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## *Colosteus scutellatus* (Newberry), a Primitive Temnospondyl Amphibian from the Middle Pennsylvanian of Linton, Ohio

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## ABSTRACT

*Colosteus scutellatus* (Newberry), known exclusively from the classic Coal Measure locality of Linton, Ohio, is the genotype and youngest representative of the Colosteidae, an archaic group of temnospondyls that also includes *Pholidogaster* and *Greererpeton*. The colosteids are a monophyletic group distinguished from other temnospondyls by massive stapes and no otic notch; elongate prefrontal contacting narial border, premaxilla, and maxilla; intertemporal reduced or absent with broad postorbital-parietal contact; single pair of premaxillary tusks; and single, elongate Meckelian fenestra. The use of the superfamily Colosteioidea

(Tatarinov, 1964) is recommended in the absence of shared derived characters indicating a close relationship between the colosteids and any other known temnospondyls. The structure of the stapes and skull roof suggests that the colosteids may represent the plesiomorphic sister group of all other temnospondyls.

An overview of the status of the Temnospondyli indicates that exclusion of the loxommatoids is justified, but that a possible microsaur-temnospondyl relationship circumvents the possibility of temnospondyl monophyly.

## INTRODUCTION

The Temnospondyli are the largest and possibly most diverse order of fossil amphibians. Despite an impressive representation of Late Paleozoic and Triassic forms, temnospondyls older than Pennsylvanian or Westphalian age are virtually unknown. Consequently, the astonishing array of temnospondyls that first appears in the Coal Measures of North America and Europe has consistently frustrated paleontologists who wish to incorporate at least a modicum of phylogeny in their classifications of the order.

The variety and abundance of Pennsylvanian temnospondyls is nowhere better documented than in collections acquired from the once-active coal mines of Linton, Ohio. In addition to a dozen species of fishes and a score of other tetrapods, this prolific locality has produced seven temnospondyl genera, four of which are unique to Linton (Hook, 1981). The most common of these indigenous temnospondyls is *Colosteus scutellatus*, a heavily scaled amphibian with an elongate body and diminutive limbs. Because similar forms are unknown from younger deposits, such as the Texas redbeds (Romer, 1935), early workers generally considered *Colosteus* as a novel adaptation to the coal swamp environment. Thus, after a somewhat checkered taxonomic history, *Colosteus* and the family to which it gives its name, the Colosteidae, were removed from the main line of temnospondyl evolution (Romer, 1947, 1966).

With the 1969 description of *Greererpeton*

*burkemorani* Romer, a *Colosteus*-like form from the Mississippian of West Virginia, it became evident that the colosteids represent an archaic lineage that might provide insights into the early evolution of temnospondyls, if not all Paleozoic amphibians. Subsequent study of additional colosteid material (Romer, 1972; Panchen, 1975; Smithson, 1982) has identified the need for a more detailed understanding of the genotype of the family.

The objective of the present paper is to provide a thorough description of the genus *Colosteus* and an accurate characterization of the Colosteidae. Although the affinities of the family are also considered, re-evaluation of other primitive temnospondyls is necessary before the problem of interrelationships can be fully addressed.

## ACKNOWLEDGMENTS

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## ABBREVIATIONS

### INSTITUTIONAL

- AMNH, American Museum of Natural History
- BM[NH], British Museum (Natural History)
- CM, Carnegie Museum of Natural History
- FMNH, Field Museum of Natural History
- MCZ, Museum of Comparative Zoology, Harvard University
- OSU, Orton Museum, Ohio State University
- PU, Museum of Natural History, Princeton University
- UMMP, Museum of Paleontology, University of Michigan

YPM, Peabody Museum of Natural History, Yale University

### ANATOMICAL

- a, angular
- a.p.f., anterior palatal fenestra
- art, articular
- c, clavicle
- cb, ceratobranchial ossifications
- ch, choana
- c.r., conical recess
- ct, cultriform process
- cth, cleithrum
- co, coronoid
- d, dentary
- ect, ectopterygoid
- eo, exoccipital
- f, frontal
- h, humerus
- hb, hypobranchial cartilage
- i, interclavicle
- ic, intercentrum
- im.f., intermandibular fenestra
- j, jugal
- l, lacrimal
- m, maxilla
- n, nasal
- p, parietal
- pal, palatine
- pa.f., para-articular foramen
- pra, prearticular
- pc, pleurocentrum
- pf, postfrontal
- pl, pleuracanth shark tooth
- pm, premaxilla
- po, postorbital
- pp, postparietal
- prf, prefrontal
- pt, pterygoid
- qj, quadratojugal
- r, radius
- sa, surangular
- sp, splenial
- spp, postsplenial
- st, supratemporal
- t, tabular
- u, ulna
- u.p., uncinate process
- v, vomer
- I-IV, digits of manus

### METHODS

Vertebrate remains from Linton have been reduced to virtually two dimensions by post-mortem crushing. Early descriptive efforts

were further vexed by the partial or complete pyritization of the original bone material (see Moodie, 1915). It was not until the 1950s, when the technique of acid-etching was followed by the use of latex as a microcasting compound (Baird, 1955), that detailed study of Linton specimens became feasible. In this innovative manner, Baird has prepared most of the important vertebrate material from this locality. Using the spray technique described by Heaton (1980b), I have cast the remaining unprepared temnospondyl specimens of Linton collections of North American museums. These latex "peels" provide detailed casts from which study of *Colosteus* and other Linton amphibians can proceed.

The drawing of significant Linton specimens is necessitated by the generally inadequate representation achieved by photography alone. Rather than using standard camera lucida or grid ocular techniques (Carroll and Gaskill, 1978), drawings were traced from twofold photographic enlargements onto mylar drafting film while the corresponding peel was examined under high magnification. This method is not only faster than those cited above, but also more accurate because it reduces the amount of peripheral distortion and allows free movement of the specimen during drawing.

Reconstructions were drafted on paper and based largely on specimen drawings. Restoration of the skull in dorsal view (fig. 1A) is derived from several nearly complete subadult skulls of intermediate size (average skull length of 9 cm.). The reconstruction of the palate (fig. 1B) is based on four subadult specimens whose estimated skull lengths range from 5.5 to 12 cm. Palatal areas not represented by actual remains (about 35% of the composite) were restored with slight modifications after *Greererpeton*, a colosteid whose palatal architecture is reasonably well documented (Smithson, 1982). In the absence of adequate information on the occiput of *Colosteus*, no reconstruction of this region has been attempted.

Accurate measurement of Linton fossils is made difficult by the crushed and incomplete nature of specimens. As such, it is not practical to attempt a conventional tabulation of dimensions. Incidental measurements are re-

corded with the description; further dimensions may be taken directly from the specimen drawings if necessary.

The present study considers the morphology of an animal whose remains present no perceivable characteristics from which sexual maturity or absolute age can be inferred. Consequently, the terms subadult and adult are based arbitrarily on absolute size, not developmental stage: specimens with an estimated skull length (measured along the dorsal midline) less than 15 cm. are considered to be subadults. Although semantically incongruent, this usage provides a means by which large, diagnostic materials can be differentiated from smaller specimens that may lack the apomorphic states produced by allometric growth (A. R. Milner, 1980a). Without this discrimination, subadults may form the basis of erroneous phylogenetic statements—the classic example being the infamous "order" Phyllospondyli (Romer, 1939).

## REVIEW OF PREVIOUS WORK

The taxonomic histories of most specimens presently referred to *Colosteus* are tortuously complex. Since such details are of little general interest, their treatment has been relegated to the Appendix. It is appropriate, however, to summarize previous work by way of tracing the publication history of the genus *Colosteus* and the family Colosteidae.

The first report of fossil vertebrates from the Ohio Diamond Coal Company Mines at Linton was given by J. S. Newberry in 1856; it included a brief description of *Pygopterus scutellatus*, a supposedly new species of paleoniscoid fish. Although no figures were supplied or specific specimens adequately described, a general picture of a heavily scaled, elongate form with flattened head and pointed snout was established.

In 1869, E. D. Cope erected the batrachian genus *Colosteus* on the basis of Linton material lent him by Newberry. Cope cited three species, *C. crassiscutatus*, *C. marshii* and *C. foveatus*, and provided measurements by which the type specimens can be identified today. However, Cope later admitted (1871a, p. 41) that in describing the type species, *C. crassiscutatus*, he had "overlooked" New-

berry's original account of *P. scutellatus*, thereby implying that both taxa were inadvertently based on the same specimen. Since *Pygopterus* was (and is) a valid fish genus, and the material in question was certainly not piscine (Cope, 1873), Cope recognized the proper combination of *Colosteus scutellatus* (Newberry, 1856) for the type species. With this synonymy, *Colosteus* predates *Amphibamus* ("Raniceps," "Pelion") *lyelli* (Wyman, 1857) as the first tetrapod recorded—albeit as a fish—from the Linton deposit.

Newberry also described (1856) and later figured (1873, pl. 39, fig. 6) *Rhizodus angustus*, a presumed crossopterygian fish from Linton. Romer (1930) noted that the type of this species was unknown and, on the basis of Newberry's figure, recorded *R. angustus* as a synonym of *C. scutellatus* since the latter species has page priority. However, because the description and figure of *R. angustus* are nondiagnostic (there is nothing to bar it from being any one of the larger Linton labyrinthodonts) and renewed search for the specimen has been unsuccessful, it may be thankfully regarded as a *nomen dubium* and *nomen oblitum*.

In an 1871b summary of the "Batrachian Fauna" of Linton, Cope erected a new form, *Oestocephalus marshii*, without description. He later referred this name to *Ptyonius marshii* (Cope, 1874) and revealed that both taxa were based on his 1869 description of *C. marshii*; recent review of the urocordylid neotriids has upheld this synonymy (Bossy, MS). In the same 1871b report, Cope erected another *nomen nudum*, *Colosteus pauciradiatus*, only to supply description and figures in subsequent papers (1874, 1875). The holotype (AMNH 6920, fig. 11A) of this taxon is an interclavicle that was originally included in the *C. crassiscutatus* paratype series (Cope, 1869, p. 23; contra 1874, p. 275 and 1875, p. 408); however, it does not merit specific separation because it cannot be differentiated from comparably sized interclavicles of the type species.

The family Colosteidae was erected by Cope in 1875 to accommodate *Colosteus*, *Sauropleuria*, and *Amphibamus*. However, in one of his last papers, Cope (1897) made the mistake of synonymizing *Colosteus* with *Sau-*

*ropleuria*, and the familial name lapsed to the Sauropleuridae (Hay, 1902). This oversight was amplified by R. L. Moodie, who, in a series of papers culminating in a 1916 monograph, compounded existing taxonomic problems with additional errors of his own invention (see Appendix).

In an ambitious, if not commendable, attempt to obtain "a reduction in the number of species" at Linton, A. S. Romer (1930, p. 79) resurrected *Colosteus* but retained only the type species in his redescription of the genus. Although he corrected many existing mistakes, Romer "committed some new ones" himself (Romer, 1968, p. 67). Particularly unfortunate was his attempt to augment the postcranially impoverished sample of *Colosteus* with a sizable quantity of headless "lepospondyl" material, described originally by Cope as *Molgophis* and *Pleuroptyx*. The improbable nature of this graft was elaborated upon by Steen (1931) and merits no further consideration.

Romer (1930) also reinstated the family Colosteidae in which he associated a second Linton genus, *Erpetosaurus*, with the genotype while transferring *Sauropleuria* to the Urocordylidae and *Amphibamus* (as "Pelion") to the Pelontidae (subsequently assigned to the Dissorophidae by Carroll, 1964). Because most of his material consisted of poorly ossified, branchiosaur-like subadults, Romer placed the family among the Phyllospondyli; similarly influenced by the work of Watson (1921), Steen (1931) followed this mistaken interpretation. Upon dissolution of the phyllospondyls, Romer deemed *Colosteus* and *Erpetosaurus* to be primitive rachitomes (1939) that had descended from ichthyostegids (1945), and separated, therefore, from the main line of temnospondyl evolution (1947).

Jarvik (1948, 1952) rejected the possibility of a close relationship between *Ichthyostega* and colosteids, but proposed no alternative placement for either *Colosteus* or *Erpetosaurus*. This dissent was followed by Lehman (1955), who recognized the "?Colosteidea" as a superfamily of the suborder Rachitomi [sic]. Through four volumes of the *Bibliography of Fossil Vertebrates* (Camp and Allison, 1961; Camp et al., 1964, 1968, 1972),

the Colosteidae was included with the Elpistostegidae and Otocratiidae in the non-rachitomous suborder Elpistostegalida. More appropriately, Tatarinov (1964) erected the superfamily Colostoidea under the Rachtomi and recognized two families, the Colosteidae and Otocratiidae. Romer, in the last edition of *Vertebrate Paleontology* (1966), questioned his own assignment of the colosteids to the superfamily Edopoidea, and, at a later date, indicated further apprehension in stating that the two Linton forms "approach the metoposaurs more closely than the trimerorhachids" (1968, p. 78).

The discovery of a Mississippian-age colosteid did surprisingly little to clarify the phylogenetic position of the family. As the first describable non-loxommatoid temnospondyl from the Lower Carboniferous, *Greererpeton burkemorani* Romer (1969) appeared to be identical in many respects to the Pennsylvanian-age *Colosteus*. Panchen (1975) subsequently concluded that two problematical labyrinthodonts from the British Lower Carboniferous, *Otocratia modesta* Watson (1929) and *Pholidogaster pisciformis* Huxley (1862), represented a single taxon that was very similar to *Greererpeton*. Although these important discoveries led to the realization of the great antiquity of the colosteid stock (Panchen, 1972, 1973), no attempt was made to reconcile such with existing classifications. Thus, in the most recent comprehensive scheme of amphibian classification (Carroll and Winer, 1977), the Colosteidae consisted of *Pholidogaster*, *Greererpeton*, *Colosteus*, and *Erpetosaurus*, and was assigned to the Trimerorhachoidea.

As reported by various workers (Romer, 1968; Panchen, 1975), the late Dr. John N. Chase, in collaboration with Dr. Baird, had begun a redescription of *Colosteus* and *Erpetosaurus*. Before his death in 1977, Dr. Chase had photographed peels of appropriate specimens and had initiated drawing efforts of important material. In 1979, with the assistance of Dr. Baird, I was able to recover the peels formerly in Dr. Chase's possession and to critically evaluate the association of *Erpetosaurus* with the Colosteidae. On the basis of this work, which will be reported in full at a later date, it is apparent that the

affinities of *Erpetosaurus* lie closer to saurerpontid trimerorhachoids than to colosteids (Hook, 1980).

## SYSTEMATICS

CLASS AMPHIBIA  
ORDER TEMNOSPONDYLI  
SUPERFAMILY COLOSTEOIDEA  
TATARINOV, 1964, *SENSU NOVUM*

**EMENDED DIAGNOSIS:** Primitive temnospondyl amphibians characterized by massive stapes, extensive tabular-squamosal contact, and no otic notch; elongate prefrontal reaches external naris, contacting premaxilla and maxilla, excluding lacrimal and nasal from narial opening; intertemporal minute or absent, broad postorbital-parietal contact; single pair of premaxillary tusks on posterolateral palatal flange; single, elongate Meckelian fenestra; approximately forty presacral vertebrae; extensive dorsal and ventral scalation, ventral scales rhomboidal with crenulated posterior margins.

Differentiated from edopoids by well-developed lateral line system, marginally situated external nares, no exposure of septomaxilla on skull roof, orbital lacrimal, accessory tusks on palatine and ectopterygoid, separate sphenethmoid and otico-occipital braincase regions, and retention of anterior flange and entepicondylar foramen on the humerus.

Distinguished from trimerorhachoids by laterally directed external nares, narrow interpterygoid vacuities completely enclosed by pterygoids, thin cultriform process not sutured to vomers on palatal surface, premaxilla borders choana, no vomerine tusks, and dentary teeth markedly larger than maxillary.

### FAMILY COLOSTEIDAE COPE, 1875

**DIAGNOSIS:** As for the superfamily, which is monotypic.

### GENUS COLOSTEUS COPE, 1869

**TYPE SPECIES:** *Colosteus scutellatus* (Newberry, 1856).

**DIAGNOSIS:** Colosteoid temnospondyl characterized by only three bones, jugal, lacrimal, and postfrontal, forming orbital mar-

gin; open lateral line system; single row of minute coronoid teeth. Dorsal sculation resembles gastralria.

*Colosteus scutellatus* (Newberry, 1856)

SYNONYMY:

*Pygopterus scutellatus* Newberry, 1856, p. 98.

*Colosteus crassiscutatus* Cope, 1869, p. 23.

*Colosteus scutellatus*, Cope 1871a, p. 41; 1874, p. 275; 1875, pp. 407–408, pl. 33, fig. 1, pl. 34, fig. 2; 1877, p. 578. Romer, 1930, pp. 100–108, figs. 8 (part), 9, 11. Steen, 1931, pp. 858–860, figs. 6, 7, pl. 2, fig. 1.

*Colosteus pauciradiatus* Cope 1871b, p. 177 (*nomen nudum*); 1874, p. 275; 1875, p. 408, pl. 40, figs. 1, 2.

*Sauroploera scutellata*, Cope, 1897, pp. 86, 88. Moodie, 1909a, p. 26; 1916, pp. 156–157, pl. 14, fig. 3, pl. 21, fig. 5.

*Sauroploera pauciradiata* Cope, 1897, p. 88. Moodie, 1916, pp. 158–160, fig. 34.

*Sauroploera longidentata* Moodie, 1909b, pp. 74–76, figs. 18, 19; 1916, pp. 160–161, pl. 16, figs. 2, 3.

*Macrerpeton deani* Moodie, 1916, pp. 184–185, fig. 40, pl. 21, figs. 1, 2.

NON:

*Rhizodus angustus* Newberry, 1856, p. 99; as *C. scutellatus*, Romer, 1930, pp. 100–101, 106. = *nomen dubium*, *nomen oblitum*.

*Molgophis macrurus* Cope, 1868, pp. 220–221; questionably assigned to *C. scutellatus*, Romer, 1930, pp. 101, 106. = *M. macrurus*, Romer, 1952, p. 76.

*Colosteus foveatus* Cope, 1869, p. 24. = *Saurerpeton obtusum* (Cope, 1868); NEW SYNONYMY.

*Colosteus marshii* Cope, 1869, p. 24. = *Ptyonius marshii* Cope, 1874, p. 265.

*Molgophis brevicostatus* Cope, 1875, p. 369, pl. 44, fig. 1; questionably assigned to *C. scutellatus*, Romer, 1930, pp. 101, 106. = *M. macrurus* Cope, 1868; NEW SYNONYMY (Wellstead, personal commun.).

*Pleuroptyx clavatus* Cope, 1875, pp. 370–371, pl. 44, fig. 2; questionably assigned to *C. scutellatus*, Romer, 1930, pp. 101, 106. = *P. clavatus*; Steen, 1931, p. 860.

*Sauroploera newberryi* Cope, 1875, pp. 404–405, pl. 37, fig. 2; as *C. scutellatus*, Romer, 1930, p. 100 (only).

= *Stegops newberryi* (Cope, 1875); Hook and Baird, in press.

*Leptophractus lineolatus* Cope, 1877, p. 576; as *C. scutellatus*, Romer, 1930, pp. 100–101, 106. = *Megalcephalus lineolatus* (Cope, 1877); Beaumont, 1977, pp. 73–76.

*Anisodexis enchodus* Cope, 1885, p. 406; as *C. scutellatus*, Romer, 1930, pp. 100–101, 106. = *M. lineolatus* (Cope, 1877); NEW SYNONYMY.

*Diceratosaurus robustus* Moodie, 1909b, pp. 67–69, fig. 5; as *C. scutellatus*, Romer, 1930, pp. 101, 106, fig. 10.

= *Erpetosaurus radiatus* (Cope, 1874); NEW SYNONYMY.

SPECIFIC DIAGNOSIS: As for genus.

HOLOTYPE: AMNH 6916, formerly 8584G and 8666G of Columbia University, collected by Prof. John S. Newberry (ca. 1855); laterally compressed anterior portion of a subadult individual, including skull, mandibles, partial ribs, incomplete pectoral girdle and sculation; preserved in counterpart blocks.

HORIZON: Cannel coal below coal seam identified as the Upper Freeport Coal (Newberry, 1871, 1874), Allegheny Group, Middle Pennsylvanian; equivalent to late Westphalian D of Europe (Baird, 1964).

LOCALITY: Coal mines originally owned by the Ohio Diamond Coal Company (Murphy, 1980), Linton, Saline Township, Jefferson County, Ohio; approximately 2.5 km. south of Wellsville, Ohio.

HYPODIGM: See Appendix.

## DESCRIPTION

### SKULL ROOF

The skull is a flat, posteriorly broad structure with gently sloping cheeks. In dorsal view (fig. 1A), the outline of the skull and position of the orbits bear resemblance to the long-snouted trimerorhachoid *Neldasaurus* (Chase, 1965); smaller skulls show proportionally larger orbits and shorter snout lengths. Whether or not the antorbital length of the largest skulls would have equaled that of *Greererpeton* is not known. The skull width is greatest just anterior to the jaw articulation and is roughly 75 percent of the skull length. Although the posterior margin of the skull is modestly embayed in the area of the post-parietal-tabular suture, there is no suggestion of an otic notch. The orbits are directed dor-

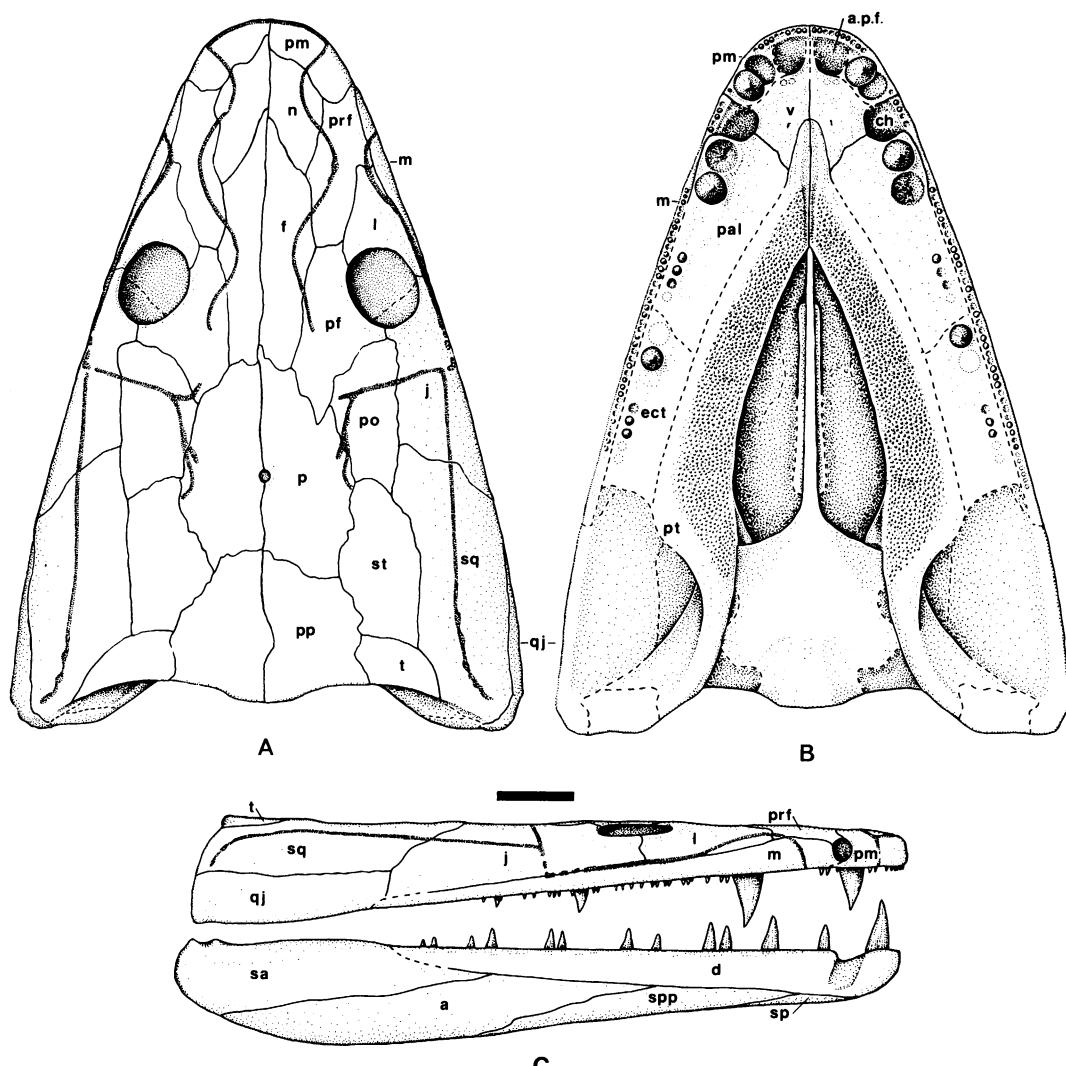


FIG. 1. *Colosteus scutellatus* (Newberry). Restoration of subadult skull and mandible. A, skull in dorsal view; B, skull in ventral view; C, skull and detached mandible in lateral view. Scale equals 1 cm.

sally with their lateral margins slightly lower than the medial. In contrast to contemporary edopoids and trimerorhachoids, the external nares are situated near the skull margin and have no dorsal exposure.

The premaxilla is a robust, tusk-bearing element that forms the bluntly rounded anterolateral margin of the skull. Because crushing has favored exposure of the more massive vertical portions of this bone at the expense of the dorsal and palatal components, the ex-

act nature of the anterior portion of the premaxillary-nasal suture is uncertain. Although the evidence is equivocal, rostral fenestrae, as found occasionally in the loxommatid *Megalcephalus pachycephalus* (Beaumont, 1977), may have perforated the dorsal surface of the snout in this region to accommodate the tips of the parasymphyseal tusks.

At about the level of the anterior margin of the external naris, the premaxilla contacts the prefrontal. From this point on the dorsal

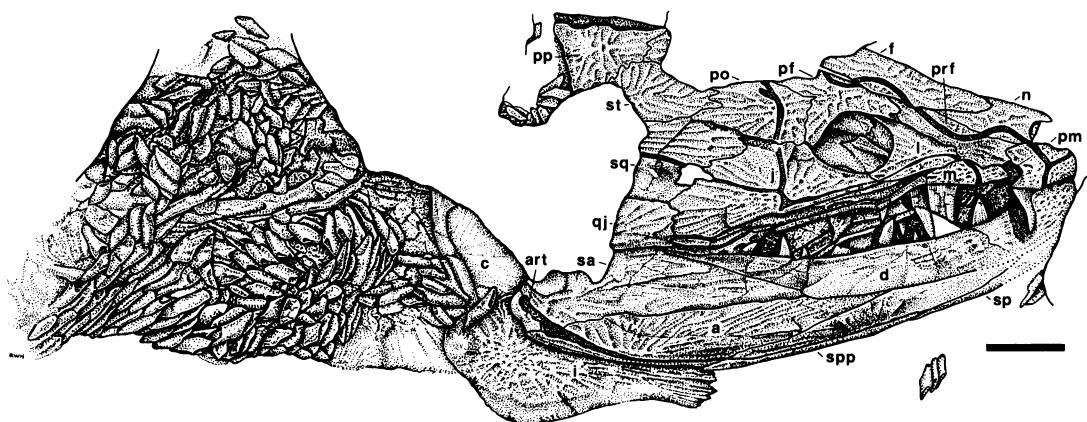


FIG. 2. *Colosteus scutellatus* (Newberry). Subadult skull, mandible, and anterior postcranial skeleton. Right counterpart block of holotype specimen, AMNH 6916. Scale equals 1 cm.

surface, the premaxilla gives rise to a wedge-shaped, posterolateral extension that overlaps the anterior edge of the prefrontal before passing laterally and downward to the external naris. The anterior half of the narial opening is bordered by the premaxilla. Immediately above the premaxillary tusk, a short, unsculptured flange forms the ventral rim of the naris; this flange obviously communicated with an anterior extension of the maxilla, but the precise configuration is unclear.

The maxilla occupies about 75 percent of the lateral skull margin. It attains its greatest height and concomitant dorsal exposure where the infraorbital lateral line sulcus intersects the dorsal edge of the bone, near the level of the vomerine tusk. Immediately above the marginal tooth row, the external surface of the maxilla is nearly vertical and only weakly sculptured. Posteriorly, the maxilla appears to contact the quadratojugal, but the evidence for this is equivocal.

The nasal is a flat bone that is preserved only in subadult specimens (AMNH 6916, fig. 2; 6945, fig. 3A; BM[NH] R.2547, fig. 3B). For half of its length, the nasal is a broad element that contacts the premaxilla laterally while sharing a common medial suture with its partner along the dorsal midline. The posterior half of the bone forms a wedge between the frontal and prefrontal.

Unlike the frontal of most temnospondyls with elongate skulls, the frontal of colosteids is the longest bone of the dorsal midline se-

ries, nearly equaling the length of the skull table. It is also the narrowest element in this series, with a width less than one-fourth its length. At a level slightly posterior to the orbits, the frontal overlaps the parietal in an interdigitating suture.

Previous reconstructions of *Colosteus* (Romer, 1945, 1947, 1966) have shown the prefrontal as not reaching the naris because of an intervening septomaxilla. However, latex casts of AMNH 6916 (fig. 2) and 6945 (fig. 3A) clearly indicate that a septomaxilla is not present and that the prefrontal continues anteriorly between the premaxilla and maxilla to comprise about one-sixth of the external narial border. This uncommon extension of the prefrontal is identical to that of *Greererpeton* (Smithson, 1982).

The configuration of the circumorbital bones is modified from that seen in other colosteids to an arrangement that is unique among all amphibians. In the aforementioned restorations, a posterolateral extension of the prefrontal enters the orbital margin. However, close examination of several well-preserved specimens (AMNH 6916, fig. 2; 6945, fig. 3A; FMNH UC 2001, fig. 4) indicates that the prefrontal is precluded from the orbital margin by an anteriorly directed lacrimal-postfrontal suture. In a somewhat similar fashion, a brief postfrontal-jugal contact on the posterior side of the orbit excludes the postorbital from the circumorbital series. The resulting arrangement of only three

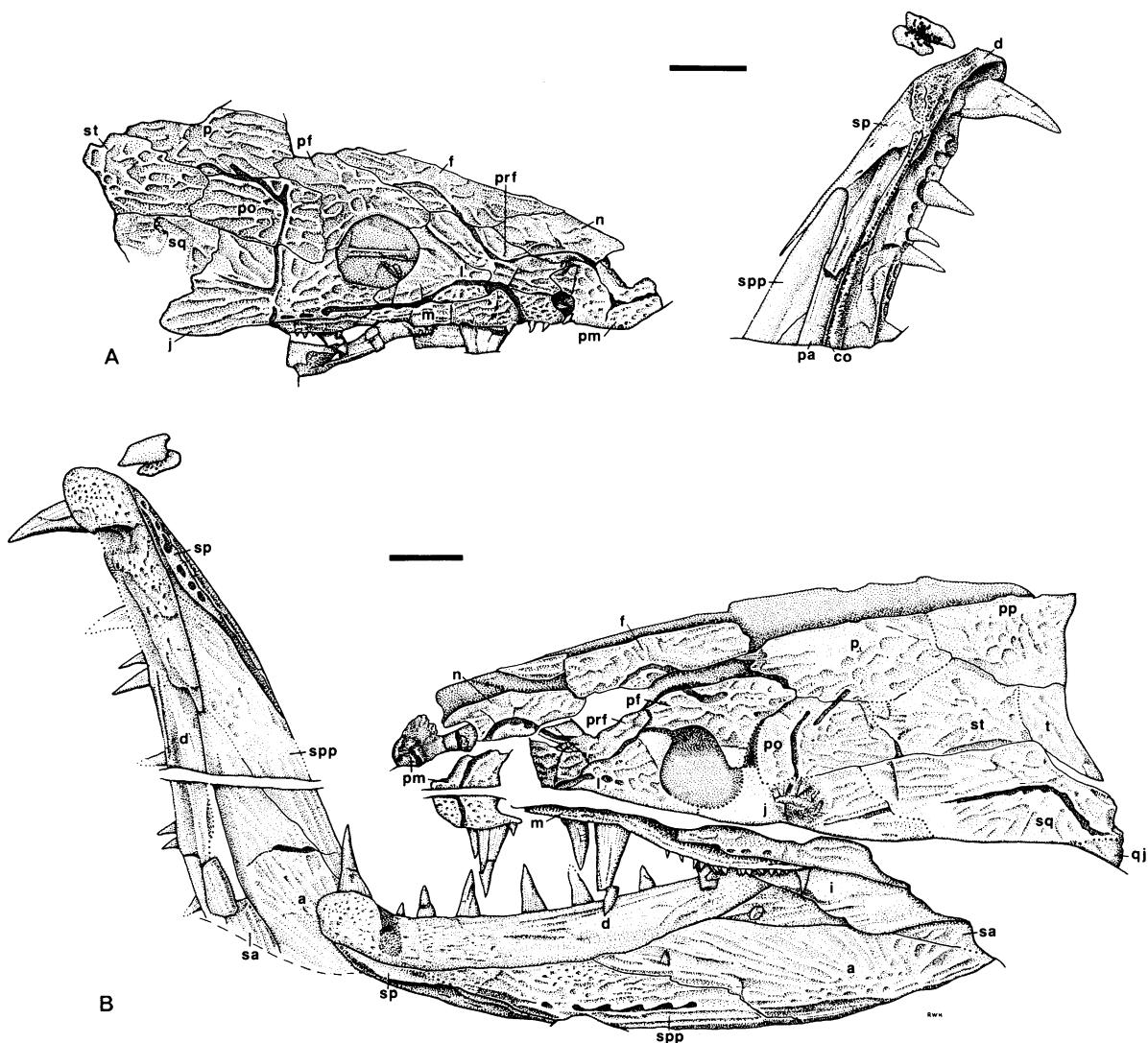


FIG. 3. *Colosteus scutellatus* (Newberry). Subadult skull and mandibles of single individual in counterpart blocks. A, holotype of *Sauroploura longidentata*, AMNH 6945; B, BM[NH] R.2547. Scale equals 1 cm.

bones—jugal, lacrimal, and postfrontal—forming the circumference of the orbit is in contrast to the standard five-bone configuration of most other primitive labyrinthodonts.

The anterior one-third of the orbital mar-

gin is formed by the triangular lacrimal. Because of the prefrontal-maxillary suture, the lacrimal fails to reach either the nasal or the external naris. The postfrontal extends anteriorly above the orbit and between the frontal and lacrimal to meet the prefrontal in a

roughly transverse suture. Posteriorly, the postfrontal expands laterally to meet the jugal and form about one-half of the posterior orbital margin. In adult specimens (AMNH 6826, fig. 5), this contact, as well as the adjoining postfrontal-postorbital suture, is a strongly interdigitating feature that is rarely disrupted by crushing. The posterolateral margin of the orbit is formed by the jugal, the largest bone of the skull roof. Below the orbit, it reaches the posterolateral corner of the lacrimal while laterally overlying the maxilla. Crushing has revealed that the jugal also overlaps the quadratojugal and squamosal posteriorly while its own mediadorsal border is overlain by the lateral edge of the postorbital.

The postorbital is a roughly pentagonal element whose margins overlap those of all surrounding bones. As Smithson (1982) has noted in describing *Greererpeton*, the absence of an intertemporal in colosteids results in an exceptional postorbital-parietal contact. Although the intertemporal is lacking in *Colosteus*, its presence is often mimicked by the truncation of the abbreviated temporal sulcus of the lateral line system near the anterior end of the parietal-supratemporal suture (see figs. 3–6); this groove, usually constricted by postmortem crushing, resembles the medial boundary of a much-reduced intertemporal element.

The remainder of the skull roof is virtually identical with that of *Greererpeton* in all respects. The parietal is the largest bone of the skull table and attains its greatest breadth at the level of the pineal foramen. The postparietal is nearly two-thirds the length of the parietal and, with its partner, comprises about one-third of the posterior skull margin as seen in dorsal view. In the reduced two-element temporal series, the supratemporal contacts the postparietal posteromedially in typical temnospondyl design, and a crescent-shaped tabular extends laterally to embay the posteromedial corner of the squamosal. On the basis of material in which the cheek had separated from the skull table (AMNH 6915, fig. 6; 6932, fig. 7A), Romer (1930) interpreted this scallop as the lower rim of an otic notch. This misconception was reinforced by the attribution of AMNH 6918, a specimen with

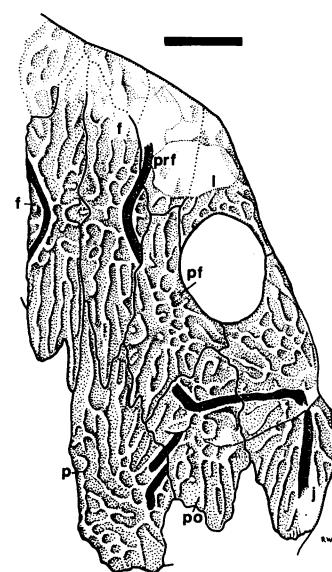


FIG. 4. *Colosteus scutellatus* (Newberry). Portion of subadult skull roof in dorsal view. FMNH UC 2001. Scale equals 1 cm.

distinct otic notches, to *Colosteus* (Romer, 1930, fig. 8, above right); this specimen is actually a large individual of *Erpetosaurus radiatus* (Baird, personal commun.).

One subadult specimen (AMNH 6915, fig. 7B) partially exposes the underside of the skull table to display the rudiments of the attachment structures for the braincase. These same features are much better developed in mature specimens of *Greererpeton* (Smithson, 1982, fig. 13B). Paired rugosities located posteriorly on each side of the dorsal midline indicate where the exoccipital reached the postparietal. Laterally, a ventral flange on the tabular received the paroccipital process from the braincase, as well as the epipterygoid from the palatal complex. An occipital "button" such as is present on the chamfered posterior edge of the tabular of *Greererpeton* and *Pholidogaster* is not exposed in the material at hand. An occipital expansion of the postparietal and tabular, as characteristically developed in trimerorhachoids (Coldiron, 1978), is absent in all colosteids.

The preservation of the skull table-cheek junction ranges from undisrupted to completely detached. The latter state is not in-

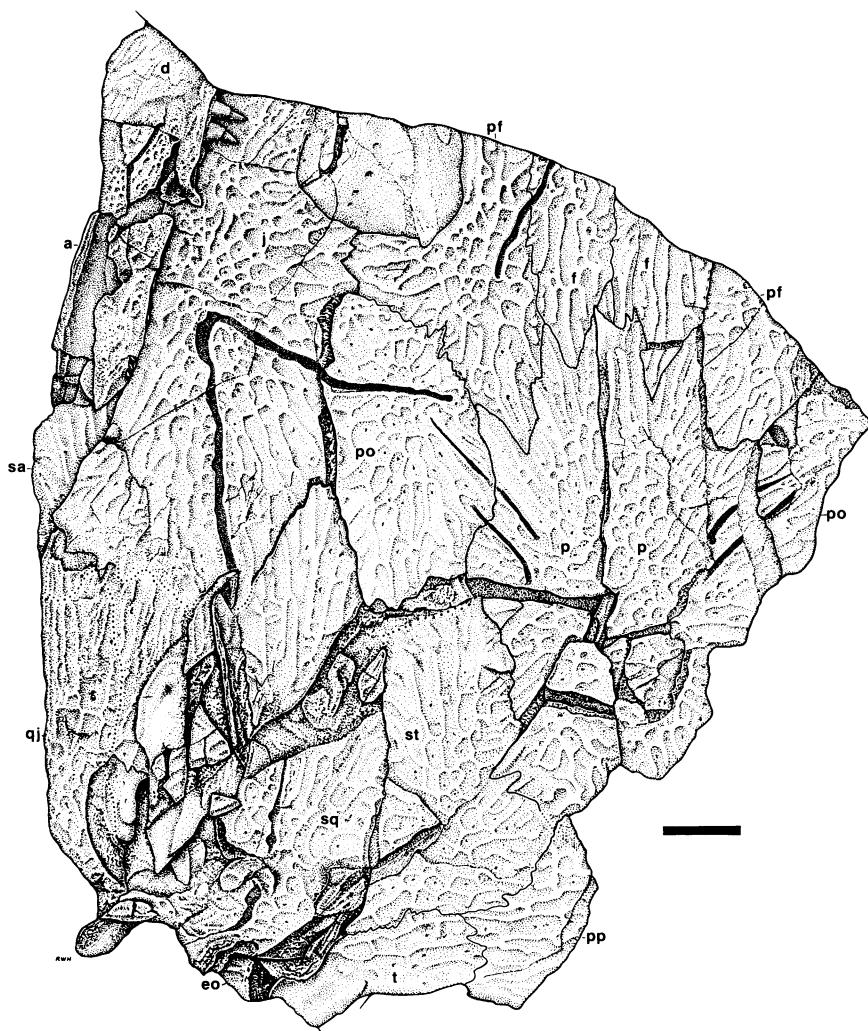


FIG. 5. *Colosteus scutellatus* (Newberry). Postorbital region of adult skull and partial mandible. Paratype of *Macrerpeton deani*, AMNH 6826. Scale equals 1 cm.

dicative of a partially kinetic skull (A. R. Milner, 1980a), but simply the poorly sutured condition of immature specimens.

The squamosal is a large bone that overlaps the edge of the skull table from the posterior skull margin to about the level of the pineal foramen. Laterally, the squamosal joins the quadratojugal, a subrectangular element that forms the greater part of the lateral wall of the subtemporal fossa. Like the maxilla, the marginal portion of the quadratojugal is weakly sculptured. Towards its posterolateral

corner, the quadratojugal has a distinct flange that continues posteriorly onto the occipital surface. Although the actual quadrate-quadratojugal suture, as well as a paraquadrate foramen, is not preserved in any specimen, the quadratojugal appears to contribute to the jaw articulation in a manner similar to that of *Eugyrinus* (A. R. Milner, 1980a).

#### PALATE

There is an unfortunate lack of reasonably well-preserved specimens to furnish infor-

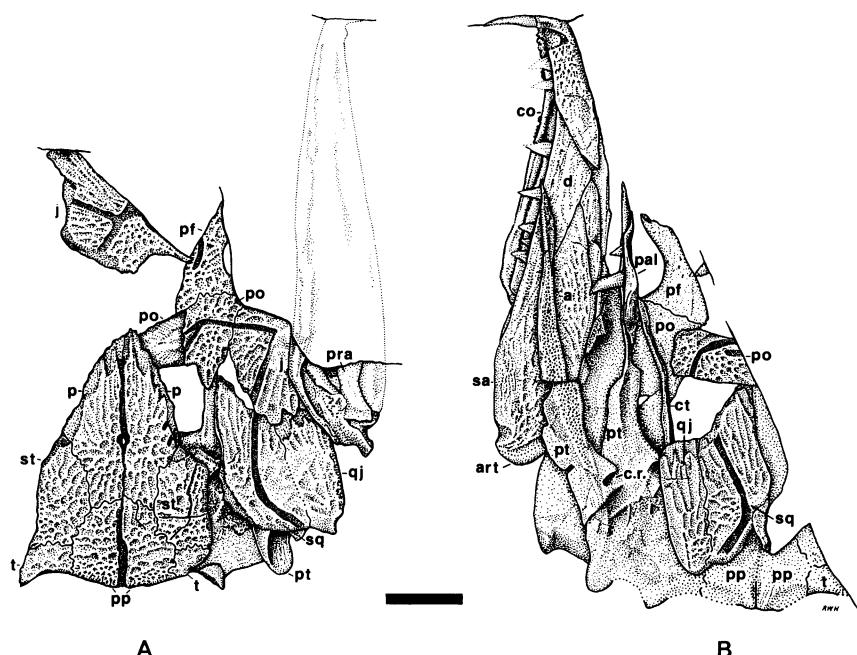


FIG. 6. *Colosteus scutellatus* (Newberry). A, B, postorbital region of subadult skull and mandible. Counterpart blocks of AMNH 6915. Scale equals 1 cm.

mation on the structure of the palate and braincase. No single specimen approaches completeness, most are subadult, and all are disarticulated. These inadequacies, combined with the erroneous assumption that *Colosteus* and *Erpetosaurus* were members of the same family, led Romer (1930, p. 104) to assert that the palate of *Colosteus* was similar "in most respects" to the relatively well-represented palate of *Erpetosaurus*. However, study of all palatal materials attributable to either form indicates that previous suppositions are unfounded and that marked differences exist. In short, the palate of *Colosteus* (fig. 1B) is characterized by anterior palatal fenestrae, a formidable complement of marginal tusks, denticulated pterygoids enclosing long but relatively narrow interpterygoid vacuities, and an unfused basal articulation.

The medial border of the choana is shared equally by the vomer and palatine. As restored from the slightly disrupted left side of AMNH 6932 (fig. 7A), the lateral margin of the choana is enclosed mainly by the maxilla,

whereas the palatal flange of the premaxilla makes a minor contribution to the anterior portion of the opening. This roughly circular outline of the choana is unlike the elongate or irregular openings commonly possessed by primitive amphibians.

In addition to the choanae, the anterior region of the palate is perforated by a second set of openings that would have received the elongate parasympathetic tusks upon closure of the jaws (AMNH 6951, fig. 8). These anterior palatal fenestrae are close-set along the midline and encircled by the premaxilla anterolaterally and the vomer posteromedially. Although this construction differs from the single median fenestra of ichthyostegids (Jarvik, 1980) and some loxommatids (Beaumont, 1977), it resembles the paired condition common to most trimerorhachoids (Chase, 1965).

The margin of the palate is bounded anteriorly by the massive tusk-bearing premaxilla. As preserved on CM 25307 (fig. 7B), the posterolateral portion of this bone is expanded beneath and thickened in front of the ex-

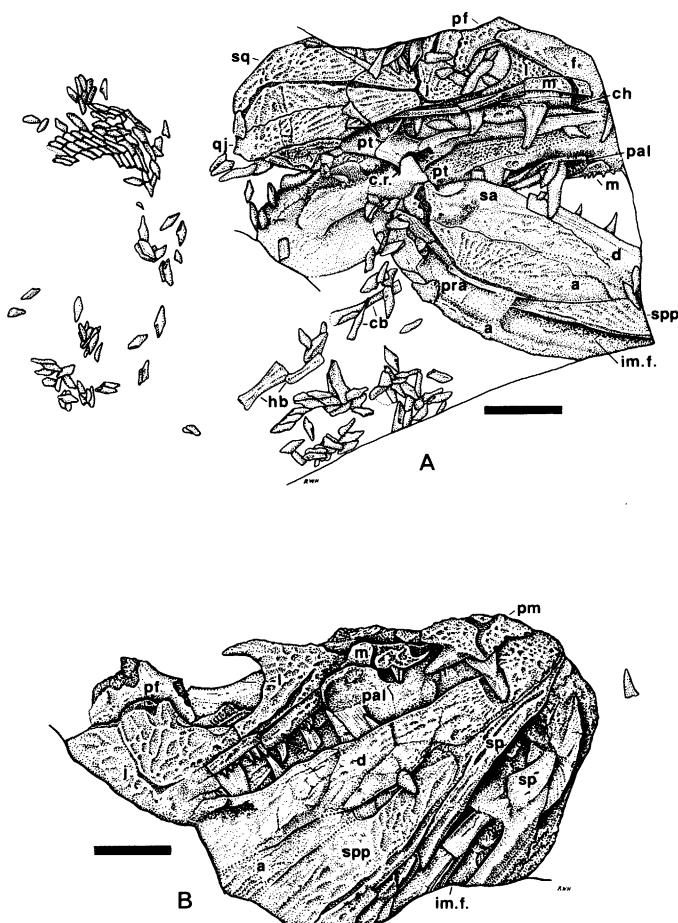


FIG. 7. *Colosteus scutellatus* (Newberry). A, postorbital region of subadult skull and mandibles with disarticulated branchial arches. Paratype of *Sauropleuria newberryi*, AMNH 6932. B, anterior portion of subadult skull and mandibles. Right counterpart block of CM 25307. Scale equals 1 cm.

ternal naris to accommodate the tusk and replacement pit. There are no specimens that delimit the medial extent of this palatal flange.

The maxilla forms much of the lateral margin of the palate. At the level of the choana, the ventral edge of the maxilla is expanded slightly to form the lateral rim of the opening. Posteriorly, this element probably contributes to the lateral wall of the subtemporal fossa.

Two specimens (AMNH 6951, fig. 8; CM 25307, fig. 7B) provide information on the structure of the vomer. A thin anterior process extends medially from the main body of each bone to contact the premaxilla and sep-

arate the anterior palatal fenestrae. Posteriorly, along the midline, the medial corner of the vomer is extensively underlain (overlain in ventral view) by a robust, finger-like anterior process of the pterygoid. Crushing has revealed that the vomer-palatine suture, a diagonal contact directed posteriorly toward the midline, is also constructed in a stepped manner. The area of the vomer that would support small palatal tusks, as seen in *Greererpeton*, is not exposed. A small but distinct foramen appears in the central portion of the bone; close scrutiny of *Greererpeton* (Cleveland Museum of Natural History 11068) reveals the presence of the same struc-

ture. In *Edops*, this opening is thought to be associated with a branch of the palatine nerve (Romer and Witter, 1942).

The sutures between the remaining dermal bones of the palate—palatine, ectopterygoid and pterygoid—are indiscernible. Presumably, there was an extensive longitudinal contact shared by the pterygoid and the two lateral elements; that this area is not well preserved in subadult specimens of either *Colosteus* or *Greererpeton* is attributable to the thin nature of the palate in this area.

Although the tusks of the palatine and ectopterygoid are visible in several specimens, the palatal surfaces of these bones are poorly exposed. Immediately behind the choana, the palatine supports a large tusk pair, whereas the posterior half of the bone bears a row of smaller accessory teeth. Exposure of the dorsal surface of the left palatine on AMNH 6915 (fig. 6B) indicates that it was overlapped posteriorly by the ectopterygoid in a well-developed tongue-and-groove suture. The palatine appears to have had little dorsal development against the marginal elements of the skull roof.

What appears to be the socketed ventral surface of the right ectopterygoid is exposed between the jaws of the holotype specimen (AMNH 6916, fig. 2). This bone apparently supported a tusk pair anteriorly at about the mid-orbit level and a row of accessory teeth posteriorly near the subtemporal fossa. The form of the anterior margin of the fossa and the development of the ectopterygoid in this area remains unknown (*contra* Coldiron, 1974).

The morphology of the pterygoid agrees in all respects with that of *Greererpeton*. In contrast to *Erpetosaurus* and other trimerorhachoids, the pterygoids of *Colosteus* join at the midline, in front of the interpterygoid vacuities, and extend forward to the postero-medial corners of the vomers; thus, the interpterygoid vacuities are completely enclosed by the pterygoids. In addition, the sides of the openings show little lateral expansion, unlike the more lyrate outlines exhibited by most temnospondyls. Further analysis of the proportions of the interpterygoid vacuities is inappropriate since their development is largely size dependent and they are only exposed in subadults.

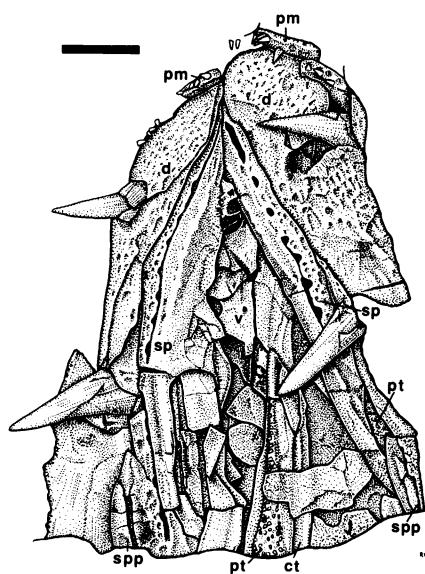


FIG. 8. *Colosteus scutellatus* (Newberry). Anterior half of subadult skull and mandibles in ventral view. Left counterpart block of AMNH 6951. Scale equals 1 cm.

The width of the flat palatal ramus of the pterygoid increases gradually from the narrow anterior process to the anterior border of the subtemporal fossa. At the latter level, the medial portion of the bone is thickened dorsally and recurved medially to form a triangular basal process (internal process of Watson, 1956). The morphology of the basal articulation, as judged from the partial medial exposure of the right pterygoid on AMNH 6915 (fig. 6B), conforms to that of *Greererpeton* (Smithson, 1982, fig. 13). A well-defined concavity in the posterior wall of the basal process represents the conical recess into which the basipterygoid process of the braincase inserts (Romer, 1947). This socket is essentially a U-shaped notch in the medial wall of the central body; it is bounded anteriorly and ventrally by the posteroventral flange of the basal process, and posteriorly by a vertical process arising from the narrowed ventral surface of the pterygoid. The low ridge present on the lateral wall of the conical recess of *Greererpeton* (Smithson, 1982) is not preserved in any specimen. Likewise, the dorsal portion of the central body

is not exposed and a pterygoid-epipterygoid suture is not visible.

Posterior to the basal articulation, the vertically oriented quadrate ramus of the pterygoid continues posterolaterally to form the internal wall of the subtemporal fossa and contact the squamosal, tabular, and quadrate. Immediately behind the conical recess, an elongate depression develops in a horizontal plane above the rounded medioventral lip of the quadrate ramus. This elongate pocket, commonly known as the excavatio tympanica because of its supposed association with a middle ear cavity (Bystrow and Efremov, 1940), has been reinterpreted recently as the homologue of the spiraculo-hyomandibular recess of rhipidistian fishes (Smithson, 1982). On the basis of *Greererpeton*, Smithson has proposed that this area of the quadrate ramus braced the ventral portion of the stapes which, in turn, supported the braincase. Unfortunately, *Colosteus* cannot be used to evaluate this hypothesis since no stapes can be identified among the remains.

The remainder of the quadrate ramus and its contact with the skull roof and quadrate are generally difficult to interpret. Only the inturned posterior edges of the squamosal and tabular on the left side of AMNH 6932 (fig. 7A) provide evidence that the construction of this region does not differ significantly from *Greererpeton* (Smithson, 1982, fig. 12). A discrete quadrate ossification is not exposed on any specimen; hence, the configuration of the jaw articulation remains unknown.

#### PARASPHENOID AND BRAINCASE

Little can be said of the detailed morphology of the parasphephenoid from the fragmentary remains present. The cultriform process conforms to the primitive temnospondyl form of an elongate, narrow structure with a V-shaped cross section (Romer, 1947). On AMNH 6951 (fig. 8), the displaced anterior end of the process is reduced to a splint of bone that appears to have been sandwiched ventrally by the pterygoids at their forward confluence. If the cultriform process reached the vomers dorsally, the contact would have been meager.

The expanded posterior section of the

parasphephenoid that apposed the underside of the braincase is exposed only in AMNH 6915 (fig. 6), but is so poorly preserved that description is not possible. What appears as a parasphephenoid body associated with the left pterygoid of AMNH 6932 (fig. 7A) is actually the severely distorted posterior half of the right pterygoid.

The predominantly subadult nature of the specimens at hand and coincident lack of endochondral ossification make identification of braincase structures tenuous at best. However, the situation is immeasurably improved in *Greererpeton* and the reader is referred to Smithson (1982) for a detailed account of the colosteid braincase and associated structures.

The lower half of the sphenethmoid is exposed in lateral view between the parted jaws of the holotype specimen (AMNH 6916, fig. 2). As reconstructed, the anterior end of this structure terminated at about the level of the anterior orbital margin. The structural relationship between the sphenethmoid and otico-occipital components cannot be determined.

Resting between the lateral margin of the skull table and right cheek of AMNH 6915 (fig. 6) is an amorphous mass of unfinished bone. The outline of the left basipterygoid process can be seen in dorsal aspect at the broadened posterior end of the cultriform process, just opposite the parietal-supratemporal suture. Adjacent to this area, a conical structure bearing a concave face at its expanded end represents the remnants of the basioccipital. A second, much larger specimen (AMNH 6826, fig. 5) provides a glimpse of what is probably an exoccipital.

#### MANDIBLE

Each mandibular ramus can be divided into three regions: a swollen posterior end that accommodates the glenoid and adductor fossae, a medially fenestrated midsection that supports coronoid and dentary tooth rows, and a bluntly rounded anterior portion that bears the characteristic labial notch and large parasymphysial tusks. Anteriorly, the rami are firmly sutured together at the jaw symphysis. In lateral aspect (fig. 1C), the jaw articulation is in line with the tooth row and

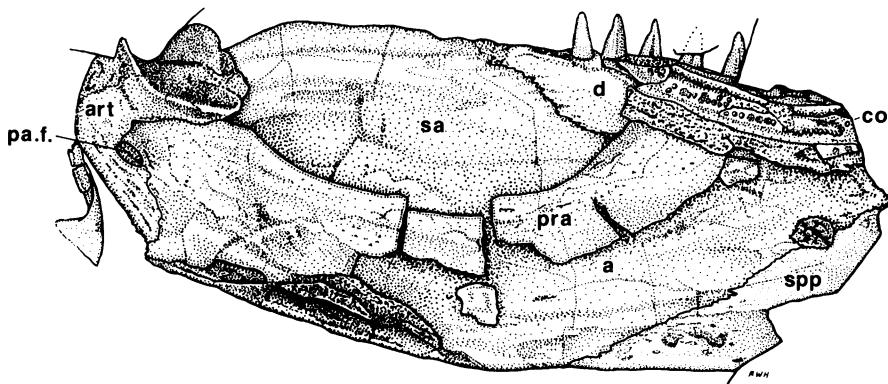


FIG. 9. *Colosteus scutellatus* (Newberry). Posterior portion of adult mandible in medial view; most of prearticular is absent to expose medial surface of angular. Holotype of *Macrerpeton deani*, AMNH 2934. Scale equals 1 cm.

the evenly rockered ventral outline attains its greatest depth at the level of the anterior limit of the adductor fossa.

The dentary is the dominant bone of the lower jaw and contacts all other mandibular dermal elements except the prearticular. Posteriorly, the dentary contributes to the anterolateral border of the adductor fossa. Over most of its dorsal exposure, the bone consists of a raised tooth-bearing platform that is stepped lingually to adjoin the coronoid shelf. As seen on AMNH 6945 (fig. 3A), the width of the platform varies with the diameter of the alveoli. At the anterior end of the tooth row, the dentary curves toward the midline and expands to contain the sizeable alveoli of the parasympathetic tusks. Externally, at this level, the bone approaches its maximum height and displays a striking U-shaped notch that afforded passage to the premaxillary tusk upon closure of the jaws. The strongly punctate anteromedial face of the dentary comprises at least three-quarters of the symphyseal surface.

The splenial forms the anterior one-third of the ventral jaw margin and makes a minor contribution to the symphysis as it joins its fellow below the dentaries. The elongate Meckelian fenestra (foramen intermandibularis communis of Heaton, 1980a) divides the posterior half of the splenial into an upper expanse that shoulders the coronoids later-

ally, and a lower splint that tapers against the postsplenial posteriorly. Between the symphysis and the fenestra, the main body of the splenial is perforated by two small foramina.

The splenial-prearticular suture above the Meckelian fenestra cannot be determined with certainty. On AMNH 6945 (fig. 3A), the splenial appears to end abruptly, but is apposed internally by an anterior extension of the prearticular. Following this interpretation, the reduced lingual wall of the Meckelian space consists almost exclusively of a considerably elongate prearticular. Posteriorly, where it encloses the adductor fossa, the prearticular appears slightly thickened but is thin elsewhere. A fairly large, ovoid para-articular foramen (Romer and Witter, 1942) for the chorda tympani is situated on the prearticular-articular suture (AMNH 2934, fig. 9). Although not completely preserved on any specimen, the prearticular-angular suture probably spanned the medial jaw surface between the articular and the Meckelian fenestra.

The sutures subdividing the coronoid series cannot be traced and the tusk-bearing anterior coronoid of *Greererpeton* is not preserved. A narrow, elongate bone possessing a single row of very small teeth, visible on AMNH 6915 (fig. 7) and 6945 (fig. 3A), is undoubtedly a coronoid element. Although its morphology differs markedly from the

broad, densely denticulated coronoid pavement of *Greererpeton*, it is very similar to that of ichthyostegids (Campbell and Bell, 1977; Jarvik, 1980) and *Doragnathus* (Smithson, 1980b). The only other coronoid segment is preserved on AMNH 2934, the posterior third of a very large mandible. Here, the same general morphology persists, but the minute teeth occasionally occur two abreast. In addition, the posterior edge of the coronoid encloses only the anteriormost part of the adductor fossa. No coronoid process is developed.

The sutures separating the splenial, post-splenial, angular, and surangular form a posteriorly directed *en echelon* pattern from the ventral edge of the dentary to the bottom of the mandible. On the lateral face, the postsplenial extends far anteriorly, nearly reaching the posterior lip of the dentary notch. This condition is more like that of *Pholidogaster* (Panchen, 1975, fig. 15) than *Greererpeton* and may indicate that the antorbital region of even the largest *Colosteus* skull was proportionally shorter than that of *Greererpeton*. The angular has an extensive lateral exposure and wraps around the ventral margin of the jaw to contact the prearticular and enclose the posteroventral corner of the intermandibular fenestra.

In form and sculpture, the surangular resembles the quadratojugal. Not only do both elements enclose the outer face of the adductor chamber, but they also contribute to the lateralmost portions of the jaw articulation surfaces. The dorsal outline of the surangular is raised slightly above the upper surface of the dentary in a subtle convexity. Crushing on AMNH 2934 has plainly revealed that the surangular constitutes about one-fourth of the jaw articulation surface; the same holds true for *Greererpeton* (Smithson, 1982), *Doragnathus* (Smithson, 1980b), and possibly *Caerorhachis* (see Holmes and Carroll, 1977, fig. 5). The presence of even a modest retroarticular process on *Colosteus* appears unlikely.

The articular occupies the posterior portion of the mandible between the lateral and medial dermal elements. As best represented by AMNH 2934, the glenoid fossa of the articular appears as a simple trough between

distinct condyloid processes. From above, the depression is an anteriorly open crescent whose tangent is perpendicular to the skull midline. In contrast to the majority of Carboniferous amphibians, the jaw articulation is not raised or depressed relative to the tooth row, but virtually on the same horizontal plane.

#### DENTITION

A complete description of the dentition is not possible because the palatal margins and lower jaws are incompletely exposed. In attempting to reconstruct dental batteries, conservative estimates were favored; therefore, it is likely that some tooth counts were actually greater than those shown in the restorations. Moreover, since postmortem crushing has dislocated and distorted most of the large teeth, their appearance in the somewhat stylized reconstructions differs from that of the specimen drawings.

The marginal teeth of the premaxilla and maxilla are simple acuminate pegs in lateral aspect ("bullet shaped" of Smithson, 1980b, p. 920). It is difficult to say how tooth replacement occurred since some marginal teeth have undoubtedly fallen away. Where the bases of the massive palatine tusks impinge upon the internal surface of the maxilla, the tooth row is discontinuous, as in *Caerorhachis* (Holmes and Carroll, 1977); since the presence of this feature cannot be verified in adult material of either *Colosteus* or *Caerorhachis*, it is possible that this condition is size-related. There is an increase (about 40%) in tooth length anteriorly along the maxillary row, but no discrete canine peaks. The maxillary tooth count cannot be estimated with any confidence because no specimens expose more than a small portion of the tooth row and the posterior extent of the series is unknown.

The marginal teeth of the premaxilla are smaller than the anterior maxillary teeth. On the premaxilla, there is room for a continuous row of 10 teeth anterior to the premaxillary tusks. An isolated, smaller marginal tooth is usually located on the posterolateral corner of the palatal flange of the premaxilla.

The occurrence of tusk pairs on the pre-

maxilla and palatine conforms to the standard replacement pattern of a single tusk accompanied by a replacement pit. Some specimens (AMNH 6915, fig. 6B; 6951, fig. 8) possess an intermediate condition in which both alveoli of the palatine are occupied by tusks of disparate sizes. The length of the premaxillary tusk is usually two and one-half times its basal diameter and about 10 percent shorter than the palatine tusk. In labial aspect, the tusks of both bones appear as evenly tapered cones with sharply defined tips.

The palatine also bears a series of at least three alveoli posterior to the tusk pair. These alveoli housed accessory teeth that were two to three times the length of the marginal teeth. On small specimens (AMNH 6932, fig. 7A), the alveoli are simple depressions that lack the coarse, radiating ridges characteristic of larger replacement pits.

As previously noted, the small teeth present on the vomers of *Greererpeton* are not preserved in any specimens of *Colosteus*. However, the general agreement between the anterior portions of the palates of these two forms justifies the reconstruction of such teeth in *Colosteus*. There are clearly no enlarged vomerine tusks present in any colosteid.

The ectopterygoid appears to support at least two tusks of intermediate size that resemble the general dagger-like form of other palatal tusks (BM[NH] R.2547, fig. 3B). The anterior ectopterygoid tusk, situated just behind the palatine-ectopterygoid suture, is the larger of the two, with a length equal to approximately two-thirds that of the premaxillary tusk. Although not exposed on any specimens, it is likely that this tusk is associated with a replacement pit. At about the level of the jugal flexure, a second tusk projects below the marginal tooth row. This smaller tusk may be one of a series of accessory teeth borne by the posterior half of the bone.

The parasympathial tusks of the lower jaw are similar in both size and shape to the large palatal tusks. They occur in the typical tusk-and-pit combination on each side of the symphysis and are slightly recurved toward their apices. The other dentary teeth are less acuminate but still of considerable size. On CM 25307 (fig. 7B), the ratio between the lengths

of dentary and maxillary teeth from the same level is about 5:1. The dentary tooth row spans the distance from the labial notch to the adductor fossa and affords space for an estimated  $21 \pm 2$  teeth.

A sequence of minute coronoid teeth is situated along a shelf below the dentary tooth row, on the lingual side of the mandible. Anteriorly, this presumably replaceable series is limited to a single row, but posteriorly, near the adductor fossa, it bears irregularly placed, side by side tooth pairs. Nowhere do the coronoids display the shagreen of denticles exhibited by *Greererpeton*.

The development of denticles on the palatal surface is limited to the palatal ramus of the pterygoid. Furthermore, the denticulated platelets commonly associated with the palates of other Linton temnospondyls (e.g., *Erpetosaurus*, *Saurerpeton*, *Stegops*) are not present in *Colosteus*.

#### DERMAL SCULPTURE AND LATERAL LINE CANALS

The dermal sculpturing of the skull roof and lower jaws has been reproduced in all specimen drawings. The predominant pattern, as described originally by Romer (1930, p. 103), is one of "pits in the center of each element, from which ridges, bifurcating, radiate toward the periphery. The enclosed valleys deepen centrally, where a pore is present."

In the absence of a sufficient number of reasonably complete specimens, the development of the dermal sculpture provides a subjective means by which proportional changes accompanying absolute growth may be discussed. More specifically, areas of the skull that exhibit a preponderance of elongated pits are considered as zones of intensive growth (Bystrow, 1935). At least three areas of this type are evident in *Colosteus*: an antorbital region posterior to the nares, a central cheek region lying between the ossification centers of the jugal, squamosal, and quadratojugal, and a dorsal midline region radiating anteriorly from the pineal foramen to about the level of the mid-orbit. The differential growth of these zones indicates that certain proportional changes are to be expected with an increase in size, namely an

elongation of the snout, a broadening and deepening of the cheek accompanied by a posterior shift in the jaw articulation, and a slight posterior migration of the pineal foramen. These trends are not unusual, however, for similar patterns have been noted in a variety of other Paleozoic amphibians (Beaumont, 1977; Bossy, ms; Boy, 1972; Langston, 1953; Panchen, 1970; Romer, 1939; Watson, 1963).

In addition to dermal sculpture, the skull surface is modified by a well-developed lateral line system. Regardless of skull size, the sulci are expressed as continuous, steep-sided, flat-bottomed channels, not unlike the grooves commonly found in other temnospondyls; however, this condition contrasts with the partially enclosed networks of *Greererpeton* and *Pholidogaster* (Smithson, 1982; Panchen, 1975).

The exact pattern of the lateral line system is somewhat variable in the postorbital region and can even differ between opposite sides of the same skull. The temporal sulcus is usually split into two short, subparallel branches situated on the lateral third of the parietal. These canals are connected anterolaterally before joining the supraorbital and infraorbital canals in the center of the postorbital. Temporal grooves are not developed posteriorly as they are sometimes on the supratemporals of *Greererpeton* (Romer, 1969, fig. 2).

In its fullest development, the posterior part of the supraorbital sulcus consists of a very short groove that is limited to the postorbital and conjoined to the temporal and infraorbital canals posteriorly. After disappearing from the skull roof at the postorbital-postfrontal contact, the supraorbital lyra is visible again near the ossification center of the postorbital; from this point the canal undulates anteriorly over the frontal, prefrontal, nasal, and premaxilla. Close to the anterolateral corner of the snout, the channel receives the ethmoid commissure medially before terminating near the anterior border of the premaxillary tusk.

From the meeting of the temporal and supraorbital canals on the postorbital, the infraorbital sulcus extends anterolaterally across the medial half of the jugal and receives the

jugal canal before forming the jugal flexure. The sulcus is usually "bridged over" several times in the vicinity of this right-angle bend. Continuing anteriorly along the jugal-maxillary suture, the infraorbital canal is flexed anteromedially at the level of the anterior margin of the orbit to form a medially convex arch on the lacrimal. At the intersection between the lacrimal, maxilla and prefrontal, the canal turns laterally and meets the skull margin at the level of the posterior rim of the choana.

The jugal sulcus is continuous from the posterior margin of the squamosal to the middle of the jugal, where it is joined to the infraorbital sulcus.

The occipital commissure of the lateral line system figured by Steen (1931, fig. 6) cannot be traced on any specimens. Examination of a latex peel of her material (BM[NH] R.2547, fig. 3B) reveals that the supposed sensory canal is actually poorly preserved dermal sculpture.

The mandibular sulcus extends the length of the jaw ramus and is continuous across the jaw symphysis. Posteriorly, the canal is superimposed upon the articular-surangular suture before turning inward slightly and continuing anteriorly along the ventral rim of the jaw where it is frequently constricted or enclosed. A faint longitudinal groove is present near the upper margin of the lateral face of the dentary of some specimens (BM[NH] R.2547, fig. 3B; AMNH 6829). This may represent a poorly developed oral sulcus of the lateral line system.

#### BRANCHIAL ARCHES

There are at least two subadult specimens which exhibit remains of the partially ossified branchial apparatus. AMNH 6932 (fig. 7A) displays an association of three or four branchial elements among a disrupted patch of scales. Two of these structures are subrectangular in outline with rough, unfinished surfaces and slightly expanded ends. These are probably hypobranchials. The identities of the two more elongate structures are less obvious, but may be regarded as ceratobranchials. Support for this interpretation is provided by AMNH 6917 (fig. 12A, B), a

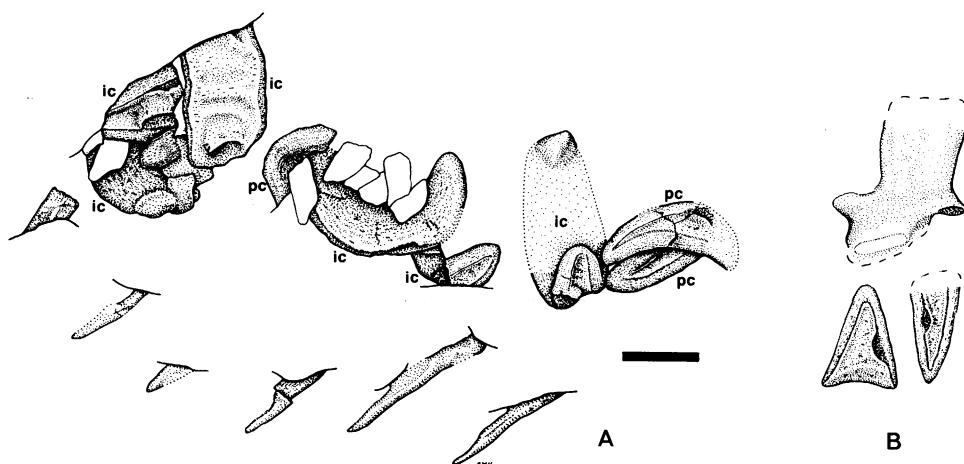


FIG. 10. *Colosteus scutellatus* (Newberry). Posterior presacral vertebrae. A, central elements as preserved on MCZ 2158; B, "exploded" restoration. Scale equals 1 cm.

specimen that exhibits an assemblage of plain bladelike and minute toothed structures. When present in other juvenile temnospondyls, the toothed elements have been regarded as gill rakers of the ceratobranchials (Bereman, 1973; Boy, 1972; Milner, 1982).

The significance of these partially ossified branchial elements is difficult to judge on such exiguous material. Although both specimens represent small subadults, comparably sized individuals (e.g., AMNH 6915, 6916, 6945) do not exhibit such remains. The retention of branchial arches in adults cannot be verified because the pharyngeal region is not favorably exposed on such specimens. Similarly, the mechanical techniques employed in the preparation of *Greererpeton* largely preclude recognition of branchial remains.

#### POSTCRANIAL REMAINS

The postcranial skeletons of Linton edopoids, loxommatids, and anthracosaurs are virtually unknown. This necessitates a degree of conservatism in attributing isolated postcranial materials to any particular labyrinthodont genus. However, recognition of the distinct colosteid scalation and study of the similar postcranial skeleton of *Greererpeton* facilitate the identification of postcranial remains of *Colosteus*. Nonetheless, there is an

inadequate record of the axial skeleton and a total lack of information on the pelvic girdle and hindlimbs.

**AXIAL SKELETON:** Although the uniqueness of the dermal scales aids in the identification of postcranial remains, their profusion frequently obscures the morphology of underlying elements. Vertebrae, for example, are usually represented solely by bulges in the pavement of body armor. Consequently, much significant information, such as atlas-axis construction, presacral length, and regional variation, remains inaccessible.

The following description and reconstruction of vertebral elements is based primarily on MCZ 2158 (fig. 10A). This specimen includes parts of 14 ribs, 10 intercentra, and an undetermined number of pleurocentra and neural arches, all exposed by postmortem disruption of the dorsal scalation. Direct comparison with articulated skeletons of *Greererpeton* indicates that the preserved area represents a far-posterior segment from the dorsal series of a large individual.

The general form of the vertebrae (fig. 10B) approaches the schizomeric condition first elucidated by Romer (1964) in *Pholidogaster*. A moderately large notochordal space is partially enclosed by a dorsally open intercentrum and paired pleurocentra. In their crushed and dissociated state, it is difficult to establish

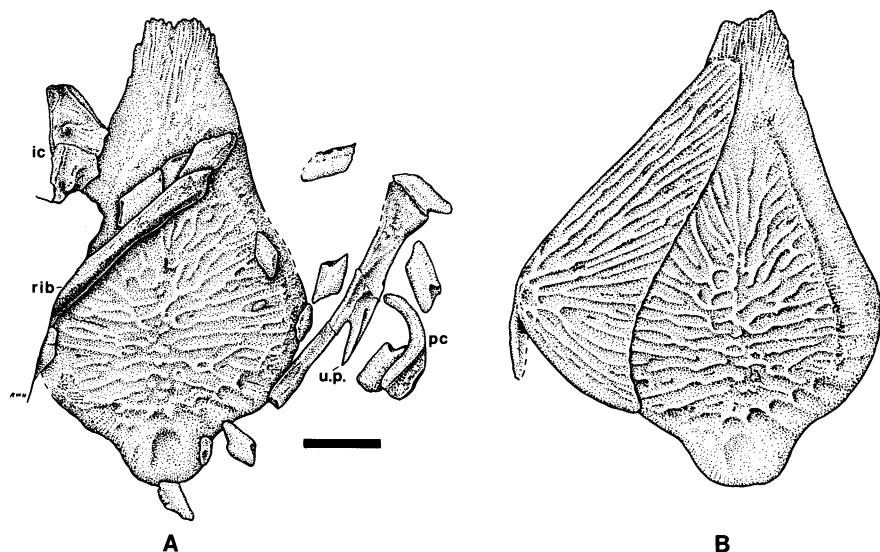


FIG. 11. *Colosteus scutellatus* (Newberry). A, anterior intercentrum, pleurocentrum, ribs, and interclavicle. Paratype specimen, holotype of *Colosteus pauciradiatus*, AMNH 6920; B, restored interclavicle and right clavicle in ventral view. Scale equals 1 cm.

the proper alignment of the pleurocentra relative to other vertebral components. Since all exposed edges of the pleurocentra are unfinished, however, it is probable that modest dorsal and ventral gaps were filled by cartilage in life. This functionally diplospondylous configuration is the same as that seen in the more completely ossified *Greererpeton*.

The intercentra of posterior presacral vertebrae conform to the general rhachitomous design of a crescentic, ventrally robust husk, with wedge-shaped, upturned sides. Anteriorly in the presacral series, the ascending processes extend farther dorsally than in the posterior sections of the column. Internally, the bone surface is rough and unfinished. This texture continues around the edges and onto the external surface, where it is modestly developed ventrally, but widely exposed on the ascending process. Elsewhere, the external surface is covered with dense periosteal bone that bears minute, irregular pits.

The ventral surface of the intercentrum is thickened near its anterior and posterior margins to produce a generally concave profile. A distinct longitudinal ridge is situated medially and is flanked by two less developed

ridges that denote the roots of the ascending processes. The periosteal field of the process is deeply recessed except where it is gathers to form the anterior boundary of the protuberant rib facet. This semicircular articular surface is located about halfway up the posterior side of the ascending process and is more pronounced anteriorly along the column, as well as in smaller individuals (AMNH 6958, 7493, BM[NH] R.2664).

A single intercentrum is preserved in ventral view on AMNH 6920 (fig. 11A). Although considerably smaller than those of MCZ 2158, this element is noteworthy for its buckled ventral midline and paired, postero-laterally directed tubercles. These pronounced bosses are located on the posterior half of the base along the lateral ridges. Similar features are present on the anterior intercentra of *Trimerorhachis* (Case, 1935) and *Greererpeton* (personal observ.).

The pleurocentra are developed to a greater extent than in typical rhachitomes (i.e., *Eryops*; Moulton, 1974), but are not fused ventrally, as in *Caerorhachis* (Holmes and Carroll, 1977). Viewed laterally, the pleurocentra resemble half an inverted intercentrum: the

margins are formed by wide, unfinished continuations of the internal surface and the periosteal field is concave. An articular facet is present on the anterior half of the pleurocentrum near its expanded dorsal edge. Like their counterparts on the intercentrum, the rounded side of this facet is enclosed by raised finished bone while the opposite face merges with the unfinished border. Below the level of the rib articulation, the sides constrict to a blunt ventral point as the bone curves ventromedially.

Most of the detailed morphology of the neural arches has been obliterated by postmortem crushing. Transverse processes, typically separated from the pedicel at their roots, appear to be relatively long, broad structures, but a satisfactory view of the articular facet is not available. An articulated series of 10 posterior presacral vertebrae is preserved on AMNH 6957. The anterior zygapophyses are tilted dorsomedially to receive the ventrolaterally oriented posterior zygapophyses. The retention of the supraneural canal, as reported in *Greererpeton* (Smithson, 1982), cannot be verified.

Steen (1931) cited two subadult postcranial specimens from Linton that are almost certainly attributable to *Colosteus*. BM[NH] R.2660, formerly identified as *Erpetosaurus* (Steen, 1931), is assigned to *Colosteus* on the basis of the morphology of the interclavicle and scales. Likewise, BM[NH] R.2664, considered to be an indeterminate "phyllospondyl" by Steen (1931, p. 855 as "R. 2644" in error, pl. 4, fig. 2), is a juvenile specimen of *Colosteus* featuring dorsal and ventral squamation and an articulated string of several vertebrae. In considering the vertebrae of *Erpetosaurus*, Watson (1956, p. 375, fig. 28) reviewed this material and concluded "that all the elements are paired, none fused into crescent-shaped intercentra." This bipartite, unossified condition of the intercentra is obviously a juvenile feature.

The salient features of the thoracic ribs can be seen on AMNH 6917 (fig. 12A), 6920 (fig. 11A), and MCZ 2158 (fig. 10A). Although the proximal ends are imperfectly exposed, the articulating heads of the anterior ribs appear to be differentiated into discrete capitular and tubercular facets. When joined to

the vertebrae, the ribs are angled posteriorly at about 60° to the column and curved modestly over their distal half. The most striking costal feature is a stiletto-like uncinate process located about halfway down the shaft. This structure is well developed on all but the most posterior thoracic ribs.

A nearly complete right thoracic rib is excellently preserved in the counterpart blocks of AMNH 6920 (fig. 11A). Between the expanded proximal end and the uncinate process, the rib is moderately constricted and a sharp keel is present along the anterodorsal edge. Anterior to this keel, a deep groove is apparent, but distorted by crushing. The uncinate process is borne on a posteriorly directed flange and is strengthened along its axis by a ridge that is contiguous proximally with the shaft. Viewed medially, the posterior portion of the process is distinctly grooved; as suggested by the anterior-most exposed ribs of AMNH 6917, this groove may have rested against the leading edge of the subjacent rib shaft to form a slight costal overlap. Distal to the base of the process, the rib consists of a shaft that terminates in an unfinished expansion.

A series of 14 partially exposed thoracic ribs is visible on the right side of MCZ 2158. Anteriorly in this sequence, short uncinate processes and broad, unfinished terminal ends are present. The brevity of the posterior flanges and uncinate processes precludes the possibility of overlap. After the sixth exposed rib, the distal ends appear finished and acuminate, and uncinate processes are absent. A rapid shortening is exhibited along the posterior half of the series, with the last exposed rib measuring only 25 percent the length of the fifth. The absence of ribs on the 10 articulated vertebrae of AMNH 6957 suggests that ribs were not developed in the posterior portion of the presacral series.

Because of the lack of specimens from the pelvic and caudal regions, no information on sacral ribs or haemal spines can be reported.

**APPENDICULAR SKELETON:** The most complete representation of the dermal shoulder girdle is that of AMNH 6917 (fig. 12A, C). As reconstructed in figure 11B, the shape of the pectoral girdle is somewhat similar to that of other aquatic temnospondyls, such as tri-

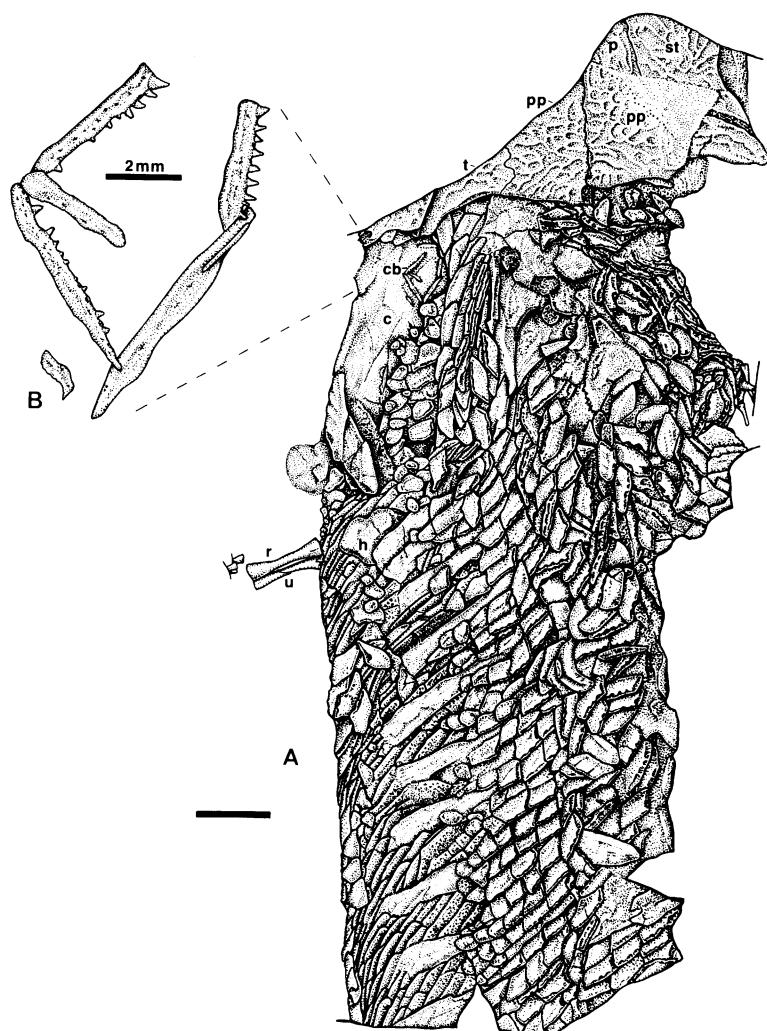


FIG. 12. *Colosteus scutellatus* (Newberry). Anterior postcranial skeleton. A, dorsal view; B, cerato-brachial ossifications (cb in A) enlarged; C, ventral view; D, restoration of left manus. Paratype specimen, counterpart blocks of AMNH 6917. Scale equals 1 cm. except in B.

merorhachids or metoposaurs. The clavicles meet anteriorly below the interclavicle to form a broad dermal shield that extends forward under the skull to about the level of the basal articulation. The width of the shield is greatest across the lateral corners of the clavicular plates and is equal to the maximum breadth of the skull. The cleithral process of the clavicle arises from the ventral shield at a low angle to join the cleithrum. The endochondral components of the shoulder girdle are

poorly represented and were probably not extensively ossified.

The largest and best preserved interclavicle, AMNH 6920 (fig. 11A), resembles an anteriorly directed spade with a very short posterior lappet. If the interclavicle is divided longitudinally into three parts of equal width, the lateral thirds are gently upturned to effect a subtle concavity (in dorsal view). The smooth dorsal surface shows only faint, irregular grooves that may represent blood ves-

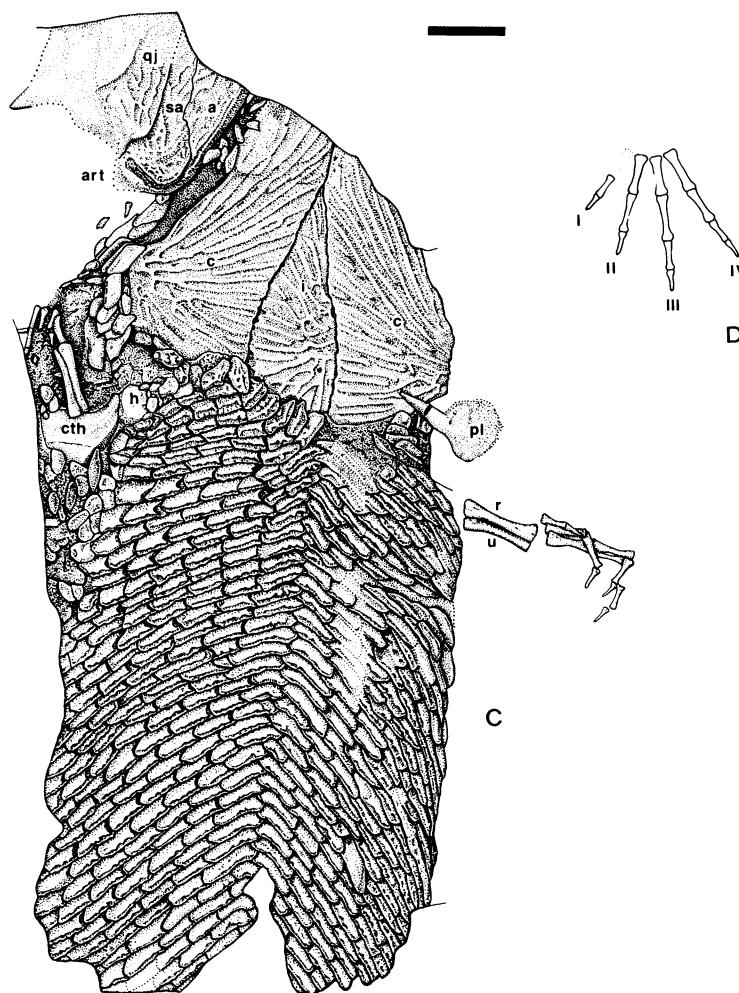


FIG. 12. Continued.

sel channels (Holmes, 1980). In contrast, the ventral face exhibits a teardrop-shaped central area bearing a dermal sculpture of furrows and bifurcating ridges. The pattern of ornamentation indicates that the center of ossification was situated along the midline, about two-thirds the length of the interclavicle from the leading edge. The periphery of the sculptured field merges with faintly striated, distally thinning extensions that apposed either the clavicles or gastralia. Where the beveled margins of the two anterior quadrants join, a pectinate texture is developed which extends to form the fimbriated leading edge of the interclavicle. Posteriorly, a para-

sternal process, as typically developed in embolomeres, is not present; rather, a tongue-shaped, medially recessed lappet is present.

The holotype specimen (AMNH 6916, fig. 2) includes an interclavicle that is about half the size of the interclavicle of AMNH 6920. In comparison, the sculpture of the type is less distinct and the longitudinal grooves leading to the fimbriated edge are more pronounced. The clavicular facets also appear to be more extensive on the smaller specimen.

The type specimen of *Colosteus foveatus* (AMNH 6919), referred tentatively to *Erypetosaurus* by Romer (1930), is an isolated interclavicle. As seen in ventral view (Cope,

1875, pl. 36, fig. 1), the sculptured ventral surface is markedly embayed by clavicular facets and finely sculptured by reticulate ornamentation. Preparation of the dorsal surface has revealed a distinct sternal trabecula. These features indicate that this specimen is attributable to *Saurerpeton*.

Each clavicle consists of a flat ventral plate and an ascending cleithral process. The ventral surface of the clavicular plate and the posterolateral face of the ascending process bear the same type of sculpturing as the interclavicle. The pattern indicates that the center of ossification is at the lateral corner of the plate, near the base of the ascending process. Internally, faint ridges radiate outward from the center of ossification to the medial edge of the plate, where additional striae are also developed.

The thin medial edge of the clavicular plate is slightly embayed where it abuts against the sculptured face of the interclavicle. Conversely, the anterolateral margin is thickened and virtually straight. This thickened edge develops posterolaterally into a low ridge that joins the posterior margin of the plate and curves dorsolaterally to form the vertical cleithral process. Although crushing has distorted the attitude of this rodlike structure, it is apparent that the process was inclined posterolaterally at a relatively low angle to the clavicular plate.

Other elements of the pectoral girdle are poorly represented by the material at hand. On AMNH 6917 (fig. 12C), a curious triangular element is partially exposed near the right clavicle. Its surface is finished but unsculptured, and bears a distinct groove on its long side. This structure probably represents the expanded dorsal blade of the right cleithrum in lateral aspect. No remains of the endochondral shoulder girdle are present. Considering the feeble ossification of such elements in *Greererpeton* (the scapulocoracoid figured by Romer, 1969, is actually a humerus), it is likely that these structures were also reduced in *Colosteus*.

Knowledge of the diminutive forelimb is obtained exclusively from AMNH 6917 (fig. 12). A small portion of the distal ventral surface of the right humerus is insufficiently exposed for description. The rather amorphous

appearance of the distal half of the left humerus indicates that the original mold was thoroughly pyritized, a condition usually associated with dense cartilaginous tissue at Linton. Proximally, the preservation of the humerus improves and some details of the dorsal surface are discernible. A small tuberosity is developed near the incompletely ossified proximal end. A similar process, found in a variety of other primitive forms, including *Greererpeton*, *Proterogyrinus*, and *Neldasaurus*, is generally regarded as the processus latissimus dorsi (after Miner, 1925). Anterolateral to this tuberosity, the outline of the anterior flange (Holmes, 1980) is preserved, but no other features of the humerus are exposed.

The radius and ulna are only slightly shorter than the humerus as preserved. Otherwise, the epipodials are unremarkable structures whose hollowed ends indicate that they were finished in cartilage. The radius is expanded at both ends, with the distal end wider and flatter than the proximal. Other surface morphologies are masked by crushing. In its incompletely ossified state, the length of the ulna is about equal to that of the radius. A modest distal expansion is visible, but the proximal end is obscured by the radius and scales.

There are no carpal remains with either forelimb. The carpus was probably unossified in subadults, if not mature individuals.

The only element missing from the right manus is the metacarpal I. The hand, therefore, can be restored confidently with a phalangeal count of 2, 2, 3, 3; digit III has the greatest length, followed by IV, II, and I (fig. 12D). Although the three preserved metacarpals are virtually identical, the proximal phalanges of the middle digits are longer than their counterparts on I and IV. Each digit ends in an elongate, bluntly pointed ungual phalanx.

No pelvic remains can be attributed confidently to *Colosteus*.

A single specimen, AMNH 6839 (fig. 13), figured by Cope as *Pleuroptyx clavatus* (1875, pl. 44, fig. 2a), preserves a partially articulated hindlimb that is similar to that of *Greererpeton*. However, since no colosteid scales accompany this material, and such a design

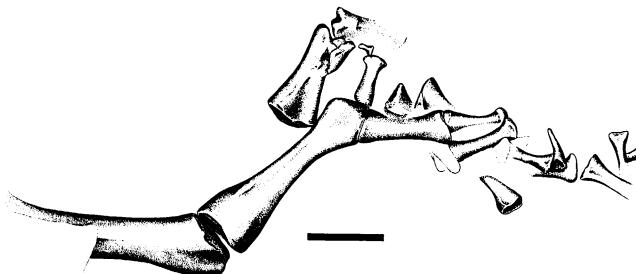


FIG. 13. Indeterminate temnospondyl. Femur, tibia, fibula(?), metatarsals, and phalanges. Paratype of *Pleuroptyx clavatus*, AMNH 6839. Scale equals 1 cm. [Drawing by P. Gaskill, courtesy of R. L. Carroll.]

may well be generalized for temnospondyls, this otherwise informative specimen must be regarded as indeterminate pending improved understanding of other forms.

**SCALES AND OSTEODERMS:** Previous descriptions of tetrapod "armor" have employed a variety of terms, often colloquially, to denote both epidermal and dermal structures. For the present purposes, the term scale refers to an ossification that was probably derived from mesenchyme within the dermis; "squamation" is a collection of scales and "gastralia" are specifically those scales of the ventral surface of the body. "Osteoderms" are structures which were formed in the superficial dermal layers directly underneath the epidermis; "squamulae" (Romer and Witter, 1941) are the concentrically arranged bony bands that comprise a particular type of osteoderm. In spite of the etymology of the animal in question, the use of the terms "scutes" and "scutellae" is avoided in that these usually connote cornified epidermal structures of a sort not seen in *Colosteus*.

Excepting the skull, mandibles, pectoral girdle and limbs the entire body is clad in one of four types of dermal ossifications. The most extensive are the gastralia which cover the underside of the body and continue onto the lower half of the flanks. Resembling these in appearance, but less widespread posteriorly, are the dorsal scales. The remaining body surfaces—the upper flanks—are covered by two varieties of osteoderms: ovoid forms similar to the "scales" of *Trimerorhachis* (Colbert, 1955), and minuscule, granular aggregates similar to the pebble-shaped

dorsal "scales" of *Ophiderpeton* (Baird, 1964, fig. 1C). The scales of the pharyngeal region are variable in form (like those of *Trimerorhachis*; Olson, 1979), but are probably modified from the ventral series.

Both the dorsal and ventral scales usually possess distinctly crenulate to punctate posterior borders. On the basis of AMNH 6917 (fig. 12), Romer mistakenly ascribed this scale-type to *Macrerpeton* (1930, fig. 22). The crenulations are expressed fairly uniformly in the dorsal squamation, but are often reduced to simple grooves near the ventral midline, and posteriorly in the gastralia (OSU 4481, UMMP 3573). Similar ornamentation is present on some ventral scales of *Greererpeton* (Carroll, 1980, fig. 2), but differences in types of preservation and preparation invalidate direct comparison.

The configuration of the gastralia is excellently preserved in AMNH 6917 (fig. 12C). A series of highly sculptured scales rabbet onto the posteroventral face of the interclavicle. Commencing at the posterior lappet of this bone, an anteriorly directed chevron is formed at the midline by opposing, postero-laterally trending rows of scales. The number of scales in each row increases from seven near the shoulder girdle to 11 or more near the pelvis; if one assumes that the body circumference does not increase significantly, the contribution of the ventral squamation to the dermal covering of the flanks increases caudally. Excluding those scales subjacent to the pectoral girdle, the anterior and medial sides of each ventral scale are internal (overlapped in ventral perspective) to its neigh-

bors. Further, because the rows are staggered at the midline, an interlocking pattern is formed along the apex of the chevron.

The outline of individual ventral scales is essentially that of a rhomboid with large acute angles. As seen in AMNH 6958 and MCZ 2158, the internal surface bears a distinct lateral recess which receives the medial flange of the adjacent scale. The anterior and medial edges are very thin, the former evenly beveled and the latter abruptly notched from the thickened middle of the scale. It is the posterior portion of this somewhat inflated area that is variously sculptured to produce the distinct crenulations of the trailing edge. All of these features become less apparent along the lateral extent of the ventral squamation; thus, the ventrolateral scales are generally thin and unsculptured with rounded corners. Additional variation is seen on the scales that form the apex of the chevron; the medial end of these scales is usually enlarged or bent at an angle to the long axis of the scale to effect the interlocking pattern of the midline.

The extensive dorsal squamation is preserved best on AMNH 6917 (fig. 12A). In general arrangement and individual form, these scales are remarkably similar to the gastralia: not only is the manner of overlap identical, but the dorsal scales are also arrayed in anteriorly directed chevrons. Because the dorsal midline is not intact on any specimen, it is difficult to determine if the opposing diagonals met as seen in the ventral squamation. There is no evidence to suggest that the dorsal scales were in any way joined to, or supported directly by the vertebrae.

On the basis of three specimens representing various levels along the vertebral column, it appears as though the lateral extent of the dorsal squamation diminishes posteriorly as the width of the ventral field increases. From AMNH 6917, a count of seven or eight rhombic scales per diagonal is estimated; in MCZ 2158, an approximation of five per row is established; and on AMNH 6957, no discrete rows are present and a total of only eight irregularly shaped dorsal scales is observed. Concurrently in this material, an increase in the number of ventral scales per row is noted.

Isolated dorsal and ventral scales can be differentiated from each other by the rela-

tively wider and thinner dimensions of the former. Equally evident is a variation in the form of the medial articulating facet. On dorsal scales, the lateral side of the notch is virtually straight, whereas the same feature on ventral scales is semicircular; this difference reflects the more angular posterolateral corner of dorsal scales.

Romer (1972) noted that the dorsal scalation of *Greererpeton* consists of an extensive mosaic of small, subcircular scales. In *Colosteus*, a few ossifications of this type are present in the pharyngeal region and the lateral extremes of the dorsal squamation. Examination of Romer's material indicates that dorsal rhomboids, as commonly seen in *Colosteus*, are totally absent in *Greererpeton*. Unfortunately, a definitive account of the scalation of *Pholidogaster* is lacking.

The remaining dermal ossifications are considered to be osteoderms on the basis of Romer and Witter's (1941) work on the squamation of *Eryops* and Olson's (1979) investigation of the integument of *Trimerorhachis*. Little can be said about the disposition of either type of osteoderm, other than that they occur together on the otherwise barren flanks, between the posteriorly directed ventral and dorsal series. The larger osteoderms (greatest diameter of 4.5 mm.) are formed by extremely thin squamulae and usually occur in patternless layers. In this respect, they resemble the general "cycloid scale" morphology (Colbert, 1955) and erratic arrangement (Olson, 1979) of osteoderms in *Trimerorhachis*. The second type of osteoderm is a tiny (greatest diameter of 0.4 mm.), subcircular granule that usually occurs in aggregates (see isolated scales near symphysis of right mandible on BM[NH] R.2547, fig. 3B). On small individuals (AMNH 6917), these ossifications are poorly formed and appear as undefined, rough surfaces. Where the dorsal scales are reduced, both types of osteoderms comprise the greater portion of the dorsal covering.

The gastralia of Linton urocordylids, particularly *Ctenerpeton remex* (Moodie, 1916, pl. 23, fig. 2), have been confused with the squamation of *Colosteus* in the past because they also bear posterior pits. For instance, BM[NH] R.2548, a small patch of ventral scales in articulation, was referred to *Cte-*

*nerpeton* by Steen (1931, p. 881); as first recognized by Baird (Bossy, ms), these gastralia are actually those of *Colosteus*. Nectridean scales are generally fusiform and more delicate than those of colosteids, making confusion upon critical examination unlikely. However, it should be noted that isolated ventrolateral scales of *Colosteus* are very difficult to differentiate from the flat, plain ventral scales of *Erpetosaurus* (Steen, 1931) and *Saurerpeton*.

In summary, the thoracic integument of *Colosteus* was armored with ventral and dorsal pavements of rhombic, posteriorly sculptured scales. As the lateral extent of the ventral squamation increased posteriorly, the width of the dorsal series decreased. In the absence of dermal scales, two types of osteoderms covered the dorsolateral flanks of the body. With reduction of the dorsal squamation posteriorly, these superficial dermal ossifications formed the dorsal covering.

#### OCCURRENCES OF COLOSTEID REMAINS

Seven localities spanning a stratigraphic interval from the mid-Viséan to the uppermost Westphalian D have produced colosteid remains (fig. 14). The oldest colosteid, and indeed the first non-ichthyostegid labyrinthodont, is *Pholidogaster [Otocratia] pisciformis*, known from the Burdiehouse Limestone and Gilmerton Ironstone of the Viséan of Scotland (Panchen, 1975). *Greererpeton* occurs in the Bickett and Hinton Shales (roughly equivalent to the upper Viséan and Namurian A, respectively) of the Mauch Chunk Group of West Virginia (Smithson, 1982). An additional Mississippian-age colosteid has been reported from the Point Edward Formation (Namurian A) of Nova Scotia (Carroll et al., 1972; PU 20100). Poorly preserved colosteid material is present in the famous Westphalian A amphibian assemblage known from Jarrow, Ireland (A. R. Milner, 1980a). The youngest stratigraphic record of the family is *Colosteus scutellatus*, known solely from the classic Pennsylvanian locality of Linton, Ohio.

In view of the longevity and geographic distribution of the family, it is somewhat dif-

ficult to account for the absence of colosteids in other Carboniferous assemblages. These include the Linton-like thanatocoenosis of Nýřany (A. R. Milner, 1980b), the meager vertebrate records of Mazon Creek (Gregory, 1950; Milner, 1982) and Cannelton (Baird, 1978), the embolomere-dominated collection of Newsham (Land, 1974), and the Namurian-age assemblages of Scotland (Smithson, 1980a; the preliminary report of colosteid remains from Cowdenbeath in Andrews et al., 1977, is unfounded [Smithson, personal commun.]). Although it is beyond the scope of this paper to entertain the reasons for these absences, I suggest that the chances of preservation and recognition of colosteid remains, particularly the scalation, rate among the highest of any Paleozoic vertebrate. Thus, their non-appearance may merit greater paleoecologic and paleogeographic recognition than is usually accorded to such negative evidence.

#### CHARACTERISTICS AND COMPOSITION OF THE COLOSTEIDAE

##### SHARED DERIVED CHARACTERS OF THE FAMILY

*Pholidogaster*, *Greererpeton*, and *Colosteus* comprise a clade of primitive amphibians. They are united by the following synapomorphies:

(1) *Elongate prefrontal entering the margin of the external narial opening, contacting the premaxilla and maxilla, thus excluding the lacrimal and nasal from the naris.* As originally noted by Smithson (1982), this feature is unique to colosteids. Although the prefrontal may reach the naris in some amphibians (adelognathids, nectrideans, *Acheroniscus*, *Micrarotter*, some trematopsids), it is almost universally separated from the premaxilla and maxilla by the nasal and lacrimal, respectively (the widely reproduced reconstruction of *Sauroplectron scalaris* from Steen, 1938, is in error; Bossy, ms; A. C. Milner, 1980). Only in the highly derived keraterpetontid *Diploceraspis* (Beerbower, 1963), in which both the nasal and lacrimal are absent, does the prefrontal reach the naris and contact both marginal elements.

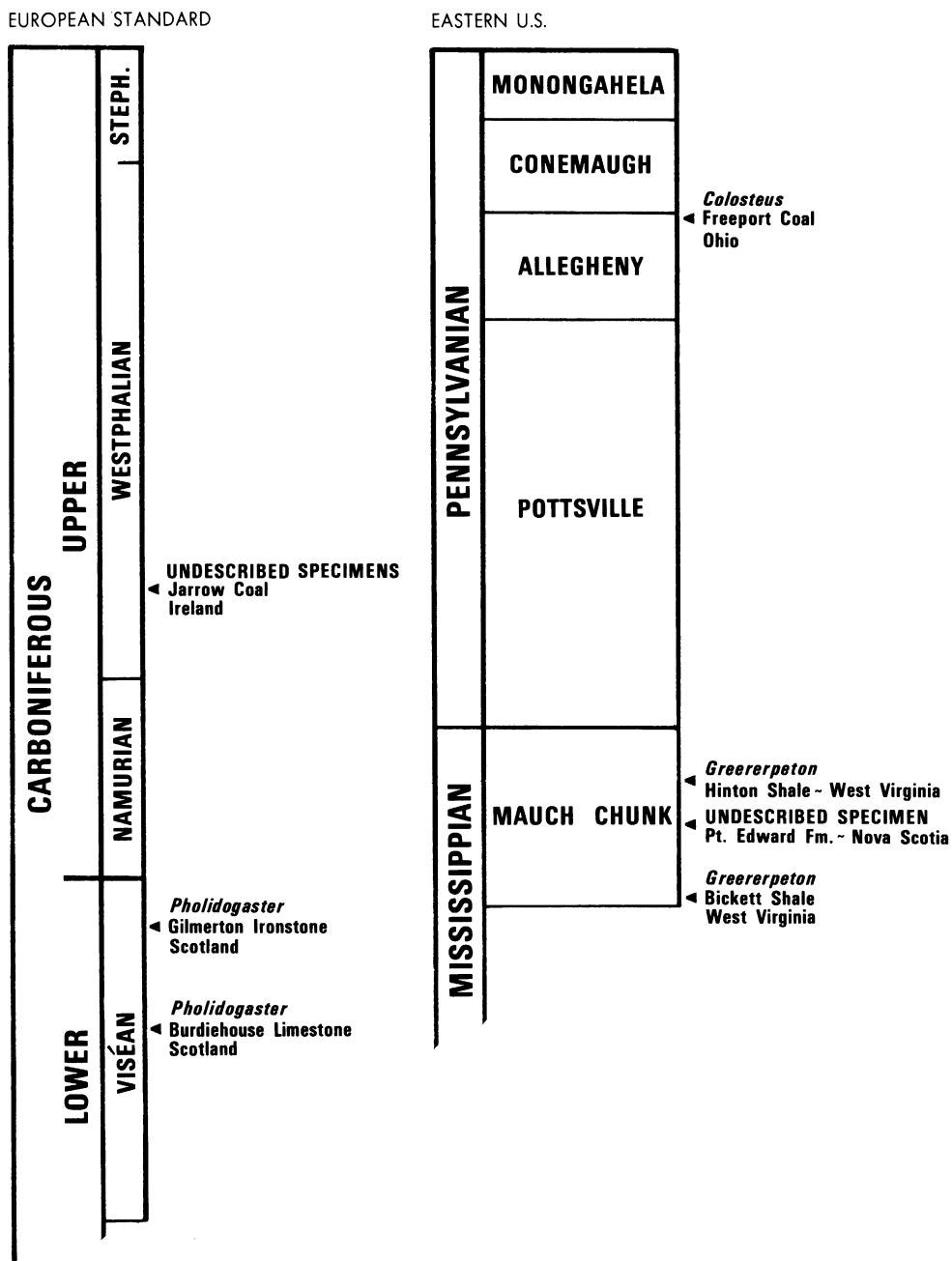


FIG. 14. Stratigraphic correlation of colosteid localities. Nova Scotia material appears with eastern United States for convenience. Adapted from Panchen, 1970.

(2) *Broad postorbital-parietal suture.* Within the Temnospondyli, this character is also seen in *Erpetosaurus* and the brachyopoids (*sensu* Warren, 1981) *Dvinosaurus*

*primus* and *Tupilakosaurus wetlugensis* (Shishkin, 1973); brief postorbital-parietal contacts appear in the rhinesuchoid *Chomatobatrachus* (Cosgriff, 1974) and the poorly

known *Broomulus* (Romer, 1947). Other temnospondyls possess either an intertemporal-postfrontal suture or, in the absence of an intertemporal, develop a supratemporal-postfrontal contact. Ichthyostegids, nectrideans, some adelognathids (assuming the "postorbital" is indeed that), and some microbrachiomorph microsaurs are among the non-temnospondyl stocks that exhibit this feature.

(3) *Extensive tabular-squamosal contact.* In the presumed absence of a tympanic membrane, colosteids have completely closed the quadrate angle (see below) by extending the tabular-squamosal contact posteriorly to the occipital surface. A similar condition is found in trimerorhachids and some brachyopoids, but in these instances there is a slight occipital recess which probably supported a tympanum. Microsaurs and nectrideans also elaborate the tabular-squamosal contact in the presumed absence of a tympanum.

(4) *Premaxillary tusk borne on postero-lateral palatal flange and accommodated by dentary notch.* Excluding *Erpetosaurus*, which differs further in having an additional tusk pair shared by the premaxillae at the midline, premaxillary tusks are not known in any other amphibians. Some forms (*Ichthyostega*, *Edops*, most embolomeres) exhibit large, marginally situated premaxillary teeth, but do not develop the tusk-replacement pit combination typical of palatal tusks.

(5) *Elongate Meckelian fenestra.* No temnospondyls other than *Colosteus* and *Greererpeton* are known to possess a single, long, narrow fenestra on the medial face of the mandible (this surface is unknown in *Pholidogaster*). A single anthracosaur, *Anthracosaurus* (Panchen, 1981), and several diadectomorphs (Heaton, 1980a) possess large, solitary Meckelian fenestrae.

(6) *Approximately 40 presacral vertebrae.* Although the trunk length of *Colosteus* is unknown, *Greererpeton*, *Pholidogaster*, and the undescribed Jarrow colosteid appear to have approximately 40 presacral vertebrae (Panchen, 1975; A. R. Milner, personal commun.). This exceptional length is known in only one other temnospondyl, the problematical *Kourerpeton bradyi* (Olson and Lammers, 1976).

The occurrence of characters 2 and 4 in

*Erpetosaurus* is not regarded as evidence of a close relationship between *Erpetosaurus* and the Colosteidae. Several shared derived characters indicate that *Erpetosaurus* is more closely related to *Saurerpeton* than to the colosteids. These include moderately developed tympanum-supporting structures; palatine incorporated in skull roof; broad interpterygoid vacuity bordered by vomer, palatine, and pterygoid; lateral border of choana formed mainly by palatine; accessory tusks only on vomer; and reduced lateral line system. Further consideration of the affinities of the Saurerpetontidae (Chase, 1965) awaits redescription of these Linton genera.

#### RELATIONSHIPS WITHIN THE FAMILY

It is difficult at this time to evaluate the validity of the generic distinction afforded the Lower Carboniferous colosteids. Whereas *Greererpeton* is represented by numerous exquisitely preserved and virtually complete individuals, *Pholidogaster* is based on only two specimens whose preservation leaves much to be desired. Because most of the cranial detail of the latter genus is obscured, any critical comparison is necessarily limited to the more informative postcranium. It is expected that Stephen Godfrey (McGill University) will address this matter upon completion of his current study of the postcranial skeleton of *Greererpeton*.

By the same token, analysis of the differences between *Colosteus* and earlier colosteids must be based largely on comparisons with *Greererpeton*. Many potential differences seen in *Colosteus*, such as relatively larger dentary teeth, shorter antorbital length and smaller forelimbs, cannot be considered in the absence of more representative adult material. Although the presence of a single row of coronoid teeth cannot be verified in adults, this feature is regarded as a valid character since drastic change in coronoid dentition is not seen in other labyrinthodont growth series. Among early labyrinthodonts, only ichthyostegids (Campbell and Bell, 1977; Jarvis, 1980) and *Doragnathus* (Smithson, 1980b) possess a single row of coronoid teeth. Highly denticulated coronoids similar to those of *Greererpeton* occur in several primitive forms, including *Megalcephalus*, *Caero-*

*rhachis*, and *Edops*. Because the densely denticulated condition is more common and the affinities of ichthyostegids and *Doragnathus* are unresolved, the single-row coronoid dentition of *Colosteus* is considered apomorphic within the Colosteidae.

The characteristic circumorbital configuration of *Colosteus* is seen in specimens of all sizes and is certainly a valid generic character. The exclusion of the prefrontal from the orbital margin appears to be unique among Paleozoic amphibians; less exceptional, but equally derived among labyrinthodonts, is the omission of the postorbital from the same margin. The resulting three-bone configuration enclosing the orbit is an autapomorphy of *Colosteus*.

An assessment of the character states represented by the different types of dorsal sculation possessed by *Colosteus* and *Greererpeton* is impaired by a general lack of information on such ossifications in other forms.

#### RELATIONSHIPS OF THE COLOSTEIDAE

Consideration of the phylogenetic relationships of the colosteids raises two fundamental problems. The first is the difficulty encountered in attempting a diagnosis of the Temnospondyli; that is, while it may be possible at present to delimit the order, the number of inadequately described taxa makes cladistic analysis infeasible. Related to this is the second problem of the development of the otic notch within the order. These general areas will be addressed before discussing the more particular concern of the taxonomic placement of the Colosteidae.

#### THE STATUS OF THE ORDER TEMNOSPONDYLI

The composition of the Temnospondyli and the affinities of the Colosteidae have been considered most recently by Smithson (1982). Building upon the suggestion that loxommatoids (loxommatids and spathicephalids; Beaumont, 1977) should not be regarded as temnospondyls (Panchen, 1980), Smithson has drawn attention to the manner in which the braincase is held within the skull of prim-

itive labyrinthodonts. In loxommatids and anthracosaurs, the braincase is attached to the skull roof by areas derived from the auditory capsules; primitive temnospondyls (colosteids, edopoids, trimerorhachoids) reduce these attachment surfaces and elaborate a connection between the exoccipitals and postparietals (Smithson, 1982, fig. 22). Smithson regards the temnospondyl condition as derived relative to the rhipidistian-like condition shared by loxommatoids and anthracosaurs. In addition, both loxommatids (Beaumont, 1977) and anthracosaurs (Panchen, 1970) appear to have retained a kinetic basal articulation characterized by opposing articular facets on the basipterygoid process and the conical recess; such facets are not present in primitive temnospondyls (Smithson, 1982).

Further consideration of a possible loxommatoid-temnospondyl relationship indicates that the characters common to both groups represent generalized amphibian conditions. These plesiomorphic characters include (1) supratemporal-postparietal contact; (2) quadratojugal-maxilla contact; (3) orbital lacrimal (conceivably secondary in loxommatoids); (4) marginally situated, laterally directed external nares; (5) widely separated choanae; (6) pterygoids joined anteromedially; (7) paired tusks on vomers, palatines and ectopterygoids; (8) parasympophysial tusks accommodated by palatal fenestrae; and (9) vertebrae with compound centra. Thus, with fundamentally different braincase-skull roof connections and basal articulations, and an apparent absence of shared derived characters, loxommatoids do not appear to share a unique common ancestry with other amphibians classified as temnospondyls.

With the loxommatids and spathicephalids removed, Smithson (1982) asserts that the Temnospondyli represent a monophyletic group "in the context of Paleozoic tetrapods" (acknowledging that anurans are generally regarded as temnospondyl descendants, but excluded from the order). But in the same paper, it is demonstrated that the very character used to consolidate the temnospondyls—an exoccipital-postparietal contact—also occurs in the order Microsauria. Smithson further notes that temnospondyls and microsaurs

share additional features that are derived relative to other primitive amphibians: akinetic skull roof, immobile basal articulation, and four digit manus. If these features, along with the mode of braincase attachment, are regarded as synapomorphies uniting the two orders, then the claim of temnospondyl monophyly appears to lack the support of any unique characters.

Consideration of a close relationship between microsaurs and temnospondyls is retarded by the chronic lack of pre-Westphalian specimens. Nonetheless, the proposal clearly merits further attention, and study of the atlas-axis complex of *Greererpeton* seems particularly warranted in light of the specialized atlas-axis configuration of microsaurs (Carroll and Baird, 1968). Equally important is the need for accurate analysis of character distributions among other lepospondyl groups: in genera in which the occiput is known, both adelognathids (*Adelospondylus*; Carroll, 1967) and nectrideans (*Diploceraspis*; Beerbower, 1963) exhibit exoccipital-postparietal contacts. Colosteids further resemble adelognathids, a group once suggested as "an early-divergent family of microsaurs" (Baird, 1965, p. 292), as well as the enigmatic *Acherontiscus* (Carroll, 1969), in the possession of lateral lines (uncommon in lepospondyls), prefrontal that contributes to both the orbital and narial margins, postorbital-parietal contact, and no otic notch (the "notch" of adelognathids is probably an elaborated surface for muscle attachment; Carroll, 1967). A re-examination of these problematical Lower Carboniferous forms may well be of use in testing a possible microsaur-temnospondyl association.

#### THE DEVELOPMENT OF THE TEMNOSPONDYL OTIC NOTCH

The suggestion that the temnospondyl otic notch was derived from a notchless ancestor (see Panchen, 1975, 1977a; Carroll, 1980; A. R. Milner, 1980a), combined with the convincing argument that the colosteid stapes represents the primitive temnospondyl morphotype (Smithson, 1982), seems to indicate that an extensive tabular-squamosal suture as seen in colosteids is primitive for the order.

Such a conclusion, however, largely ignores the manner by which cranial kinesis appears to be reduced in labyrinthodonts, as well as the wide variety of otic configurations seen in primitive temnospondyls.

There is no conclusive evidence to indicate that an extensive tabular-squamosal contact is requisite to the stabilization of the skull. In *Ichthyostega*, loxommatoids, most primitive temnospondyls, and advanced embolomeres which lose skull table-cheek kinesis (*Anthracosaurus*; Panchen, 1977b), this suture is either short or absent. Yet, these forms appear to have consolidated the skull roof mainly through a posterior shift in the position of the parietal-postparietal suture and a change in the relative positions and sizes of the postfrontal, postorbital, and intertemporal bones (Panchen, 1972). It is, therefore, difficult to argue that the broad tabular-squamosal contact seen in colosteids represents an archetypical temnospondyl design for the reduction of cranial kinesis.

The otic notch has been defined as "the bony emargination enclosing (usually anteriorly) the tympanum" (Thomson and Bossy, 1970, pp. 18-19); thus, the recognition of an otic notch postulates the existence of a tympanic membrane. A second type of posterior embayment of the skull roof is the space between the lateral edge of the skull table and the margin of the squamosal. This space, termed the quadrate angle by Thomson and Bossy, often coincides with the topological position of the otic notch.

Colosteids may be considered as notchless forms with no distinct quadrate angle because the morphology of the stapes indicates that a tympanum was probably absent (Smithson, 1982), and an extensive tabular-squamosal suture supersedes any posterior embayment of the skull roof. The only other primitive temnospondyl that has been cited as notchless is *Caerorhachis bairdi*, known only from a single specimen in which the skull roof is poorly preserved. On the basis of a natural cast that represents the ventral surface of the right tabular and squamosal, Holmes and Carroll (1977, p. 493) stated "that the existence of a well developed otic notch is unlikely." This description, and an equally equivocal figure of the skull, have been in-

terpreted as a probable indication of the notchless or tympanumless condition (Panchen, 1977a; A. R. Milner, 1980a; Smithson, 1982). However, since no stapes accompany this material, it seems more judicious to exclude *Caerorhachis* from consideration.

A survey of the remaining early temnospondyls does not reveal any compelling evidence for a common ancestor that lacked both the otic notch and quadrate angle. A plethora of notch types occurs in Westphalian temnospondyls, ranging from slight (*Saurerpeton*), to moderate (*Eugyrinus*, *Erpetosaurus*), to markedly embayed (*Stegops*, *Cochleosaurus*, *Amphibamus*, *Dendrerpeton*). In fact, the majority of Westphalian forms possesses well-developed otic notches and quadrate angles in which the tabular is almost completely separated from the squamosal on the skull roof.

If an abbreviated tabular-squamosal contact is common among early temnospondyls, then colosteids may be regarded as a primitive group of aquatic specialists that maintained the supporting function of the stapes, never developed a tympanic membrane, and secondarily reinforced the skull roof through closure of the quadrate angle. The precursors of other early forms, such as *Dendrerpeton*, *Amphibamus*, and *Edops*, would have elaborated the anterior portion of the quadrate angle into a bony, tympanum-supporting otic notch while modifying the stapes for transmission of airborne vibrations (Smithson, 1982). Further, the problematical "otic slits" of saurerpetontids do not represent tympanum-supporting structures at all (Milner, 1982), but more plausibly an intermediate condition in which the quadrate angle is not completely occluded by a tabular-squamosal contact. If a tympanum were present, as suggested by the form of the stapes in these genera, it would have been supported by a slight recess on the occipital expansion of the skull (see Warren, 1981, for further development of the saurerpetontid plan in brachyopids).

It is concluded that the extensive tabular-squamosal suture of colosteids is derived relative to other primitive temnospondyls, and that the otic notch developed from a non-colosteid form that possessed a short tabular-squamosal contact and distinct quadrate angle. Finally, if colosteids are regarded as an

early apomorphic group that closed the quadrate angle while retaining the stapes as a braincase support, then they constitute a monophyletic taxon that may be the plesiomorphic sister group of all other temnospondyls.

#### COLOSTEIDS, EDOPOIDS, AND TRIMERORHACHOIDS

As previously noted, colosteids have been associated most commonly with either the edopoids or the trimerorhachoids, two groups that have been regarded traditionally as primitive temnospondyl grades. Although it is not the intent of this section to diagnose these groups (the edopoids are being revised by A. R. Milner, and a statement on the trimerorhachoids awaits redescription of several saurerpetontid species), members from these two superfamilies can be used to consider possible relationship to the colosteids. As used here, the Edopoidea contains two families, the Edopidae and Cochleosauridae, with *Dendrerpeton* and *Caerorhachis* removed to separate families of uncertain position (A. R. Milner, 1980a). The Trimerorhachoidea is considered to consist of three families, the Eugyrinidae (A. R. Milner, 1980a), Saurerpetontidae (Chase, 1965), and Trimerorhachidae, with the monogeneric Dvinosauridae removed to the Brachyopidea (Shishkin, 1973).

Edopoids are known from as early as the Westphalian A of Jarrow. In addition to a well-developed otic notch and stapes adapted for an impedance matching system (Romer and Witter, 1942), a diagnostic complex of characters is also present that distinguishes the superfamily from other early temnospondyls (A. R. Milner, 1980a): no lateral lines, lacrimal excluded from orbit by jugal-pre-frontal contact, septomaxilla incorporated in dermal skull roof, and broad separation of the maxilla and quadratojugal. Only on the palate, where narrow interpterygoid vacuities, thin cultriform process not sutured to the vomers, and reduced vomerine tusks occur, are any similarities to colosteids evident. These may be considered as primitive temnospondyl features and do not in themselves indicate close relationship.

Colosteids have most recently been asso-

ciated with trimerorhachoids (Carroll and Winer, 1977). Although the otic notch is poorly expressed in trimerorhachoid genera, their slender, dorsolaterally oriented stapes suggest that an impedance-matching system was developed. Other cranial features, including dorsally oriented external nares, broad cultriform process sutured to vomers, and enlarged interpterygoid vacuities bordered in part by vomers, represent character states that are derived relative to those seen in colosteids. However, similarities exist between the postcranial skeletons of the two groups: the pectoral girdle is extended anteriorly to form a dermal plate beneath the braincase, and the limbs are generally reduced. In addition, the vertebrae of *Neldasaurus* (Chase, 1965) resemble the schizomericous condition of colosteids. But in the absence of comparative material from other early amphibians, the taxonomic significance of these similarities is difficult to evaluate objectively for the recognition of polarities within groups comes to rely heavily upon *ad hoc* adaptational or functional interpretations.

In the apparent absence of derived cranial features linking colosteids to trimerorhachoids or any other group, it is proposed that the superfamily Colostoidea, first erected by Tatarinov (1964) and recently employed by Shishkin (1973), be utilized. Like some Permo-Triassic temnospondyl superfamilies, this taxon would consist solely of the monophyletic type family, and the familial diagnosis would be elevated accordingly. Although this may not be as economical as tentatively associating the colosteids with the Trimerorhachoidea, it does not handicap a higher taxon that is slowly staggering toward monophyly (see Coldiron, 1978). In an even less Hennigian perspective, this prudence underscores the difficulties of establishing the interrelationships of Westphalian temnospondyls when so few Lower Carboniferous representatives are known.

#### SYSTEMATIC CONCLUSIONS

*Colosteus*, *Greererpeton*, and *Pholidogaster* represent the family Colosteidae, a clade of closely related, primitive temnospondyls. Despite a preponderance of plesiomorphic characters, these forms also possess a suite

of specialized features that precludes them from being direct ancestors of any other presently known temnospondyls. Because they can be associated with the Trimerorhachoidea or Edopoidea only on the basis of characters of questionable polarity or certain primitiveness, the colosteids are placed in a separate superfamily, the Colostoidea (Tatarinov, 1964), that is possibly the plesiomorphic sister group of all other temnospondyls. A revised classification of primitive temnospondyls based on these conclusions and those of A. R. Milner (1980a) is as follows:

Superfamily: Colostoidea Tatarinov, 1964

Family: Colosteidae Cope, 1875

*Pholidogaster pisciformis* Huxley, 1862

*Greererpeton burkemorani* Romer, 1969

*Colosteus scutellatus* (Newberry, 1856)

Superfamily: Trimerorhachoidea

Families: Saurerpetontidae, Eugyrinidae, Trimerorhachidae

Superfamily: *incertae sedis*

*Caerorhachis bairdi* Holmes and Carroll, 1977

Superfamily: Edopoidea

Families: Edopidae, Cochleosauridae

Superfamily: *incertae sedis*

Family: Dendrerpetontidae

#### APPENDIX

##### Hypodigm of *Colosteus scutellatus* (Newberry)

AMNH 2934: J. S. Newberry Collection. Posterior portion of adult mandible; association with AMNH 6826 (Moodie, 1916, p. 185) unlikely. Holotype of *Macrerpeton deani*. Moodie, 1916, figure 40; plate 21, figure 1; figure 9 of this paper.

AMNH 6826: formerly 8535G, Newberry Collection. Postorbital region of adult skull and left mandible; association with AMNH 2934 (Moodie, 1916, p. 185) unlikely. Paratype of *M. deani*; erroneously cited as holotype by Romer (1930, pp. 102–103); erroneously cited as holotype of *Megalcephalus lineolatus* by Beaumont (1977, p. 75). Moodie, 1916, plate 21, figure 2; Romer, 1930, figure 9 right, below; figure 5 of this paper.

AMNH 6829: formerly 1088G, Newberry Collection. Right dentary of subadult. Erroneously cited as holotype of *Leptophractus lineolatus* by Moodie (1916, p. 169).

AMNH 6833: formerly 8563G, 8570G, 8673G, 8693G, 9031G, Newberry Collection. Isolated dorsal and ventral scales, not associated. 8673G referred to *Sauropleuria* by Moodie (1916, p. 160).

AMNH 6915: formerly 8587G (or possibly 8687G), Newberry Collection. Postorbital region of subadult skull, palate and mandibles; in coun-

terpart blocks. Romer, 1930, figure 9 left, above and below; figure 6 of this paper.

AMNH 6916: formerly 8584G and 8666G, Newberry Collection. Subadult skull, mandibles, and anterior portion of body, including partial ribs, pectoral girdle, and scalation; in counterpart blocks. Holotype of *Pygopterus scutellatus*, *Colosteus crassiscutatus*, *Sauropleurus scutellata*, and *C. scutellatus*. Cope, 1875, plate 33, figure 1; Moodie, 1916, plate 21, figure 5 as *S. scutellata*; Romer, 1930, figure 8 left, above and below; figure 2 of this paper.

AMNH 6917: formerly 8657G and 9027G, Newberry Collection. Posterior portion of subadult skull and mandibles, and anterior segment of body, including pectoral girdle, forelimbs, and scalation; in counterpart blocks. Paratype of *C. crassiscutatus* and *C. scutellatus*. Cope, 1875, plate 34, figure 2; Moodie, 1916, plate 14, figure 3 as *S. scutellata*, but also *S. pauciradiata* (pp. 159-160); Romer, 1930, figure 22 as *M. huxleyi*; figure 12 of this paper.

AMNH 6920: formerly 8670G, Newberry Collection. Isolated interclavicle, ribs, scales, intercentrum, and pleurocentrum; in counterpart blocks. Paratype of *C. crassiscutatus*, holotype of *C. pauciradiatus* and *S. pauciradiata*. Cope, 1875, plate 40, figure 1 as *C. pauciradiatus*; Moodie, 1916, figure 34A as *S. pauciradiata*, but also *S. scutellata* (p. 156); figure 11A of this paper.

AMNH 6921: formerly 8671G, Newberry Collection. Isolated left clavicle in counterpart blocks; not associated with AMNH 6920. Paratype of *C. pauciradiatus*; erroneously designated as holotype of *S. pauciradiata* by Moodie (1916, p. 158). Cope, 1875, plate 40, figure 2 as *C. pauciradiatus*; Moodie, 1916, figure 34B as *S. pauciradiata*.

AMNH 6932: formerly 8612G, Newberry Collection. Incomplete subadult skull, mandibles, branchial arches, and scalation. Paratype of *S. newberryi*; erroneously designated as type by Moodie (1916, p. 158) and Romer (1930, p. 101). Cope, 1875, plate 41, figure 5 as *S. Newberryiana* in error; Romer, 1930, figure 8 right, below; figure 7A of this paper.

AMNH 6936: formerly 8674G, Newberry Collection. Segment of subadult gastralria. Referred to *S. pauciradiata* by Moodie (1916, p. 160).

AMNH 6937: formerly 2412G, Newberry Collection. Segment of subadult gastralria.

AMNH 6945: formerly 8619G, Newberry Collection. Partial subadult skull and mandible; counterpart of BM[NH] R.2547. Holotype of *S. longidentata*; erroneously cited as *S. dentatus* by Romer (1930, p. 103). Moodie, 1909b, figure 18; 1916, figures 2, 3; Romer, 1930, figure 9 right, above; figure 3A of this paper.

AMNH 6949: formerly 951G, Newberry Collection. Anterior portion of an adult palate and mandibles.

AMNH 6950: formerly 8572G, Newberry Collection. Anterior portion of a subadult skull and left mandible, very poorly preserved; in counterpart blocks. Referred to *M. huxleyi* by Moodie (1916, p. 184), but not associated with 8532G (=AMNH 6954, an edopid) as stated.

AMNH 6951: formerly 8709G, Newberry Collection. Antorbital region of subadult skull and mandibles; in counterpart blocks. 6951 was cited in error by Romer (1930, pp. 127-128) under *L. lancifer*; 6954 was intended. Figure 8 of this paper.

AMNH 6957: formerly 8554G, Newberry Collection. Adult posterior presacral vertebrae; counterpart of OSU 4481. Referred to *S. pauciradiata* by Moodie (1916, p. 160). Possibly from same individual represented by PU 16532 or AMNH 6958.

AMNH 6958: formerly 8668G, Newberry Collection. Section of adult presacral vertebral column, ribs, and scales. Referred to *S. pauciradiata* by Moodie (1916, p. 160). Possibly from same individual represented by AMNH 6957, OSU 4481, or PU 16532.

AMNH 7491: Newberry Collection. Incomplete subadult mandible; in counterpart blocks.

AMNH 7493: formerly 8333G, Newberry Collection. Portion of presacral dorsal and ventral scalation, intercentra partially exposed; in counterpart blocks.

AMNH 20866: formerly 8558G (incorrectly associated with AMNH 6965), Newberry Collection. Isolated left subadult clavicle.

BM[NH] R.2547: T. Stock Collection, purchased by Museum in April 1895 (A. C. Milner, personal commun.). Subadult skull, mandibles, and partial interclavicle; counterpart of AMNH 6945. Steen, 1931, figure 6; plate 2, figure 1; figure 3B of this paper.

BM[NH] R.2548: Stock Collection (see BM[NH] R.2547). Segment of gastralria. Referred to *Ctenoperpeton remex* by Steen (1931, p. 881).

BM[NH] R.2660: J. W. Davies Collection, purchased by Museum in October 1895 (A. C. Milner, personal commun.). Disarticulated subadult postcranial remains, including vertebrae, ribs, interclavicle, and scales. Referred to *Erpetosaurus radiatus* by Steen (1931, pp. 852, 856).

BM[NH] R.2664: Davies Collection (see BM[NH] R.2660). Segment of subadult postcranial skeleton, including vertebrae, ribs, and dorsal and ventral scalation in counterpart blocks. Steen, 1931, plate 4, figure 2 as a phyllospondyl.

BM[NH] R.9949: formerly BM[NH] R.2675 (B.M.63), Davies Collection (see BM[NH] R.2660).

Portion of postorbital region of adult skull; adjoins OSU 4545. Steen (1931, p. 886) as unidentified labyrinthodont.

CM 25307: R. Lund, collector. Preorbital region of subadult skull and mandibles; in counterpart blocks. Figure 7B of this paper.

FMNH UC 2001: A. S. Romer, collector(?), 1932. Portion of subadult skull roof. Figure 4 of this paper.

MCZ 2136: D. and L. Baird, collectors, 1953, 1954. Lateral portions of dorsal and ventral scalation, vertebrae and ribs partially exposed. Two specimens from possibly the same individual.

MCZ 2158: R. N. Fearon Collection, 1883. Section of adult posterior presacral region, including vertebrae, ribs, and dermal ossifications; counterpart of UMMP 3573. Figure 10A of this paper.

MCZ 2159: Fearon Collection, 1883. Incomplete adult mandibles.

OSU 4481: Newberry Collection. Adult posterior presacral gastralia; counterpart of AMNH 6957. Possibly from same individual as represented by AMNH 6958 or PU 16532.

OSU 4545: Newberry Collection. Small portion of adult skull roof; adjoins BM[NH] R.9949.

OSU 4560 and 4562: Newberry Collection. Poorly preserved squamation; in counterpart blocks.

PU 16532: Newberry Collection. Section of adult postcranial skeleton including vertebrae, ribs, and scalation; in counterpart blocks. Possibly from same individual as represented by AMNH 6957, 6958, or OSU 4481.

PU 16540: D. Baird, collector, 1957. Subadult skull. Smallest known individual, skull length = 7.5 mm.

UMMP 3573: Fearon Collection, 1883. Portion of gastralia; partial counterpart of MCZ 2158.

YPM 4604: F. H. Bradley, collector. Postcranial remains, including scales and vertebrae, of two individuals of disparate size on same bedding plane; in counterpart blocks.

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