no lateral line in this region of the skull.

Intertemporal.—No intertemporal is present. Among colosteids this compares to *Colosteus* and *Pholidogaster* and most *Greerherpeton* specimens (Hook, 1983; Panchen, 1975; Smithson, 1982). A minute intertemporal is present on one side of one specimen of *Greerherpeton* (Smithson, 1982).

Jugal.—Both jugals are preserved though that on the left, along with the quadratojugal, has been rotated away from the rest of the skull. The jugal has the largest surface area in the skull roof and its sutures with most of the surrounding bones are very clear. The suture with the squamosal is raggedly interdigitated and those with the lacrimal, postorbital and quadratojugal less so. The suture with the maxilla is relatively straight and without interdigitations and the suture with the lacrimal is inclined somewhat posterodorsal to anteroventral. The jugal forms the posteroventral orbital margin and about 18% of the total margin. Though the maxilla is not optimally exposed, it appears that it does not reach posteriorly to the quadratojugal. Thus the jugal forms a small portion of the ventral skull margin. The surface ornament has a “starburst” pattern with its center at the junction of the lateral line canals. This is comparable to that illustrated for *Ichthyostega* by Jarvik (1996), for *Greerherpeton* by Romer (1969) and Smithson (1982), as well as for many temnospondyls. The presence of this pattern reinforces the boundaries determined by tracing the sutures. The infraorbital lateral line enters the jugal from the lacrimal and turns dorsally to enter the postorbital. Shortly after turning dorsally, the infraorbital canal gives off the jugal canal that runs over the cheek to enter the squamosal. Canals are open almost everywhere in the jugal but are crossed by bony bridges in the area where the jugal canal joins the infraorbital canal.

Lacrimal.—Only the right lacrimal is preserved. The lacrimal is a roughly triangular bone, with the exact boundaries of its anterior angle uncertain. Its other two angles lie at the anteromedial edge of the orbital opening and at the sutural junction with the maxilla and jugal. The lacrimal has a clear sutural border with the maxilla and with the jugal. It makes the largest contribution to the orbit (38%) of any

bone, forming its entire anterior margin. Medially a clear, straight suture marks the separation of the lacrimal from either the postfrontal and prefrontal or the prefrontal alone. This ambiguity arises from the uncertain placement of the postfrontal–prefrontal suture which could be either at the medial border of the orbit or somewhere anterior to the orbit. Either placement would be consistent with other colosteids (*Greererpeton* in the former, *Colosteus* in the latter), see Discussion section on roofing bones of the snout. Our placement of the readily interpretable sutures is reinforced by the surface ornament, which radiates from near the lacrimal's lateral edge about midway along its length. Unfortunately, deformation and disruption of the skull posterior to the external naris (likely caused by a fang on the palatine) precludes tracing either the terminal sutural borders of the lacrimal or its ornamentation pattern. Thus, whether the lacrimal reaches the external naris or has sutural contact with the nasal cannot be determined with certainty. The orientation of the suture with the postfrontal/prefrontal, when projected anteriorly, does suggest that the lacrimal does not reach the external naris. Hook (1983) reconstructed the anterior-to-posterior course of the post-narial infraorbital lateral line in *Colosteus* as arching from the maxilla into the posteroventral corner of the prefrontal and then into the lacrimal. Smithson (1982) (Fig. 5.5) reconstructed its course in *Greererpeton* as passing from the maxilla directly into the lacrimal–maxilla suture. In the *Deltaherpeton* specimen, the canal as it crosses the border of the maxilla is discernible, but the exact bone into which it immediately passes is not. More certainly, in its more posterior segment it lies in the ventral margin of the lacrimal or in the joint between the lacrimal and maxilla.

Maxilla.—The right maxilla is preserved in its entirety, and the left as a small portion adjacent to the jugal only. Careful excavation of the anterior portion allowed examination of the right maxilla along its entire length. The anterior half of that bone is in its natural vertical position but the posterior half is rotated 90° around its long axis so that the marginal dentition is splayed out laterally. Posteriorly it tapers to become very slender and ends, after the last tooth, in a delicate process which terminates just before the suture between the jugal and quadratojugal. The anterior half of the maxilla has pit and ridge ornament but the surface of the posterior half (containing about half the dentition) is unornamented. The maxilla bears approximately 44 teeth plus tooth spaces; the teeth are similar in size to the premaxillary teeth and both are about half the size of the teeth on the dentary. At its anterior end, the maxilla ends as finished periosteal bone in approximation to a similar surface on the premaxilla and forms the smooth posteroventral quadrant of the external naris. Just posterior to the external naris, the dorsal bounding suture of the maxilla is clear, though the identity of the bone on the other side of the suture is uncertain and might be either the lacrimal, prefrontal, or anterior tectal. Further posteriorly, the maxilla is in contact with the lacrimal and jugal. The post-narial segment of the infraorbital canal begins anteriorly at an opening on the ventral margin of the maxilla just posterior to the external naris. This pattern is present also in *Colosteus* and *Greererpeton*, uniquely among tetrapods (Figs. 4.1, 4.3–4.5, 5.5). After crossing the lacrimal(?) / anterior tectal(?) / prefrontal(?)–maxilla suture the canal runs posteriorly in the lacrimal.

Nasal.—The region of the nasal is disrupted on both sides such that neither sutures nor ornament pattern allow confident reconstruction of its complete shape. Rostrally, a suture with the premaxilla is partially traceable on the right at

the point where the supraorbital lateral line canal crosses, and on the left side the premaxilla appears to have separated from the nasal at their common suture. The suture between the nasal and the frontal can be determined with minimal confidence only (Fig. 2). In the midline, the possibility of interfrontonasals, or alternatively extended frontals, would reduce the extent of nasal to nasal contact or might preclude it altogether though this seems unlikely. Laterally, the suture with the prefrontal posteriorly and the same bone or others anteriorly cannot be determined with confidence. Finally, it cannot be determined whether or not the nasal attained the boundary of the external naris.

Parietal.—The boundaries of the parietals are well defined on both sides (Figs. 2, 3). Most of the bounding sutures display modest interdigitation similar in scale to that between the jugal and lacrimal. A small parietal opening is present posteriorly at about 75% of the anterior to posterior length of the interparietal suture. There is no intertemporal. No lateral line canals are evident.

Postfrontal.—The sutures with the postorbital, parietal and frontal are readily determined as well as its contribution to the border of the orbit. The placement of the suture with the prefrontal, however, is not certain because of disruption in the region of the orbit and in the preorbital region (Fig. 2). If *Deltaherpeton* is comparable to *Greererpeton*, *Pholidogaster*, and many other early tetrapods then this suture would run from the orbital border medially to the frontal. If, however, it is similar to *Colosteus* then the suture is anterior to the orbit and runs medially from the lacrimal to the frontal or nasal; see section on roofing bones of the snout in Discussion. The pattern of dermal ornament does not provide a useful indicator of the territory of the bone in this case. The supraorbital lateral line canal crosses the suture with the frontal to pass into the prefrontal for a short distance. This is directly comparable to the pattern seen in other colosteids.

Postorbital.—The sutural boundaries of both postorbitals can be reliably determined and the pattern of ornamentation is consistent with the sutural evidence. All sutures are interdigitated though those with the squamosal and with the jugal posterior to the infraorbital canal are less strongly so. The postorbital forms about 22% of the orbital border. The infraorbital canal crosses the jugal–postorbital suture and appears to come to a blind end within the postorbital as it does in other colosteids. There is no indication of branching as described in *Colosteus* by Hook (1983) (Fig. 4.2).

Postparietal.—The postparietal is unpaired, presumably representing fused right and left elements. Among early tetrapods this state is shared only with *Ichthyostega* (Jarvik, 1996). The bone is roughly triangular and has a transverse break approximately through the middle of its anteroposterior extent. Clear sutures indicate that the bone articulates with the parietals, supratemporals, and tabulars. The postparietal forms most of the posterior edge of the skull roof. There is no indication of lateral line canals.

Prefrontal.—Breaks and distortions prevent a detailed determination of the prefrontal in *Deltaherpeton* (Figs. 2, 3). The postfrontal–prefrontal suture could be either at the medial border of the orbit (cracked and disrupted on both sides) or further anteriorly on the snout and running from the lacrimal laterally to either the nasal or frontal medially but other possibilities cannot be excluded. The former placement would be as described in *Greererpeton* (Smithson, 1982), the latter as described in *Colosteus* (Hook, 1983). The prefrontal has been interpreted in both *Greererpeton* (Smithson, 1982) and *Colosteus* (Hook, 1983) as extending anteriorly to border the

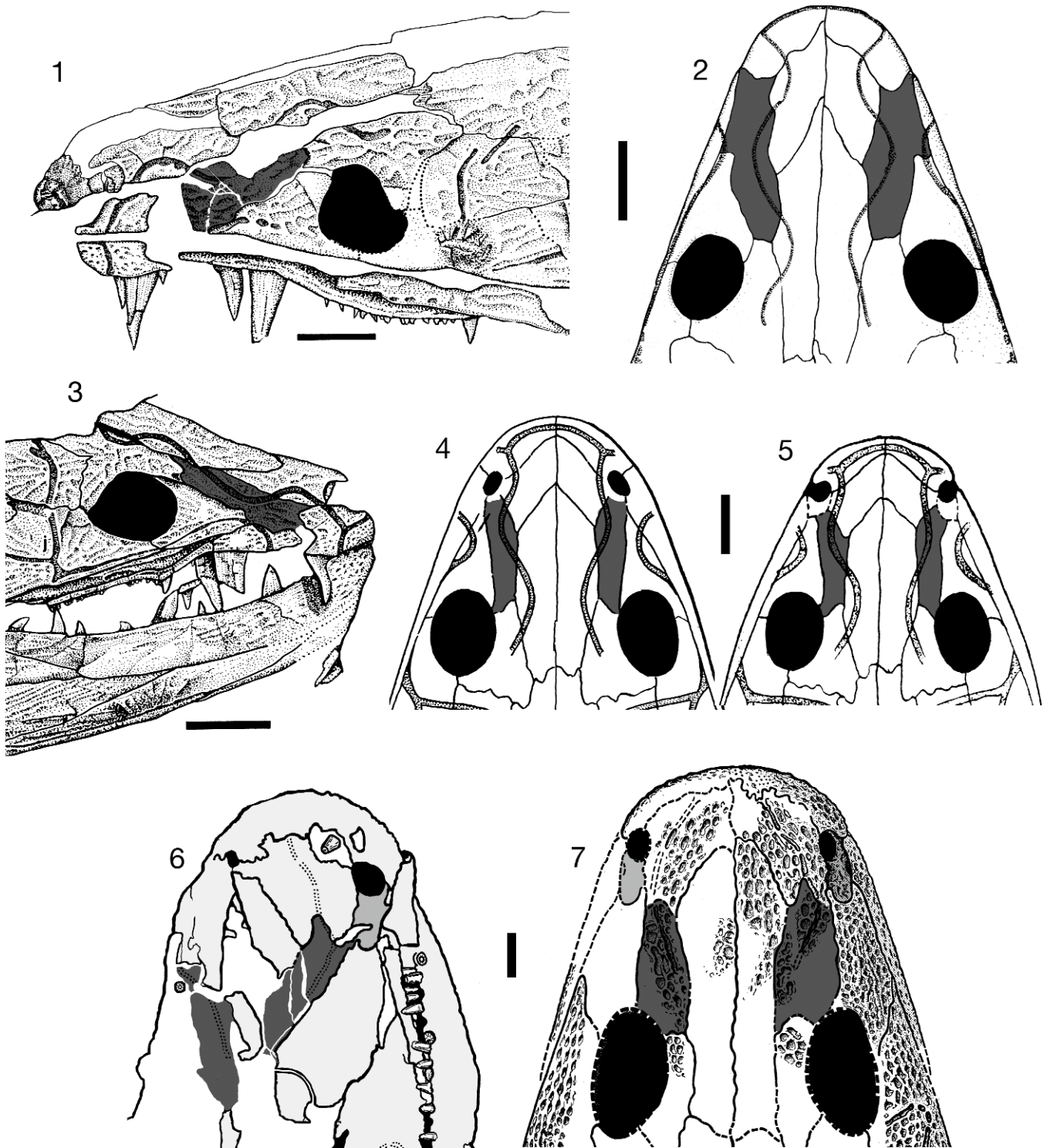


FIGURE 4—Snout region in *Colosteus* and *Pholidogaster*. All drawings are modified from originals by shading the prefrontal (dark shade) and in 6 and 7 the anterior tectal/septomaxilla (light shade posterior to external naris), cropping, and (where necessary for clarity) removing osteological detail and altering shading. 1–5, *Colosteus*: 1, BMNH R.2547, Hook, 1983, note the prefrontal does not border the orbit and is in two portions though the scale of the drawing does not allow this to be visualized; 2, Hook, 1983, note that the prefrontal reaches the external naris excluding the nasal from doing so and does not border the orbit; 3, AMNH 6916 (holotype), Hook, 1983, note the prefrontal appears to be in one piece; 4, Romer, 1930, note the nasal as attaining the border of the external naris and the prefrontal as “nearly” attaining the border, and that the prefrontal borders the orbit; 5, Romer, 1947, note that a “septomaxilla” is uncertainly indicated by dotted lines excluding the prefrontal, nasal, and lacrimal from the border of the external naris, and that the prefrontal borders the orbit; 6–7, *Pholidogaster*: 6, BMNH R30534, Panchen, 1975, note the “septomaxilla”; 7, Panchen, 1975, note the “septomaxilla” (light shading posterior to external naris) excludes the lacrimal and prefrontal from the naris but that the nasal attains the narial border.

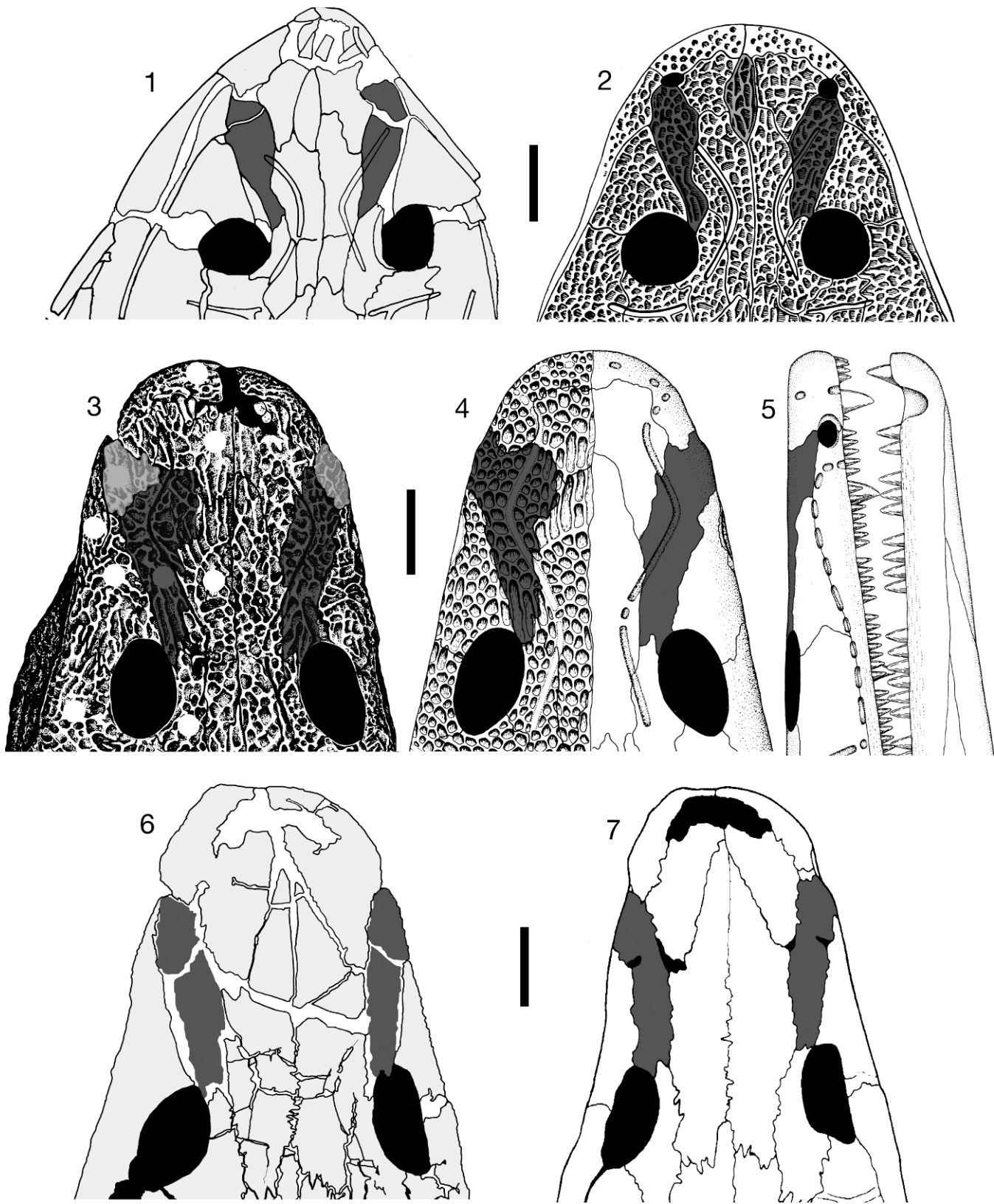


FIGURE 5—Snout region in *Greererpeton*. All drawings are modified from originals by shading the prefrontal (dark shade) and in 6 and 7 the anterior tectal/septomaxilla (light shade posterior to external naris), cropping, and (where necessary for clarity) removing osteological detail and altering shading. 1, CMNH 10931, Romer, 1969, note that the prefrontal is divided into two portions and an “internasal” (interfrontonasal) is present; 2, Romer, 1969, note the prefrontal is not in two portions and the nasal attains border of external naris; 3, CMNH 11068, Carroll, 1980, note the prefrontal and “anterior tectal” are indicated as separate bones; 4, Smithson, 1982, note the prefrontal has incorporated what was previously indicated as “anterior tectal” and the nasal is excluded from the external naris; 5, Smithson, 1982, note the path of the post narial infraorbital lateral line and prefrontal bordering the external naris excluding lacrimal and nasal from doing so; 6, KMNH 87695, original drawing, note the prefrontal is in two portions; 7, Schultze and Bolt, 1996, note how the prefrontal is restored as single and excludes the nasal from the external naris, directly comparable to the restoration in 4 and 5 by Smithson.

external naris and suturing with both the premaxilla and maxilla. In that interpretation it excludes both the nasal and lacrimal from the border of the naris. The prefrontal of *Pholidogaster* has been interpreted by Panchen (1975) as not reaching the external naris and having a very different sutural arrangement. The anterior extent of the prefrontal cannot be traced in *Deltaherpeton*. It is possible that its relationships to the maxilla, premaxilla, and external naris are as have been reconstructed in *Greererpeton* and *Colosteus*, or as in *Pholidogaster*, but other interpretations are possible as well. We therefore defer consideration to the section on roofing bones of the snout in the Discussion. Whatever the posterior boundary and anterior extent of the prefrontal, it would have carried a portion of the supraorbital lateral line canal as it curves sharply medially to enter the nasal. The canal is open in this region.

Premaxilla.—Both premaxillae are present. The left, still sutured to the internasal, is detached from the remainder of the skull but retains what appears to be a relatively undamaged sutural edge for contact with the nasal. The right retains sutural contact with the skull and preserves a sutural edge for the internasal. Each preserves its border to the external naris, an identical complement of teeth, ornamentation, and indications of the lateral line. A smooth periosteal surface of the premaxilla approximates a similarly finished surface of the maxilla beneath the naris (preserved on the right) and also has a smooth surface forming the anterior internal border of the narial opening. The dentition consists of 11 teeth + tooth spaces for teeth equal in size to those on the maxilla, as well as a fang and replacement space. Nine of the teeth and tooth spaces occur medial to the fang, two lateral. The premaxillary fang is positioned to fit into the notch on the dentary. The surface ornamentation consists of a complete covering of subcircular pits and ridges which contrast with the relatively smooth surface of the internasal. The premaxilla contains the triple junction where the supraorbital, ethmoid commissure and pre-narial segment of the infraorbital join. The supraorbital canal enters the premaxilla at the nasal-premaxilla suture. The ethmoid commissure passes from the triple junction medially to the internasal and from that bone to the premaxilla on the other side. The pre-narial segment of the infraorbital canal passes ventrally from the junction to end in an opening on the ventral margin of the premaxilla just posterior to the fang and anterior to the external naris. While in the premaxilla, the canal is completely enclosed and opens to the surface by three or four foramina. The ethmoid commissure of the lateral line is completely enclosed and opens to the surface via several foramina.

Quadratojugal.—The quadratojugal is preserved in situ on the right and appears to be intact on the left, where it is included in the partly detached cheek. On the right, the jugal-quadratojugal and quadratojugal-squamosal sutures are evident. The pattern of ornament reinforces the perception of the territory occupied by the quadratojugal. The maxilla does not appear to extend far enough posteriorly to reach the quadratojugal. The jugal branch of the lateral line reaches the quadratojugal-squamosal suture but does not extend into the quadratojugal.

Septomaxilla.—The territory that might be occupied by a septomaxilla is disrupted and uninterpretable. See Discussion section on roofing bones of the snout.

Squamosal.—The squamosal is preserved in situ on the right, and on the left is part of the detached cheek. The right squamosal is distorted in the vertical plane with resulting cracks and the left appears to be incomplete. Sutures on the

right are discernible and the pattern of the ornament on the squamosal and neighboring bones aids in delineation of the bone's territory. The squamosal forms the posterior border of the skull roof between the supratemporal and quadratojugal. The jugal-squamosal suture, visible on the right, is highly interdigitated. Also on the right, the posterior third of the squamosal-supratemporal joint is open, revealing morphology that indicates a beveled joint in which the supratemporal overlies the squamosal. It is not possible to determine how far anteriorly this beveled joint surface extends. On the left, despite the promise that separation of the cheek at that point would seem to have, the joint surfaces of the squamosal and supratemporal are damaged and so do not provide useful information. The nature of the squamosal-supratemporal joint in colosteids has received differing interpretations; see section on the squamosal-supratemporal joint in the Discussion. The jugal lateral line canal enters the squamosal from the jugal. In the squamosal it arches upward before turning ventrally towards the quadratojugal, but there is no indication that it enters that bone.

Supratemporal.—The supratemporal is complete on the right and, except for its lateral edge, is complete on the left. On both sides, the sutures are discernible and the pattern of ornamentation reinforces perception of the boundaries of the bone. The supratemporal sutures to the postorbital, squamosal, tabular, postparietal, and parietal. A slender posterolateral process reaches the posterior border of the skull roof, separating the squamosal from contact with the tabular. This process is interrupted by a crack on the right. The suture with the parietal is broadly interdigitated and the suture with the squamosal is, at least posteriorly, a scarf joint with the supratemporal overlapping that bone. This latter joint is discussed further in the section on the squamosal-supratemporal joint in the Discussion. The medial portion of the suture with the tabular is highly interdigitated on a fine scale. There is no indication of a lateral line canal.

Tabular.—The tabular is present in situ on both sides. A small bone, it is sutured to the supratemporal and the postparietal. On the left, the suture with the postparietal is disrupted by a crack and similarly on the right with the supratemporal. The ornamented surface ends at the posterior edge of the skull but clearly there is an occipital flange. From the occipital face a short "tabular horn," preserved on both sides, projects straight posteriorly. The horn on the left appears to be more complete and relatively undamaged, preserving small flanges of bone projecting from the horn and horn base. The horn on *Deltaherpeton* is comparable to that described for *Greererpeton* (Smithson, 1982) and *Pholidogaster* (Panchen, 1975). There is no evidence of a lateral line in the tabular.

DISCUSSION

General.—*Deltaherpeton* is clearly a colosteid, with the characters unique to that group (characters 1–5, Appendix). Where preserved, *Deltaherpeton* has the other characters of the skull and jaws that occur in colosteids though they may be primitive, or derived but shared with limited numbers of other taxonomic groups. These are listed in the Appendix scattered among characters 6–40.

Deltaherpeton differs from other colosteids in that it has an unpaired postparietal, a feature shared however with the stem tetrapod *Ichthyostega*. The unpaired internasal may be unique among colosteids but is also shared with *Ichthyostega*, and paired internasals occur in several other early tetrapods. The potential paired interfrontonasal might also mark

Deltaherpeton as unique, though a similar element is present in other, non-colosteoid, taxa. Whether or not an internasal and/or interfrontonasal is unique to *Deltaherpeton* among colosteids is not certain at this point due to the distortions present in the snout region of other colosteoid specimens (see following section).

The roofing bones of the snout.—Individual colosteids have been reported to have, or maybe have, or not to have, one or more of the following: internasal fontanelle; internasal bone(s), interfrontonasal bone(s); anterior tectal; septomaxilla; and a prefrontal that reaches the border of the external naris in a specific way. The latter has generally been viewed as one of the major characteristics of the family. We conclude after the following review and discussion that until better preserved specimens are available, the pattern of dermal bones in the snout of colosteids should at present be considered uncertain.

Colosteus.—Romer's redescription of *Colosteus* (1930) indicated (p.104) "The prefrontals are narrow, but extend forward nearly to the nares lateral to the nasals.... The lacrymals [sic] were wedged in between maxilla and prefrontals, and I cannot be certain whether they reach the nares." His reconstruction, based on specimens such as Figure 4.1 and 4.3 did not show definitive sutural relationships around the nares for the nasal, prefrontal, and lacrimal (Fig. 4.4). There was no mention of a septomaxilla. In his text *Vertebrate Paleontology*, Romer next figured *Colosteus* with a dotted in and labeled septomaxilla (Fig. 4.5) (First Edition 1933, fig. 86, Third Edition, 1966, fig. 121). In *Review of the Labyrinthodontia* (1947), the image was repeated without labeling in a composite figure (fig. 15, p. 81) that illustrated *Elpistostege*, *Ichthyostega*, "*Otocratia*" (syn. *Pholidogaster*, Panchen, 1975), *Colosteus*, and *Erpetosaurus*—all shown with unlabeled septomaxillae. The accompanying text (p. 82) indicates "A superficial element lying medial (or dorsal) to the external naris—Westoll's postnarial—appears to represent the septomaxilla in a primitive stage of its history." He further states, "The lacrimal does not enter the narial margin, from which it is separated by the septomaxilla." Subsequent authors have interpreted *Elpistostege*, *Ichthyostega* (Jarvik, 1996), *Pholidogaster*, and "*Otocratia*" (Panchen, 1975) as having a septomaxilla, but not *Colosteus*.

In his redescription of *Colosteus*, Hook (1983, p. 6) illustrated and stated that *Colosteus* and *Greererpeton* share "Elongate prefrontal entering the margin of the external narial opening, contacting the premaxilla and maxilla, thus excluding the lacrimal and nasal from the naris." He noted Romer's previous interpretation that the prefrontal does not reach the naris because of an intervening septomaxilla but indicated "However, latex casts...clearly indicate that a septomaxilla is not present." Hook's interpretive reconstruction of *Colosteus* is reproduced in (Fig. 4.2).

Pholidogaster.—In his 1929 description of the only specimen of *Pholidogaster*, Watson found the specimen "disappointing" because the dorsum of the head was embedded in ironstone. He was therefore unable to say anything certain about the bones of the snout region (fig. 10). Romer (1964) indicated that his attempt at the same skull was quickly abandoned as the initial work of his preparator exposed "a mass of crushed bone fragments impossible of interpretation" (fig. 3). Panchen (1975), after further preparation (Fig. 4.6), reconstructed the snout in a configuration with the external naris bounded by the premaxilla, nasal, septomaxilla, and maxilla (Fig. 4.7). The lacrimal and prefrontal are excluded from the external naris by the septomaxilla and nasal, and the prefrontal contacts neither

the premaxilla nor maxilla. We note that Panchen's septomaxilla might also be reasonably interpreted by position as an anterior tectal as used elsewhere in the present paper. Subsequently, Smithson (1982) indicated that the snout of *Pholidogaster* is "...severely disrupted and poorly preserved..." making interpretation difficult. He considered it "possible" that the septomaxillaries of Panchen might actually be broken continuations of the prefrontals. In this view the prefrontals would border the external naris excluding the lacrimal from the border and excluding contact between the lacrimal and nasal as has been reconstructed in *Greererpeton* and *Colosteus*. It would differ from those taxa in that the prefrontal would not contact the premaxilla, so that the nasal would still border the naris though the prefrontal would suture to the maxilla. Smithson (1982, p. 75) indicated that *Colosteus*, *Greererpeton*, and *Pholidogaster* share "...sutural connection between the prefrontal and maxilla..." Panchen (1975, p. 617) actually said about *Pholidogaster*: "The whole region of the right nostril is well preserved. It is bordered by the premaxillary, the maxillary, a septomaxillary and the nasal. The septomaxillary is well preserved and quite distinct...-boundaries clear...different surface ornament..." As a consequence, a septomaxilla plus a prefrontal that neither contacts the maxilla nor borders the external naris were illustrated for *Pholidogaster* by Panchen (Fig. 4.6, 4.7).

Greererpeton.—In his original description of the holotype, CMNH 10931, Romer (1969) described the prefrontal of both sides of the skull as apparently broken into anterior (smaller) and posterior (larger) segments. He reconstructed the prefrontal as a single element, which borders the external naris and, in contacting the maxilla, excludes the lacrimal from the narial border and the nasal from contact with either the lacrimal or maxilla. The prefrontal does not contact the premaxilla in his reconstruction and so the nasal enters the border of the naris (Fig. 5.1, 5.2). His text expressed some uncertainty (p. 10): "The state of preservation makes it impossible to give details of the region of the external naris: apparently premaxilla, maxilla, nasal and prefrontal enter into its borders. The lacrimal appears to have been excluded." He reconstructed the snout with an unpaired midline "internasal?" (more like an interfrontonasal as defined in the present work). As noted above, Romer (p. 10) based the potential presence of an "internasal" on "...a median strip of bone... [where] the sculpture pattern...shows no relation to that adjacent on either nasal..." (Fig. 5.1, 5.2). We have been unable to examine the dorsal surface of the holotype, which is presently unavailable due to preparation after Romer's study.

Subsequently, Carroll, 1980, illustrated the skull of an intact but dorsoventrally compressed *Greererpeton* specimen (CMNH 11068) as having an anterior tectal that would be the equivalent of the anterior segment of the prefrontal of Romer (Fig. 5.3). This interpretation excludes the prefrontal from the narial border and has the anterior tectal in that role excluding the lacrimal and nasal from the border while contacting the maxilla and premaxilla. Carroll did not depict an interfrontonasal. In his thorough redescription of *Greererpeton*, Smithson 1982 found that further preparation indicated that the "suture" between Carroll's prefrontal and anterior tectal is actually a crack and the area identified by Carroll as anterior tectal is in his view more correctly identified as an anterior continuation of the prefrontal as in Romer's interpretation. He repeated Carroll's illustration but with amended sutural lines in the snout (fig. 5, p. 38) (Fig. 5.4). He indicated that other specimens, especially CMNH 11090 and 11093, have not suffered post-mortem

disturbance in the snout region and support his interpretation. Neither Smithson nor, subsequently, Godfrey (1989b) indicated anything like an interfrontonasal in *Greererpeton*.

Most recently, a Goreville *Greererpeton* specimen (KUPV 87695) described by Schultze and Bolt (1996) was reconstructed with an extended prefrontal that borders the naris, thus excluding the lacrimal (Fig. 5.6, 5.7). The prefrontal is also shown in contact with the maxilla and premaxilla, excluding the nasal from the narial border. No midline internasal or interfrontonasal bones are illustrated, though a significant gap, as is usual in *Greererpeton* specimens from Greer, and containing the tips of the parasymphysial fangs, is present where an internasal would be placed. We note that the specimen, however, could be differently interpreted. Each prefrontal is in two pieces, with a smaller anterior segment bordering the naris that could be interpreted as an anterior tectal (Fig. 5.6) as in the holotype described by Romer (Fig. 5.1). Significantly, the Goreville specimen is the only one known that is not crushed dorsoventrally. Indeed, it is remarkably undistorted and thus may well indicate that an anterior tectal is in fact present.

Deltaherpeton.—The snout region of *Deltaherpeton* cannot be interpreted with certainty. The anterior extent of the prefrontal cannot be determined at all. The premaxilla and maxilla certainly border the external naris anteriorly and ventrally but the contributions to the external naris of the lacrimal, prefrontal, anterior tectal (if it exists), and nasal are not evident (Figs. 2, 3). The relations of these bones to one another in the region of the naris are not evident, either. That an internasal is present can be stated with some confidence, an interfrontonasal less so. We believe the internasal in the *Deltaherpeton* specimen to have been preserved because the lower jaws were disarticulated from the skull before dorsoventral crushing, which prevented the parasymphysial fangs from disrupting the region. Elongate frontals that shorten the internasal suture characterize all other colosteids as reconstructed (Figs. 4, 5). Romer (1969) reconstructed *Greererpeton* with the nasals separated at the midline by an unpaired interfrontonasal (?internasal; Fig. 5.2). Nasals that do not join at the midline are rare in early tetrapods. They are separated by a gap in *Acanthostega* as reconstructed by Clack (2003b) and are separated by a large midline ossification ("interfrontal") in the temnospondyl *Zatrachys* (Langston (1953). The nasals may not have been in contact in *Deltaherpeton*, but rather separated by either the frontals or possibly an interfrontonasal.

In summary, interpretation of the anterior snout of colosteids appears to be uncertain due to both the 'tight' and somewhat obscure sutures of the region, and disruptions consequent to preservation. Because both the specimens of *Greererpeton* from the Greer locality and *Pholidogaster* are crushed dorsoventrally, and those of *Colosteus* are nearly two dimensional impressions, the topography of the snout could have been distorted by the strongly vertical palatine fangs just caudal to the naris and by the parasymphysial fangs on the dentary medial to the naris. The former disrupt the area where the maxilla, lacrimal and septomaxilla/prefrontal enter the region of the naris and the latter the area where the premaxilla, nasal, and an internasal, might come together. It is usual, therefore, for specimens to be difficult to interpret around the medial and posterior aspects of the naris. This general preservation problem undoubtedly underlies the fact that no illustrations of specimens in any of the works referenced above traces sutures in the snout and why a number of experienced paleontologists over an extended period have produced varied

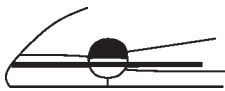




interpretations, clearly-figured reconstructions notwithstanding. In our view, the bones present in this region and their dispositions are yet to be known in any colosteid with certainty.

Cheek articulation.—The cheek-skull table junction of early tetrapods has traditionally been an area of particular functional-morphological and phylogenetic interest, because it is often thought to be a kinetic joint inherited from osteolepiform crossopterygians (e.g., Carroll 1988). The articulation of the skull table (supratemporal, tabular) on the cheek (squamosal) has been depicted as firmly sutured in Greer specimens of *Greererpeton* by Smithson (1982) who states "The solid connection between the skull table and cheeks, and the firm union of the bones of the palate with the skull roof, almost certainly preclude cranial kinesis." Likewise in *Colosteus*, Hook (1983) writes "The preservation of the skull table-cheek junction ranges from undisrupted to completely detached. The latter state is not indicative of a partially kinetic skull...but simply the poorly sutured condition of immature specimens." To the contrary, Romer (1969) said of the holotype *Greererpeton*, from Greer, "...area of junction of cheek and table is disturbed on both sides. That the suturing was not too tight between the two regions is demonstrated by the clean break between cheek and table seen on the left."

More recently, Schultze and Bolt (1996) argued for a moveable joint based on sutural morphology for *Greererpeton* from both the Goreville and Greer localities, and Bolt and Lombard (1996, 2001) extended these observations on favorably preserved material from the Goreville locality. In summary, we now believe that there is a continuous scarf joint devoid of interdigitation between the supratemporal and postorbital on the table and the squamosal and jugal on the cheek for *Greererpeton* from Goreville and Greer. In this joint the cheek bones have a flange that lies internal to the bones of the table. Bolt and Lombard (2001) showed that, in *Greererpeton* from both localities, the lower jaw is characterized by a "brassicata" intermandibular joint between the adsymphysials that likely permitted the two mandibles to move relative to one another in the horizontal plane. They suggested that at the posterior end of the jaws this movement would have been accommodated by movement of the cheek on the skull table, in other words, that there might have been a functional correlation between this moveable cheek and a mobile symphysial joint. In *Deltaherpeton* the left cheek has been pulled away from the skull table and the scarf joint is visible (Figs. 2, 3). Here, too, the skull table-cheek joint is not interdigitated, in contrast to other sutures on the skull roof. *Deltaherpeton* also has the "brassicata" joint between its mandibles, so in both respects it is comparable to the anatomy described for *Greererpeton*. At present we consider the evidence for a mobile scarf joint between the table and the cheek to be convincing for *Greererpeton* and *Deltaherpeton*, and unavailable for *Colosteus* and *Pholidogaster* where preservation does not reveal the relevant anatomy in sufficient detail.

Mandible.—The mandibles of PR1637, the *Deltaherpeton* holotype, were compared in detail with several *Greererpeton* specimens in Bolt and Lombard (table 1, 2001). Among the mandibular characters listed in that work that are preserved in PR1637 (105 of 226), none differs from those in *Greererpeton*. The dentary notch, a colosteid synapomorphy, is well preserved. A single, elongate exomeckelian fenestra, another colosteid synapomorphy, may be present, but it is not possible to delineate it completely because of crushing.

TABLE 1—Schematic representation of the course of the infraorbital lateral line canal ventral to external naris in some Paleozoic and Mesozoic anamniote sarcopterygians. The focus is on pattern relative to individual dermal bones, the external naris, and the margin of the upper jaw. In most taxa the canal is detectable as a series of openings that connect to a tube within bones or as a groove on the surface of the bones. Absence of these morphological indicators does not necessarily mean that the canal is absent as it could lie completely superficial to the bone surface in soft tissue. Bones included in the pathway are indicated under the drawings (LAC, lacrimal; MAX, maxilla; PEM, premaxilla). Patterns below the heavy line are those that include the maxillary bone in the pathway. *Microbrachis* is included based on Steen (1938) and Vallin and Laurin (2003), in which illustrations appear to indicate pattern (c) but supportive text is lacking.

Pattern	Taxa
(a) Continuous ventral to naris within lateral rostral	<i>Marsdenichthys</i> (Long, 1985) <i>Eusthenopteron</i> (Jarvik, 1980) <i>Panderichthys</i> (Vorobyeva, 1971, Vorobyeva and Schultze, 1991) <i>Ichthyostega</i> (Jarvik, 1996)
	
(b) Discontinuous across ventral naris	<i>Whatcheeria</i> (Lombard and Bolt, 1995) <i>Palaeoherpeton</i> (as “ <i>Palaeogyrinus</i> ” Panchen, 1964) <i>Pholiderpeton attheyi</i> (as “ <i>Eogyrinus</i> ” Panchen, 1972) <i>Archeria crassidisca</i> (Holmes, 1989) <i>Discosauriscus austriacus</i> (Klembara, 1994)
	
(c) Apparently discontinuous ventral to naris across maxilla to premaxilla	<i>Acanthostega</i> (Clack, 1994) <i>Baphetes</i> (Beaumont, 1977) <i>Megaloccephalus</i> (Beaumont, 1977) <i>Neldasaurus</i> (Chase, 1965) <i>Microbrachis pelikani</i> ? (Steen, 1938; Vallin and Laurin, 2003)
	
(d) Continuous ventral to naris in maxilla and premaxilla	<i>Dvinosaurus</i> (Bystrow, 1938) <i>Trimerorhachis</i> (Holmes, 2000) <i>Benthosuchus sushkini</i> (Bystrow and Efremov, 1940) Benthosuchidae <i>Compsoceros cosgriffi</i> (Warren, 2000) Chigutisauridae <i>Deltacephalus whitei</i> (Hewison, 1996) Lydekkerinadae <i>Lydekkerina huxleyi</i> (Hewison, 2007) Lydekkerinadae <i>Trematosaurus brauni</i> (Schoch and Milner, 2000) Trematosauridae
	
(e) Deflected ventrally and opening to ventral skull margin anterior and posterior to naris	<i>Deltaherpeton</i> (Lombard and Bolt, present paper) <i>Colosteus</i> (Hook, 1982) <i>Greererpeton</i> (Smithson, 1983)
	

Teeth.—All features of number, size, and placement in the dentition of *Deltaherpeton* are comparable to those of *Greererpeton* and *Colosteus*. The large size of the dentary marginal teeth compared to the smaller teeth on the premaxilla and maxilla is seen in *Greererpeton* and *Colosteus*, as well. In *Pholidogaster*, Panchen (1975) indicated that the “dentary teeth... may have been on average slightly larger [than the premaxillary and maxillary teeth].” His reconstruction does not show the striking difference in size seen in other named colosteids.

Lateral line.—The skull and jaws of *Deltaherpeton* preserve evidence of a well-developed lateral line system that in all respects is arranged like that of other colosteids (Figs. 2, 3). In the process of determining the lateral line pattern, we undertook a literature review particularly of the pattern ventral to the external naris. The results of that review are presented in Table 1.

The information available is incomplete due not only to the expected limitations of preservation, but also because a detailed description of the course of the lateral line is not

usually made. Such an effort might require, for example, time consuming preparation of small surface detail in order to elucidate the path of a canal that might open to the surface only periodically. It is thus not uncommon for some form of only a general character “lateral line—present/absent” to be included as a diagnostic feature in a description or in phylogenetic analyses. One receives the distinct impression that students of early tetrapods have lapsed into a set of expectations about the lateral line in the skull. For example: “the infraorbital canal passes forward ventral to the external naris.” We will show there are perhaps four or five patterns for the lateral line ventral to the naris that can tentatively be recognized at present. This variation may carry a useful phylogenetic signal.

Table 1 indicates five patterns for the infraorbital lateral line ventral to the external naris. In colosteids (e), the infraorbital canal appears to terminate in the ventral margin of the maxilla just posterior to the external naris. In addition, a segment of canal that connects with the supraorbital canal and ethmoid commissure appears to terminate in the ventral

margin of the premaxilla just anterior to the naris. This pattern has been known for almost eighty years, having been first figured by Romer in *Colosteus* (1930). Subsequent work on *Colosteus* (Hook, 1983) and *Greerpeton* (Smithson, 1982; Godfrey, 1989a, 1989b) confirmed and expanded this description. None of these papers discussed this morphology as unusual or compared the colosteid pattern to that of other early tetrapods. Similarly, none of the numerous publications on non-colosteid early tetrapods has noted the colosteid pattern as unique, either. Indeed, save for work that includes consideration of the lateral rostral in sarcopterygian fish and stem tetrapods either as basic description or in relation to the origin of choanae (for example: Vorobyeva and Schultze, 1991; Clack, 1994), the lateral line in this region has apparently received no comparative study in early tetrapods. The pattern found in sarcopterygian fish and *Ichthyostega* where the canal passes ventral to the external naris within the lateral rostral (Table 1a) is reasonably considered, *a priori*, primitive for tetrapods; that of colosteids is then both derived, and a synapomorphy of Colosteidae.

Three additional derived patterns may be recognized. In Table 1b, the canal appears not to be continuous in bone: opening in the lacrimal at the posteroventral corner of the naris and in the premaxilla at the anteroventral corner. It is reasonable to hypothesize this pattern as a derived transformation of the most primitive condition through loss of the lateral rostral, though it could represent a failure to preserve a fragile lateral rostral (such as is reported in *Ichthyostega*, Jarvik, 1996) in some or all of those taxa represented. Its distribution in the stem tetrapod *Whatcheeria*, the anthracosaurs *Palaeoherpeton*, *Pholiderpeton*, and *Archeria*, and the seymouriamorph *Discosauriscus* is intriguing. In (a) and (b) the infraorbital canal proceeds anteriorly from the lacrimal to the premaxilla via either a lateral rostral or via an hypothetical non-osseous route. In no case is the maxilla involved. In (c), (d), and (e) however, the canal passes anteriorly from the lacrimal to the maxilla. In (c) an indication of the canal is discontinuous and in (d) continuous from the maxilla to the premaxilla. Pattern (c) is found in the stem tetrapod *Acanthostega*, the stem-tetrapod baphetids, some early temnospondyls, and the one microsauro described with evidence for a lateral line, *Microbrachis*. Pattern (d) is widely represented among both basal and derived temnospondyls, and the number of temnospondyl taxa with this pattern is almost certainly greater than indicated in the table.

Colosteid relationships.—It has long been recognized that colosteids are primitive tetrapods. Historically, most authors considered them to be primitive temnospondyls, e.g., Romer, 1945; Panchen, 1975; Smithson, 1982; Hook, 1983; Laurin and Reisz, 1997). Over time, however, the long-held conception of colosteids as temnospondyls has waned. This retreat has been coincident with the evolving sense that the features used to associate colosteids with temnospondyls are either plesiomorphic for tetrapods, shared more broadly than with temnospondyls alone, or that the anatomy on which some individual characters were based had originally been misinterpreted. Movement of colosteids out of the crown group tetrapods to the tetrapod stem has been associated with the increasing application of cladistic techniques with ever larger data sets. A recent study of early-tetrapod relationships includes 339 characters for 102 taxa (Ruta and Coates, 2007). Ruta, Coates and Quicke (2003) presented a sample of the diverse phylogenetic relationships that have been proposed for colosteids.

The putative synapomorphic features that unite colosteids (Appendix Characters 1–5) are presently not known to occur in other taxa. Colosteidae may thus be recognized as a monophyletic taxon. Features that are derived for tetrapods and present in colosteids as well as other diverse early tetrapods (Appendix Characters 6–13) are each homoplastic to some degree depending on the phylogenetic hypothesis suggested. None-the-less, of characters presently known, these have the best chance, with more refined knowledge, of linking colosteids to another taxon. For example, character 12, the presence of a brassicate symphyseal joint surface on the adsymphyseal, is presently known only in the colosteids *Greerpeton* and *Deltaherpeton* (Bolt and Lombard, 2001) and the baphetid *Megalocephalus* (Ahlberg and Clack, 1998). No Devonian or other Carboniferous taxon where the jaw is adequately known possesses this character. If further discovery confirms its presence in colosteids, whatcheerids and baphetids only, it could well prove to be a synapomorphy that unites these taxa. An additional 5 characters (Appendix Characters 14–18) are of uncertain polarity at present and so cannot with confidence be used to unite colosteids with any other taxon though they might ultimately prove of use as knowledge increases. The remaining presently valid 21 characters that have been identified in colosteids appear to be primitive at a higher level and are broadly shared with diverse early tetrapods (Appendix Characters 19–39).

CONCLUSIONS

Colosteidae is a monophyletic taxon defined by five unique features of the skull and jaw. *Deltaherpeton* shares all of the colosteid synapomorphies where its anatomy is preserved and is distinguished from other colosteids by two, possibly three, features of the skull roof: the presence of an internasal, an unpaired midline postparietal, and the possible presence of paired interfrontonasals. Colosteids are recognized here as having an infraorbital lateral line with a unique and derived pattern: the post narial segment ends in the ventral margin of the maxilla and the prenarial segment ends in the ventral margin of the premaxilla. The infraorbital line in early tetrapods displays four additional patterns; two in which the pre and post narial segments appear to connect from the lacrimal to the premaxilla through the ventral aspect of the external naris, and two in which the post narial segment passes from the lacrimal to the maxilla before turning anteriorly beneath the naris. The dermal bones of the snout region of colosteids are difficult to interpret despite multiple specimens, some of which are well-preserved. We conclude that key aspects of the relationships of the premaxilla, maxilla, prefrontal, nasal, lacrimal and possible (anterior tectal/septomaxilla) to one another at the external naris are presently uncertain. *Deltaherpeton* adds further evidence (brassicate adsymphyseal joint and lap/scarf joint between the skull table and cheek) to the likelihood that colosteids had a kinetic skull. Systematic relationships of colosteids are uncertain but there is weak support for status as a stem tetrapod group at present.

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APPENDIX

All osteological character states that have been previously suggested by other authors as diagnostic for Colosteidae, and new ones proposed in this paper, are included here. They have been subdivided into groups that indicate character states that we propose as synapomorphies of the Colosteidae; those derived for early tetrapods but not unique to the Colosteidae; those of uncertain polarity and not unique to the Colosteidae; those generally hypothesized as primitive for tetrapods; and those known not to apply to all colosteids or that may be based on questionable interpretations of morphological conditions.

Previous diagnostic statements, originally expressed in diverse formats, are here modified or restated to a consistent form that includes separation into more than one character of some that originally combined potentially independent features. Statements are in the format: [PART feature state], where PART is the nominal minimum anatomical element that can possess the feature and state. This will usually be a single bone. Alternative state(s) are known for each though alternatives are not indicated here. Unless noted, character states described are known for all colosteid genera. If noted as unknown for an indicated taxon, specimens available do not permit determination due to the fortunes of preservation, incompleteness, or lack of preparation. In all cases, character states that have been suggested to be common to all colosteids may turn out to not be so. Citations indicate first formal use of a character state to define the Colosteidae.

Derived characters that we presently conceive as synapomorphies for the Colosteidae:

1. DENTARY notch present (Smithson, 1982). Romer (1930, fig. 15) illustrates a dentary notch in AMNH 6927 identified as *Erpetosaurus*, as well as in an accompanying reconstruction (fig. 16). Subsequent work on colosteids neither mentions the specimen nor remarks on its identity. Otherwise, clearly present in all colosteids.
2. MANDIBLE single exomeckelian fenestra length > 4 × width (Hook, 1983 as “meckelian fenestra”). Unknown: *Pholidogaster*, and suggestive but not certain in *Deltaherpeton* (Bolt and Lombard, 2001). Though presently unknown in any other primitive tetrapods, this character state may be part of a transformation series between the single, exomeckelian slit opening posteriorly found in diverse primitive tetrapods and the multiple exomeckelian fenestrae as occur in the more derived early tetrapods such as anthracosaurs and temnospondyls (Bolt and Lombard, 2001).
3. MAXILLA post-narial infraorbital lateral line terminates at ventral margin just posterior to external naris (Lombard and Bolt, this paper). Unknown: *Pholidogaster*. Clearly illustrated in *Colosteus* (Romer,

- 1930; Hook, 1983) and *Greererpeton* (Smithson, 1982; Godfrey, 1989a, 1989b) and noted in the text of the first three authors, as well.
4. PREMAXILLA fang pair present (Smithson, 1982). *Erpetosaurus*, at one time placed in the colosteids (Romer, 1930), but presently indicated, though not formally, as a trimerorhachid temnospondyl (Hook, 1983, p31; Hook and Baird, 1986), has two pairs of fangs on the premaxilla.
 5. PREMAXILLA infraorbital lateral line terminates at ventral margin just anterior to external naris (Lombard and Bolt, this paper). Unknown: *Pholidogaster*. Clearly illustrated in *Colosteus* (Romer, 1930; Hook, 1983) and *Greererpeton* (Smithson, 1982; Godfrey, 1989a, 1989b) and noted in the text of the first three authors, as well.

Derived characters in colosteids that also occur in other early tetrapods:

6. ADSYMPHYSEAL joint with antimere brassicata (Lombard and Bolt, this paper). This morphology was first noted in the baphetid *Megaloccephalus* (Ahlberg and Clack, 1998). They later coined the term “brassicata” to describe the morphology (after the family Brassicaceae to which cauliflower belongs: personal communication) and it was first used in print by Bolt and Lombard (2001). Unknown: *Colosteus*, *Pholidogaster*.
7. DENTARY fang not bounded laterally by marginal tooth row (as “parasymphysial tusks,” Godfrey, 1989a). This state is now known in *Ichthyostega*, *Crassigyrinus*, and *Megaloccephalus*, for example (Ahlberg and Clack, 1998). Unknown: *Pholidogaster*.
8. HEAD (skull plus lower jaws) dentary teeth larger than maxillary teeth (Smithson, 1982). In *Pholidogaster*, Panchen (1975) indicated that “dentary teeth... may have been on average slightly larger.” Panchen’s reconstruction does not present the striking difference in size seen in *Colosteus*, *Greererpeton*, and *Deltaherpeton*. Also occurs in temnospondyls *Isodectes* (Sequeira, 1998) and *Balenerpeton* (Milner and Sequeira, 1994).
9. INTERTEMPORAL bone minute or absent (Smithson, 1982). Occurs in diverse early tetrapods. Does not completely correlate with 10.
10. PARIETAL joint with postorbital present (Hook, 1983). Occurs in diverse early tetrapods. Does not completely correlate with 9.
11. SKULL frontal length relative to nasal length parallel to midline two to three times longer (Smithson, 1982). Stated as “elongate frontals” in Smithson without reference to any other part of the skull. Configured in the reverse of our statement (as nasal relative to frontal) by Ruta, et al, 2003; Ruta and Coates, 2007, as their character NAS 2. Also present in some lepospondyls.
12. SKULL nasal area relation to postparietal area lesser or equal (Ruta, et al, 2003 as character POSPAR 10). Present in adelospondyls, some aistopods, and some keraterpetontid neotrideans.
13. SKULL notch between squamosal and tabular absent (Smithson, 1982). This is the “squamosal embayment” or “otic notch” of previous works on colosteids, but not the same as character SQU 3 “Squamosal... with... semicircular embayment” of Ruta, et al (2003). A notch is also absent in all lepospondyl groups and some temnospondyls.

Characters of uncertain polarity for colosteids and not unique to them:

14. PRESACRAL VERTEBRAE count about 40 (Smithson, 1982). Unknown: *Pholidogaster*; *Deltaherpeton*. This is not an unusual number of vertebrae in Paleozoic tetrapods.
15. SCAPULOCORACOID supraglenoid foramen absent (Godfrey, 1989a). Unknown: *Deltaherpeton*.
16. TABULAR horns small, rounded, and blunt (Ruta, et al, 2003 as character TAB 3 “...rounded, subdermal, button-like posterior process of tabular”). Unknown: *Colosteus*. Also present in baphetids.
17. TRUNK ventral scale shape rhomboidal (Hook, 1983). Unknown: *Deltaherpeton*.
18. TRUNK ventral scale shape posterior margin crenellated (Smithson, 1982). Unknown: *Deltaherpeton*; *Pholidogaster*.

Characters of colosteids that are primitive for tetrapods:

19. ADSYMPHYSEAL bone present (Bolt and Lombard, 2001) Unknown: *Pholidogaster*, *Colosteus*.
20. ADSYMPHYSEAL teeth present (Bolt and Lombard, 2001). These are of approximately the same size as the dentary marginal teeth. Indicated as “fangs” in some works (Ahlberg and Clack, 1998). Unknown: *Pholidogaster*, *Colosteus*.
21. DENTARY postdental process present (Bolt and Lombard, 2001). Unknown: *Pholidogaster*, *Colosteus*.

22. ECTOPTERYGOID small accessory teeth present (Smithson, 1982). Unknown: *Pholidogaster*; *Deltaherpeton*.
23. ECTOPTERYGOID fang pair present (Smithson, 1982). Unknown: *Pholidogaster*; indirect evidence indicates presence in *Deltaherpeton*.
24. HEAD lateral line indication present (Smithson, 1982).
25. HEAD lateral line enclosure mostly open with short sections enclosed (Smithson, 1982).
26. HUMERUS entepicondylar foramen present (Smithson, 1982). Unknown: *Pholidogaster*; and *Deltaherpeton*.
27. HUMERUS anterior flange present (Smithson, 1982). This is the “supinator” flange of some authors (Godfrey, 1989a). Unknown: *Pholidogaster*; *Deltaherpeton*.
28. INTERCENTRUM shape crescentric (Smithson, 1982). Unknown: *Deltaherpeton*.
29. NEURAL ARCH supraneural canal present (Smithson, 1982). Later work indicates this is true only for more rostral vertebral segments (Godfrey, 1989a). Unknown: *Pholidogaster*; *Deltaherpeton*.
30. PALATINE small accessory teeth present (Smithson, 1982). Unknown: *Pholidogaster*; *Deltaherpeton*.
31. PALATINE fang pair present (Smithson, 1982). Unknown: *Pholidogaster*; indirect evidence indicates presence in *Deltaherpeton*.
32. PLEUROCENTRUM ventral joint with antimere unfused (Smithson, 1982). Unknown: *Deltaherpeton*.
33. PTERYGOID joint with antimere anteriorly (Smithson, 1982). Unknown: *Pholidogaster*; *Deltaherpeton*.
34. SKULL anterior palatal vacuity present (Smithson, 1982). Unknown: *Pholidogaster*; *Deltaherpeton*.
35. SKULL interpterygoid vacuity narrow (Smithson, 1982). Unknown: *Pholidogaster*; *Deltaherpeton*.
36. STAPES bone “massive” (Hook, 1983). At the time Smithson (1982) described the stapes of *Greererpeton* as a “major supporting element for the back of the braincase” its form was unique among those known for fossil tetrapods. Smithson noted that this stapes form is “almost certainly primitive for temnospondyls (and possibly for Amphibia as a whole)...” The term “massive” used by Hook (1983), and Godfrey (1989a), is imprecise and awaits a more refined description, likely involving two or more independent characters. Subsequent discovery of similar stapes in *Pholiderpeton* and *Acanthostega* led Clack (1989) to confirm that this stapes form is plesiomorphic for tetrapods, and additional examples are now known. In any case, the stapes form is unknown in: *Pholidogaster*; *Colosteus*; *Deltaherpeton*.
37. TRUNK scales extensive (Hook, 1983). Unknown: *Pholidogaster*; *Deltaherpeton*.
38. VERTEBRA cross section primarily notochordal (Smithson, 1982). Unknown: *Pholidogaster*; *Deltaherpeton*.
39. VERTEBRA elements schizomorous (Smithson, 1982). Unknown: *Deltaherpeton*.

Characters that are presumably derived or of uncertain polarity and that are now known not to apply to all colosteids, and/or may apply to taxa outside the colosteids, and/or may be based on questionable interpretations of morphological conditions:

40. PREFRONTAL bone elongate (Smithson, 1982). Later succinctly stated by Hook (1983) for colosteids as: “elongate prefrontal reaches external naris, contacting premaxilla and maxilla, excluding lacrimal and nasal from narial opening.” This statement is actually six potentially independent characters: PREFRONTAL bone elongate (which does not indicate how “elongate” is determined); PREFRONTAL joint with premaxilla present; PREFRONTAL joint with maxilla present; PREFRONTAL border to external naris present; LACRIMAL border to external naris absent; and NASAL border to external naris absent. We argue that this suite of characters is uncertain in all known colosteids. See section on the roofing bones of the snout in DISCUSSION. An “elongate” prefrontal that borders the external naris also occurs in the trimerorhachid temnospondyls *Acroplous* and *Isodectes* (Foreman, 1990; Sequeira, 1998) and many lepospondyls: the microsaur *Batropetes*, *Carrolla*, and *Utaherpeton* (Carroll, 1998a); most neotrideans (Bossy and Milner, 1998); some (?) aistopods (Carroll, 1998b); lysorophids (Wellstead, 1998); some(?) adelospondyls (Carroll and Andrews, 1998); and perhaps *Acherontiscus* (Carroll, 1998c). In all but *Utaherpeton*, the prefrontal does not exclude the lacrimal or nasal from bordering the naris and does not contact the maxilla or premaxilla. In *Utaherpeton* the prefrontal appears to contact the premaxilla, thus excluding the nasal from the naris.

41. PREMAXILLA fang pair located on palatal flange (Hook, 1983). The “flange” appears to be a local swelling of the premaxilla to accommodate the large base of the fang and not independent of that tooth. Cannot be examined in *Pholidogaster*; *Deltaherpeton*.
42. SKULL orbit placement midway between snout and occiput (Smithson, 1982). This is true for *Greerherpeton*, *Pholidogaster*, and *Deltaherpeton* (orbit center projected to center line of skull is at about 47% from tip of snout for all). In *Colosteus*, however, the figure is about 39%. Orbit placement midway between snout and occiput is also common to several non-colosteid fossil tetrapods.
43. SQUAMOSAL joint with tabular present (Hook, 1983). Expressed as “extensive tabular-squamosal contact” by Hook (1983) it is sometimes taken as equal to “squamosal embayment” by others but the two are not always coincident. In any case, in *Deltaherpeton*, the supratemporal attains the posterior margin of the skull separating the tabular and the squamosal and there is no “squamosal embayment” (see “SKULL notch between squamosal and tabular,” above). Intercession of the supratemporal between the tabular and squamosal in the skull roof is by far the most common condition among post Devonian tetrapods.