

The Carboniferous Amphibian *Proterogyrinus scheelei* Romer, and the Early Evolution of Tetrapods

Author(s): R. Holmes

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**THE CARBONIFEROUS AMPHIBIAN
PROTEROGYRINUS SCHEELEI ROMER, AND THE
 EARLY EVOLUTION OF TETRAPODS**

BY R. HOLMES

*Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal,
 Quebec, Canada, H3A 2K6*

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Proterogyrinus scheelei Romer, from the Upper Mississippian of Greer, West Virginia, is one of the earliest known members of the amphibian infraorder Embolomeri. The primitive, eogyrinid-like skull conforms to Panchen's allometric plot of the British eogyrinids. It has no identifiable autapomorphies, but shares with two other, as yet undescribed genera attributed to the same family, a unique skull table with a raised pineal foramen rim and an acuminate median ridge on the skull table posteriorly, flanked on each side by a deep depression. The kinetic junction extends from the otic notch anteriorly to the posterodorsal corner of the orbit. The braincase, bearing no ossified roof, is composed of separate otic-occipital and sphenethmoid units, the latter bearing no sagittal or parasagittal septa. The vertebrae are similar to those of other embolomeres, except that the pleurocentrum retains a dorsal suture in adults, and the intercentrum, unossified dorsally in adults, is a ventral crescent. The presacral count is 32. The atlas-axis is reptiliomorph. The limbs and girdles are similar to those of *Archeria*, except that they are slightly stouter. Humerus structure is primitive. Range of limb movement, at least in the pectoral limb, is very restricted. The possession of few autapomorphies indicates that *Proterogyrinus* is a member of the stem family (Proterogyrinidae) of the infraorder Embolomeri. Although most of the putative autapomorphies of anthracosaurs that were formerly thought to preclude them from reptile ancestry are not considered to be valid, there are no undisputed synapomorphies with reptiles either, making it impossible to support close relationship between the two groups.

INTRODUCTION

The class Amphibia is commonly divided into three subclasses: the Lissamphibia (the three extant orders), the rather rare, exclusively Palaeozoic Lepospondyli, most of which are small and bear holospondylous ('one piece') vertebral centra, and the Labyrinthodontia, comprising forms generally larger and more common than the lepospondyls that range from the Upper Devonian to Lower Jurassic in age. The Labyrinthodontia is considered by Romer (1966) to be composed of three orders:

- (i) order Ichthyostegalia, known mainly from the Upper Devonian of east Greenland with some recently discovered fragmentary material from Australia;
- (ii) order Temnospondyli, ranging from the Lower Carboniferous to the Lower Jurassic. This group is the most numerous and diverse of the three orders;
- (iii) order Anthracosauria, ranging from the Lower Carboniferous to the Lower Triassic.

However, the characters traditionally used to diagnose the Labyrinthodontia, such as a multipartite vertebral column, labyrinthine in-folding of the teeth, and suture pattern of the dermal skull roof (Romer 1947, 1966) are also present in many Palaeozoic sarcopterygian fish (Panchen 1977a). Such primitive characters cannot be used to define a monophyletic group, and the term 'Labyrinthodontia' must be discarded as it designates a paraphyletic (unnatural) grouping (Smithson 1982).

The poorly known Ichthyostegalia is probably not monophyletic either, and even the integrity of the type genus *Ichthyostega* has been questioned (Gaffney 1979; Panchen 1975). However, except for *Ichthyostega*, all genera attributed to the order are so fragmentary that a resolution to the problem is impossible at this time.

The monophyly of the Temnospondyli as defined by Romer (1966) has also been questioned by Panchen (1980) and Smithson (1982) (see also Gardiner 1983). They have pointed out that members of the Loxommatoida share no synapomorphies with other temnospondyls, and *contra* Romer (1966) should be removed from the order. At least two synapomorphies, the

large interpterygoid vacuity and exoccipital-postparietal contact characterize the remaining temnospondyls, which appear to form a monophyletic assemblage (Smithson 1982).

It has long been recognized that all anthracosaurs possess well-developed tabular horns (modified in seymouriamorphs), a well-developed 'otic' notch, and diplospondylous vertebrae in which the pleurocentrum is always better developed than the intercentrum. Since these specialized features are not encountered in precisely the same form in either osteolepiform fish or in other amphibians, the Anthracosauria as defined by Romer (1966) is generally considered to be a monophyletic group (but see also Heaton 1980). Following Panchen (1980), the Anthracosauria (*sensu* Romer) is here considered to have subordinal status, and together with the loxomatids (formerly considered to be temnospondyls) and the primitive *Crassigyrinus* comprise the order Batrachosauria.

Not only were the 'labyrinthodonts' the dominant amphibians of the Palaeozoic and early Mesozoic, but they have long been considered ancestral to amniotes, as well as to at least some of the modern amphibian groups. Of the three 'labyrinthodont' groups, batrachosaurs show the greatest similarity to reptiles, and have traditionally been identified as their closest relatives among the Amphibia.

Despite the significant phylogenetic position allotted to the Batrachosauria, relatively little is known of their structure and evolution, largely because of the rarity of adequate fossils. The mode of preservation and past collecting techniques have also hampered our efforts. The majority of descriptions of early batrachosaurs are based on isolated skulls and a few postcranial elements of questionable association from the Upper Carboniferous of Great Britain. Descriptions of generally poorly preserved coeval American genera add little to our understanding of the group. Until recently, the only well-documented information on the batrachosaur postcranial skeleton came from descriptions of *Gephyrostegus* from the Upper Carboniferous of Bohemia and *Seymouria* and *Archeria* from the Lower Permian of North America. The postcranial skeleton of *Kotlassia* (Bystrow 1944), a highly terrestrial seymouriamorph from the Upper Permian of Russia, provides no information on the early evolution of the group. *Discosauriscus* (Špinar 1952) from the Middle Permian of Russia, is secondarily aquatic and possibly paedomorphic. These features make the evolutionary significance of its postcranial skeleton uncertain.

The recent discovery of several well-preserved skeletons of a new batrachosaur from the Upper Mississippian of West Virginia is therefore of considerable significance. The first specimen to be excavated and prepared, that of an incomplete and relatively immature individual, was described in a preliminary fashion and named *Proterogyrinus scheelei* (Romer 1970). Several more complete and mature specimens from the same locality have subsequently been prepared, and form the subject of this paper. *Proterogyrinus* is one of the best preserved and most complete of all batrachosaurs, permitting a virtually complete description of the skeleton (figure 1). It is also one of the earliest known members of this group.

To appreciate the phylogenetic significance of *Proterogyrinus* it is necessary to review briefly the presently hypothesized phylogeny of batrachosaurs (figure 2). The best known subdivision of the Batrachosauria, the suborder Anthracosauria, is composed of two infraorders: the Seymouriamorpha and the Embolomeri. The Seymouriamorpha is thought to include *Seymouria* (once considered either a reptile or a structural intermediate between reptiles and amphibians), discosauriscids (but see Heaton 1980), and a number of highly derived forms from the Russian Upper Permian and Lower Triassic of questionable affinities (see The relation between embolomeres and seymouriamorphs, below). The small terrestrial gephyrostegids from the

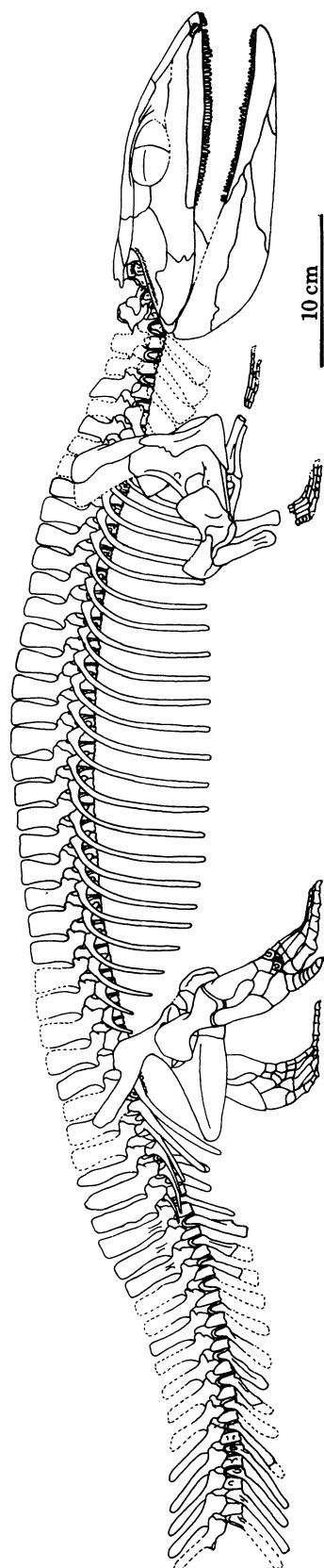


FIGURE 1. *Protogyrinus scheelei* Romer, skeletal restoration.

Upper Carboniferous of Bohemia and *Eoherpeton* from the Lower Carboniferous of Great Britain are thought to be either primitive seymouriamorphs or constitute their plesiomorphic sister group. An assemblage termed the Diadectomorpha by Heaton (1980), including *Diadectes*, *Limnoscelis*, and *Tseaajaia*, may be seymouriamorph derivatives. Heaton further argues that the Seymouriamorpha and Diadectomorpha form a monophyletic group more closely related to reptiles than to any other known batrachosaurs.

The Embolomeri includes the British and American eogyrinids and *Anthracosaurus* of Carboniferous age, and the archeriids from the American Lower Permian. With the exception of the incompletely known carnivorous *Anthracosaurus*, they all appear to have been long-bodied, aquatic piscivores.

Below the anthracosaur level of organization, batrachosaur phylogeny is poorly understood. The suborder Palaeostegalia, originally founded on a partial skull of *Crassigyrinus* (Panchen 1973) but further characterized by additional information from a recently discovered, nearly complete skeleton of the same genus (Andrews *et al.* 1977; Panchen 1980) appears to be a very primitive offshoot. The problematical loxommatids, with their distinctive 'keyhole-shaped' orbits, share many primitive features with batrachosaurs, but with the exception of vestigial tabular horns, and the structure of the basal articulation (Smithson 1982), no unequivocal shared derived characters can be identified. Nevertheless, Panchen considers them as batrachosaur derivatives more advanced than the palaeostegalians, but diverging from the mainline before the embolomere-seymouriamorph dichotomy.

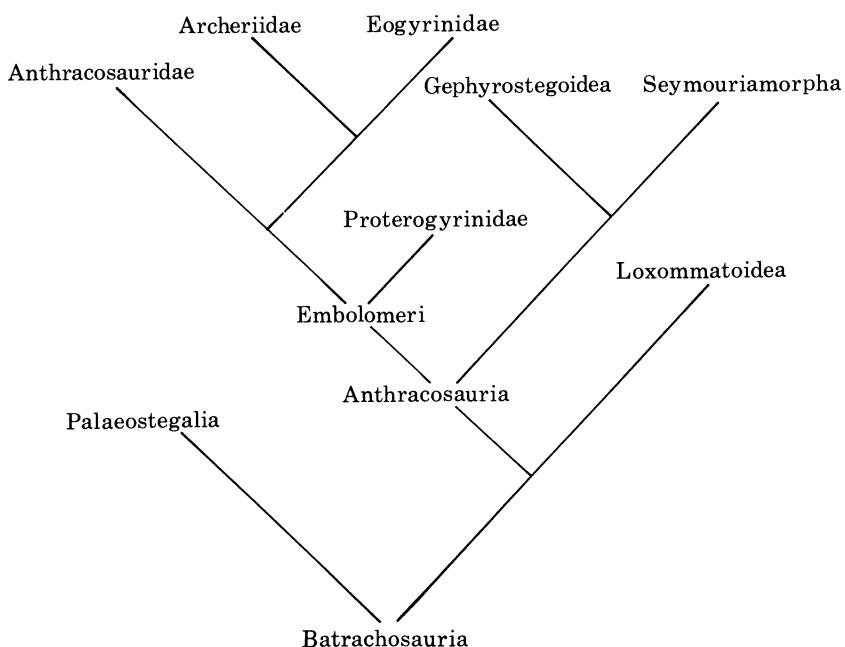


FIGURE 2. Hypothesized phylogeny of the Batrachosauria, modified from Panchen (1980).

Of all known fish, the osteolepiform crossopterygians share the greatest number of characters with primitive tetrapods, and have long been considered tetrapod ancestors. This has been disputed by Rosen *et al.* (1981), who argue that the characters used to establish this relation are either primitive characters (plesiomorphies) and therefore not reliable indicators of affinity, or invalid due to misinterpretation of fossilized structures. They believe that the dipnoans share

more derived characters with tetrapods, and should be considered the sister group of tetrapods (but see also Jarvik 1981). Whatever their phylogenetic relation, the *known* dipnoans, living or fossil, possess many specialized characters (autapomorphies) not present among osteolepiforms, and are much farther from the morphotype expected for tetrapod ancestors. Consequently, known lungfish are poorly suited as a starting point in an analysis of the fish–amphibian transition. Although many of the characters used to define osteolepiforms may be primitive for choanate fish and do not necessarily indicate affinity with tetrapods, these fish nevertheless provide a more plausible basis for the origin of tetrapod structures (cf. Gaffney 1979, p. 97).

Since *Proterogyrinus* occurs very early in the geological history of the batrachosaurs, it can be used to construct hypotheses concerning polarity of character states in this group. In addition, outgroup comparisons show that it is plesiomorphic in most characters, establishing *Proterogyrinus* as a primitive member of the infraorder Embolomeri. Because it occupied a position very close to the embolomere–seymouriamorph dichotomy, it also provides much information on the polarity of character states in both major groups of anthracosaurs. *Proterogyrinus* also allows us to evaluate the possibility of batrachosaurs having a significant relation to reptiles.

In addition to contributing to an understanding of the structure and phylogeny of the batrachosaurs, knowledge of the anatomy of *Proterogyrinus* clarifies important aspects of the early evolution of tetrapods. *Proterogyrinus* is one of the few known pre-Pennsylvanian tetrapods in which well developed, articulated limbs are available for three-dimensional study, rendering it a valuable source of information on the level of development of limbs at this early stage in the evolution of tetrapods.

SPECIMENS EXAMINED

All specimens were recovered from one localized lenticular deposit of the Upper Mississippian Bickett Shale, Bluefield Formation, Mauch Chunk Group located in the Greer Quarry, 10.5 km southeast of Morgantown, West Virginia. Busanus (1976), based on his work on macroscopic invertebrates and on his and other authors' work on ostracods from Greer, believes the Mauch Chunk to be equivalent to the Glen Dean and possibly as young as the Menard Formation of the Illinois Basin. These two units have been identified as lowermost Namurian (Henry & Gordon 1979; Swann 1963).

The specimens were prepared in the laboratories of the Cleveland Museum of Natural History with an S.S. White dental air abrasive machine, model F, using dolomite powder. Additional preparation was done by the author with an air-powered vibrating tool and mounted needle.

All specimens are from the collection of the Cleveland Museum of Natural History (CMNH), the Museum of Comparative Zoology, Harvard (MCZ), and the U.S. National Museum (USNM).

(i) CMNH 10950. Type specimen. Small individual preserved in three blocks containing a skull and scattered postcranial elements.

(ii) CMNH 10938. Articulated, reasonably complete postcranial skeleton of a small individual.

(iii) CMNH 11035. Isolated skull table with a few postcranial elements of a small individual.

(iv) CMNH 11067. Exceptionally well preserved, complete articulated skeleton of a large individual.

- (v) CMNH 11091. Disarticulated rear limbs of a large individual.
- (vi) CMNH 11111. Upper and lower jaws of a large individual.
- (vii) CMNH 11112. Disarticulated skull table and cheek with scattered postcranial elements.
- (viii) MCZ 4537. Reasonably complete, although somewhat disarticulated, large individual.
- (ix) USNM 22573. Type of '*Mauchchunkia bassa*' (Hotton 1970). A large individual with a good skull and numerous postcranial elements.
- (x) USNM 26368. Disarticulated postcranial remains of a large individual.
- (xi) USNM 26399. Disarticulated postcranial remains of a large individual.

SYSTEMATICS

In 1970, preliminary descriptions of two anthracosaur specimens from the Greer quarry appeared in the journal *Kirtlandia*: *Proterogyrinus scheelei* Romer (CMNH 10950) in April and *Mauchchunkia bassa* Hotton (USNM 22573) in September. The former is a small individual with a poorly ossified, scattered postcranial skeleton. The latter, with a skull approximately 50% longer, is much better ossified and more complete. Despite the differing states of maturity, both authors believed that there were enough significant differences to justify generic distinction. The following is a summary of apparent differences that suggested the presence of two anthracosaurs at Greer: a higher maxillary tooth count in *Proterogyrinus* (at least 40, compared with a total marginal count of 26 for *Mauchchunkia*), an unusually long tabular and a relatively elongated snout in *Proterogyrinus*, and a vertebral structure in *Proterogyrinus* in which both the pleurocentrum and intercentrum are incomplete rings, open dorsally in contrast to the 'protoreptilian' pattern in *Mauchchunkia*. Additional preparation of the type specimens reveals that some of the apparent differences are due to misinterpretation. Additional information gained from more recently discovered specimens from Greer indicates that the other differences can be attributed to the different states of maturity or to intraspecific variation. *Mauchchunkia* is therefore a junior synonym of *Proterogyrinus*.

Panchen (1975) erected the infraorder Herpetospondyli to include *Eoherpeton* and *Papposaurus*, both from the Scottish Namurian A, and *Proterogyrinus*. He considered the infraorder to be a primitive offshoot of the line leading to the Embolomeri. However, the concept of the Herpetospondyli was considerably weakened when *Eoherpeton* was removed from the group (Panchen 1980). Consequently, it appears more reasonable to consider the 'herpetospondyls' (essentially *Proterogyrinus*) as a primitive family of the Embolomeri rather than as comprising a separate infraorder. Since the term Proterogyrinidae (Romer 1970) has priority over the term Herpetospondyli (Panchen 1975), the latter should be dropped and all genera previously included in that taxon should be transferred to the family Proterogyrinidae.

Order Batrachosauria Efremov (see Panchen (1980) for diagnosis)
Suborder Anthracosauria Säve-Söderbergh

Diagnosis. (Revised from Panchen 1975, 1980.) Primitive batrachosaurs retaining the lateral kinetism between the skull table and cheek and large, posteriorly directed horns on the tabular bones (both characters absent in the advanced seymouriamorphs). Palatal tusks on at least palatine and ectopterygoid, with or without accessory teeth on ectopterygoid. Preopercular bone lost, postorbital length measured to posterior lip of postparietal always shorter than the preorbital length, tabular-parietal contact achieved with elimination of the postparietal-

supratemporal suture, broad frontal-parietal contact. Vertebral pleurocentra primitively horseshoe-shaped although complete cylinders in post-Mississippian genera, and except in atlas and posterior caudal segments, are longer than their corresponding intercentra.

Greatest transverse dimension of the interclavicle always closer to the anterior margin of bone, resulting in a more or less distinct parasternal process.

Limbs well developed, phalangeal count of five-toed manus 2, 3, 4, 5, 4, and of pes 2, 3, 4, 5, 4 or 5.

Infraorder Embolomeri Cope

Diagnosis. (Revised from Panchen 1975.) Anthracosaurs with body proportions primitively comparable with those associated with a terrestrial tetrapod, but tending toward secondary adaptations for aquatic anguilliform locomotion in at least one family. Skull of crocodilian piscivorous shape, snout elongated in some specialized forms, quadrate condyles well behind occipital condyle, especially in large genera, deep 'otic' notch, full kinetism between skull table and cheek present primitively, although partly fused anteriorly or completely absent in later genera. Lateral line sulci often conspicuous, dermal ornamentation of the normal anthracosaur type. Nasolabial groove primitively present, but lost in at least one genus. Prefrontal excludes lacrimal from orbit in all but the most primitive forms. Post-temporal fossae absent, basal tubera not conspicuously developed. Palatal dentition of tusks on palatine and ectopterygoid, and small teeth on ectopterygoid, vomers tuskless.

Lower jaw with two large Meckelian fenestrae in all but *Anthracosaurus* where the bony division separating the two fenestrae has been lost. Coronoid teeth primitively present, but lost in advanced groups.

Thirty-two presacral vertebrae primitively, but column more elongate in at least one family. Well-ossified pleurocentra always larger than intercentra except in atlas and posterior caudal vertebrae, intercentra complete rings, although not ossified dorsally in primitive members. Atlas arches and pleurocentra paired, axis arch with broad, hatchet-shaped neural spine.

Posterior process of ilium long and narrow, dorsal process variably developed.

Five phalanges on the fifth digit of pes.

Family Proterogyrinidae Romer

Diagnosis. (Revised from Romer 1970.) Primitive embolomere with skull structure generally similar to that of *Eogyrinus* and *Palaeoherpeton*. Anteorbital region relatively short. Taking midpoint of the orbit as a reference, the distance to the anterior end of the skull is between 20 and 30% longer than the distance to the posterior termination of the postparietals measured at the midline. Pineal rimmed. Median suture posterior to the pineal on a ridge flanked on either side by a depression. Tabular horn biramous in contrast with eogyrinids. Kinetic junction extends from otic notch to posterodorsal corner of orbit in contrast with more advanced families where it is variably fused. Jugal exposed on the ventral skull margin. Maxilla makes no sutural contact with the premaxilla. Marginal dentition: premaxilla 5; maxilla 46. Tooth shape similar to that of eogyrinids. Palatal dentition: vomer ?0; palatine 2; ectopterygoid 2(4). Teeth only slightly larger than those of the marginal series present on anterior coronoid, but none on posterior coronoid. Parasymphysial tusk present. Otic-occipital portion of braincase separated from the sphenethmoid by a large gap. Atlas pleurocentrum incompletely ossified ventrally as well as dorsally. The more posterior pleurocentra, although disc-shaped in adults, are unossified

dorsally in immature specimens. Dorsal suture may persist in some adults. Intercentrum a smaller ventral crescent. Well-developed supraneural canal in neural arches. Thirty-two presacral vertebrae. Pectoral limbs, although slightly stouter, like those of *Archeria* and other embolomeres as far as known. Pelvic limb generally similar to that of *Archeria* with the following exceptions: dorsal blade of ilium poorly developed, mesial surface of ilium bears a ventrally directed foramen that traverses the ilium-pubis suture and emerges on the external surface of the pubis posterior to the obturator foramen, tibia and fibula shorter and stouter, four centralia in tarsus, the most proximal (fourth) being partly fused to tibiale.

Proterogyrinus Romer

Type species. Proterogyrinus scheelei

Diagnosis. (Modified from Romer 1970.) Same as for family except that the pleurocentrum is unossified dorsally in immature individuals and although it forms an ossified floor for the neural canal in mature individuals, still bears a dorsal suture.

Proterogyrinus scheelei Romer

Mauchchunkia bassa Hotton

Diagnosis. Same as for genus.

DESCRIPTION OF SKULL

The dermal skull and palatoquadrate

See figures 3 and 4. Reconstructions of the skull are based on all available material and are not meant to represent any particular specimen. The dorsal and lateral aspects were based primarily on MCZ 4537 and USNM 22573, that of the palate on USNM 22573, CMNH 11067 and CMNH 10950. In areas where information is available on one side only, bilateral symmetry is assumed (see tables 1, 2 and 3 for skull data).

Of all the well-preserved embolomeres, the skull structure of *Proterogyrinus* is closest to that of the eogyrinids *Palaeoherpeton* and *Eogyrinus* (Panchen 1964, 1972a). It is high, bears large dorsolaterally facing orbits, and shows none of the marked aquatic specializations seen in later eogyrinids and archeriids. The cheeks are steep, forming an angle of about 60° with the skull table. The skull has a narrow, triangular outline as viewed dorsally. The shallow preorbital region is very short compared with most batrachosaurs, producing a primitive appearance. Taking the midpoint of the orbit as a reference, the distance to the anterior end of the skull is between 20 and 30 % longer than the distance to the posterior termination of the postparietals measured at the midline. Since the quadrates are positioned considerably posterior to the occiput, the orbits are approximately midway between the tip of the snout and the quadrate condyles. The adductor chambers are long and narrow. Anterior to the basal articulations, the mesial edges of the pterygoids diverge little from the midline. The palate hence retains the primitive 'closed' appearance.

The ornamentation is similar to that of later embolomeres. The pits, rounded and distinct at the centres of ossification, radiate outward to become faint, elongated streaks toward the edges of each bone. They are never as strongly developed as they are in temnospondyls.

As in all embolomeres, except *Anthracosaurus*, the skull of *Proterogyrinus* possessed lateral line sulci. They are poorly developed, however, appearing only as shallow, elongated grooves on

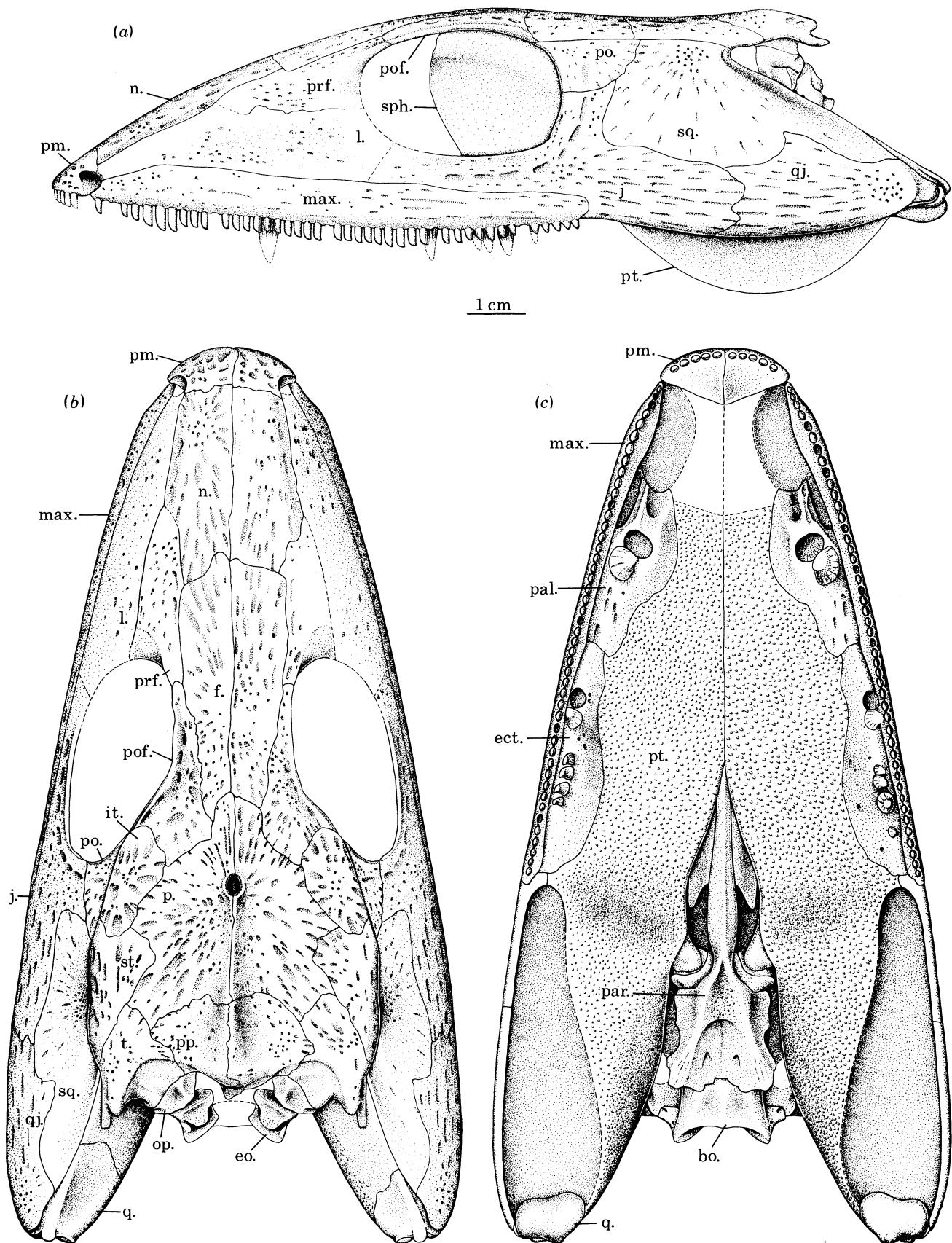


FIGURE 3. *Proterogyrinus scheelei* Romer, restoration of skull. (a) Lateral view; (b) dorsal view; (c) palatal view.

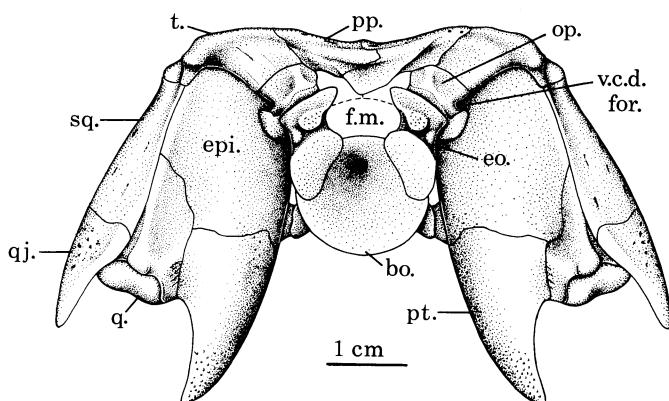


FIGURE 4. *Proterogyrinus scheelei* Romer, occipital restoration.

the postfrontal, postorbital, the suborbital ramus of the jugal, and on the lateral edge of the nasal. If a complete lateral line system existed, most of it was too superficial to have left an impression on the dermal skull bones.

The rectangular nasals are somewhat shorter than the frontals in all but CMNH 11035 (figure 5). Elongated pits on the posterior portion of the bone indicate that this area grew much more rapidly than the anterior portion during ontogeny. Although the anterior margin is well preserved in several cases, none shows any evidence that the nasal participated in the rim of the external naris.

As in other embolomeres, the frontals are narrow between the orbits, but gradually become wider anteriorly. The ornamentation indicates that the area of most rapid growth was in the anterior portion of the bone.

The parietals are similar to those of *Eogyrinus* (Panchen 1972a), *Anthracosaurus* (Panchen 1977b), and *Palaeoherpeton* (Panchen 1964). The specializations of the parietal seen in *Eoherpeton* (Panchen 1975), including an extreme anteroposterior shortening and possibly a posterolaterally directed suture with the tabular are not developed in *Proterogyrinus* (the latter occurs in CMNH 11035, see below). As in other embolomeres, the pineal is located anterior to the midpoint of the bone.

The size and shape of the pineal foramen varies considerably (figure 6), ranging from 2.5 mm in CMNH 11067 (a large individual) to 4.5 mm in CMNH 11035 (a relatively small individual) and from circular (CMNH 11035) to ovoid (CMNH 11067). The rim is distinctly raised in all cases. Posterior to the pineal, the common suture of the parietals can be traced along an acuminate median ridge that continues onto the postparietals. On either side of the ridge, the bone surface drops away into a deep, elongated depression. Laterally, the bone surface abruptly rises once more to the general level of the surface of the skull table. Although the raised pineal and associated depressions on the parietals are unknown in other described embolomeres, the features are present in an isolated skull table from the Namurian A of Scotland and an undescribed partial skull table from the Point Edward Formation (Namurian A), Nova Scotia (Smithson 1980). These animals and *Proterogyrinus* are all roughly contemporaneous and may be closely related.

The postparietals are roughly pentagonal in shape. The parietal depression continues onto the postparietal, deepens slightly posterior to the parietal-postparietal suture, and then shallows to produce the raised posterior rim of the table.

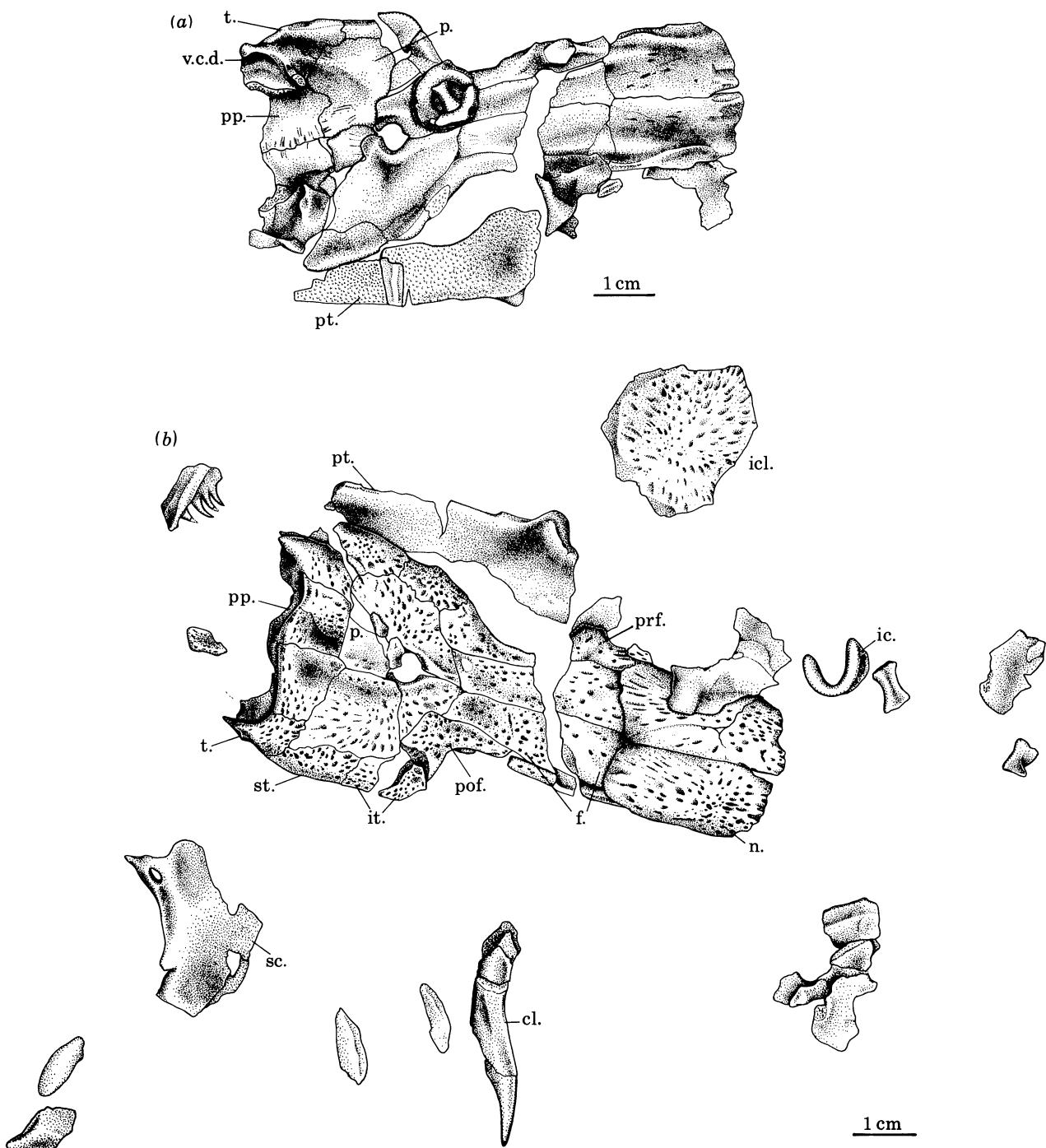


FIGURE 5. *Proterogyrinus scheelei* Romer, incomplete skull and postcranials (CMNH 11035). (a) Ventral view of skull; (b) dorsal view.

The tabular is generally of the type found in other embolomeres. (Romer (1970) overlooked the tabular-supratemporal suture in CMNH 10950, and the resulting 'tabular' in his reconstruction includes the supratemporal.) It forms a long posterolaterally directed suture with the supratemporal and an anterolaterally directed suture with the parietal, except in CMNH 11035 (figure 5) in which the suture is oriented posterolaterally as in *Eoherpeton*.

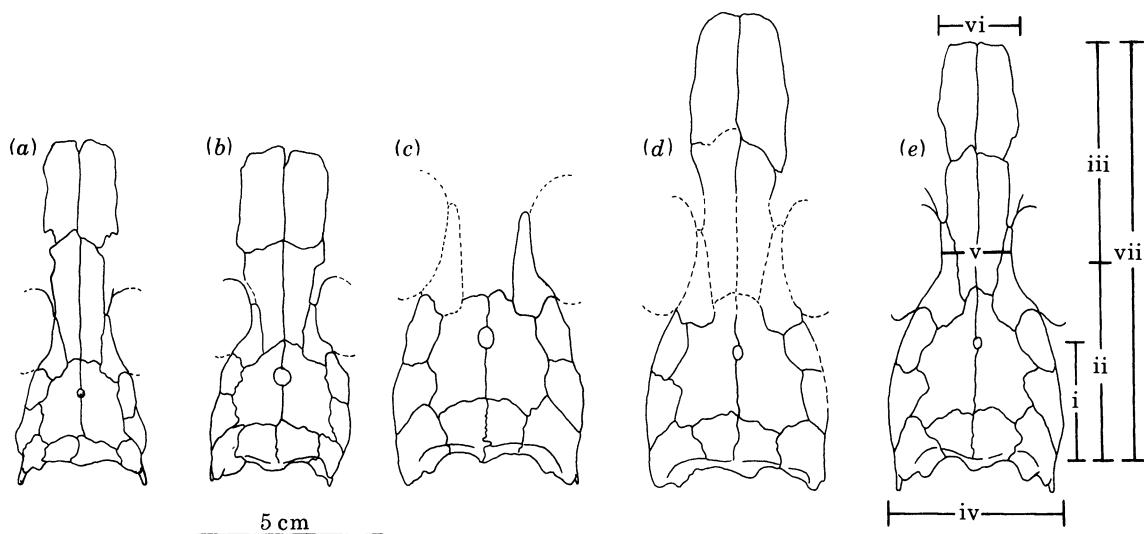


FIGURE 6. *Proterogyrinus scheelei* Romer, skull table restorations of five specimens to show variation in proportions. (a) CMNH 10950 (type); (b) CMNH 11035; (c) MCZ 4537; (d) CMNH 11067; (e) USNM 22573. Selected dimensions for each (indicated on (e)) are recorded in table 1.

Panchen (1975) placed considerable emphasis on this unusual feature in *Eoherpeton*, but its occurrence in one specimen of *Proterogyrinus* indicates that it may be of little taxonomic significance. Posteromesially, the tabular forms the lateral portion of the deeply concave posterior margin of the skull table. The moderately well-developed tabular horn is biramous. The dorsal ramus is actually a posterior extension of the posterolateral corner of the bone and bears faint dermal pitting. The ventral ramus, often broken off near its base, is a delicate posteriorly directed blade that originates from the ventrolateral surface of the tabular near the base of the dorsal ramus. The blade is somewhat dorsoventrally flattened and its ventral surface is convex if viewed laterally. Although the horns of *Palaeoherpeton* and *Eogyrinus* are also divisible into two parts (Panchen 1970, 1972a), the relation of the two parts is quite different than those of *Proterogyrinus*. In the former genera the blade, although directed slightly ventrally, is an extension of the posterolateral corner of the tabular rather than a discrete process arising separately from the ventrolateral surface of the bone. The topographic relation between the two processes of the tabular of *Proterogyrinus* is essentially the same as in *Anthracosaurus* (Panchen 1977b), although neither process is as massively developed. Panchen (1977b) suggests that the condition in *Eogyrinus* is primitive for embolomeres, and that the intermediate condition seen in *Eobaphetes* represents a transitional stage approaching the more advanced bifurcated horn present in *Anthracosaurus*. The presence of a biramous horn in *Proterogyrinus* as well as *Anthracosaurus* suggests that this highly distinctive feature (i) is a synapomorphy of the two genera; or (ii) was developed in parallel; or (iii) is primitive for embolomeres. Since *Proterogyrinus* shares no other derived features with *Anthracosaurus*, the first alternative seems unlikely. Until the functional significance of the bifurcated horn is understood, the second alternative is difficult to evaluate. The third alternative is tentatively accepted here. According to this interpretation, the intermediate condition in *Eobaphetes* represents a stage in degeneration from the hypothesized primitive biramous condition approaching an essentially uniramous condition seen in known eogyrinids and archeriids. Panchen (1977b) suggested that the down-turned ventral process in *Anthracosaurus* supported the back of the tympanum. However,

in *Proterogyrinus* this process turns up rather than down, making it less suitable for this purpose. No ventral process is described in *Eoherpeton*. As in other embolomeres, the ventral surface of the tabular forms the dorsal margin of the 'otic' notch.

The triangular supratemporal forms about half of the convex, lateral margin of the table. Ventrally, the posterior third of the bone contributes to the dorsal rim of the 'otic' notch, resulting in a deeper notch than is characteristic of other embolomeres. The remainder of the ventral surface forms a loose, non-sutural joint with the squamosal. The surface of the facet is convex, and does not show the groove for the accommodation of connective tissue seen in *Palaeoherpeton* and *Eogyrinus* (Panchen 1964).

The rectangular intertemporal is somewhat longer and narrower than in other embolomeres. Anteriorly it forms a loose, overlapping suture with the postfrontal. In both CMNH 10950 (figure 7) and 11035 (figure 5), the two bones have separated, showing the rounded pocket at the back of the postfrontal that received the intertemporal. Mesially and posteriorly, the



FIGURE 7. *Proterogyrinus scheelei* Romer, CMNH 10950. Type skull.

intertemporal is firmly sutured to the parietal and supratemporals, respectively. Laterally, it forms the anterior part of the smoothly curved edge of the skull table. At no point is its ventral surface suturally attached to the cheek, allowing the kinetic junction to extend unbroken from the 'otic' notch to the posterodorsal corner of the orbit. The ventral facet is convex. This condition is distinct from that of eogyrinids in which the junction is sealed anteriorly by the development of an interdigitating suture between the intertemporal and postorbital, but similar to that of *Eoherpeton* and possibly the contemporaneous Cowdenbeath embolomere (Smithson 1980). A full kinetic junction is no doubt a primitive character inherited from the osteolepiform fish condition.

The squamosal is well preserved in MCZ 4537 (figure 8). The dorsal facet for the articulation with the supratemporal is deeply concave, presumably to accommodate connective tissue (Panchen 1964). Posterior to the facet, the edge of the squamosal slopes posteroventrally at an angle of about 25° from the horizontal. Although roughly comparable to the condition in most embolomeres, it is distinctly different from that of *Eoherpeton* (Panchen 1975) and *Gephyrostegus* (Carroll 1970), in which the posterior margin of the bone is much closer to the vertical plane. It also lacks the distinct sigmoidal outline that has been attributed to all embolomeres except *Anthracosaurus*. This gives the otic notch a triangular outline that does not appear to have been suitable for supporting a tympanum. Recent re-examination of *Palaeoherpeton* and *Pholidopeltis* indicates that in neither of these genera could the notch have supported more than a tiny tympanum (Clack 1983), and Smithson (1982) has suggested that a tympanum was absent in primitive batrachosaurs and the notch was a remnant of the sarcopterygian spiracular cleft. It is uncertain whether such a spiracle would have been functional in batrachosaurs, but this hypothesis is compatible with the occurrence within the group of many apparent aquatic adaptations. Immediately anteroventral to the margin, and parallel with it, is a groove. Although well developed immediately behind the dorsal facet, it gradually broadens and shallows as it passes posteriorly. A similar groove in *Eoherpeton* is thought to have held the tympanum (Panchen 1975), but may simply represent the limit of dermis attachment (Clack 1983). Ornamentation is crisp and punctate around the ossification centre immediately ventral to the posterior termination of the dorsal facet, but rapidly lightens with distance from the centre, and is reduced to a few faint streaks at the opposite borders of the bone. Posteriorly, the squamosal wraps around the dorsal process of the quadrate.

The large quadratojugal comprises about 40 % of the height of the cheek. In USNM 22573 (figure 9) the left cheek has been folded during preservation to expose an extensive surface that underlapped the posterior part of the squamosal. Posteriorly, the quadratojugal covers most of the lateral surface of the quadrate leaving only the condyle exposed. In both USNM 22573 (figure 9) and MCZ 4537 (figure 8), punctate ornamentation covers the ossification centre located near its posterior end. More anteriorly, deep elongated striations run parallel to the gently convex ventral border of the skull.

The ossification centre of the jugal is marked by small round pits located at the level of the posterior rim of the orbit. Elongated striations, similar to those on the quadratojugal, pass posteriorly parallel to the ventral margin of the skull toward the jugal–quadratojugal suture (figures 8, 9). Although its precise position is difficult to locate owing to damaged bone surface, the sculpture patterns of the two bones place the suture well behind the posterior tip of the maxilla, allowing the jugal considerable exposure on the ventral margin of the skull (figure 3). This derived condition is shared by *Palaeoherpeton*, *Eogyrinus*, *Archeria*, and *Neopteroplax*.

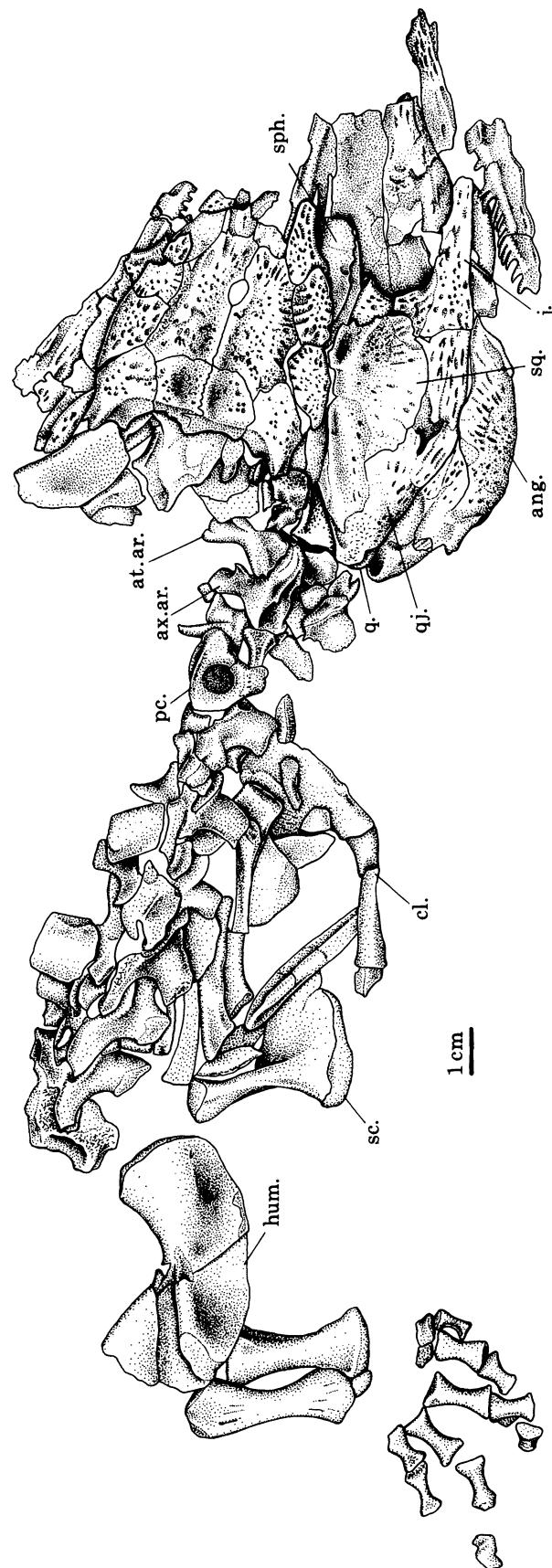


FIGURE 8. *Proterogyrinus schiedei* Romer, MCZ 4537. Partial skull and anterior trunk, dorsal view.

(Romer 1963), but not *Anthracosaurus*, *Eoherpeton* or *Gephyrostegus*, which retain the osteolepiform fish condition in which the large quadratojugal makes contact with the maxilla anteriorly and excludes the jugal from the ventral skull margin. An analogous condition is shown by the eogyrinid *Eobaphetes* (Panchen 1977b). However, in the latter, the quadratojugal is short anteroposteriorly, and the jugal is excluded from the skull margin by a posterior extension of the maxilla. This condition is probably derived from that seen in *Palaeoherpeton* rather than primitive.

The orbits, as in other embolomeres, are subcircular with some ‘squaring off’ posteriorly and ventrally, although not nearly as square in outline as in *Eoherpeton*.

Posteriorly the postfrontal is expanded in dorsal view, constricting the anterior part of the parietal mesially, and producing a convexity in the rim of the orbit laterally. It makes an underlapping suture with the intertemporal, and ventral to this forms a short contact with the anterior tip of the postorbital, thus completing the superior facet of the kinetic joint anteriorly and barely excluding the intertemporal from the rim of the orbit.

The postorbital is preserved in MCZ 4537 (figure 8) and USNM 22573 (figure 9). In the former it clearly shows the trough-shaped anterior continuation of the inferior facet of the kinetic joint already described in the squamosal.

The part of the orbital margin formed by the jugal is not smoothly curved. Posteriorly, it is close to vertical. However, as the edge is traced anteroventrally, it abruptly approached the horizontal, beyond which the ventral rim is almost straight. This contributes to the ‘squared off’ appearance of the orbit. In no specimen is the bone surface anteroventral to the orbit well preserved, leaving the position of the jugal–lacrimal suture in doubt.

The lacrimal, where present, is crushed and its form difficult to interpret. However, some data are available from USNM 22573 (figure 9) in which post-mortem crushing has folded the left cheek under the skull roof. The fold continues anteriorly through the orbit and separates the prefrontal from the lacrimal along their common suture, exposing clearly defined matching surfaces. The lacrimal is a large bone, with parallel dorsal and ventral borders except anteriorly, where the dorsal border turns ventrally. The dorsal margin can be traced posteriorly to within about 9 mm of the position of the anterior margin of the orbit, at which point the bone shows no indication of narrowing. This suggests that the lacrimal–prefrontal suture continued to the orbit, and that the lacrimal contributed to the orbital margin. This primitive condition is known in *Gephyrostegus* and is approached in *Eoherpeton*, in which the lacrimal comes to within 3 mm of the orbit. In all later embolomeres, the lacrimal is excluded from the orbital margin by a ventral process of the prefrontal that makes contact with the jugal. Anteriorly, the bone is broken, but appears to have sent a narrow process to form part of the rim of the external naris.

The long, thin prefrontals are preserved in part in CMNH 11035, 10950 and USNM 22573 (figures 5, 7 and 9). The flat dorsomesial surface of each bears conspicuous pits. In the anterodorsal corner of the orbit, each bears an expansive bevelled area, devoid of dermal ornamentation, that turns into the orbit. The two surfaces are separated by a distinct ridge that begins as an anterior continuation of the lateral edge of the postfrontal and passes anteriorly in a broad lateral arc. A similar morphology is figured in *Eoherpeton*.

Premaxillae are preserved in CMNH 11067 (figure 10). Their size and form show quite clearly that the snout of *Proterogyrinus* was narrow anteriorly as in other embolomeres. Posterolaterally, the external surface of each turns sharply inward to form the concave anterior and part of the dorsal wall of the ‘vestibule’ of the external naris, much as in *Eoherpeton*. In

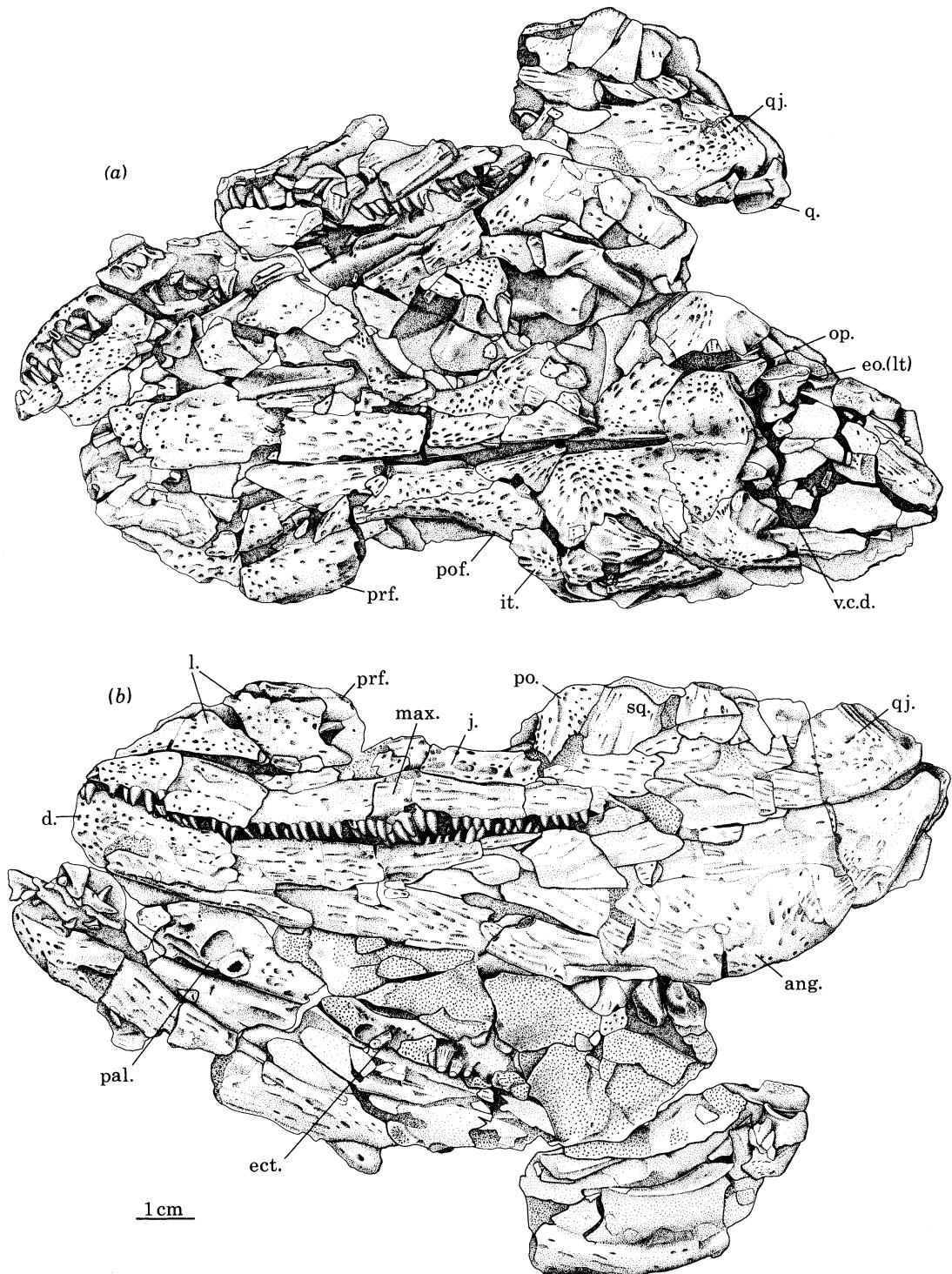


FIGURE 9. *Proterogyrinus scheelei* Romer, USNM 22573. Type skull of '*Mauchchunkia bassa*'. (a) Dorsal view; (b) ventral view.

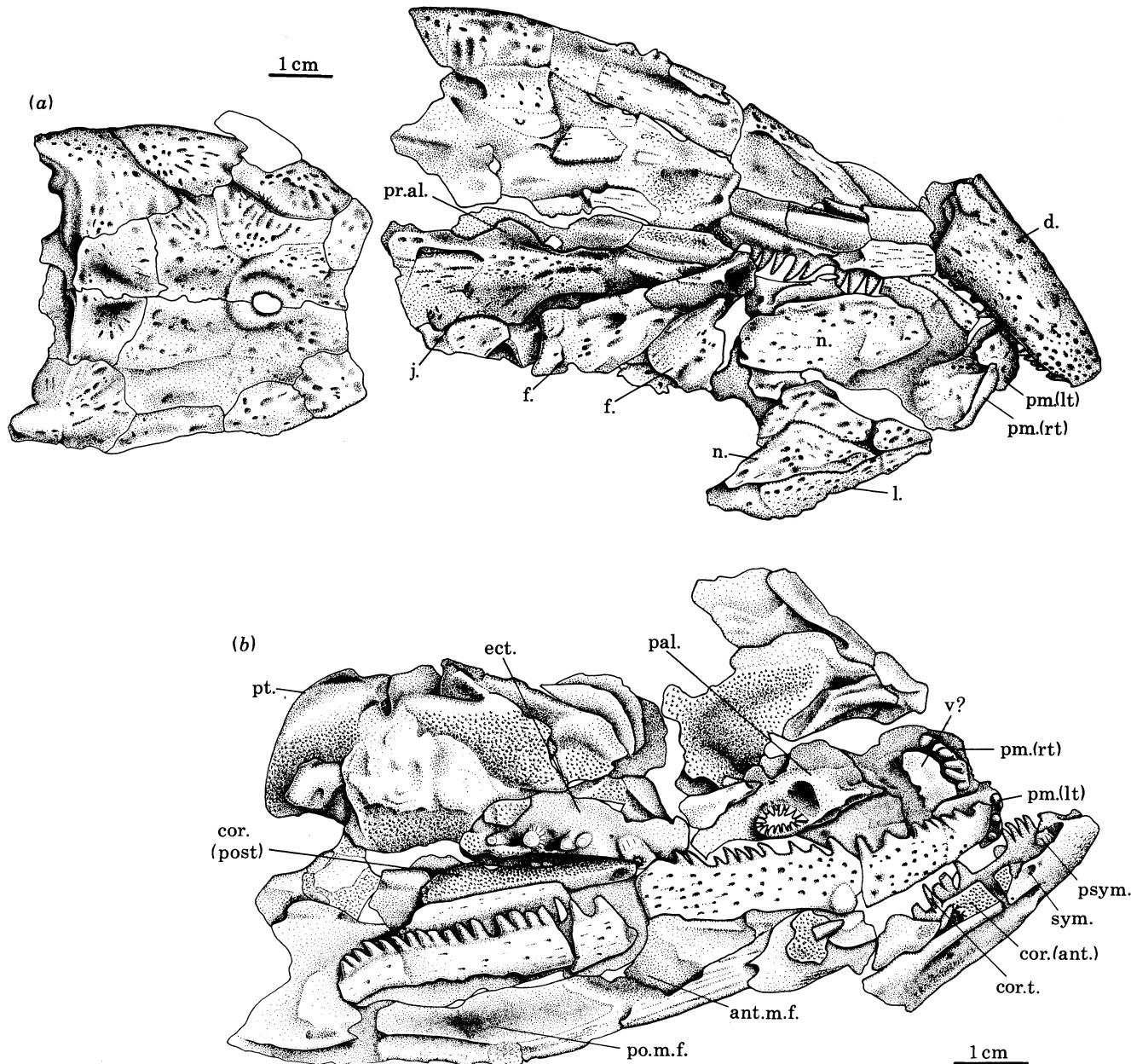


FIGURE 10. *Proterogyrinus scheelei* Romer, CMNH 11067. Skull. (a) Dorsal view; (b) ventral view.

Proterogyrinus, this wall continues posteromesially to the midline. The teeth are discussed in a separate section.

The anterior end of the maxilla is well preserved in CMNH 10950, 11067, and USNM 22573. In all specimens, the smooth, round termination shows no evidence of a sutural contact with the premaxilla. The lateral margin is bevelled anteriorly, indicating the presence of a nasolabial groove. Dorsally, it bears a gentle but distinct excavation that serves as the ventral margin of the external naris. As in most anthracosaurs, the maxilla has little lateral exposure. Its ventral margin is gently convex. The teeth are discussed in a separate section.

None of several well-preserved nasals shows a narial margin. It is probable that the premaxilla formed most of its dorsal rim making contact with the lacrimal and excluding the nasal from the rim of the naris.

The narial margin of the lacrimal is not preserved. No septomaxilla could be identified.

The skull tables of five specimens are represented with a minimum of reconstruction in figure 6. Although all specimens show the same qualitative characters, there are noticeable differences in proportions, none of which can be attributed to post-mortem distortion (table 1). In CMNH 10950 (type) the lateral margins of the table diverge posteriorly, its widest point being at the level of the tabular-supratemporal suture, and the snout is quite long and narrow. The table of CMNH 11035 is more square in proportions, it is wider between the orbits, and the snout is much broader and somewhat shorter. The type of '*Mauchchunkia bassa*' (USNM 22573) is intermediate in most proportions with the convex lateral margins of the table being widest near the supratemporal-intertemporal suture, and a moderately elongated snout. The skull tables of CMNH 11067 and MCZ 4537 are similar to that of USNM 22573 and, although the interorbital region of the former is not preserved, the elongate nasals indicate that the snout was slightly longer, approaching the proportions in CMNH 10950. There is no tendency to elongate the snout with increased absolute size as might be expected in an ontogenetic series: in fact the smallest individual (CMNH 10950) has the greatest relative snout length. However, such a trend might not be apparent in a small sample in which the skull size spans such a narrow range.

Although it is possible that these specimens constitute more than one taxon, there are no distinct morphological breaks, and for the want of any additional evidence, it is simplest to consider all as members of one taxon possessing a considerable degree of variation in skull proportions.

TABLE 1. SKULL DIMENSIONS OF *PROTEROGYRINUS*

| | I pp.-pin. | II pp.-midorbit | III midorbit- nasal | IV maximum table width | V maximum interorbit | VI maximum nasal width | VII pp.-nasal |
|------------|---------------|--------------------|---------------------------|---------------------------------|----------------------------|---------------------------------|------------------|
| USNM 22573 | 31 | 49 | 60 | 46 | 19 | 26 | 109 |
| CMNH 10950 | 20 | 38 | 49 | 34 | 15 | 19 | 86 |
| CMNH 11035 | 22 | 38 | 45 | 37 | 17 | 23 | 77 |
| CMNH 11067 | 28 | ?54 | ?63 | 48 | — | ?26 | ?111.5 |
| MCZ 4537 | 28 | 52 | — | 49 | 21 | — | — |

All measurements in millimetres.

TABLE 2. SELECTED RATIOS OF MEASUREMENTS IN TABLE 1

| | min. midorbit- nasal | max. interorb. width | max. nasal width | max. nasal width | min. interorb. width | max. table width |
|------------|----------------------------|----------------------------|------------------------|------------------------|----------------------------|------------------------|
| | pp.- midorbit | max. table width | max. table width | pp.- nasal | pp.- nasal | pp.- nasal |
| USNM 22573 | 1.225 | 0.413 | 0.565 | 0.239 | 0.174 | 0.422 |
| CMNH 10950 | 1.289 | 0.441 | 0.559 | 0.221 | 0.174 | 0.395 |
| CMNH 11035 | 1.184 | 0.459 | 0.622 | 0.229 | 0.221 | 0.481 |
| CMNH 11067 | — | — | 0.542 | 0.222 | — | — |
| MCZ 4537 | — | 0.429 | — | — | — | — |

Panchen (1970) hypothesized that the British eogyrinids form an allometric series. To demonstrate this, he plotted the total skull table length from the back of the postparietal to the anterior termination of the snout ('postparietal length') against a number of other skull measurements (see figure 11). Although his data were limited, it indicated that the British eogyrinids belong to a morphocline beginning with the small *Palaeoherpeton* and terminating with the large *Eogyrinus*. In small skulls, the table is long relative to the snout and as the absolute size of the skull increases, the length of the preorbital region increases at the expense of the postorbital region.

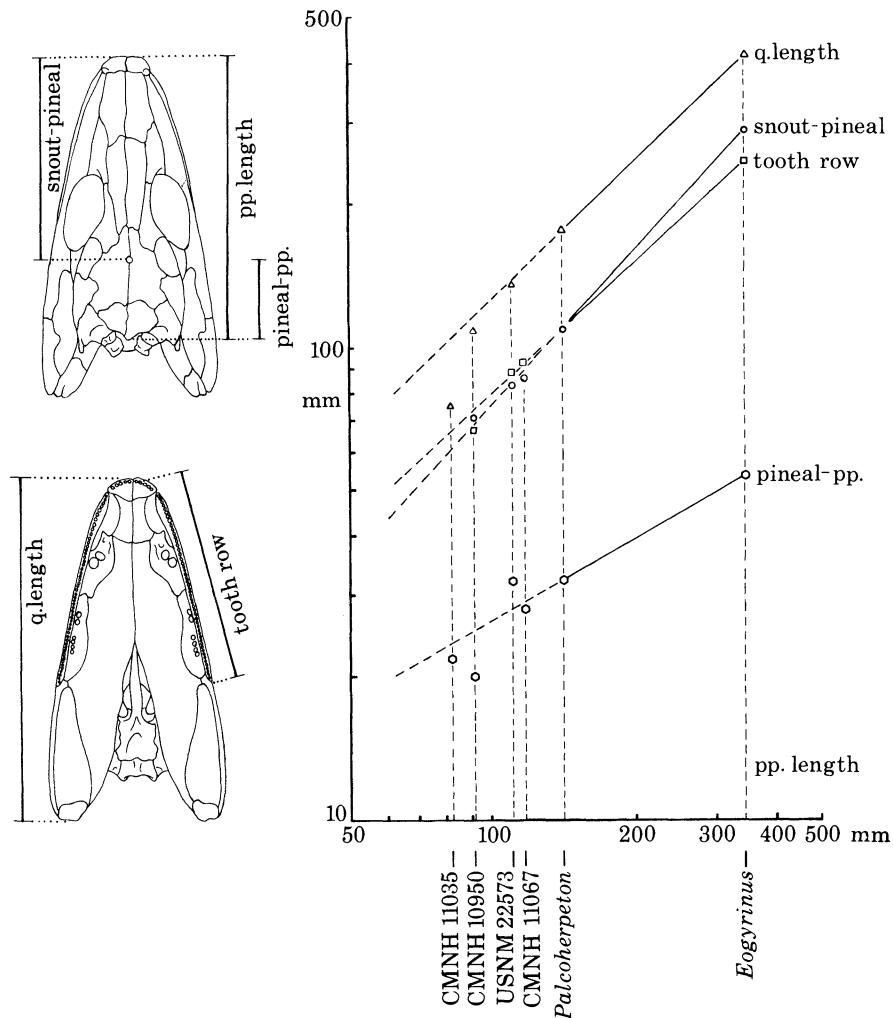


FIGURE 11. Allometric plot of selected skull measurements of British eogyrinids (solid lines) and four specimens of *Proterogyrinus*. *Proterogyrinus* measurements, indicated on skull figures, from table 3.

Although a sample of four specimens is statistically not significant, an attempt has been made to take comparable measurements in *Proterogyrinus* (table 3). It was possible to determine the pineal-postparietal length accurately in all specimens. The remaining measurements were estimated by assuming a 6 mm long premaxilla in CMNH 10950 and CMNH 11035. In CMNH 11067 the smashed interorbital region was reconstructed assuming that the back of the tooth row was in line with the pineal as it is in other specimens.

Although the plotted data fall slightly below the extrapolated line in most cases (figure 11), the points are close enough to suggest that the smaller *Proterogyrinus* skulls either conform approximately to the eogyrinid allometric series or form another series not greatly divergent from it. In either case, the relatively short snout of *Proterogyrinus* is primarily a function of the small absolute size of the skull, and is not necessarily a more primitive condition than that of later embolomeres, although a short antorbital region, being characteristic of osteolepiform fish might be expected in a primitive tetrapod.

TABLE 3. SKULL MEASUREMENTS OF *PROTEROGYRINUS* USED IN ALLOMETRIC PLOT (SEE FIGURE 15
FOR EXPLANATION OF MEASUREMENTS AND PLOT.)

| | pp.-length | q.-length | pineal-pp. | tooth row | snout-pineal |
|------------|------------|-----------|------------|-----------|--------------|
| CMNH 10950 | 91 | 108 | 20 | 67 | 71 |
| CMNH 11035 | 82 | — | 22 | — | 65 |
| CMNH 11067 | 117.5 | — | 28 | 93.5 | 87 |
| MCZ 4537 | — | — | 28 | — | — |
| USNM 22573 | 115 | 136 | 31 | 89 | 84 |

All measurements in millimetres.

Elements of the palate are best preserved in MCZ 4537 (figure 12) and USNM 22573 (figure 9), although additional information is available from CMNH 10950 (figure 7), CMNH 11035 (figure 5) and CMNH 11067 (figure 10).

No readily identifiable vomer is preserved in any of the specimens. A badly preserved bone, partly overlying the palatal surface of the right premaxilla of CMNH 11067, may be a vomer, but gives little information concerning its structure. There is no trace of vomerine fangs in any specimen. These fangs are large, conspicuous structures in many temnospondyls. If they were present in *Proterogyrinus* they probably would have been evident in some specimens. It is hence concluded that, as in other embolomeres, they were absent. The narrow outline of the snout, obtained by reconstruction of the relatively well-preserved dorsal aspect, indicates that the vomers must have been narrow and elongate as in other embolomeres, and unlike those of many temnospondyls, which are larger and more robust, to support fangs.

The palatine is preserved in USNM 22573, CMNH 11067 and CMNH 10950. The two large tusks, like those present in other embolomeres, are borne on the greatly thickened central region that projects their bases somewhat ventral to the general surface of the palate. The larger anterior tusk, represented in CMNH 11067 and USNM 22573 by subcircular pits of a maximum diameter of 5 mm, is surrounded by a raised, rather rugose rim as in *Eoherpeton*. The rim forms a buttressed ridge anterior to the tusk. A sharp ridge continues anteriorly from the rim to merge with the edge of the internal naris at its posterolateral corner. Mesial to this ridge is an elongate concavity that begins anterior to the ridge and slopes anterodorsally to the posterior rim of the internal naris. In CMNH 11067, the concavity bears two nutrient foramina. The morphology of this part of the palatine is very similar to that of *Eoherpeton*.

Lateral to the ridge and buttress, the palatine bears a laterally facing concave excavation. This matches well with the concavity on the mesial surface of the maxilla in CMNH 10950 between the maxillary teeth 9 and 15. These excavations contribute to the walls of a deep fenestra between the anterior end of the palatine and the maxilla. The form of the maxillary excavation indicates that the fenestra opened dorsally as a large elongate foramen into the region

of the nasal capsule. A similar fenestra is described in *Eogyrinus* (Panchen 1972a). It may be associated with the Jacobson organ. It is possible that the fenestra in *Proterogyrinus* was continuous with the internal naris. The slightly smaller posterior tusk is located immediately behind as in most other embolomeres, but unlike *Eoherpeton*, where the two tusks are separated by a considerable distance. Posterior to the tusks, the surface of the palatine bears deep, irregular pits in USNM 22573 similar to those in *Eogyrinus*. In CMNH 10950, it also bears irregular patches of closely spaced denticles. These denticles, also present on the ectopterygoid of USNM 22573, were probably not directly associated with the bone surface, but were imbedded in the dermis and lost in most specimens when the dermis decayed before preservation.

The ectopterygoid bears six tusks. The first pair, although smaller than the palatine tusks, are distinctly larger than the remaining four, from which they are separated by a distinct gap, as in *Eogyrinus*. In *Eoherpeton* all ectopterygoid tusks are about the same size. In *Proterogyrinus* the smallest tusks are approximately the size as a large maxillary tooth. As in the palatine, the bone is thickened around the tusk roots, projecting their bases ventral to the general palatal surface. The lateral margins of the tusk rims are raised. Where not covered by patches of denticles, the surface bears pits similar to those on the palatines.

The relation between the posterior end of the ectopterygoid and the jugal is not clear in any of the articulated specimens. However, in CMNH 11067 the right jugal clearly shows a modest processus alaris that would almost certainly have made contact with the pterygoid mesially and excluded the ectopterygoid from the rim of the adductor chamber, as it does in *Eogyrinus* and *Palaeoherpeton*.

The pterygoid can be considered to be composed of an anterior horizontal palatal ramus, a central region around the basal articulation, and a more nearly vertical posterior quadrate ramus.

The palatal ramus is covered by small, closely spaced denticles. Striations on the thickened mesial surface of the long, anterior portion of the palatal ramus of the right pterygoid in CMNH 10950 indicate that the pterygoids met anteriorly to form a long common butt-joint, producing the 'closed' palate present in anthracosaurs and loxomatids. Posteriorly, the mesial edges of the pterygoids diverge slightly from the midline, exposing the cultriform process of the parasphenoid.

The denticle-covered central region of the pterygoid, characterized by its concave ventral surface, effects a smooth transition between the horizontal palatal ramus and the vertical quadrate ramus. It is not clear whether the pterygoid participates in the basal articulation, as the pterygoid–epipterygoid suture is not visible in this region.

The mesial aspect of the quadrate ramus is preserved in CMNH 10950, showing a rounded, ventrally projecting flange, characteristic of embolomeres, that begins in the region of the basal process and sweeps well below the ventral edge of the cheek. The ramus, almost devoid of denticles except near its ventral rim, does not show the shallow pit and ridge ornamentation seen in *Eogyrinus*. In all other specimens, post-mortem crushing has badly distorted the quadrate ramus, obscuring the natural shape of the mesial rim of the subtemporal fossa. Posteriorly, the pterygoid shows a common suture with the quadrate, and dorsally with the epipyterygoid.

The mesial aspect of the right epipyterygoid is also preserved in CMNH 10950 (figure 7). The basal process, with its saddle-shaped terminal surface, is well-preserved, but the posterior and dorsal portions of the articular surface are obscured. Posteriorly, the pterygoid–epipyterygoid suture is clearly visible. The quadrate–squamosal ramus of the epipyterygoid is complete except

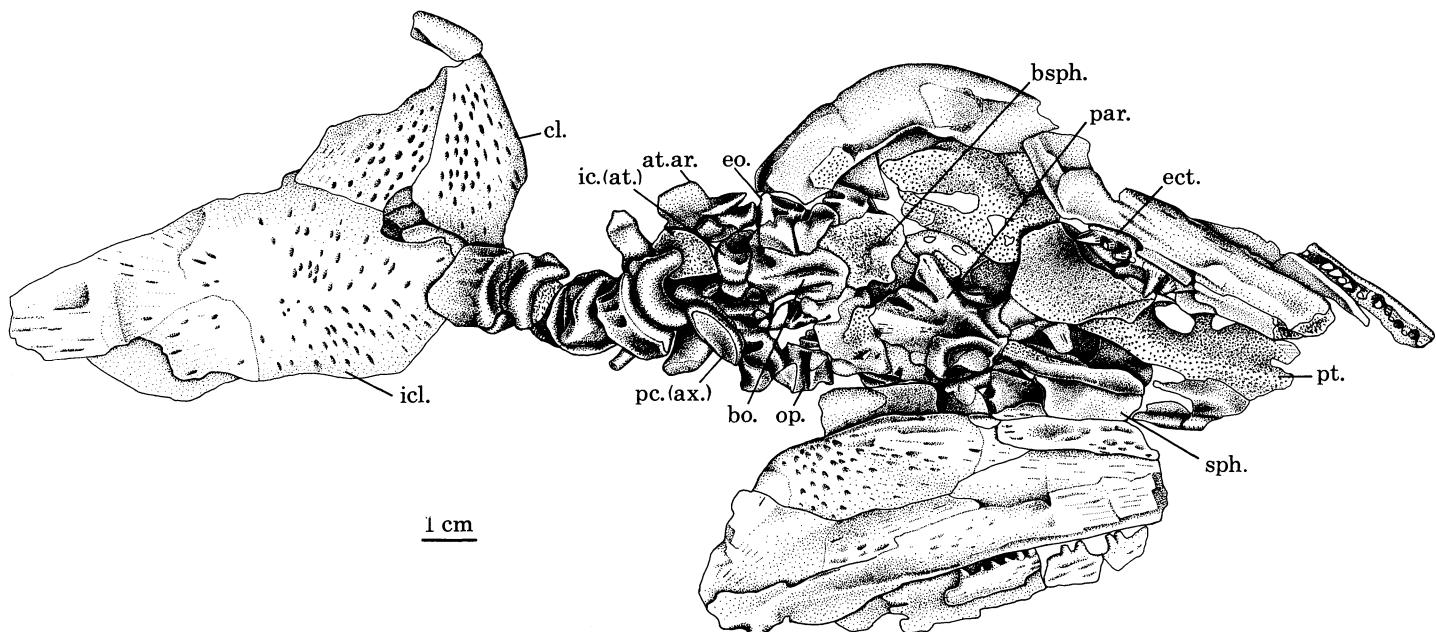


FIGURE 12. *Proterogyrinus scheelei* Romer, MCZ 4537. Partial skull and anterior trunk, ventral view.

for a few small gaps along its edge. The columella cranii, located at the anterior end of the quadrate-squamosal ramus and apparently continuous with it, is in the form of a mesially turning, vertical flange arising immediately posterior to the root of the basal process. The columella appears to be incomplete dorsally and therefore it is uncertain whether it bore the dorsal fork seen in *Palaeoherpeton*. The epipterygoid may have sent a palatal ramus anteriorly along the dorsal surface of the pterygoid adjacent to the midline but a suture separating the two bones in this area is lacking, making this impossible to confirm.

The quadrate, also present in CMNH 11067 and 10950, is best preserved in USNM 22573, in which its ventrolaterally facing condyle is partly exposed on the right side (figure 9). Additional information on the contours of the condyle is inferred from the glenoid of an isolated articular (CMNH 11112, figures 14 and 15). The condyle's double surface is composed of a large, mesial convexity and a smaller lateral convexity separated by a shallow longitudinal groove.

Dorsal and anterior to the condyle, the quadrate forms a plate-like, mesially facing dorsal process. Its smooth surface bears a shallow, anterodorsally directed concavity. Although fractured bone surface obscures the position of the quadrate-pterygoid suture, the appearance of denticles in the mesial surface of the suspensorium roughly 15 mm in front of its posterior termination indicates its approximate position. No quadrate foramen is preserved. The posterodorsal edge of the dorsal process is formed by an acuminate ridge, visible laterally, that terminates posteroventrally as a blunt boss at the dorsal edge of the condylar surface. The dorsal edge of the dorsal process forms a simple butt joint with the mesially facing dorsal edge of the squamosal and quadratojugal. The quadratojugal-quadratojugal suture appears to have been poorly consolidated, since it separated cleanly on both sides in one specimen (figure 9).

The braincase

The braincase of the British embolomeres has been studied extensively by Panchen (1964, 1970, 1972a, 1975, 1977b). All are massive, well-ossified structures composed of a posterior otic-occipital region housing the brain and inner ears, and an anterior sphenethmoid region through which several nerves passed toward the snout. Although the two units are distinct, they are firmly co-ossified. This condition has been tacitly assumed to be primitive for the following reasons.

- (i) It superficially resembles that in the presumed ancestral osteolepiform fish, in which both otic-occipital and sphenethmoid are heavily ossified and connected by an extensive, albeit moveable joint.
- (ii) It resembles closely that of the rather distantly related temnospondyls, and particularly that of loxommatids. The appearance of a similar braincase in these groups suggest that it is primitive for tetrapods. This argument has recently been complicated by the suggestion that loxommatids may be more closely related to embolomeres than to temnospondyls (Panchen 1980; Smithson 1982).
- (iii) Reptiles, generally considered to be more advanced than any amphibian, have very poorly ossified braincases, suggesting a progressive reduction in ossification as reptilian status was approached and ostensibly establishing the polarity for this character.

Parts of the braincase of *Proterogyrinus* are preserved in MCZ 4537 (figures 8 and 12) and USNM 22573 (figure 9). Although both specimens appear to be quite mature and little disturbed during preservation, the braincases are incomplete and elements have become disarticulated from each other and from the dermal roof. This indicates that the braincase was poorly ossified in life in marked contrast to the condition in later embolomeres. Nevertheless, the preserved portions generally follow the embolomere pattern.

Because components of the dermal skull roof, particularly the tabulars and postparietals, provide important areas of contact with the posterior parts of the braincase in embolomeres, relevant aspects of their morphology will be considered here.

The occipital plate of each postparietal slopes posteroventrally, making an angle of about 35° with the transverse plane. A ridge begins at the midline and sweeps dorsolaterally across the posterodorsally facing surface of each postparietal and onto the tabular. Below each ridge is a pocket for muscle attachment. A triangular median process projects ventrally between the opisthotics and almost reaches the dorsal margin of the foramen magnum.

On the ventral surface of the tabular, a double-faceted tabular-opisthotic contact, similar to that in *Palaeoherpeton* (Panchen 1964) forms the major attachment between the skull roof and otic-occipital. As in *Palaeoherpeton*, there is a deep, posterolaterally directed groove between the two facets. This groove will be discussed below. A depression, probably homologous to a similar one located anterior to the tabular facets in *Palaeoherpeton* is weakly developed in *Proterogyrinus*. As in antracosaurs generally (including *Seymouria*) the tabulars have extensive occipital exposure, restricting the postparietal exposure to a narrow area flanking the median line.

The ventral surface of the postparietal bears a few striations (figure 5A), but these provide no specific additional information about the attachment between the braincase and skull roof.

The occipital surface of the opisthotic bears a shallow pocket bordered mesially by a low rounded ridge, but there is no evidence for a fossa bridgei (figure 4). Mesially, there is a large

gap in the occipital plate between the ventral margins of the postparietals and the foramen magnum. Although the complementary facets of the opisthotic and tabular match well, indicating a close fit, the two bones never co-ossified and the opisthotics are displaced in both specimens.

Although the gap in the occipital plate ventral to the postparietals and mesial to the preserved opisthotics may have contained an unossified supraoccipital, this element is not included in the restoration. The position that it occupies in early reptiles is occupied by the occipital exposure of the opisthotics in other embolomeres such as *Eoherpeton* (Panchen 1980) *Anthracosaurus* (Panchen 1977b). Panchen now believes that the suture between the 'supraoccipital' and the postparietals of *Palaeoherpeton* (Panchen 1964) is an artefact of preservation (A. L. Panchen, personal communication). If this is true, then there is no evidence that the supraoccipital existed as a separate ossification. There is no supraoccipital preserved in *Gephyrostegus* (Carroll 1970) or *Seymouria* (White 1939), although Carroll provisionally added one in this reconstruction of the former, following Panchen's original description of *Palaeoherpeton*. The supraoccipital is also absent in loxomatids (Beaumont 1977), and temnospondyls such as *Eryops* (Sawin 1941) and *Edops* (Romer & Witter 1942).

The exoccipital is similar to that of *Pholidherpeton* (Clack 1983) and *Eogyrinus* (Panchen 1972a) in most respects. Ventrally it contributes to a small part of the occipital condyle. Above the distinct 'waist' the expanded dorsal portion articulates with the opisthotic. Between the two expansions, its occipital surface bears a large convex condyle for articulation with the proatlas. A deep groove, possibly marking the passage of the first spinal nerve, turns laterally from the foramen magnum, passes ventral to the articular surface for the proatlas, and then promptly bifurcates.

As in other embolomeres and loxomatids, the basioccipital forms most of the occipital condyle.

The opisthotics are well preserved in MCZ 4537 (figures 8 and 12) and USNM 22573 (figure 9). Although the ventral surface of the tabular clearly indicates that the opisthotic is attached by two facets as in other embolomeres, the opisthotic is poorly ossified anteriorly and only the posteromesial facet is preserved. Nevertheless, it is clear that the double opisthotic–tabular contact of *Proterogyrinus* encloses a large channel that passes from the dorsolateral corner of the occiput anteromesially into the dorsal cranial cavity. Panchen (1964) identified this foramen in *Palaeoherpeton* as the passage of the vena capitis lateralis. However, in vertebrates generally, this vein does not pass out of the posterodorsal corner of the braincase, but rather runs lateral to the wall of the braincase where it receives the vena capitis medialis as it leaves the cavum crani with the facial (VII) nerve, and then passes lateral to the otic capsule to become the jugular vein posteriorly (Goodrich 1930). This is certainly the case in *Salamandra* (Francis 1934) and *Sphenodon* (O'Donoghue 1921) in which it passes ventrolateral to the paroccipital process. Jarvik (1954) has reconstructed a similar pattern in *Eusthenopteron* in which the vein pierced the ventral portion of the ventrolaterally expanded paroccipital process. If the course of the vena capitis lateralis of *Palaeoherpeton* was that suggested by Panchen, it would be unique among vertebrates. A more likely possibility is that the foramen admitted the vena capitis dorsalis into the cranial cavity. Although unknown in modern amphibians, the vein commonly occurs in living and fossil reptiles (O'Donoghue 1921). In *Sphenodon* it drains the muscles in the spino-occipital region, passes into the posttemporal fenestra and pierces the dorsal occipital surface of the skull by way of a foramen in the parietal, or between it and the otic or

supraoccipital bone. The vein drains into the transverse sinus of the cranial cavity, which in turn drains into the vena capitis medialis, a major tributary of the vena capitis lateralis (O'Donoghue 1921).

A similar pattern is present in *Lacerta* and *Natrix* ('*Tropidonotus*') (Bruner 1907). A 'vena capitis dorsalis' has been reconstructed in the Triassic temnospondyls *Capitosaurus* (Watson 1919), *Metoposaurus* (Wilson 1941), and in several trematosaurs (Säve-Söderbergh 1936), the Permian temnospondyls *Edops* (Romer & Witter 1942), *Eryops* (Sawin 1941), the Carboniferous loxommatids (Beaumont 1977), and crossopterygians (Säve-Söderbergh 1936). However, in all cases, the vein is reputed to have passed anteriorly from the post-temporal fossa (fossa bridgei) through a foramen ('post-temporal foramen' of Romer & Witter (1942)) on the anterior wall of the fossa into the cavum epipteriticum rather than into the cavum cranii as is the case in recent forms. The reason for this incongruity is uncertain, but may be traced to an original misunderstanding of the structure of extant forms by Watson (1919). The actual function of the 'post-temporal foramen' in fossil tetrapods and fish is therefore uncertain, although in *Amia*, an extant actinopterygian fish, a similar foramen carries the oticus facialis, a branch of the seventh cranial nerve, into the fossa bridgei (Allis 1897). A nerve composed of fused rami of the fifth and tenth cranial nerves (ramus ophthalmicus superficialis V and ramus auricularis) exits through a separate foramen on the dorsal surface of the braincase and passes posteriorly into the fossa bridgei. More posteriorly, the ramus supratemporalis lateralis (IX) pierces the floor of the fossa (Allis 1897). All nerves serve the sense organs of the lateral line system. This pattern is probably primitive for actinopterygians (Patterson 1975). No blood vessel foramina passing from the fossa bridgei into the cavum cranii have been described. The foramen between the tabular and opisthotic in embolomeres, although clearly not homologous to the 'post-temporal foramen' that has been incorrectly identified as the passage for the vena capitis dorsalis, may, none the less, have carried that vein from the occipital region into the cavum cranii as in living reptiles. The 'post-temporal fossa' of *Seymouria* (White 1939), quite distinct from that of any of the above, is essentially identical (and no doubt homologous) to the foramen of embolomeres as it follows the same course between the tabular and opisthotic into the cavum cranii (see The relationships between embolomeres and seymouriamorphs, below). As in embolomeres, there is no development of a pocket-like post-temporal fossa (fossa bridgei) of the type seen in temnospondyls, and certainly no fenestra opening into the cavum epipteriticum. Beaumont described two foramina in the braincase of *Baphetes kirkbyi*, number B.M. (N.H.) R2753 (Beaumont 1977, pp. 84 and 86, and figure 20). One foramen, located anterior to the fenestra ovalis and piercing the prootic thus opening into the post-temporal fossa, is no doubt the 'post-temporal foramen'. She identified this foramen as the place of entry of the vena capitis dorsalis, in accord with the then generally understood course of that vessel in fossil tetrapods (see above). Beaumont described another foramen as a perforation of the posterolateral wall of the otic capsule marking the point of emergence of the vena capitis dorsalis from the post-temporal fossa. This foramen, depicted in figure 20 (Beaumont 1977), clearly passes between the opisthotic and tabular much as the vena capitis dorsalis foramen does in embolomeres and *Seymouria*. It is uncertain, however, whether this foramen could have admitted the vena capitis dorsalis into the cavum cranii. A vein passing from the occipital region through the foramen would have had to have passed mesially across the dorsal portion of the post-temporal fossa before gaining access to the cavity. The appropriate bone surface is not exposed in the specimen, making it impossible to confirm this course. Beaumont does not describe the foramen

in any other loxommatid, although unless the specimens are of exceptional quality, such a small foramen could easily have been obscured during preservation or preparation, or simply have gone unnoticed unless a specific effort were made to locate it. The common occurrence of this foramen in embolomeres, seymouriamorphs, many modern reptiles, and possibly loxommatids suggests a unique pattern of venous circulation that distinguishes these groups from other known Palaeozoic tetrapods.

The opisthotic of *Proterogyrinus* is deeply notched just ventral to the lateral termination of its posteromesial tabular facet. The notch, visible in occipital aspect, is confluent with the groove for the vena capitis dorsalis on the dorsolateral surface of the opisthotic. The groove widens as it turns anterodorsally into the cavum cranii. Hotton (1970), who had only one specimen available to him, misidentified this groove as part of the margin of the fenestra ovalis. Immediately ventral to the notch is a prominent posterolaterally facing facet that may have served as an attachment surface for the dorsal process of the stapes.

A small fragment of bone located ventral to the right tabular in USNM 22573 may be part of the pro-otic. Hotton (1970) tentatively identified the concave margin of this element as the anterior border of the fenestra ovalis. However, this curved border more closely resembles the anterior margin of the pro-otic of *Palaeoherpeton*, and has been restored tentatively in that position (figure 13).

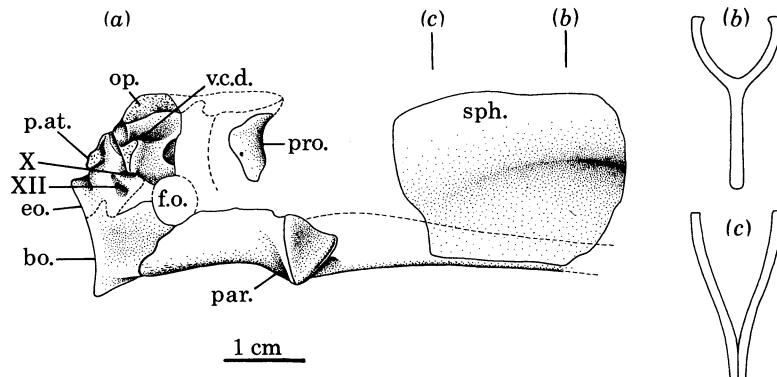


FIGURE 13. *Proterogyrinus scheelei* Romer, reconstruction of braincase. (a) Lateral view; (b, c) sections through sphenethmoid at points indicated in (a).

The otic-occipital region bears no ossified roof, which is a conspicuous feature of later embolomeres.

The region of the fenestra ovalis is poorly preserved. The maximum size of the fenestra (assuming an approximately circular shape) as determined by a reconstruction (figure 13) is comparable to that of *Palaeoherpeton*.

Exoccipitals are preserved in both MCZ 4537 and USNM 22573. One exoccipital, interpreted by Hotton (1970) as the right, is preserved in USNM 22573 (figure 9). However, examination of the more recently discovered MCZ 4537 (figure 12) in which both exoccipitals are preserved, indicates that it is the left exoccipital that has been displaced to the right side of the specimen during burial.

The vagus foramen passes between the dorsolateral corner of the exoccipital and the opisthotic as in most Palaeozoic amphibians. Ventral and slightly posterior to this foramen, the large hypoglossal foramen pierces the body of the exoccipital. *Proterogyrinus* shares this condition with loxommatids, *Edops*, *Eryops*, *Greererpeton*, and the microsaurs *Pantylus* (Romer

1969a) and *Goniorhynchus* (Carroll & Currie 1975), suggesting that this is a primitive tetrapod character.

The basisphenoid-parasphenoid complex is well preserved in MCZ 4537 (figure 12). The parasphenoid and attached basipterygoid processes of the epipterygoid were forced anteriorly during preservation, shearing them from the rest of the otic-occipital and exposing the ventral aspect of the basioccipital and the remainder of the basisphenoid. The large basisphenoid is poorly preserved, probably because it was incompletely ossified, and appears as a block of unfinished bone with indistinct edges. Posteriorly, it is firmly attached to a well-preserved basioccipital. The well-preserved articular surfaces of the basipterygoid processes are not saddle-shaped as they are shown in restorations of *Palaeoherpeton* and *Eogyrinus* (Panchen 1964, 1972a), but bear two facets: one concave and anterodorsal in orientation, the other convex and facing anteroventrally. The two facets are separated by a rounded transverse ridge passing ventrolaterally, forming an angle of approximately 55° with the frontal (horizontal) plane. Such an articular surface would allow the basal processes of the epipterygoid to slide ventrolaterally on the ridge or rotate slightly on a transverse axis inclined approximately 55° from the frontal plane, but would preclude rotation about a dorsoventral axis. This is generally consistent with Panchen's explanation of skull mechanics in embolomeres (Panchen 1964). However, it should be noted that movement of the cheek-palate complex would not have been strictly dorsoventral during rotation. The inclined axis would have produced a considerable mesiolateral component, causing some rotation about an anteroposterior axis through the joint between the cheek and skull roof. Thomson (1967) hypothesized that since little dorsoventral movement between the skull roof and the palate was possible anterior to the orbit, the palatoquadrate-cheek complex could not have rotated in a dorsoventral plane around the basipterygoid articulation as Panchen hypothesized, but must have moved as a lever hinged at its anterior end, presumably with the inferior epipterygoid surface of the basipterygoid articulation sliding ventrolaterally on the superior (basisphenoid) surface, causing ventrolateral movement of the quadrates. However, in *Proterogyrinus*, the axis of the basal articulation is roughly parallel to the outer surface of the cheek. Consequently, any mesiolateral sliding at the articulation, although producing ventrolateral movement of the quadrate, would involve mainly tension-compression at the kinetic junction, and little rotation through its anteroposterior axis.

Only the most posterior part of the dorsal aspect of the basioccipital is exposed in MCZ 4537 (figure 8) showing its contact with the atlas intercentrum.

The parasphenoid is very similar to that of other embolomeres. The triangular basal plate is deeply concave. The lateral, posteriorly diverging ridges bear deep longitudinal striations. The surface of the plate bears scattered clumps of denticles that were probably embedded in the skin rather than attached to the bone during life. A pair of carotid foramina for minor branches of the internal carotid pierce the plate.

The parasphenoid is solidly attached to the basipterygoid processes of the basisphenoid. A pair of sharp ridges, anterior extensions of the lateral ridges of the plate, converge mesially between the processes. Between each ridge and the base of the corresponding process is a deep groove that provided passage for the internal carotid and palatine branch of the seventh cranial nerve. The region of the fenestra ovalis is obscured by bone fragments.

The cultriform process is V-shaped in cross section and bears a ventral ridge. It expands laterally immediately anterior to the basipterygoid processes and then gradually narrows anteriorly as far as preserved.

The sphenethmoid is preserved only in MCZ 4537 (figures 8 and 12). It differs considerably

in structure from those of other embolomeres, but resembles that of 'batrachosaurian' amphibians such as *Seymouria* (Heaton 1980), primitive reptiles (Heaton 1979) and the primitive temnospondyl *Greererpeton* (Smithson 1982). As in the latter groups except *Greererpeton*, but unlike most embolomeres, there is no ossified roof nor is there any evidence that the sphenethmoid is composed of a dorsal and a ventral ossification of the type described in *Palaeoherpeton* (Panchen 1964).

Viewed posteriorly, the sphenethmoid is V-shaped, showing a median suture. Anteriorly it is Y-shaped, restricting the olfactory tracts and vomeronasal nerves to the dorsal part of the braincase. The thin interorbital septum shows no median suture at its anterior termination. Unlike *Palaeoherpeton*, *Eogyrinus* and most later temnospondyls, there are no longitudinal osseous septa dividing the cavity of the sphenethmoid, nor is there evidence for a membranous septum.

There is a large gap between the sphenethmoid and the otic-occipital, unlike other, later embolomeres, but as in *Eoherpeton* (A. L. Panchen, personal communication).

Anteriorly, the bone thins and terminates slightly anterior to the midpoint of the orbit. The broken anterior margins indicate that the bony sphenethmoid probably extended somewhat further anteriorly in life, but there is no evidence that the region of the openings for the olfactory tracts and vomeronasal nerves ossified.

The lower jaw

See figures 14 and 15. The lateral aspect of the lower jaw is preserved in USNM 22573 (figure 9). Its general form differs from that of other embolomeres in being much shallower posteriorly. This primitive osteolepiform feature is shared by *Eoherpeton*. Not all sutures are evident on its heavily fractured surface, but each bone is easily delineated by its distinctive pattern and intensity of sculpturing. The dentary bears punctate ornamentation anteriorly. Posteriorly, it gradually thins to a wedge and bears elongated striations parallel with the tooth row. Except posteriorly, the teeth are concealed by the maxilla, making a tooth count impossible. The dentition is discussed in a separate section.

Most of the ventrolateral surface of the ramus is formed by the presplenial and postsplenial. Both bear deep, elongated pits running parallel to the ventral margin of the ramus.

Coarse, elongated pits of the angular radiate dorsally and anteriorly from its ossification centre near its ventral margin towards the suture with the surangular. A narrow anterior process, virtually devoid of sculpturing, forms a limited contact with the dentary.

The surangular, bearing faint, approximately horizontal grooves, is distinct from the coarsely ornamented angular. Although only part of their common suture can be seen, its course can be inferred by the abrupt change in sculpture pattern. The dorsal portion of the surangular is obscured by the cheek in USNM 22573. However, a portion of a large surangular crest is preserved in CMNH 11111 (figure 14). This derived character is shared by later embolomeres.

The articular is almost completely sheathed laterally by the surangular. Posterior to the glenoid, the articular bears a prominent boss similar to that on the quadrate that is continuous with a ridge on the posterior edge of the jaw. With the jaw in articulation with the skull, the bosses face each other across a short distance (about 4 mm) when the jaw is closed. A stabilizing ligament probably ran between them. Similar bosses occur in *Archeria*. A stout process in *Eoherpeton*, identified by Panchen (1975) as a retroarticular process, may be homologous. Otherwise this process is unknown in other anthracosaurs. The deeply concave glenoid of the articular, rhomboidal in shape dorsally, is divided into a large mesial depression and a smaller

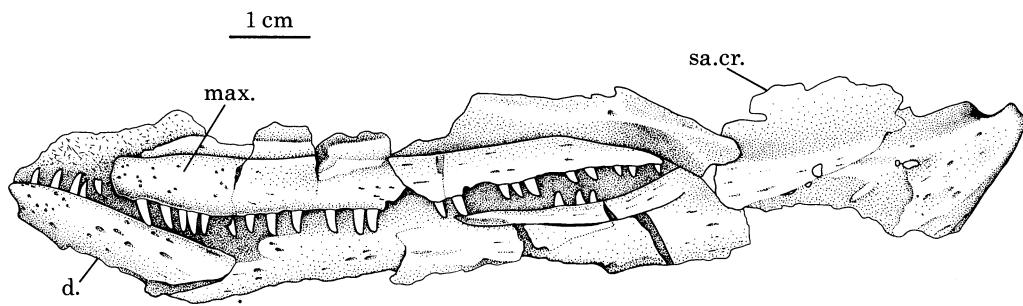


FIGURE 14. *Proterogyrinus scheelei* Romer, CMNH 11111. Partial upper and lower jaws.

lateral depression by an anteroposterior ridge (figure 15). Mesially and posteriorly, the edge of the glenoid bears a thickened lip.

The middle portion of the fragmentary mesial aspect of the lower jaw is difficult to interpret. The posterior portion of the ramus is well preserved in USNM 22573 (figure 9). The articular appears to be sheathed posteriorly by the surangular and mesially by the prearticular, leaving little but the glenoid rim exposed. The prearticular forms the smooth, gently concave dorsal bevelled border of the mesial wall of the adductor fossa. The anterior portion of this border is not preserved. Ventral to the bevelling, an acuminate ridge, similar to that seen in *Eogyrinus* and *Eoherpeton* runs quasiparallel to the rim.

The anterior three-quarters of the mesial aspect of the jaw, in varying states of preservation, is exposed in CMNH 11067 (figure 10). The prearticular bears a thick, horizontal reinforcing ridge in its dorsal border from the adductor fossa to the anterior end of the bone. Anterior to the adductor fossa and apparently forming part of its border, is a long narrow posterior coronoid bearing closely spaced denticles. Its suture with the prearticular has opened, showing clearly that the longitudinal reinforcing ridge is associated with the prearticular as in *Eogyrinus* and not the coronoid, as in *Eoherpeton*. The dorsal, presumably denticle-bearing, part of the middle coronoid is obscured by the displaced left maxilla. The more ventral portion, bearing an anterior continuation of the reinforcing ridge described above, is separated from the splenial by a diagonal suture. Posteroventrally, the middle coronoid forms the anterior border of a foramen (see below).

Most of the anterior coronoid is exposed in CMNH 11067. In addition to closely spaced denticles, it bears at least one large tooth. Another loose tooth, too large to be from the marginal series is probably associated with the anterior coronoid. This primitive condition is distinctly unlike that of *Eoherpeton*, in which the anterior coronoid is devoid of both denticles and teeth.

The presplenial bears the anterior-most part of the longitudinal reinforcing ridge on its dorsal border. Ventral to the ridge is a rugose depression, similar to that in *Eoherpeton*, identified by Panchen (1972a) as the origin of an intermandibularis muscle.

In CMNH 11067, the ventral margin of a moderate-sized fenestra is preserved near the anterior end of the postsplenial. Crushing of bone surface or subsequent preparation with air abrasives has obscured its other borders. The Meckelian space passing through the ramus appears to terminate just anterior to this fenestra. Immediately posterior to the fenestra, a thickening of the postsplenial resembles the ventral part of the bar separating the two Meckelian fenestrae in *Eogyrinus*. Unfortunately, the displaced maxilla, located dorsal to this point, obscures the critical area of the prearticular and deprives us of conclusive evidence of a large

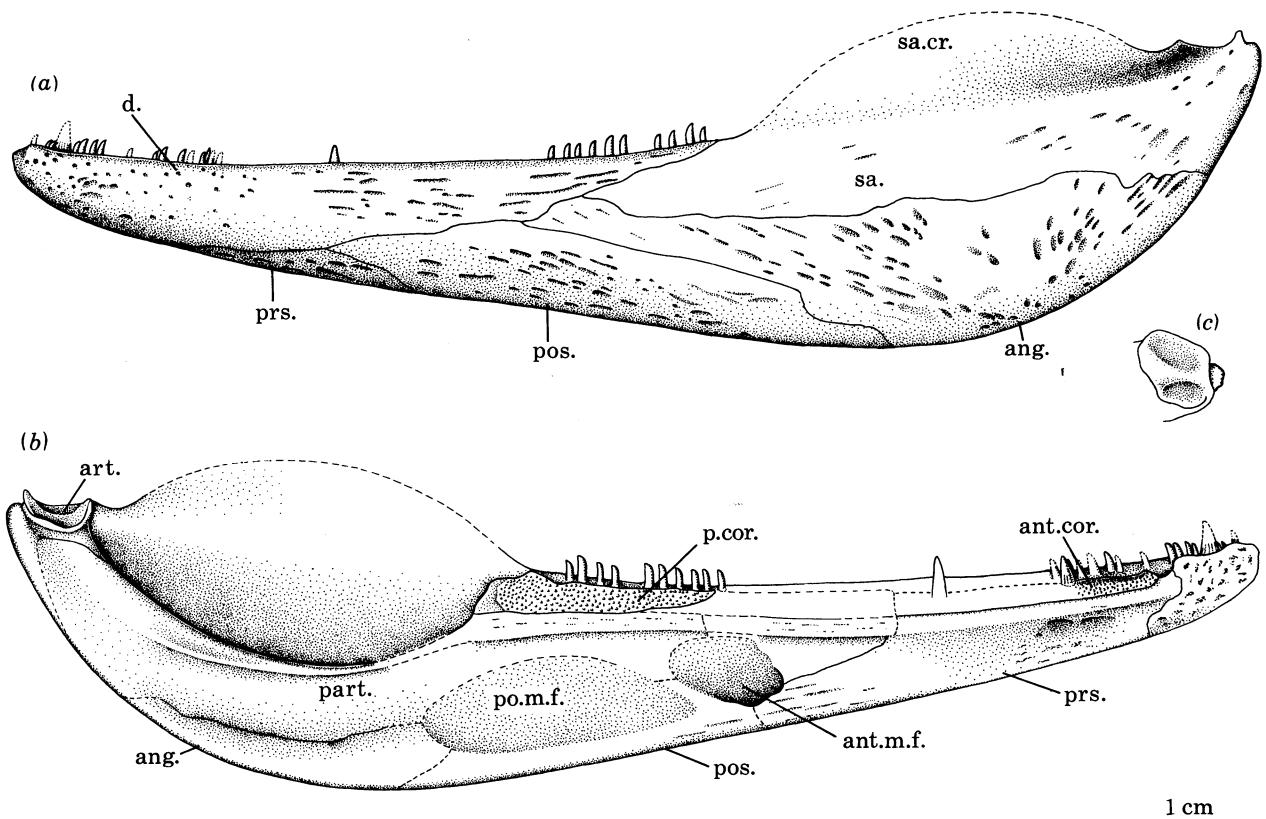


FIGURE 15. *Proterogyrinus scheelei* Romer, reconstruction of lower jaw. (a) Lateral view; (b) mesial view; (c) articular, dorsal view.

posterior Meckelian fenestra. The Meckelian space is 'open' ventral to where it is obscured by the maxilla, suggesting the presence of the fenestra. However, the ventral margin of the ramus appears to be broken, indicating that the mesial wall of the ramus, formed by the postsplenial and prearticular in most primitive amphibians, may simply have been broken away and lost during preservation. It is felt that the balance of evidence slightly favours the presence of a large posterior Meckelian fenestra. If this is the case, *Proterogyrinus* would resemble other embolomeres, but not *Eoherpeton* which, like most other primitive amphibians, retains small Meckelian foramina.

The mesial exposure of the dentary is limited to the symphysis. Between the symphysis and the tooth row it bears a prominent parasymphseal tusk. This feature, although present in the primitive antracosaur *Gephyrostegus* and common in temnospondyls, is unknown in other embolomeres except the Point Edward embolomere (Romer 1958), to which *Proterogyrinus* is probably closely related. '*Antracosaurus lancifer*', a Linton embolomere that has since been synonymized with *Leptophractus obsoletus* (Panchen 1977b), has been cited as having symphyseal dentition that consists of three teeth, smaller than those of the marginal series and located posterior to the symphysis (Romer 1963). Their small size, number (symphyseal dentition is normally represented by a solitary tusk and a companion replacement pit in each jaw), and somewhat posterior position suggest that they are probably more appropriately identified as coronoid teeth.

Dentition

Both premaxillae, preserved in CMNH 11067, bear poorly preserved, blunted teeth (figure 10). Including replacement pits, there is room for five teeth in each. This is high for anthracosaurs, the count ranging from two in *Anthracosaurus* to five in *Eoherpeton*. Including replacement pits, each maxilla has room for about 46 teeth. Hotton (1970) estimated that there were about 26 marginal teeth (including premaxilla) in USNM 22573. However, more complete preparation reveals room for about 46 teeth in the maxilla, as in CMNH 11067 and CMNH 10950. This count is much higher than in other anthracosaurs with short preorbital regions, for example, *Palaeoherpeton*, 30, *Eoherpeton*, 18–24, but is closely comparable to that in the primitive *Gephyrostegus* (45–47) and '*Pholiderpeton bretonensis*' (about 46) from Point Edward. *Eogyrinus* and *Archeria*, which have elongated snouts adapted to a piscivorous diet, have counts (including empty pits) in excess of 46 (Panchen 1970, 1972a).

The maxillary teeth in *Proterogyrinus* are variable in length. In USNM 22573, the most anterior are about 2 mm in length measured from the ventral margin of the maxilla (viewed laterally) to the tip. Beginning at mx. 6, the tooth row begins to rise to a 'canine peak' at mx. 7 and 8, both of which is about 3.5 mm in length. Posterior to mx. 8, the teeth abruptly return to a length of 2 mm and, with very minor variations, remain that length until about mx. 28, where there begins a second peak culminating at mx. 30 (3.5 mm). From that point, the teeth become reduced gradually in length to the back of the maxilla. Although the teeth are somewhat shorter in the smaller CMNH 10950, the pattern described above is the same. Relative to the size of the skull, the teeth in *Proterogyrinus* are much smaller than in later embolomeres, but show a similar relation to that in *Gephyrostegus*.

Tooth shape is similar to that of eogyrinid embolomeres. Viewed laterally, the sides of the shaft of all but the most posterior teeth are parallel except toward the tip, where the anterior margin sweeps back to join the straight posterior margin. However, in CMNH 10950 some of the teeth between the two peaks do not taper at their ends, but end abruptly in laterally compressed chisel-like blades, resembling the tooth structure thought highly characteristic of archeriid embolomeres. A similar trend is present in *Pholiderpeton scutigerum* from the British coal measures (J. Clack, personal communication). The posterior five teeth become progressively shorter and more bulbous in outline. The considerable variation in tooth structure and apparent overlap in structure with archeriids dictates cautious use of tooth shape as a taxonomic character.

Following the method of formulating dental count in 'labyrinthodonts' proposed by Chase (1963), *Proterogyrinus* would be characterized as follows:

- (i) marginal dentition: pmx, 5; mx, 46; canine peaks, +.
- (ii) palatal dentition: v-p-ec; ?0-2-2(4).

The dentary teeth are similar to those of the maxilla in size and shape.

No dentary is sufficiently complete to allow a tooth count, although based on the size and spacing of visible teeth and the upper jaw count, an estimate of 50 is plausible.

As previously noted, a parasymphysial tusk, missing the crown, is present in CMNH 11067. Its base is 2.5 mm in diameter, indicating that it would have been considerably longer than the marginal teeth.

The anterior coronoid bears at least one large tooth. Coronoid teeth, characteristic of osteolepiform fish, are not known in embolomeres with the possible exception of *Leptophractus*

obsoletus (see above) and *Anthracosaurus*, although only the posterior coronoid bears tusks in the latter (Panchen 1981). *Eoherpeton* possesses coronoid teeth on the middle rather than the anterior coronoid.

A shagreen of fine denticles covers the ventral surface of the pterygoids and mesial surface of the coronoids. Similar denticles were embedded in the dermis overlying the palatal elements during life.

VERTEBRAL COLUMN OF *PROTEROGYRINUS*

A well-preserved vertebral column, missing only the first few cervical vertebrae and the posterior caudals is preserved in CMNH 11067 (figure 16). Additional information is provided by five large, complete articulated vertebrae (MCZ 4537, figure 17), and by an incomplete jumbled column in CMNH 10938 (figure 18).

Each vertebra of *Proterogyrinus*, as in other 'labyrinthodonts', is composed of a neural arch and a multipartite centrum comprising an intercentrum and a separate pleurocentrum supporting the neural arch. As in other embolomeres, the pleurocentrum (figure 17) is considerably larger than the intercentrum, both in its anteroposterior length and dorsal development. Its concave lateral and ventral surfaces are covered by smooth periosteal bone. The remaining surfaces are unfinished. Dorsally, two anterodorsally facing facets received the pedicels of the neural arch. The pleurocentrum is deeply amphicoelous. However, unlike the condition seen in other embolomeres such as *Eogyrinus* (Panchen 1966), *Calligenethlon* (Carroll 1967), and *Archeria* (Cope 1884), where the element is in the form of a complete disc perforated by a small notochordal canal, the pleurocentrum of *Proterogyrinus* is a horseshoe-shaped structure (figure 17), in which the dorsomesial surfaces of the element abut in large specimens, but do not fuse below the neural canal. In immature specimens (figure 19), there is a gap dorsally. Although the suture may have closed completely in old individuals this is not observed in any specimen. A similar structure is present in the anthracosaur *Gephyrostegus* (Carroll 1970) and the temnospondyl *Caerorhachis* (Holmes & Carroll 1977). In these smaller forms, however, ossification is less complete, and there is a large gap between the dorsomesial surfaces.

As in *Eogyrinus*, the periosteal bone of the intercentrum is limited to its concave ventral and lateral surfaces. The unfinished, convex anterior and posterior faces complement the concave surfaces of the pleurocentrum. Taken as a unit, the two-part centrum is therefore functionally opisthocoelous. Superficially, the structure of the intercentrum is not typically embolomeric. In other embolomeres the intercentrum, although shorter anteroposteriorly, is like the pleurocentrum in being a complete disc perforated by the notochordal canal. In *Proterogyrinus* the ossified intercentrum is limited to a ventral crescent, resembling that of temnospondyls, seymouriamorphs and an undescribed 'protoembolomere' from Cowdenbeath (Smithson 1980). Anteroposteriorly, the element is longest measured at the ventral midline and tapers dorsally, reaching little farther than half way up the side of the pleurocentrum (figure 17). Romer (1970) described the intercentra in CMNH 10950 as resembling the pleurocentra in being dorsally opened rings. It is probable that no intercentra were preserved in this immature specimen, and that these 'intercentra' are actually misidentified pleurocentra (figure 19). Large gaps between the dorsal portions of successive pleurocentra indicate that each intercentrum was continued dorsally in cartilage, with the two sides presumably meeting below the neural canal as suggested for *Gephyrostegus* (Carroll 1970). If this interpretation is correct, the centra differ from those of other embolomeres only in their lesser degree of ossification.

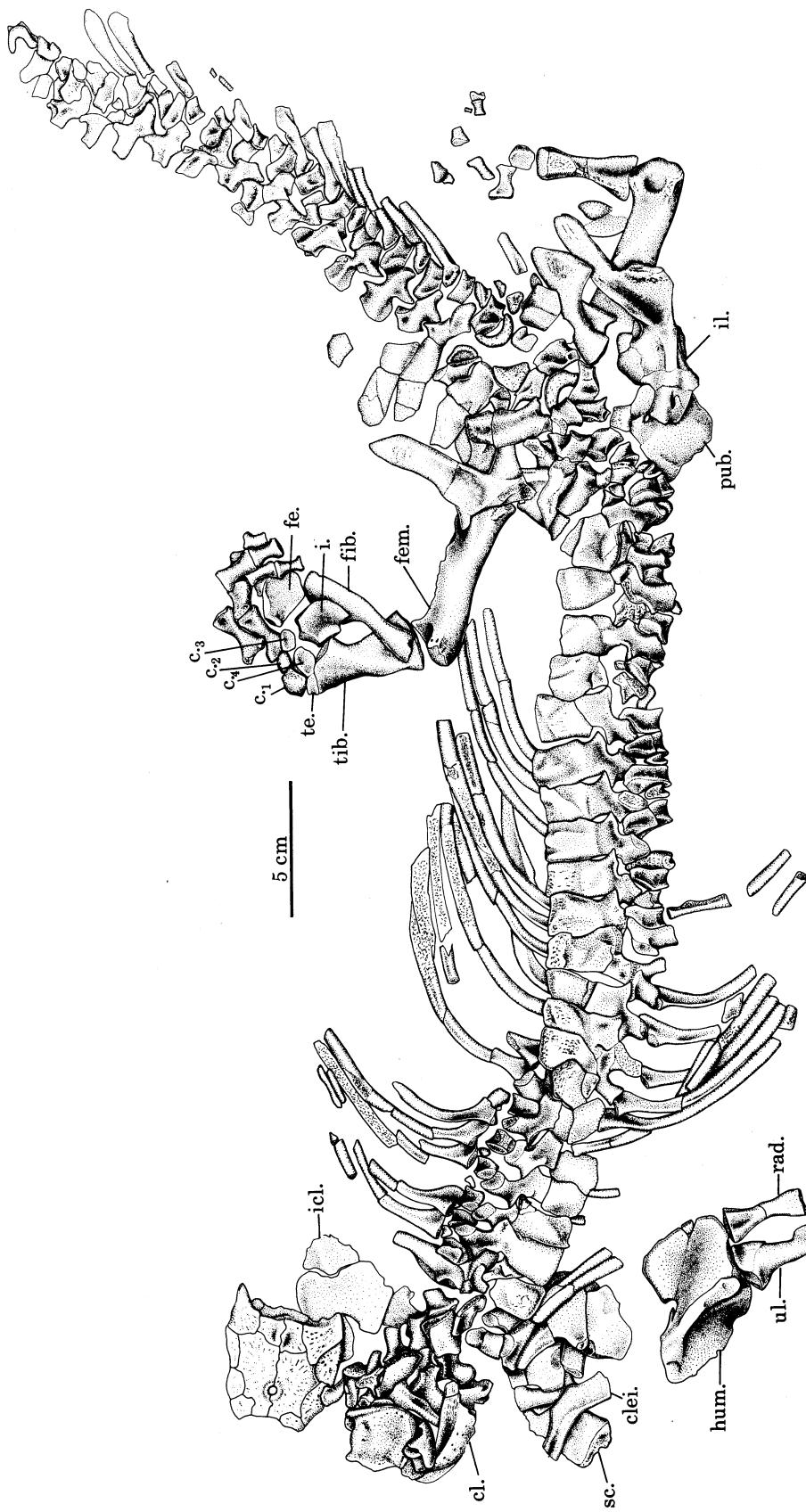


FIGURE 16. *Proterogyrinus scheelei* Romer, CMNH 11067. Articulated skeleton.

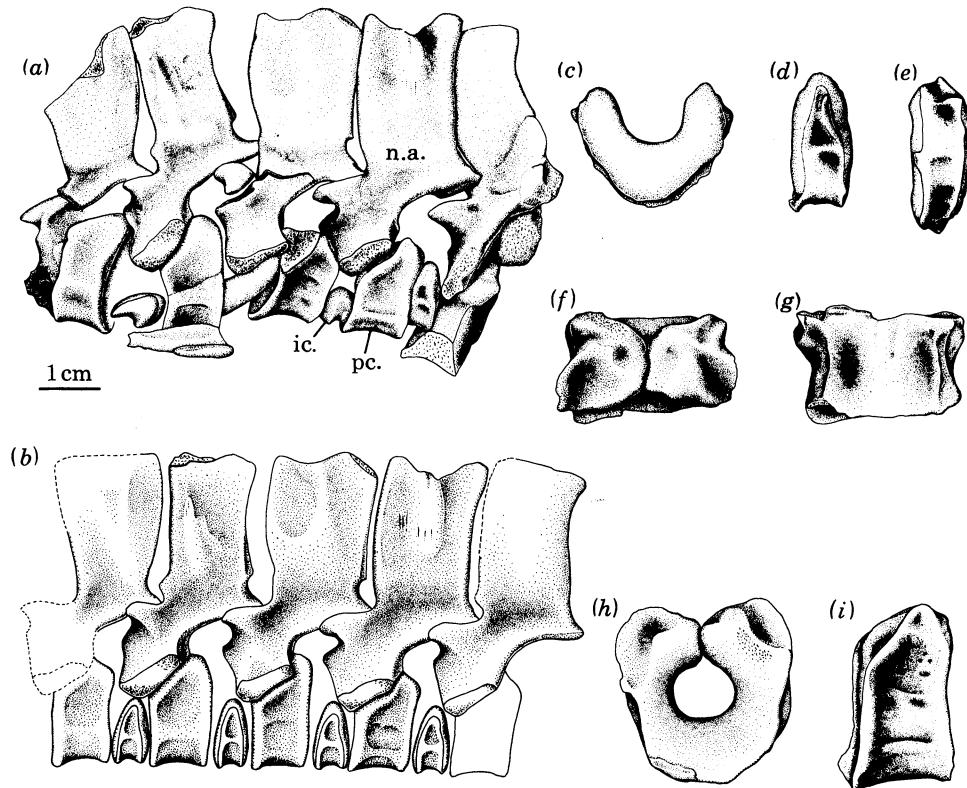


FIGURE 17. *Proterogyrinus scheelei* Romer, MCZ 4537. Vertebral elements. (a) Five articulated trunk vertebrae; (b) reconstruction of vertebrae in (a); (c)–(e) intercentrum in anterior, lateral and ventral views respectively; (f)–(i), pleurocentrum in dorsal, ventral, anterior and lateral views, respectively.

Although degree of ossification of the central elements is no doubt primarily an ontogenetic phenomenon (older individuals of any given species are better ossified), there appears to be a phylogenetic component as well. Although all known later embolomeres have well-ossified ring-shaped centra, the ‘protoembolomeres’ forms possess variably ossified centra. In *Proterogyrinus*, the pleurocentrum is open dorsally in small animals. The gap closes but does not fuse in larger individuals. The intercentrum is always crescentic. In the undescribed anthracosaur from Cowdenbeath (Smithson 1980), although the pleurocentrum forms a complete disc, the intercentrum resembles that of *Proterogyrinus*. The vertebral structure of the anthracosaur from Point Edward is more difficult to interpret as all material at this locality has been transported and disarticulated. In addition to a partial skull table closely resembling that of both *Proterogyrinus* and the Cowdenbeath specimen, there are a number of vertebral centra varying in diameter from about 8 to 30 mm. The small centra, although possibly caudals of a large individual, are much more highly notochordal, suggesting that they were from small individuals. In no cases do the pleurocentra bear dorsal sutures. In addition to a number of cylindrical caudal intercentra-bearing haemal arches are a few small crescentic intercentra, some with haemal arches, some without. This evidence, although equivocal, indicates that either there is more than one type of an anthracosaur at Point Edward, one of which has vertebrae similar to *Proterogyrinus* and the Cowdenbeath specimen, or that immature individuals of a single anthracosaur genus have crescentic intercentra that ossified dorsally in later life.

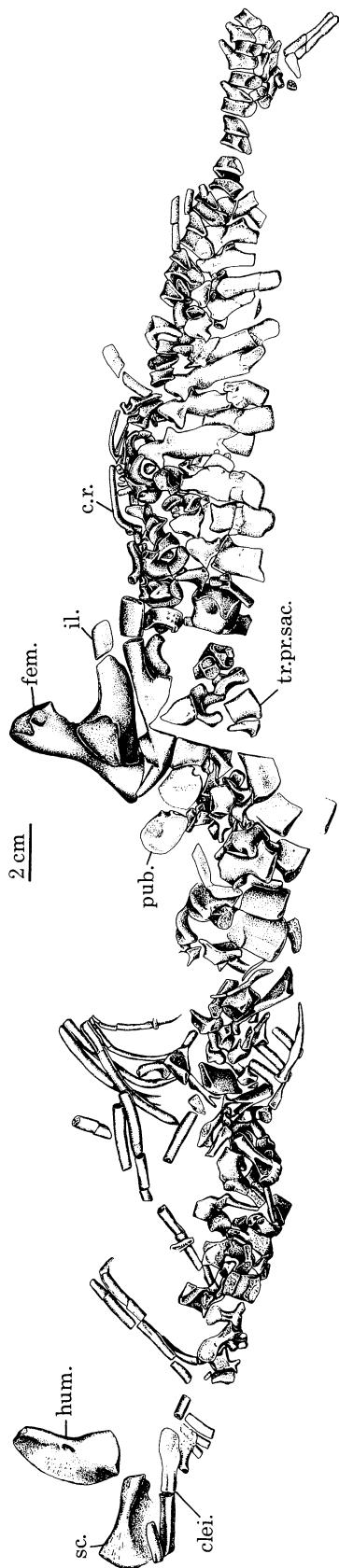


FIGURE 18. *Proterogyrinus scheelei* Romer, CMNH 10938. Postcranial skeleton.

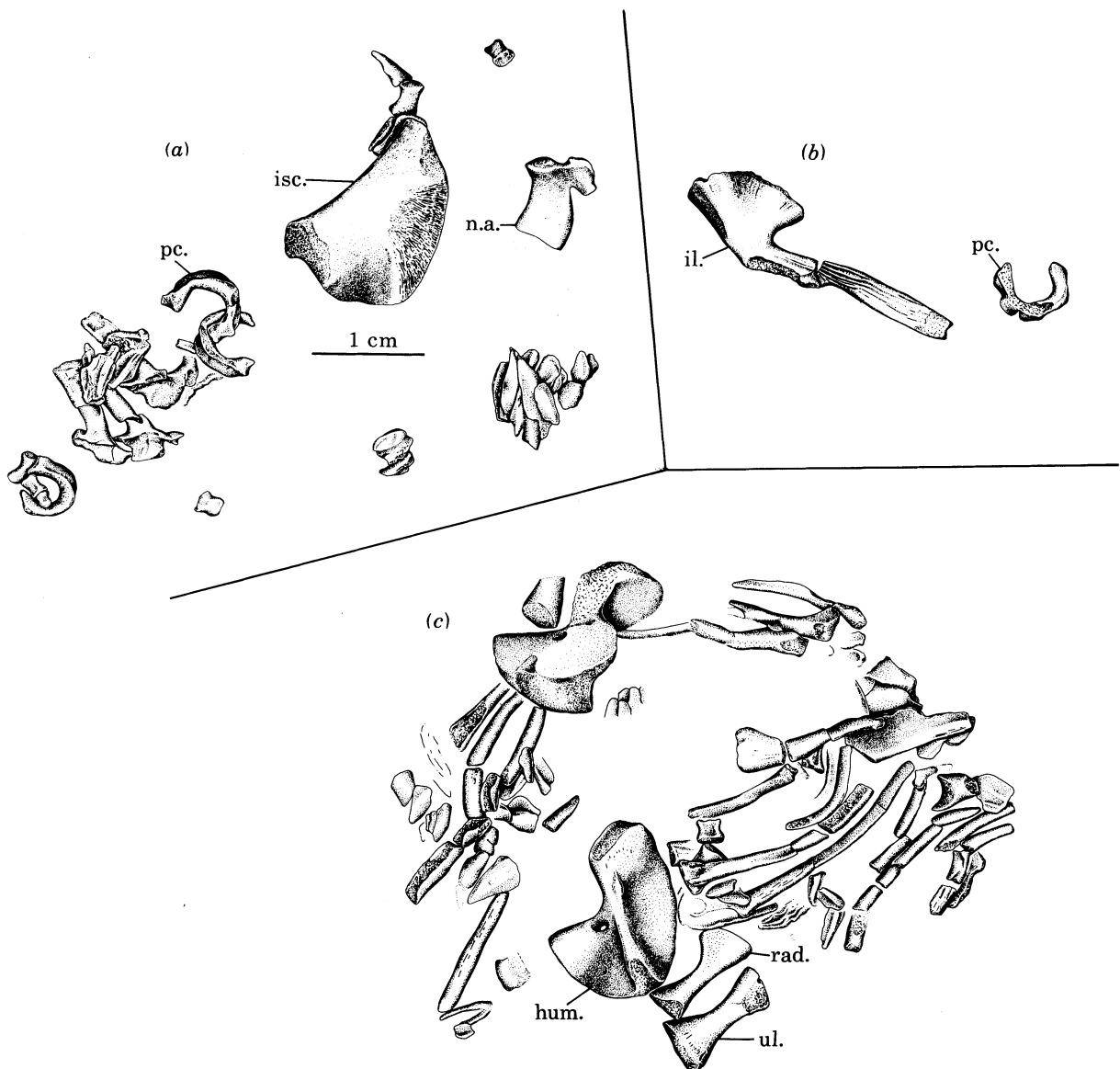


FIGURE 19. *Proterogyrinus scheelei* Romer, CMNH 10950. Selected portions of postcranial skeleton of the type. (a) Vertebral elements and ischium; (b) ilium and pleurocentrum; (c) pectoral limb elements and anterior ribs.

As in later embolomeres, the neural arches of *Proterogyrinus* have broad, short transverse processes that project little beyond the pleurocentrum facets. The processes bear broad diapophyses at their terminations. The arches also have tall rectangular spines and well-developed zygapophyses set close to the midline. Viewed anteriorly or posteriorly, the dorsomesially facing prezygapophyses and ventrolaterally facing postzygapophyses of all presacral and the most anterior caudal arches form an angle of 20° with the horizontal (figure 17). Viewed laterally, each prezygapophysis is tilted to face anterodorsally, its long axis making an angle of 9° with the horizontal plane. The posteroventrally facing postzygapophysis is inclined appropriately to articulate with the matching prezygapophysis. Viewed dorsally, the long axes of the diverging pre- and postzygapophyses form an angle of about 45° with the sagittal plane.

The internal surface of the pedicel of the neural arch forms a large facet for articulation with the central elements. The facet is triangular in outline with the base of the triangle dorsal. It is unequally divided by a ridge running from the centre of the base of the triangle anteroventrally to terminate anterior to its apex. The larger, posterior surface articulates with the pleurocentrum and the smaller surface presumably articulates with the cartilagenous dorsal extension of the intercentrum.

The neural spine, although a unitary structure dorsally, bifurcates ventrally into two lateral halves, creating a 'supraneural' space. A thin shelf of bone, often restricted to the posterior part of the arch only, extends horizontally between the two halves at the level of the zygapophyses, separating the space from the neural canal (figure 20). Essentially the same structure is shown by *Pteroplax cornutus* (Boyd 1980) and *Ichthyostega* (Jarvik 1980).

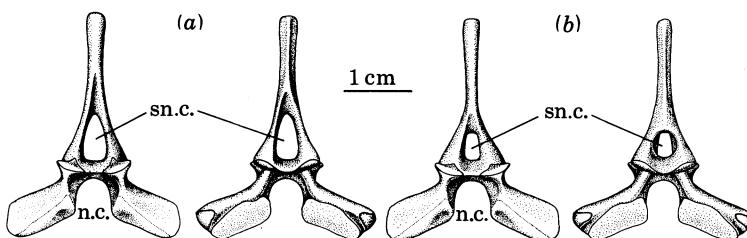


FIGURE 20. *Proterogyrinus scheelei* Romer, CMNH 10938. Neural arches. (a) Anterior and posterior views of arch from about vertebra 20; (b) anterior and posterior views of arch from about vertebra 27.

The presence of a supraneural space is presumably a primitive condition, transitional between the condition in osteoleipiform fish such as *Eusthenopteron*, in which the arch is paired, and that of more advanced tetrapods, where the arches have fused completely dorsal to the neural canal. More complete fusion has produced the condition seen in the Upper Carboniferous *Eogyrinus*, in which the two halves of the arch are connected by an osseous web in the centre, but in which deep excavations persist anteriorly and posteriorly (Panchen 1966). This 'advanced' condition may be partly a response to greater stress on the vertebral arches in a much larger animal, since some vertebral arches of *Archeria*, a Lower Permian embolomere of a size comparable to that of *Proterogyrinus*, show more restricted but distinct supraneural spaces. However, other arches also attributable to *Archeria*, not only lack the space, but also show much shallower grooves than those of *Eogyrinus*, suggesting some phylogenetic tendency toward consolidation of the neural arch in later forms. The picture is further complicated by the possibility that the progressive closing of the supraneural spaces and grooves may also be an ontogenetic phenomenon. In *Eryops*, where the grooves are moderately well developed, they are much less conspicuous in larger animals (Moulton 1974).

As noted in the description of '*Mauchchunkia*' by Hotton (1970), the neural spines of *Proterogyrinus* are taller dorsoventrally than they are wide anteroposteriorly. The lateral surfaces of the tops of many spines bear massive, blunt processes that no doubt served as ligament attachment sites.

The atlas-axis complex

See figure 21. A semiarticulated atlas-axis complex is preserved behind the skull of MCZ 4537. It is similar in form to that of primitive reptiles, *Gephyrostegus*, and temnospondyls such as *Eryops*.

No proatlantal arches could be identified. However, articular facets on both the exoccipitals and the atlas arch indicate that they must have been present.

The atlas of *Proterogyrinus* is composed of five elements: a paired neural arch, two pleurocentral ossifications, and an intercentrum. Each arch half has a prominent rectangular spine. Projecting mesially from the anterior portion of the base of this spine, immediately above the neural canal, is a shelf that made contact with, but did not fuse to, a corresponding projection of the opposite arch half.

Posteriorly the bases of the spines separate to accommodate the insertion of the axis spine. The large, gently convex prezygapophyses of the atlas arch face dorsally and slightly anteriorly. The postzygapophyseal surfaces have both ventral and mesial exposure. The oval, ventrally directed surface is larger and slightly convex. The more convex mesially directed surface is narrow dorsoventrally, and posteriorly twists ventrally to merge with the former surface.

A short, stout finger-like projection of the base of each neural arch half projects slightly posterior to the postzygapophysis. A broad surface of the anterior aspect of each pedicel presumably articulated with the occipital condyle. The short, but broad, transverse processes bear extensive attachment surfaces for atlantal ribs, although the latter are not preserved.

The atlantal intercentrum, viewed ventrally, is approximately 25% longer than other anterior cervical intercentra. It bears a prominent posteriorly facing convexity on the posterior rim of the bone near the ventral midline. Viewed anteriorly, it is a robust crescent, and laterally, a wedge. Prominent, ventrolaterally directed parapophyses are present. The anterior surface of the intercentrum is convex, matching the concave surface of the occipital condyle. Unlike more posterior intercentra, the posterior surface is deeply concave to receive the atlantal pleurocentrum.

The paired atlantal pleurocentrum shows a condition superficially similar to that seen in the vertebrae of rhachitomous temnospondyls (cf. Moulton 1974). Viewed laterally, each half presents a dorsoventrally elongated rhomboidal outline. The concave laterally facing, finished bone surface is somewhat less extensive than that of more posterior pleurocentra. The unfinished anterior surface is strongly convex, matching the concave posterior surface of the intercentrum. Dorsally, the gently notched anterodorsally facing surface received the pedicel of the atlas arch. The two pleurocentral halves did not meet dorsomesially. However, it is possible that cartilage bridged the gap below the neural canal in life as may have been the case in *Eryops* (Moulton 1974). Ventrally, however, the two halves were prevented from meeting by the midventral posterior projection of the atlantal intercentrum.

An incompletely ossified (especially ventrally) atlantal pleurocentrum and expanded atlantal intercentrum is also characteristic of some reptiliomorph amphibians (*Seymouria* (White 1939), and *Tseaiaia* (Moss 1972)) and primitive reptiles (ophiacodonts (Romer & Price 1940), *Hylonomus* (Carroll 1964), *Petrolacosaurus* (Reisz 1981) and *Procolophon* (R. Holmes, personal observation)). This similarity may not necessarily imply close relations, however. Kemp (1969) pointed out that in forms in which the spherical occipito-atlas joint behaved as a universal ball and socket joint, rotation of more than a few degrees at the joint would have resulted in severance of the spinal cord by the atlas arch unless the two halves of the arch were able to move independently. If this condition is satisfied, one half of the arch could have been pulled clear of the foramen magnum by the proatlas, while the other half would have been prevented from moving mesially and occluding the foramen magnum by its posterior articulation with the axis. It is clear that the pleurocentrum, which is attached to the pedicels of the arch, would

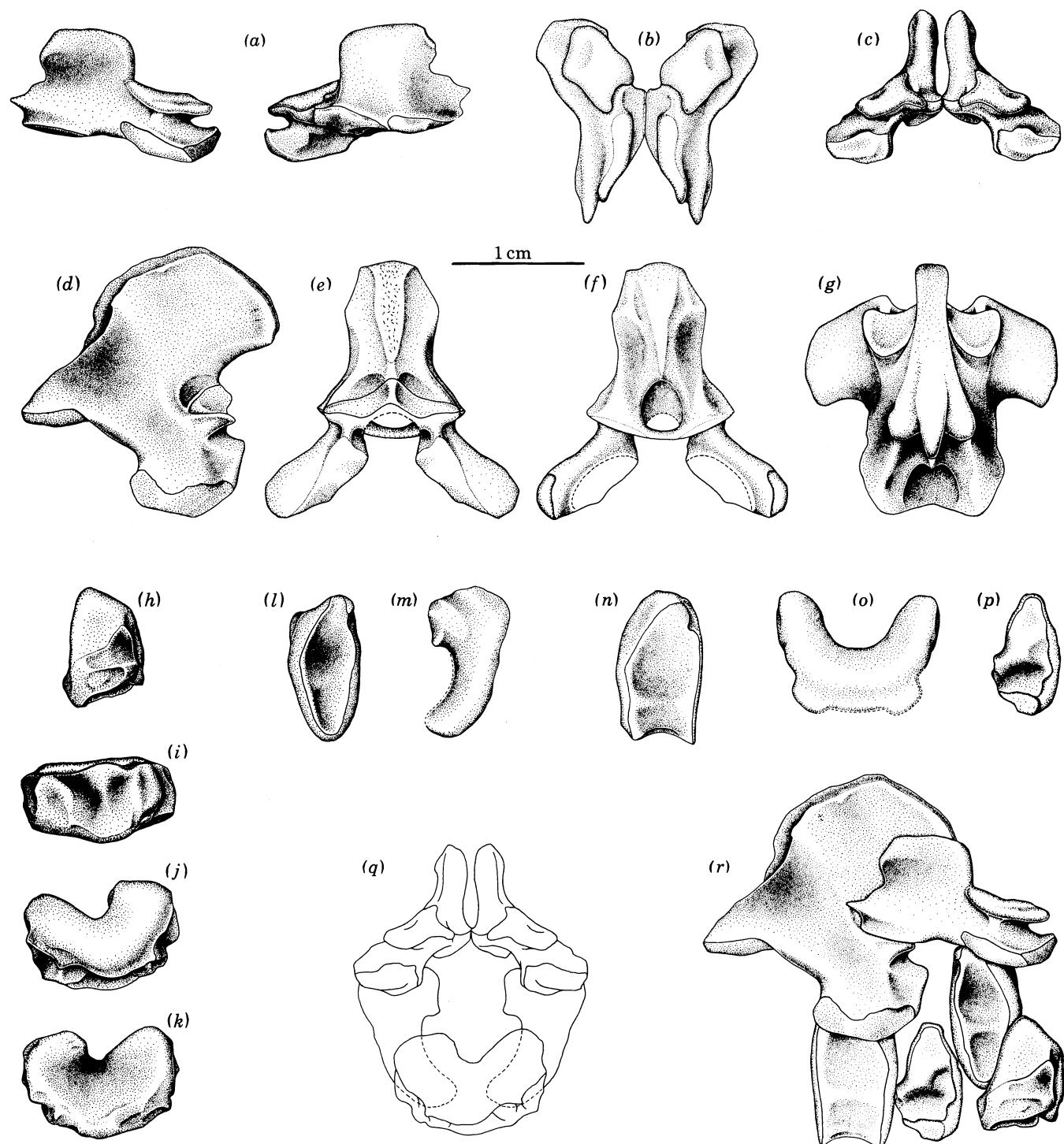


FIGURE 21. *Proterogyrinus scheelei* Romer, elements of the atlas-axis complex. (a) Right atlas arch in lateral and mesial views; (b) atlas arches in dorsal view; (c) atlas arches in anterior view; (d)–(g), axis arch in lateral, anterior, posterior and dorsal views respectively; (h)–(k), atlas intercentrum in lateral, ventral, posterior and anterior views respectively; (l)–(m), left atlas pleurocentrum in lateral and anterior views; (n) axis pleurocentrum in left lateral view; (o)–(p), axis intercentrum in anterior and right lateral views; (q)–(r), reconstructions of atlas-axis complex in anterior and right lateral views.

have interfered with the independent movement of the arches unless it too was a paired structure. It is perhaps significant that the atlantal centrum of the late but primitive anthracosaur *Gephyrostegus* is a large, unitary structure (Carroll 1970). This must have restricted the rotation at the occipito-atlas joint. However, it is uncertain whether this is a specialized or primitive condition.

The axial arch is a massive structure. The spine is elongated anteroposteriorly and thickened dorsally and posteriorly. Its anterior border projects far forward in a long sweeping anterodorsally directed curve between the atlantal arch halves. A broad, 'sagittal crest' arises on the thick dorsal border of the spine. The crest becomes more prominent on the expanded posterior border of the spine as it attenuates to a sharp ridge. On either side of the ridge is a deep depression, bordered laterally by a lesser ridge. The central ridge loses prominence as it passes ventrally and finally ends immediately above the supraneurial canal. The development of this system of ridges and depressions is clearly associated with the insertion of powerful neck musculature, probably the *spinalis capitis*.

The transverse processes of the axis arch are somewhat stouter than those of more posterior vertebrae and have very extensive diapophyses.

The dorsally facing prezygapophysis is buttressed from below in the usual manner, but the mesial portion of the surface turns to face laterally, forming a deeply concave articular surface. The two contralateral surfaces rise to meet at the midline, forming a blade continuous with the anterior margin of the neural spine. This unusual configuration no doubt protected the spinal cord from mesiolateral shearing by preventing mesial sliding of the atlas postzygapophysis during axial rotation at the occipito-atlas joint (see above). Posterior and dorsal to the prezygapophysis on the neural arch is a deep concavity that receives the most posterior portion of the atlantal arch and acted as an additional stop to limit excessive mesial rotation. The postzygapophysis is not detectably different from those of the more posterior vertebrae.

The axial intercentrum possesses strong ventrolaterally directed parapophyses, but is otherwise similar to the more posterior intercentra. The axial pleurocentrum is approximately 10% shorter measured anteroposteriorly than those of the more posterior vertebrae, but is otherwise unspecialized.

The posterior cervical column

See figure 22. Five cervical vertebrae, bearing flattened ribs, are located behind the atlas-axis. The intercentra are in the form of ventral crescents. Those of the first two post atlas-axis vertebrae (3 and 4) in MCZ 4537 (figure 12) bear strong ventrolaterally directed processes with parapophyseal surfaces at their terminations similar to those on the axis intercentrum. The first two preserved intercentra in CMNH 11067 also show similarly developed processes. This information, in addition to evidence provided by the positions of the skull and pectoral girdle in this relatively undisturbed specimen, indicates the probability that all cervical vertebrae, except the atlas-axis complex, are preserved. This gives *Proterogyrinus* a presacral count of 32 vertebrae. Posterior to vertebra 4, the prominent parapophysis-bearing processes on the exposed intercentra of CMNH 11067 begin to migrate to a more lateral position.

None of the pleurocentra possess parapophyseal surfaces. In CMNH 11067, they bear two or three excavations separated by prominent anteroposterior ridges on their ventral periosteal surfaces.

The moderately tall rectangular spines of the neural arches are broad anteroposteriorly.

Consequently, there is very little space between the posterior edge of one spine and the anterior edge of the next. This could not have allowed much independent movement particularly in the sagittal plane, between adjacent spines, and must have produced a rather rigid vertebral column. The thick transverse processes, quite narrow anteroposteriorly, have a convex dorsolaterally facing surface and a concave ventromesially facing surface. This produces a terminal diapophysis with a kidney-shaped outline.

Trunk vertebrae

As in the posterior cervical column, the anterior trunk intercentra (7–14) possess lateral processes bearing parapophyses at their terminations. However, there is a progressive reduction in the size of the processes, and posterior to vertebra 14 the parapophyses are represented as bevels on the posterior lip of the intercentrum. Between vertebrae 10 and 16, the parapophyses shift from a lateral to a more ventrolateral orientation (figure 22).

Only the last presacral pleurocentrum bears an articular surface for the capitulum of the rib. It is a concave, anterolaterally facing demifacet borne on a short, stout process arising from the anterior margin of the bone, and with the demifacet of the intercentrum of that vertebra forms the parapophysis. This pleurocentrum is noticeably shorter anteroposteriorly than neighbouring presacral pleurocentra, presumably to accommodate the massive sacral intercentrum. None of the trunk pleurocentra bear midventral excavations like those of the cervical series.

The morphology of the trunk neural arches is similar in most regards to that of the cervical series. However, the spines gradually become taller posteriorly, the spine height of the last trunk vertebra being roughly 20% greater than that of the most anterior trunk vertebrae. There is also a trend toward flattening and broadening the transverse processes posteriorly, producing long, narrow diapophyses. As in the cervical series, the neural spines are very broad anteroposteriorly, precluding all but a minor amount of dorso-ventral flexion of the trunk column. In the anterior vertebrae the triangular supraneural space is large, extending from the level of the postzygapophyses dorsally to a point midway to the dorsal tip of the spine. Posteriorly, the space becomes closed dorsally as the two halves of the arch become more completely co-ossified, and is restricted to a small circular space (figure 20). This consolidation of the arch is probably in response to increased stress near the sacrum.

The sacrum

The sacral vertebra (33), similar to that of *Eogyrinus*, is easily identified in CMNH 11067 by its massive structure (figure 22). The intercentrum, not well preserved ventrally, is longer anteroposteriorly and appears to be more massive than the presacral intercentra. The posterolaterally facing demifacet for articulation with the sacral rib, although large, is unbuttressed. Although more massive and longer anteroposteriorly, the sacral pleurocentrum is generally similar to the presacral pleurocentra. It bears a large concave anterolaterally facing demifacet for the capitulum of the sacral rib. The demifacet is supported by a buttress, similar, but more massive than that of vertebra 32. Clearly the pleurocentrum received most of the forces transmitted by the capitulum of the sacral rib from the pelvic girdle.

The massive transverse process of the neural arch is thick dorsoventrally and flares in an anteroposterior plane at its distal end. The extensive diapophysis has a flattened oval outline. However, unlike *Eogyrinus*, where the long axis of the concave surface is inclined steeply toward

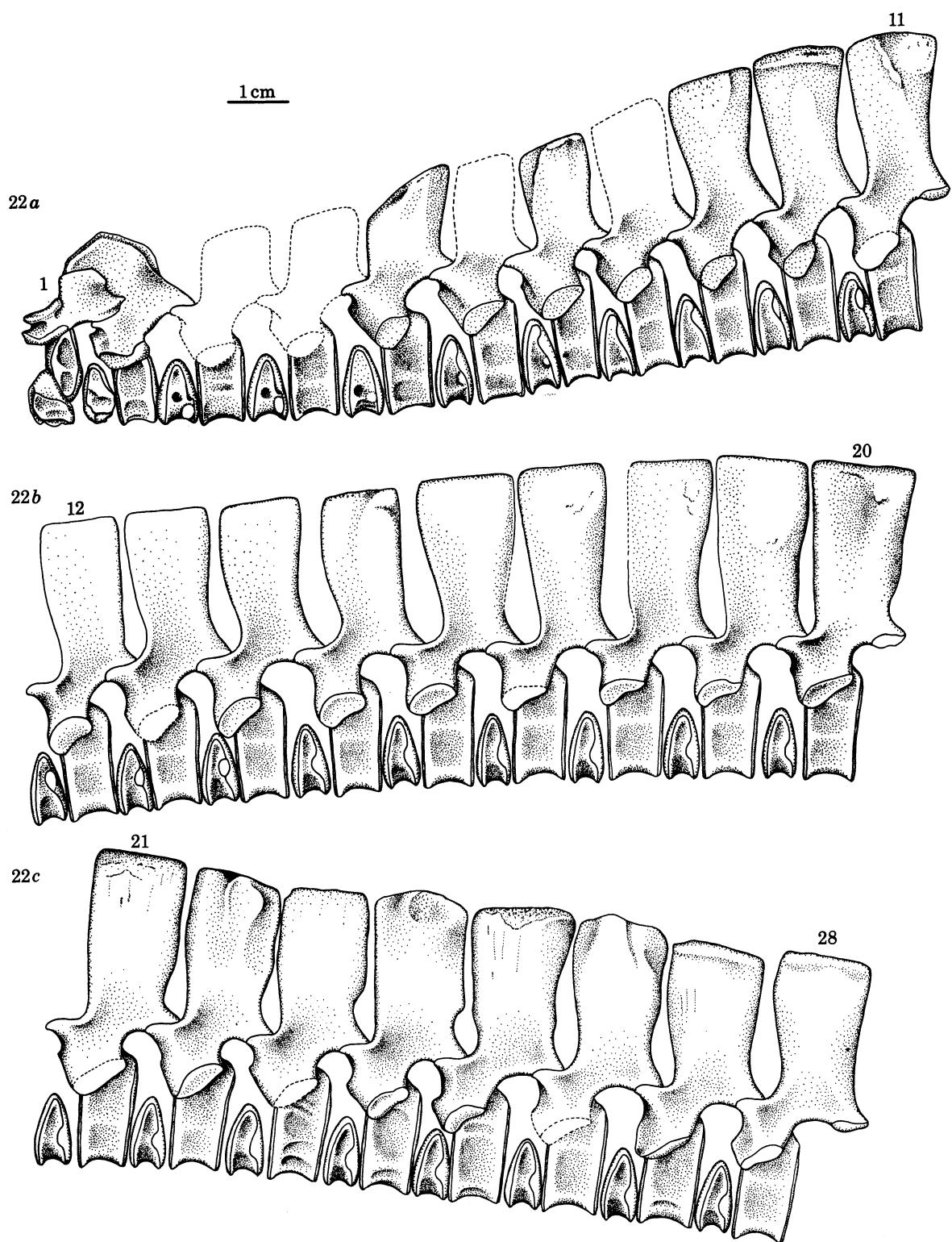


FIGURE 22 (*a–c*). For description see page 476.

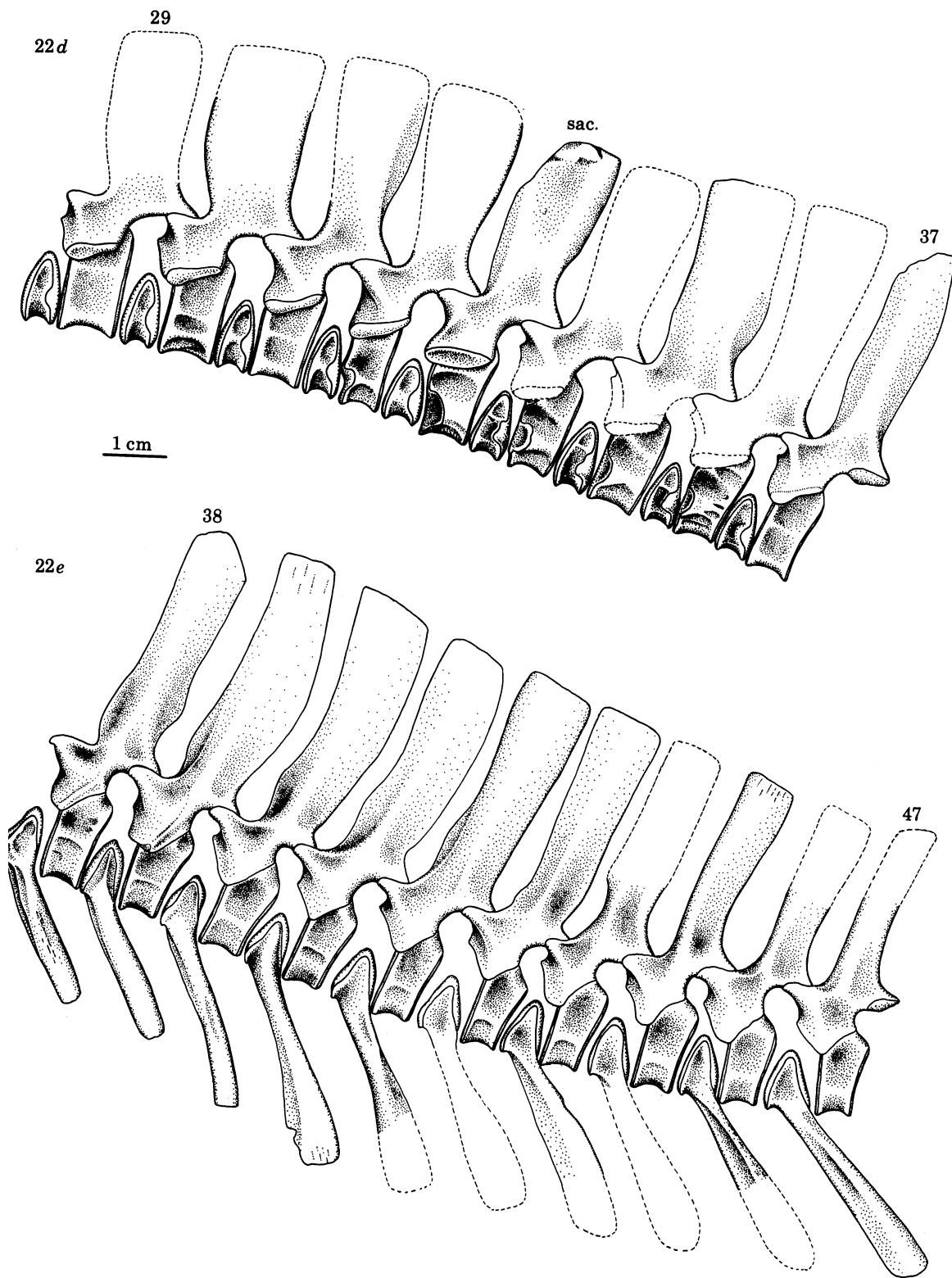


FIGURE 22 (d-e). For description see page 476.

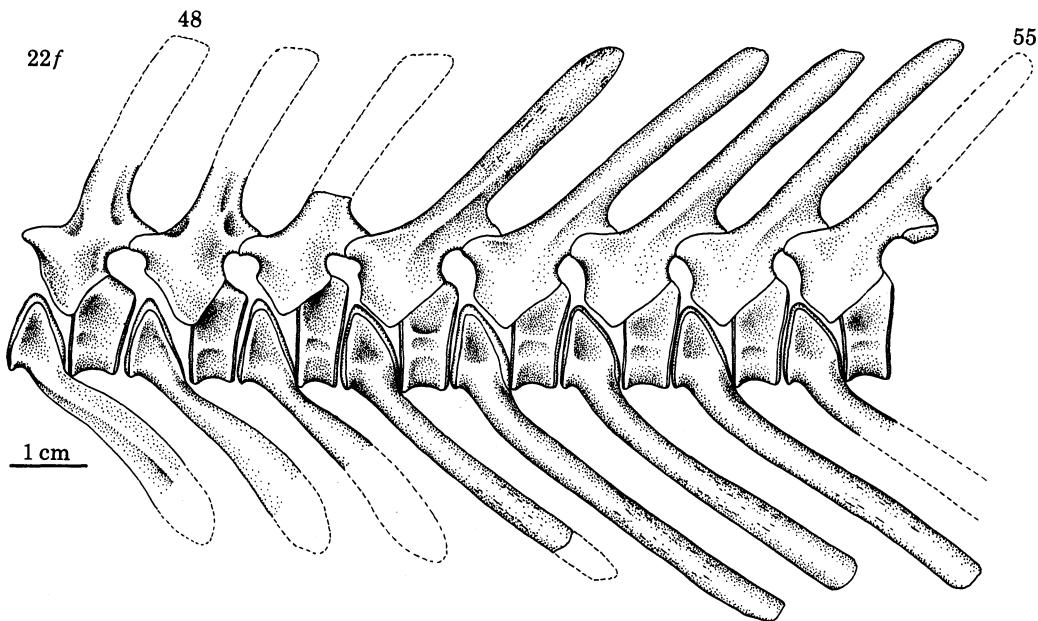


FIGURE 22. *Proterogyrinus scheelei* Romer, reconstruction of vertebral column. (a) Vertebrae 1–11; (b) vertebrae 12–20; (c) vertebrae 21–28; (d) vertebrae 29–37; (e) vertebrae 38–47; (f) vertebrae 48–55.

the vertical, the long axis of the slightly convex surface of *Proterogyrinus* is much closer to the horizontal. The neural arch is otherwise very similar to those of the presacral vertebrae.

Caudal vertebrae

Uninterrupted anterior caudal series are present in two specimens. In CMNH 11067, vertebra 34 (caudal 1) through 51 (caudal 18) are well preserved, although most neural spines are missing. Additional information obtained from a series (caudals 1–22) in CMNH 10938 allows confident reconstruction of the anterior caudal series (figure 22). The large size of the vertebral elements and great length of the neural and haemal spines in the last preserved caudal vertebra suggest that a considerable number of vertebrae, perhaps as many as twenty-five, are missing.

Each of the first four caudal intercentra has a large flat, ventrolaterally directed parapophyseal surface supported by a short, stout buttress. As in other embolomeres, they do not bear haemal spines. All more posterior intercentra possess haemal spines, each of whose length is approximately equal to the neural spine on the same vertebra. Better preserved spines show a broad spatulate outline viewed laterally. A ridge, running from the anteroproximal corner of the lateral surface and turning onto the midlateral surface of each spine as it passes distally, represents the line of attachment of the myoseptum of the caudal musculature. These ridges are most acuminate in posterior arches.

Beginning at about caudal 13, the intercentra, although retaining their crescentic shapes, gradually become larger both dorsoventrally and anteroposteriorly. This trend, concomitant with a reduction in the anteroposterior length of the pleurocentra, continues to the distal end of the preserved tail. Viewed laterally, the posterodorsal face of each of these wedge-shaped intercentra appears to have opposed the anteroventrally facing edge of the pedicel of the corresponding neural arch. Any rotational movement between the neural arch-pleurocentrum

unit and the intercentrum would have been limited to that permitted by the compressibility of the cartilage between the intercentrum and the anteroventral surface of the pedicel. None of the haemal-spine-bearing intercentra possess identifiable parapophyses.

The first three caudal pleurocentra closely resemble the last trunk pleurocentrum in the possession of a large buttressed, concave and anterolaterally facing parapophysis demifacet. No other caudal pleurocentra show this feature. Although there is little reduction in height posteriorly, the length of the ventral part of the element becomes reduced in posterior vertebrae as the intercentra become more massive.

The neural spines gradually increase in height from the sacrum to a maximum in caudal 6. Posterior to this point, the spines gradually become reduced in height as well as antero-posterior width. About caudal 13 the spines begin to lean posteriorly. This trend becomes progressively more pronounced to the end of the preserved series. The supraneural space, small in the anterior caudals, becomes further reduced posteriorly as the arches become narrower, and is obliterated at about caudal 7. The spines bear rounded ridges on their lateral surfaces marking the position of the myoseptum. The ridges are much more conspicuous in the larger individual (CMNH 11067). Although relatively undisturbed tails are preserved in CMNH 10938 and 11067, no fin rays of the type seen in *Ichthyostega* (Jarvik 1980) are apparent.

The dorsomesially facing prezygapophyses of the most anterior caudal arches are tilted from the horizontal to a degree comparable to those of the presacral vertebrae (about 20°). However, this angle gradually increases posteriorly. The zygapophyses of caudal 5 and caudal 11, which have been preserved in such a way as to allow accurate measurement, are tilted from the horizontal at 26° and 45° respectively. This increased tilting of zygapophyses in the caudal region, common in primitive tetrapods, appears to be a mechanism to restrict rotation between vertebrae.

None of the well-preserved caudal arches possesses identifiable diapophyses.

RIBS

The ribs of *Proterogyrinus* (see figure 23) are bicipital as in *Eogyrinus* and in lower tetrapods generally. A portion of the proximal head of a rib, probably associated with the axis, is preserved in MCZ 4537 (figure 8). Otherwise, the ribs of the anterior cervical series are not preserved. Preserved ribs of the pectoral region are greatly expanded distally. The rib associated with vertebra 7 in CMNH 11067 is oval in cross section at its narrowest point. Distally, its thickened anterior margin sweeps sharply anteriorly and bears a raised boss near the distal termination, presumably for the origin of serratus anterior musculature. The proximal head of a rib in the same region is preserved in the type of '*Mauchchunkia*'. It reveals that these ribs remain thickened to their proximal terminations, and although expanded proximally, there is no clear development of separate tubercula and capitula.

The shape of the ribs alters abruptly at vertebra 8. The rib associated with this vertebra has a wide, flattened proximal head, bearing a kidney-shaped tuberculum matching the diapophysis of the arch and a smaller capitulum connected to the former surface by a thin web of bone. Distally, the rib narrows rapidly as it turns ventroposteriorly. A distinct crest runs along much of the dorsoposterior surface of the shaft. Distally the rib is subcircular in cross section. Unlike the cervical ribs, it does not expand distally. A similar structure is exhibited by the rib associated with vertebra 14. Although the heads of most of the presacral ribs are obscured by vertebral

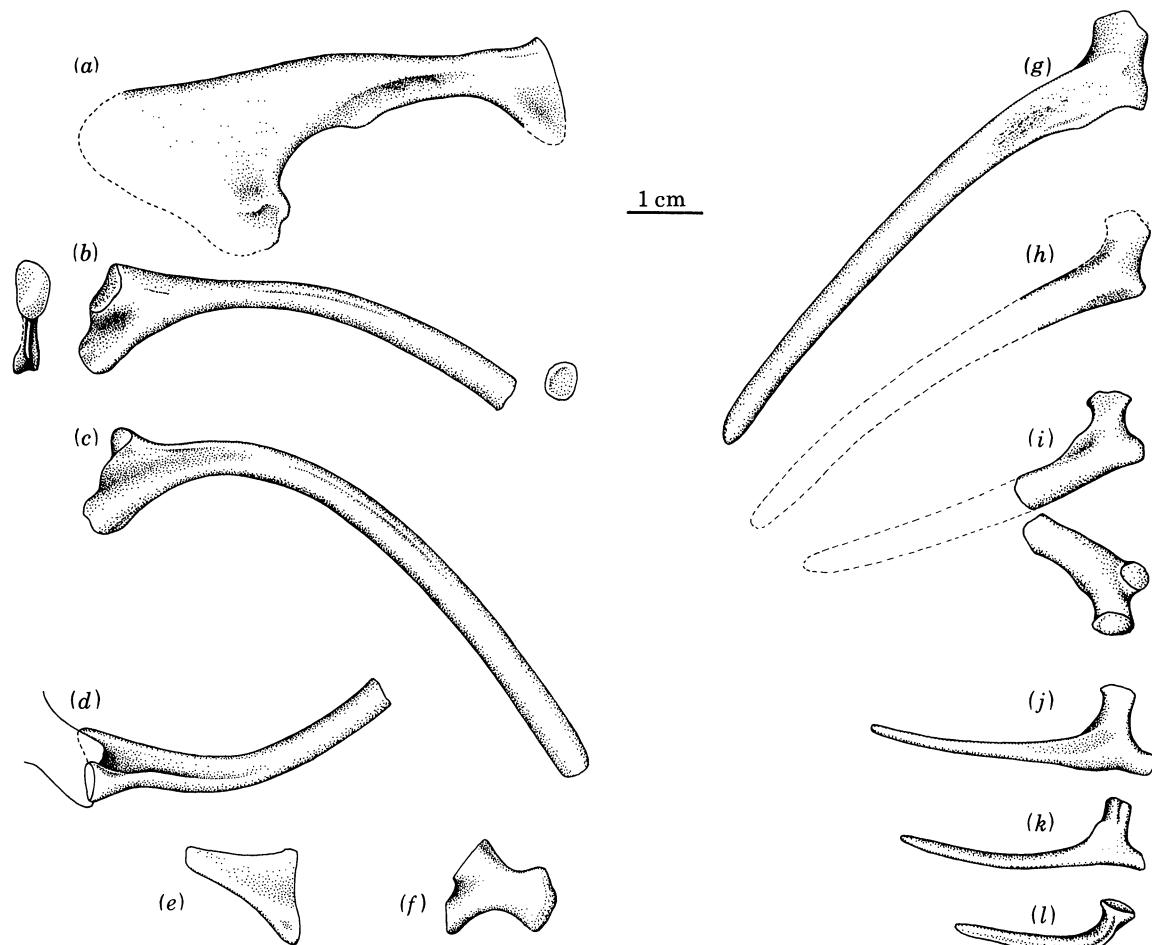


FIGURE 23. *Proterogyrinus scheelei* Romer, ribs. (a) Reconstruction of last cervical (7) from CMNH 11067 and USNM 22573, anterodorsal view; (b) first thoracic (8) in mesial anterodorsal and distal views; (c) thoracic (14) anterodorsal view; (d) thoracic (19), posterodorsal view; (e) head of thoracic (27); (f) sacral rib; (g) right caudal (34) anterolateral view; (h) right caudal (35) anterolateral view; (i) right caudal (36), anterolateral and posteromesial views; (j)–(l) right caudals (37–39), anterolateral views. (b)–(e), from CMNH 11067; (f)–(l) from CMNH 10938.

elements, many of the shafts have been preserved in CMNH 11067 (figure 16). They are long and stout, indicating that the rib cage of *Proterogyrinus* was well developed.

Although the sacral region is well preserved in both CMNH 11067 and CMNH 10938, a single sacral rib can be identified only in the latter. It lies in close proximity to the left transverse process of the sacral arch. The stout head, not unlike that of presacral ribs, bears two extensive oval facets connected by a short web of bone. Distally the rib narrows, although the shaft is thicker than those of the presacral ribs. The rib immediately expands again to form an unfinished terminal knob. Although somewhat more massive than the proximal portions of the presacral ribs, the sacral rib is relatively smaller and less specialized in structure than is that of other known Palaeozoic tetrapods.

Ribs are preserved in association with the first six caudal vertebrae. As in the presacral ribs, distinct, oval capitular and tubercular facets are present. However, unlike the presacral ribs where the tuberculum is located on the proximal termination of the shaft and the capitulum

is borne on a ventromesially directed process, in the caudal ribs it is the capitular facet that is in line with the general curvature of the shaft, while the tuberculum is borne on the dorsomesially directed process. All caudal ribs curve sharply posteriorly at the neck. The most anterior rib also turns slightly ventrally. The rib associated with caudal 3 probably projected directly posteriorly. Posterior to this, the ribs show a distinct dorsal turn. The ribs rapidly decrease in size posteriorly, the most posterior preserved rib (caudal 6) being only about 30% of the length of that associated with caudal 1. It is unlikely that the series continues for more than a few vertebrae posterior to this point.

SCALES

A large, although incomplete, section of ventral scales is preserved in MCZ 4537 (figure 24). They are arranged in the chevron pattern seen in other Palaeozoic amphibians. At the midline they meet at an angle of about 60° , in contrast to about 90° in *Archeria* (Cope 1884). Each elongate scale overlaps its distal and posterior neighbours, and bears ventral depressions and ridges to reflect this pattern of overlap. The rounded lateral terminations are somewhat asymmetrical, with the major part of its margin parallel to the sagittal plane. The much larger paramedian scales are expanded at the midline, but are not V-shaped as they are in *Archeria*. The incomplete section of scales has approximately 42 ranks anteroposteriorly, and as many as 12 rows on either side of the midline. No dorsal scales or scutes are preserved.

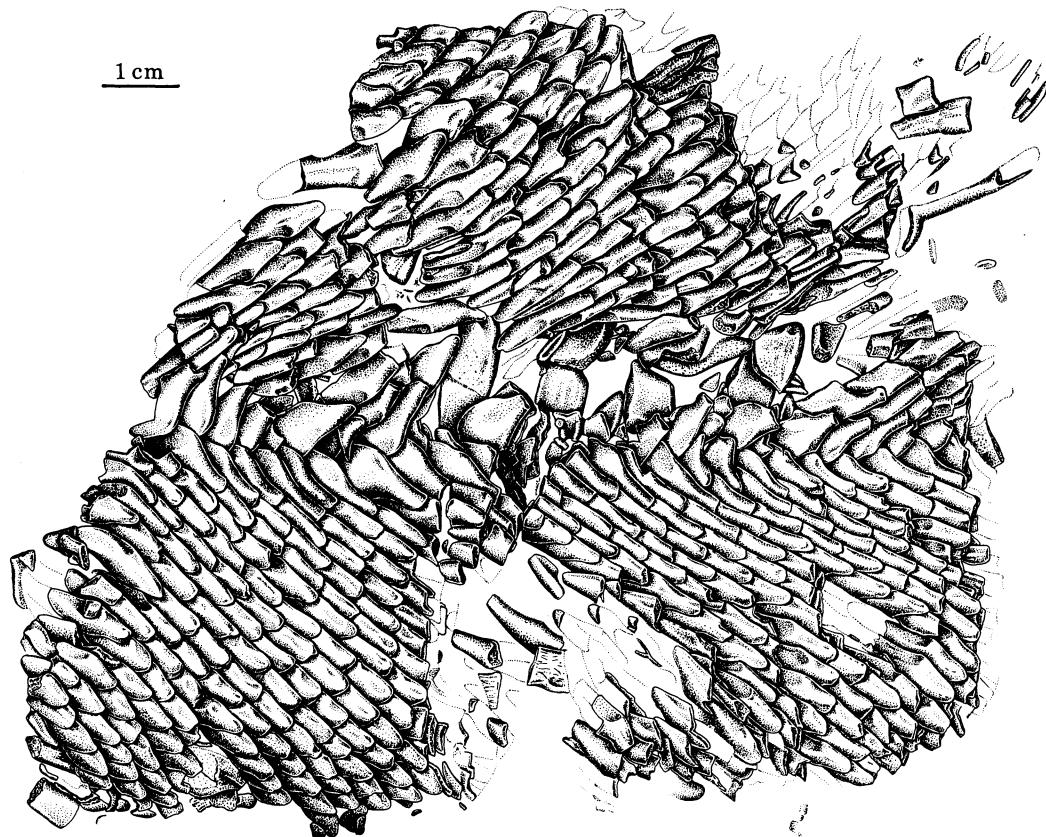


FIGURE 24. *Proterogyrinus scheelei* Romer, MCZ 4537. Ventral scales.

THE APPENDICULAR SKELETON

The pectoral girdle and limb

The pectoral limb of *Proterogyrinus* was described in detail elsewhere (Holmes 1980) and only a few brief comments will be made here.

The stout scapulocoracoid (figure 25) is similar to that of *Archeria* (Romer 1957) in being ossified from a single centre. Two foramina pierce the coracoid plate.

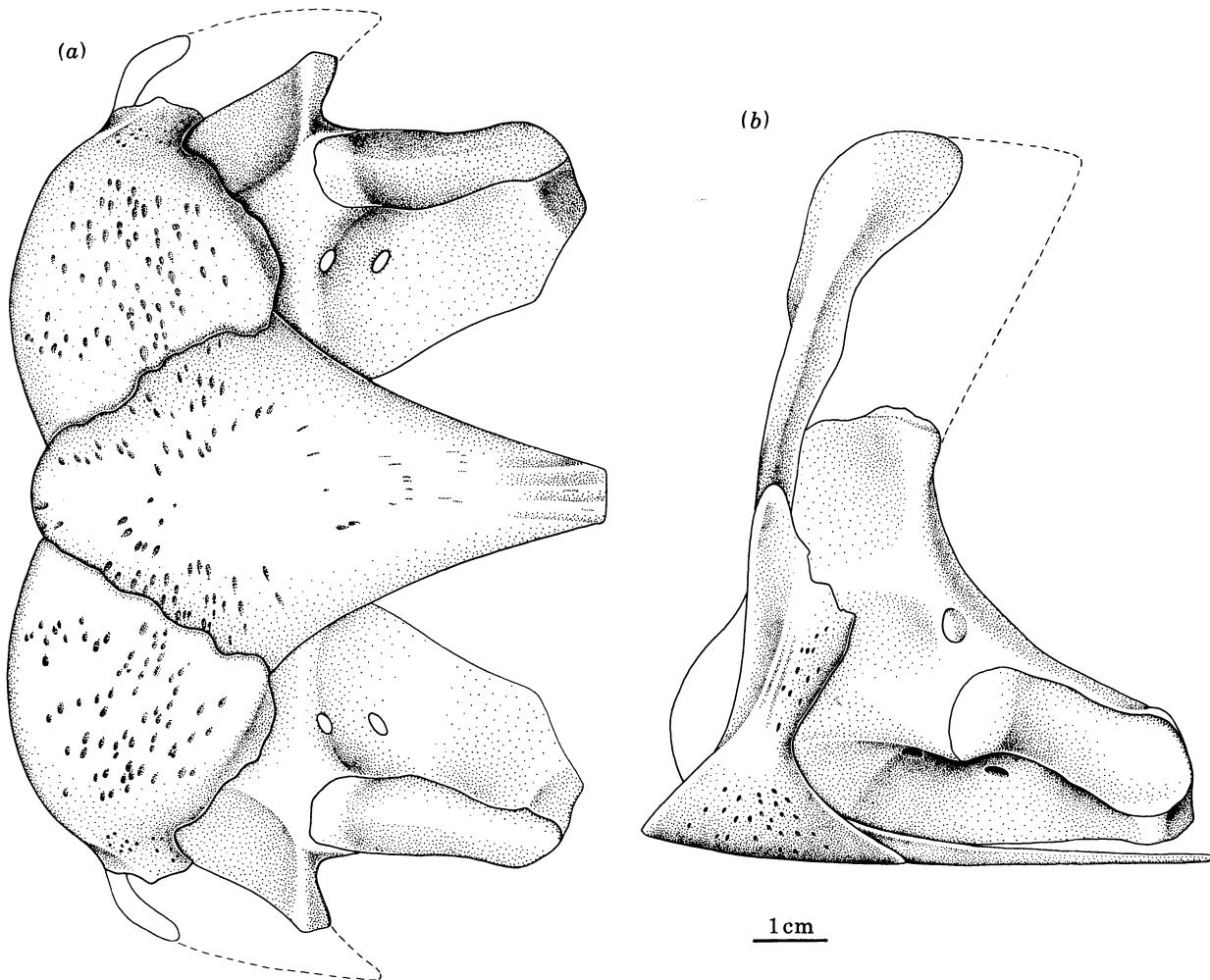


FIGURE 25. *Proterogyrinus scheelei* Romer, reconstruction of pectoral girdle. (a) Ventral view; (b) lateral view.

The dermal girdle, although generally similar in structure to that of *Archeria*, is more massive. The interclavicle (figure 25), with its broad, relatively short parasternal process is similar to that attributed to *Eogyrinus*. The short, stout dorsal process of the clavicle overlaps the lateral surface of the well developed cleithrum.

The humerus of *Proterogyrinus* (figure 26) has a tetrahedral structure common in early tetrapods (Romer 1947). As in embolomeres such as *Archeria* and an unnamed anthracosaur from Cowdenbeath (Smithson 1980), as well as in *Gephyrostegus* and *Braktererpeton*, it bears a

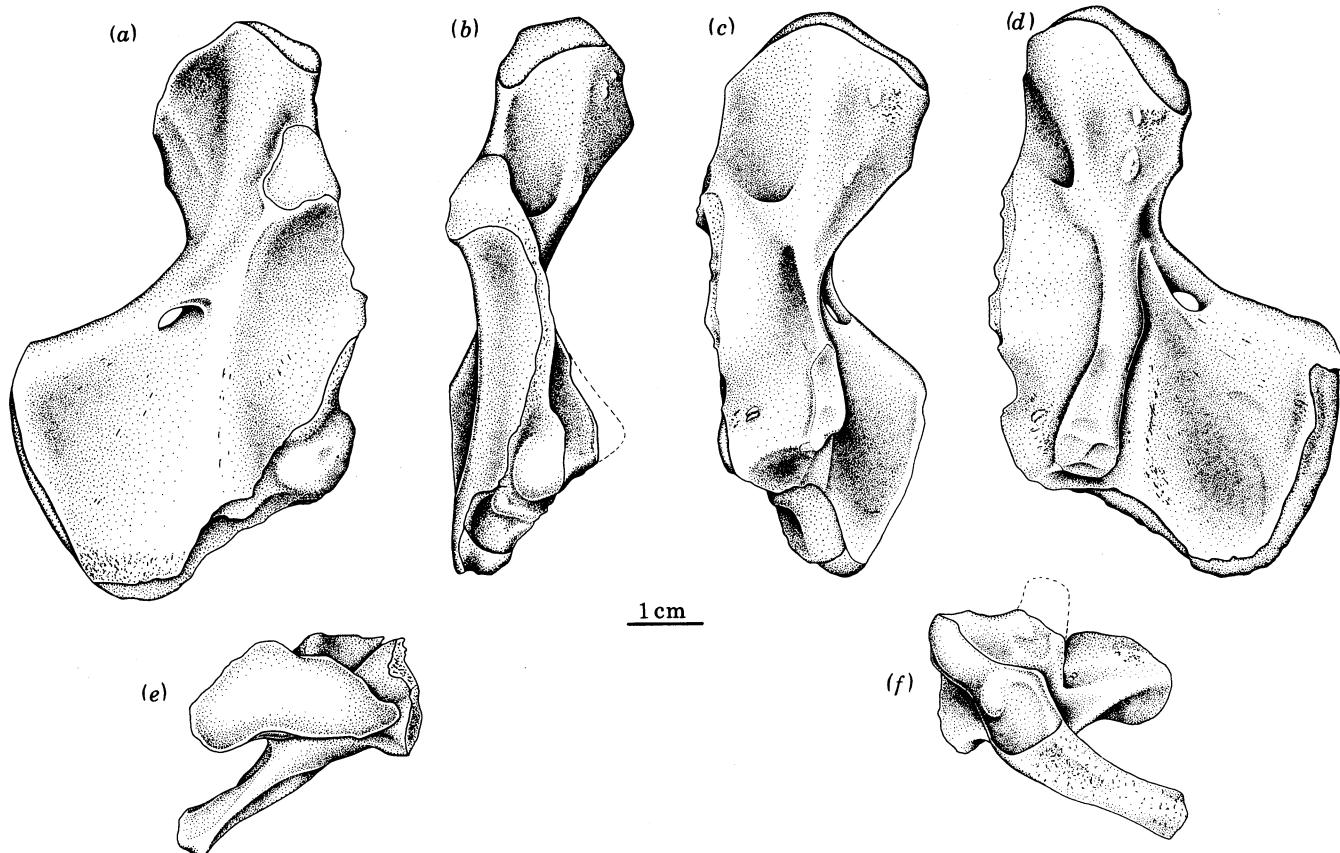


FIGURE 26. *Proterogyrinus scheelei* Romer, reconstruction of left humerus based primarily on CMNH 11067. (a) In the plane of the distal ventral surface; (b) anterior view; (c) in the plane of the proximal dorsal surface; (d) in the plane of the distal dorsal surface; (e) proximal view; (f) distal view.

large entepicondyle, a prominent anterior keel extending from the proximal expansion to the ectepicondyle, and a broad dorsal ridge passing from the middorsal surface of the shaft to the distal termination at the level of the ulnar articulation. The occurrence of a very similar humerus structure in a series of unrelated genera (*Greererpeton*, *Diceratosaurus*) indicates that it may be primitive for tetrapods. The humerus of *Ichthyostega* seems to share these features (Jarvik 1980) although the strangely flattened proximal expansion, complete absence of a constricted shaft, and possession of five foramina not comparable to those in other known tetrapods makes detailed comparisons difficult.

The ulna and radius of *Proterogyrinus* (figure 27), although relatively short and stout, are otherwise similar to those of *Archeria*. The carpus, except for the first and second distal carpals remained unossified, and the five digit manus is not complete in any specimen. However, the sizes of the most distal preserved elements makes a phalangeal formula of 2,3,4,5,4 not unreasonable (figure 28).

Although ossification of the articular surfaces of the pectoral limb elements is generally not as complete as that seen in some other Palaeozoic tetrapods such as *Captorhinus* (see Holmes 1977), some conclusions concerning limb function can be made (for a detailed analysis, see Holmes 1980).

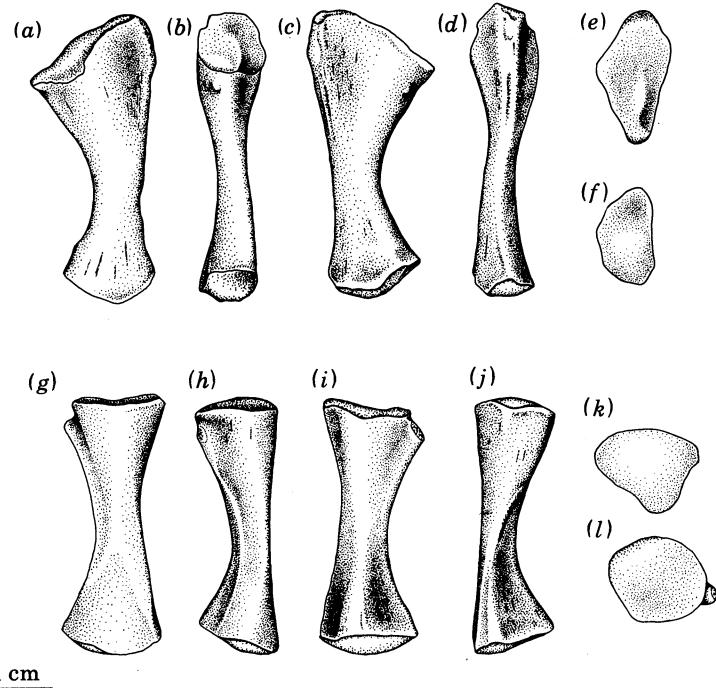


FIGURE 27. Limb elements of *Proterogyrinus scheelei*. (a)–(f) left ulna in extensor, mesial, flexor, lateral, proximal and distal views (USNM 26368); (g)–(l), left radius in extensor, mesial, flexor, lateral, proximal and distal views (USNM 26368).

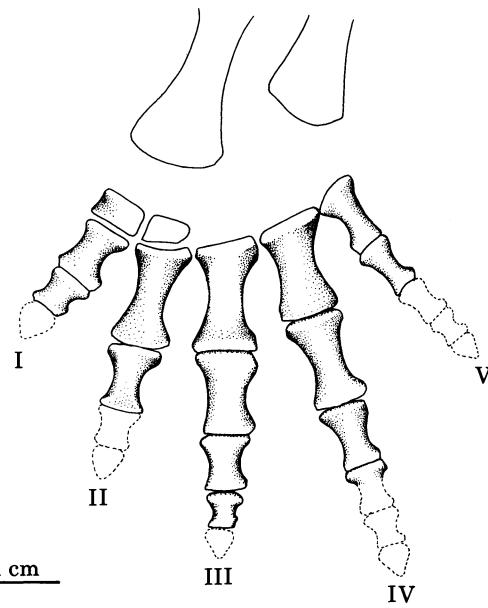


FIGURE 28. *Proterogyrinus scheelei* Romer, restoration of the left manus.

(i) The angular relation between the proximal and distal humeral expansions, as well as the structure of the elbow joint, indicate that the cartilagenous proximal articular surface of the humerus bore a diagonal groove that fitted into a ridge on the cartilagenous cap of the glenoid as was the case in most primitive Palaeozoic tetrapods such as *Captorhinus* (Holmes 1977), *Dimetrodon* (Jenkins 1971), and *Eryops* (Miner 1925).

(ii) The range of movement at the shoulder appears to have been quite restricted (figure 29). During the power stroke, the humerus probably could not have been retracted through an arc of more than 35° (the previous estimate of 25° (Holmes 1980) was probably too low) much less than in *Captorhinus*.

(iii) Movement at the elbow joint was also quite restricted. The fully flexed ulna forms a 90° angle with the long axis of the humerus, and fully extended, 84° for a total arc of only 6° . However, the spiral nature of the humero-ulnar articulation causes the distal end of the ulna to rotate 15° through an anteroposterior arc at the same time, augmenting the length of the stride.

Although the functional analysis of the forelimb of *Proterogyrinus* includes some lamentably

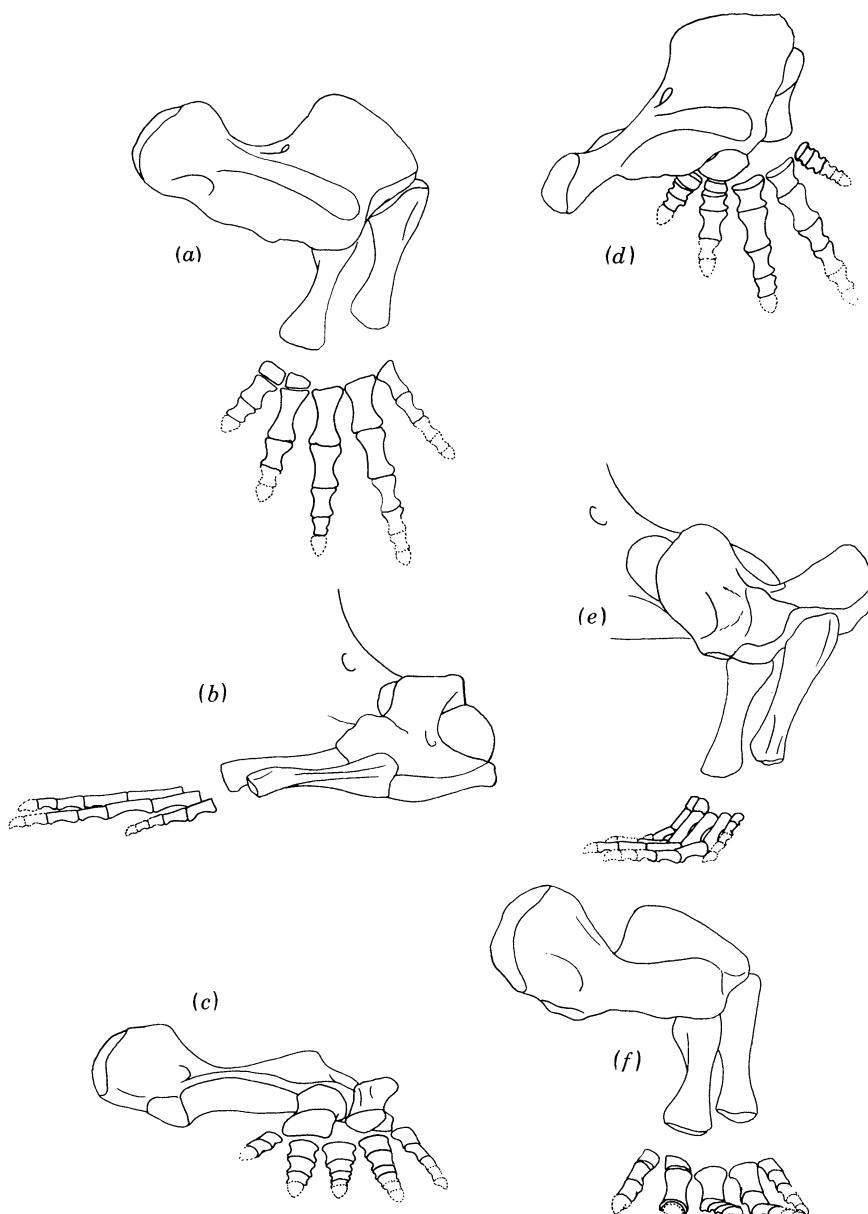


FIGURE 29. *Proterogyrinus scheelei* Romer, restoration of the pectoral limb. (a)–(c) Beginning of power stroke; (d)–(f) end of power stroke; (a), (d), dorsal view; (b), (e), lateral view; (c), (f) anterior view.

crude estimates of ranges of movement, it nevertheless provides some information on the locomotor adaptation of the genus. *Proterogyrinus* must have been a relatively poor swimmer, since the large forelimbs always projected at roughly right angles to the trunk, and could not have been retracted sufficiently to significantly reduce drag in open water. Such a forelimb would have been more suited to walking or anchoring the animal on a firm substrate (see 'Preservation, palaeoecology and life environment').

The pelvic girdle

See figure 30. Although all three elements ossified in large individuals, during ontogeny the pubis ossified more slowly than the ilium and ischium. In smaller individuals, the elements are always separated (figure 18), and even in the largest specimen, the sutures are never completely closed (figure 31).

The ilium is typical of embolomeres in the possession of both a dorsal and a blade-like posterior process but differs from those of *Archeria* and *Calligenethlon* (Carroll 1967) primarily in the shortness of the dorsal process. Primitive temnospondyls such as *Caerorhachis* (Holmes & Carroll 1977), *Dendrerpeton* (Carroll 1967), and *Greererpeton* (Romer 1969b) possess a long posteriorly directed process similar to that in embolomeres, while later, more advanced temnospondyls (dissorophids, *Eryops*) possess an iliac blade comparable to the dorsal process of embolomeres. No known temnospondyl has both. *Ichthyostega* (Jarvik 1980) appears to possess both processes, but its relation to either embolomeres or temnospondyls is uncertain.

As in *Archeria*, the iliac blade is thickest at the 'neck', and as it expands and bifurcates dorsally, thins. On the mesial surface, immediately above the 'neck' a broad, shallow depression marks the articular surface for the sacral rib. The relatively smooth nature of this surface suggests a relatively weak osseous bond that must have required considerable ligamentous reinforcement. Ridges that surround the surface, especially those located anteriorly and ventrally and extending onto the ventral surface of the posterior projection, indicate the attachment sites of these ligaments. The distinct dorsal process, its thickened dorsal margin and internal surface providing attachment for the iliocostalis and longissimus dorsi muscles, projects little above the articular surface for the sacral rib. A prominent ridge ('transverse line', Romer 1922), beginning on the lateral surface of the dorsal process curves dorsally and posteriorly onto the posterior process where it runs parallel to its ventral margin before subsiding half way to the posterior tip of the process. Striations on the ventrolaterally facing surface of the posterior process below the ridge probably indicate the origin of the iliobibialis muscle. Anterior to this, on the lateral surface of the 'neck' of the ilium ventral to the ridge and immediately above the acetabulum are the rugose attachment sites for the iliofibularis and iliofemoralis muscles. The lateral surface of the posterior process is flattened distal to the ridge and is covered by coarse striations for the posterior third of its length. The entire mesial surface of the process is flattened, giving the process a flattened oval cross-section posteriorly and a triangular cross-section anteriorly, as in *Archeria*. Longitudinal striations, most pronounced anteriorly, cover the surface. Romer suggested that the long posterior process is correlated with a long tail and aquatic habits. However, it is unclear why an aquatic animal should require a long posterior iliac process for the attachment of tail extensors. The process is well developed in terrestrial iguanid and varanid lizards, and much shorter in the amphibious *Alligator*. In modern salamanders, where the large tail is very important in swimming, there is no posterior development of the ilium. Although the long iliac process of the aquatic neotritians hooks

posteriorly near its termination (Bossy 1976), it is more nearly vertical throughout most of its length and cannot be considered equivalent to the posterior process in embolomeres. A modest posterior process is present in primitive microsaurs, some of which are aquatic, but others of which are almost certainly terrestrial. Although the process in embolomeres probably provided attachment for caudal extensors as Romer suggested, it does not necessarily indicate an aquatic habit. Its ventral edge probably also provided origin for the iliofemoralis (coccygeofemoralis) brevis muscle. This muscle, originating from a point considerably posterior to the axis of femoral rotation in embolomeres, would have been a powerful femoral retractor and rotator, giving the rear limb the capacity to produce a strong power stroke.

Below its neck, the anterior and posterior margins of the ilium diverge and turn laterally. The bone also thickens mesiolaterally to support the acetabulum, which has a cup-shaped

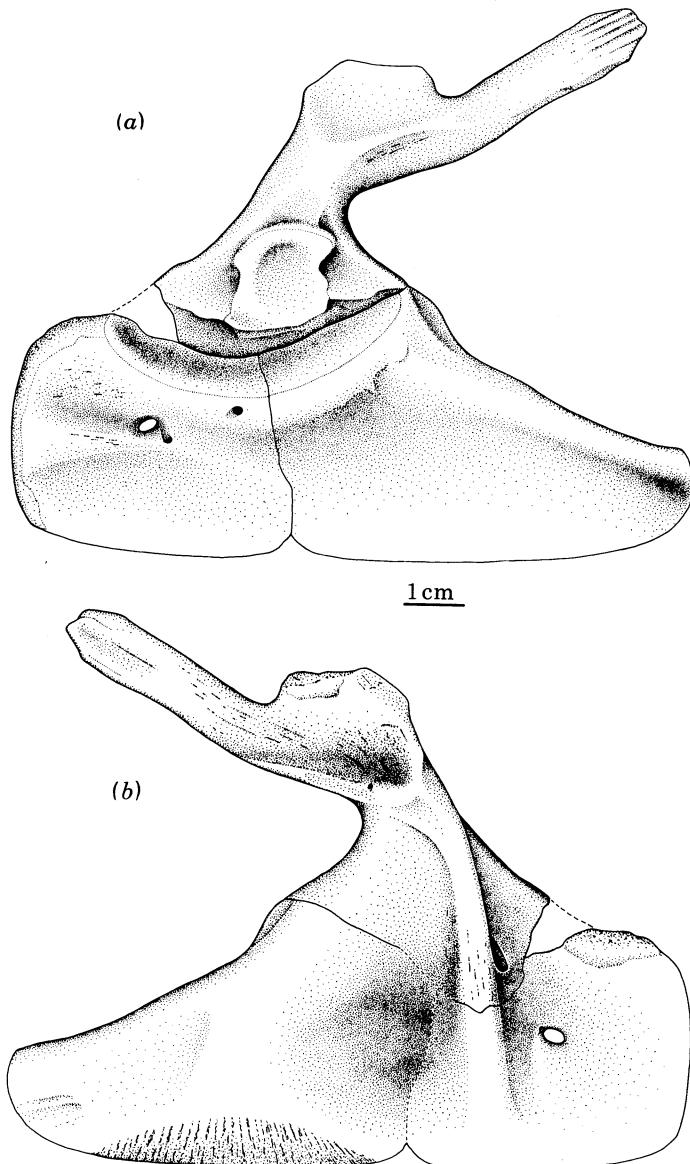


FIGURE 30. *Proterogyrinus scheelei* Romer, reconstruction of left half of pelvic girdle. (a) Viewed laterally and slightly ventrally to provide greatest exposure; (b) viewed mesially and slightly dorsally.

structure typical of early tetrapods. The protruding rim of the iliac portion of the unfinished acetabulum has an inverted U-shape. The dorsal part of the surface, supported by the prominent acetabular buttress, faces directly ventrolaterally. Mesially, the ilium extends more ventrally than it does in *Archeria*, overlapping part of the dorsal portion of the mesial surface of the pubis. A massive ridge, beginning on the anteromesial aspect of the 'neck' and passing ventrally and slightly anteriorly, divides the ventral part of the mesial surface of the ilium into two parts as in *Archeria*. The concave, anteromesially facing surface bears a channel oriented parallel to the ridge. The channel deepens as it passes ventrally, and in one large specimen (CMNH 11067) terminates in a large foramen located immediately dorsal to the suture between the ilium and pubis (figure 31). This foramen will be discussed with the pubis. In one

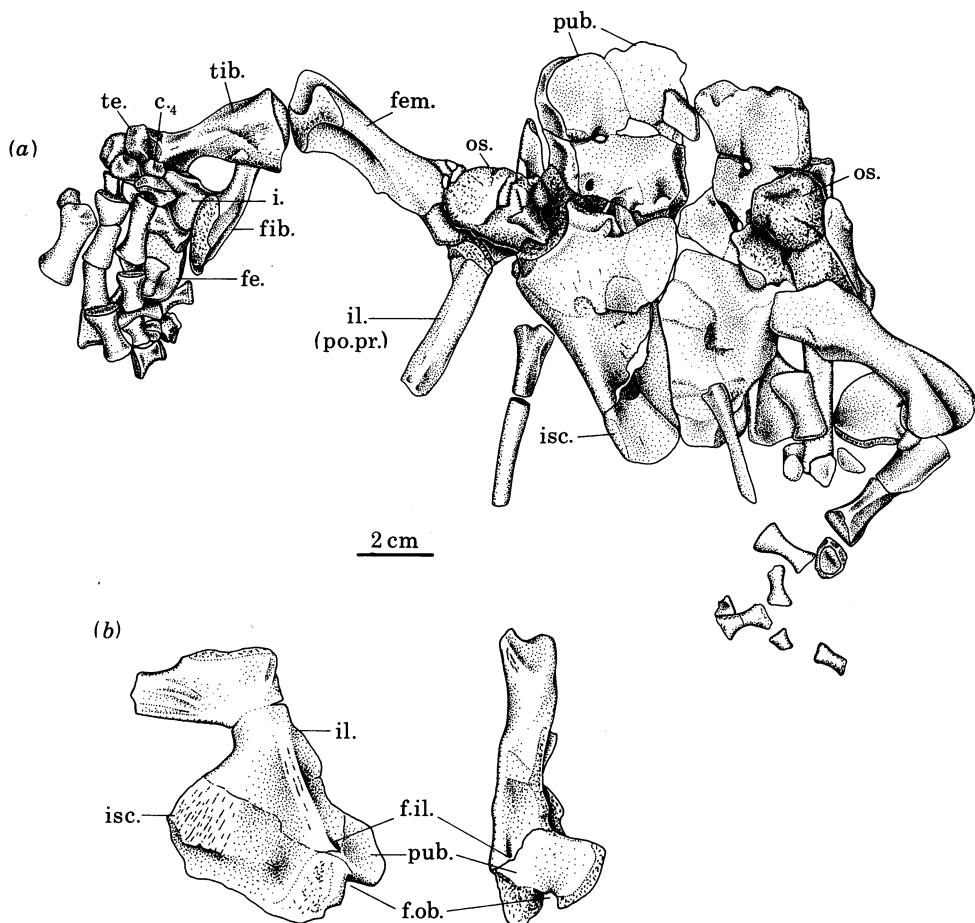


FIGURE 31. (a) *Proterogyrinus scheelei* Romer, CMNH 11067. Rear limbs and girdles in ventral view; (b) *Archeria crassidisca* Cope, MCZ 2501. Incomplete pelvis in mesial and anterior views.

specimen of *Archeria* in which the ventral portion of the mesial surface of the ilium is exceptionally well preserved, a small foramen can be seen in this position (figure 31).

The pubis is well preserved only in CMNH 11067, a large, well articulated specimen (figure 31). In another large individual, CMNH 11091 (figure 32), the pubis is missing from an otherwise articulated pelvis. In the smaller individual CMNH 10950, although an isolated ilium

and ischium are preserved, no recognizable pubis is present (figure 19). In the intermediate-sized specimen CMNH 10938 (figure 18), both pubes are preserved in place, but the portions of the bones posterior and dorsal to the obturator foramina remained unossified. This evidence suggests that the pubis was the last bone of the pelvis to ossify, and even in large individuals tends to be incompletely attached to the other elements since ossification began anteroventral to the obturator foramen and proceeded posteriorly and dorsally. As in *Archeria*, the pubis is roughly square in outline. The extensive, unfinished acetabular surface, clearly seen in CMNH 11067 (figure 31), is deeply concave. It is bounded ventrally by a prominent buttress. Although it is clear that the dorsal edge of the pubis anterior to the acetabulum is quite thick, poor ossification (or preservation) prevents a more detailed description of this part of the bone. The unfinished anterior edge was presumably continued in life by cartilage. The ventral edge is slightly thickened.

The concave lateral surface of the pubis is pierced by two foramina. A rather small obturator foramen pierces the bone ventral to the anterior end of the acetabulum. On the external surface, a low rugose ridge extends anteriorly from below the obturator foramen. One specimen (figure 31) clearly shows a small nutrient foramen between the posterior termination of the ridge and the obturator foramen. Posterior to the obturator foramen, immediately ventral to the rim of the acetabulum and not far from the pubo-ischiac suture is another, smaller foramen. This foramen is probably continuous with the previously described foramen that passes through the mesial surface of the ilium and into the dorsal part of the underlying pubis. This foramen has not been described in any other post-Devonian tetrapod. No specimen of *Archeria* shows it. In MCZ 2501, the foramen piercing the mesial surface of the ilium appears to converge with the obturator foramen, and therefore does not have a separate opening laterally. However, two obturator foramina pierce the pubis of *Icthyostega* in essentially the same positions (Jarvik 1980). This is presumably a primitive character.

The mesial surface of the pubis is slightly convex. The posterior portion is traversed by a massive vertical ridge that is a continuation of the ridge on the mesial surface of the ilium. It terminates ventrally at the symphysis. A small nutrient foramen enters the bone immediately anterior to the ridge. The obturator foramen, unlike that of *Archeria*, does not lead to a vertical groove on the mesial surface of the pubis. The nerve which it carried must not have passed in close proximity to the bone on its way from the spinal column as it did in *Archeria*, but it must have pierced the pubis at close to right angles to its surface. The position of the two foramina on the mesial surface of the pelvis suggests that the origin of the pubo-ischiofemoralis internus muscle was restricted to the ilium and dorsal part of the pubis anterior to the vertical ridge. The region of the symphysis is not well preserved in any specimen.

The ischium is similar to that of *Archeria*. The unfinished acetabular surface, only preserved in large specimens (figures 31 and 32) is deeply concave. As in the pubis, the bone is greatly thickened in this region, particularly posteriorly, where it forms a thick, rounded buttress. Dorsal to this buttress, immediately behind the acetabulum, is a mesial flange similar to that in *Archeria*. The slightly thickened dorsolateral margin turns ventrally as it sweeps posteriorly. With the exception of the acetabular area and dorsolateral margin, the plate is uniformly thin. The lateral surface is distinctly concave. The posterior part of the mesial surface is flat or slightly convex. However, the anterior one-third of the surface is occupied by a concave pocket that opens onto the pubo-ischiatic suture. The ventral portion of the mesial surface bears vertical striations similar to those in *Archeria*, indicating a fibrous connection between the two ischia.

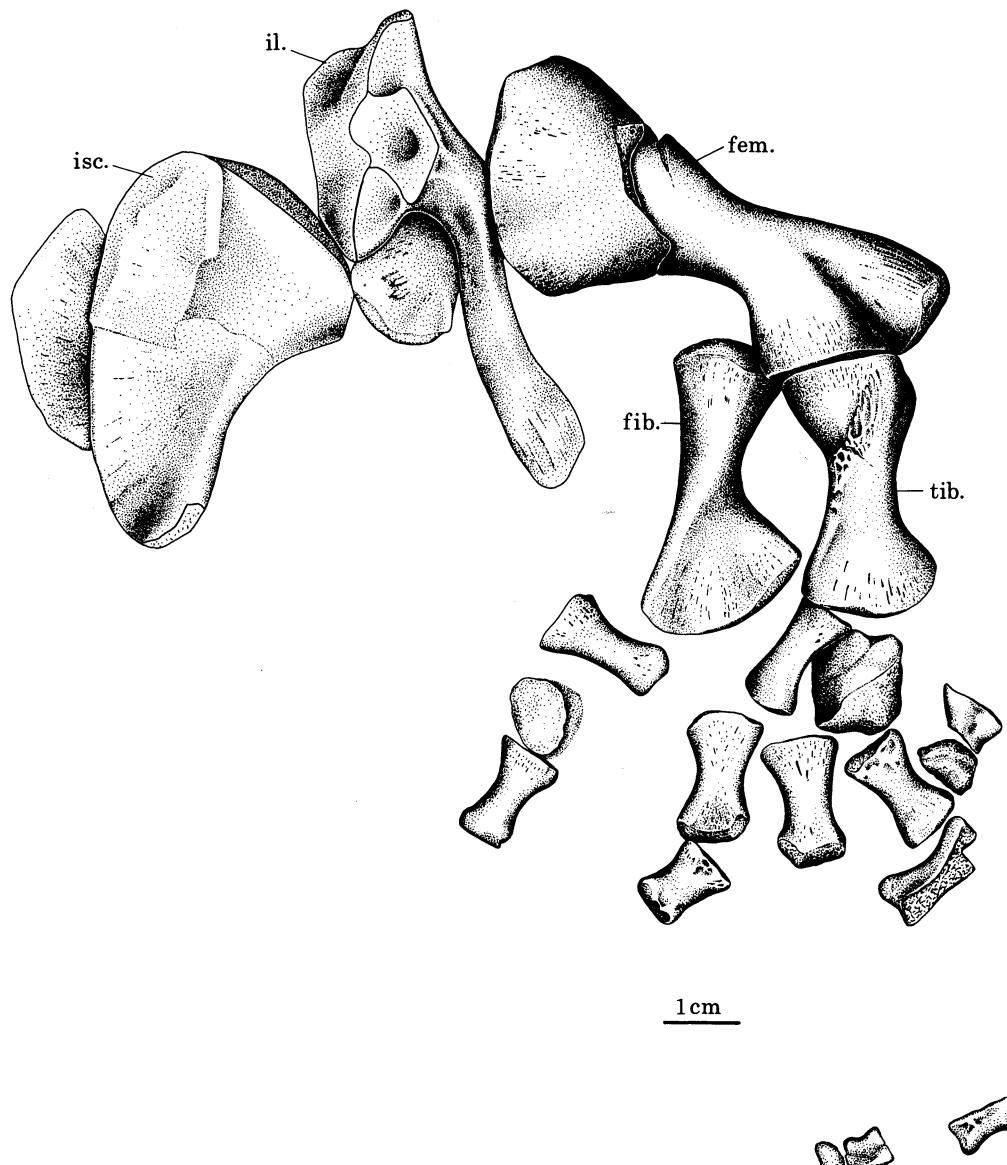


FIGURE 32. *Proterogyrinus scheelei* Romer, CMNH 11091. Left rear limb and girdle.

at the midline. The plane of this facet is set off at an angle of only 32° from the dorsoventral axis of the ischium, indicating that the pubo-ischiatic plate faced more laterally than ventrally.

In one large, well-articulated individual (CMNH 11067), each acetabulum is occupied by a rather well ossified if nondescript spherical lump of bone, each having a diameter of approximately 19 mm (figure 31). The proximal heads of the slightly displaced femora appear to be complete, making it unlikely that they are epiphyses. Although the nature of these bones is uncertain, they do not appear in any other specimens of *Proterogyrinus*, nor to my knowledge, in any other Palaeozoic tetrapod. They are almost certainly an artefact of preservation or an abnormality, possibly an osteophyte produced by a severe arthritic condition of the hip joints. However, these bones are unlike osteophytes in that they do not appear to be particularly closely

associated with either the acetabular surface or the head of the femur, but simply occupy a space between the normally opposing articular surfaces of the joint.

The pelvic limb

The femur of *Proterogyrinus* (figure 33) is similar to that of *Archeria*, the main difference being the more expanded distal condyle and thinner shaft in the former. Several Carboniferous localities have yielded femora of comparable structure. The isolated femur (*Papposaurus*) from the Scottish Lower Namurian locality of Loanhead (Watson 1914) is almost indistinguishable from that of *Proterogyrinus*, and almost certainly pertains to a very similar animal. Although somewhat less well preserved, a femur from Cowdenbeath (Lower Namurian of Scotland) is also clearly of the same type (Smithson 1980). An undescribed embolomere from the Westphalian D locality of Florence, Nova Scotia (Carroll *et al.* 1972), shows a femur of comparable length and structure to that of *Proterogyrinus*, although it is much more lightly constructed. The 'seymouriamorph' femur from the Viséan deposits of Horton Bluff, Nova Scotia (Carroll *et al.* 1972), is also quite similar to that of *Proterogyrinus*.

The mesially facing, band-shaped proximal articular surface of the femur of *Proterogyrinus* is broadly convex viewed dorsally. It is convex dorsally and concave ventrally when viewed mesially. Measured dorsoventrally, the surface is broad, the maximum width being approximately 60% of the maximum length measured along its anteroposterior axis, compared with 50% in *Archeria* and the Florence embolomere, and approximately 43% in *Papposaurus*. The

TABLE 4. LIMB BONE MEASUREMENTS OF *PROTEROGYRINUS*†

| bone | length | proximal width | shaft width | distal width |
|---------------|--------|----------------|-------------|--------------|
| femur | | | | |
| MCZ 4537 | | | | |
| left | 71 | 31 | 12 | 35 |
| right | 74 | 30 | 12 | 34 |
| CMNH 10938 | 54 | 29 | 10 | 29 |
| CMNH 11067 | | | | |
| left | 67 | — | 12 | 33 |
| right | 69 | 30 | 11 | 33 |
| CMNH 11091 | 62 | 29 | 11 | 29 |
| tibia | | | | |
| MCZ 4537 | 39 | 22+ | 11 | 25 |
| CMNH 10938 | 33 | 21 | 10 | 18 |
| CMNH 11067 | | | | |
| left | 38 | 25 | 13 | 17+ |
| right | 39 | 25 | 13 | 23 |
| CMNH 11091 | | | | |
| left | 33 | 23 | 11 | 20 |
| right | 33 | 22 | 12 | 19 |
| fibula | | | | |
| MCZ 4537 | 45 | 17 | 9 | 26 |
| CMNH 10938 | 37 | 12 | 8 | 20 |
| CMNH 11067 | | | | |
| left | 50 | 18 | 8 | 23 |
| right | 51 | 14+ | 8 | 19 |
| CMNH 11091 | 40 | 14 | 7 | 23 |

† All width measurements are taken perpendicular to the long axes and parallel to the extensor surfaces of the bones. All measurements are maximum except for width of shaft, which is the minimum. All measurements in millimetres.

anterior boundary of the articular surface is not separated from the adjacent internal trochanter by finished bone surface.

The proximal dorsal surface of the femur is much as described in *Archeria*. However, the posterior rugosities identified by Romer as the area for insertion of the ischiotrochantericus muscle and attachment areas for joint ligaments are not conspicuous. Anteriorly, the dorsal surface of the internal trochanter bears pronounced fluting, indicating the insertion of the puboischiofemoralis internus muscle.

The broadly convex dorsal surface of the anterior condyle is featureless. A distinct ridge begins immediately distal to the midpoint of the shaft and passes distally, approximately parallel to the posterior margin of the bone and finally subsides shortly before the distal extremity of the dorsal surface of the posterior condyle. The posterior condyle extends more distally than the anterior condyle, as it does in most primitive Palaeozoic tetrapods including captorhinomorph and pelycosaurian reptiles. However, the posterior condyle of *Seymouria* (White 1939) extends only slightly more distally, and in gephyrostegids (Carroll 1970; Boy & Bandel 1973) and *Tseajaia* (Moss 1972) the condyles terminate at the same level. The intercondylar groove is comparable in its degree of development to that of *Archeria* and *Papposaurus*. Longitudinal ridges, most strongly developed on the dorsal surface of the posterior condyle, mark the origin of ligaments and extensor muscles.

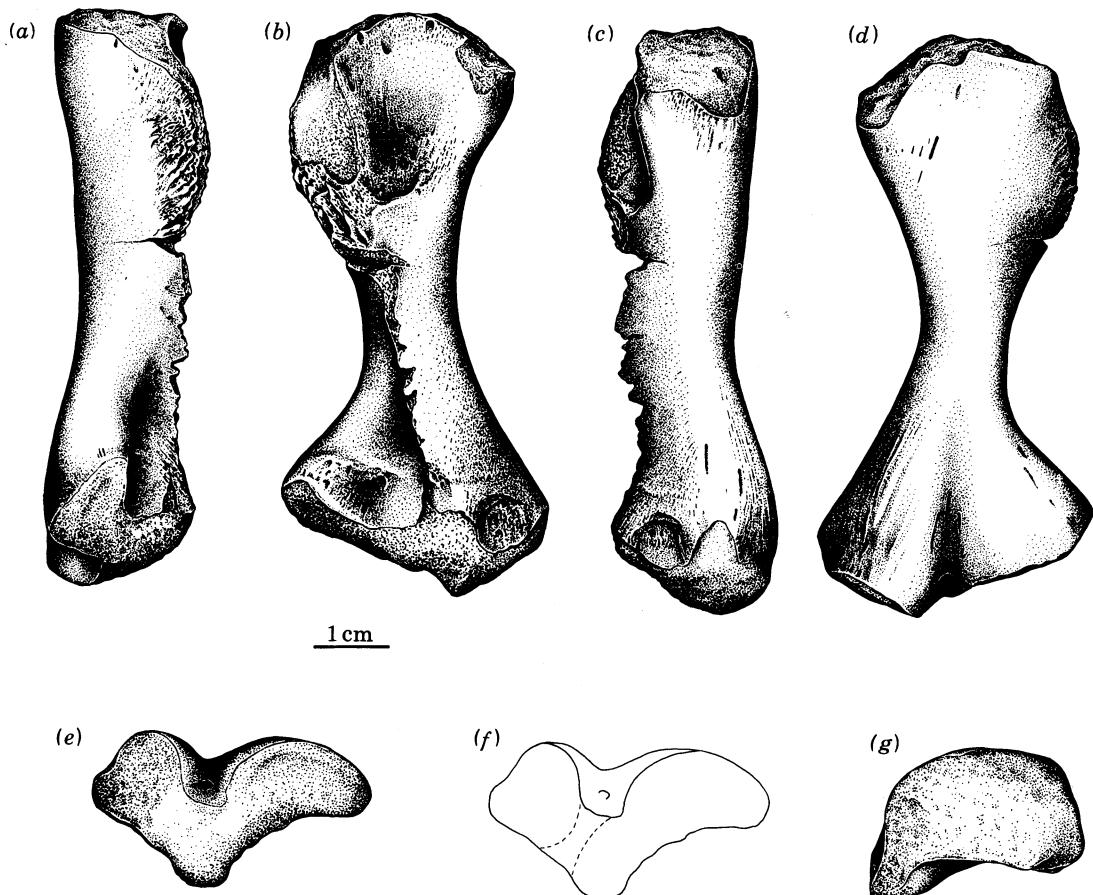


FIGURE 33. *Proterogyrinus scheelei* Romer, MCZ 4537. Right femur. (a) Anterior view; (b) ventral view; (c) posterior view; (d) dorsal view; (e) distal view; (f) distal view with fibular and tibial facets outlined; (g) proximal view.

Ossification of the distal head is insufficiently complete to allow identification of separate tibial and fibular facets. However, a ventrally turning, U-shaped lappet of finished bone at the distal termination of the intercondylar groove indicates the approximate line of division. Articulated specimens clearly show that the dorsally convex, crescentic tibial facet begins at the margin of the distal head, turns ventrally as it passes posteriorly, and terminates immediately ventral to the intercondylar groove on the distal termination of the adductor crest. The anterior portion of the anteromesially facing surface is slightly concave rather than flat as in *Archeria*. The posterior portion of the surface is convex. The smaller, subcircular, gently convex fibular facet was presumably separated from the tibial facet in older animals by a narrow band of finished bone that passed ventroposteriorly from the intercondylar notch (figure 33). A triangular extension of the fibular facet, somewhat larger than that seen in *Archeria*, turns mesially and invades the dorsal portion of the lateral surface of the posterior condyle.

The morphology of the ventral surface of the femur is extremely similar to that of the femora of *Archeria* and *Papposaurus*. The moderately prominent, ventromesially directed internal trochanter is proximal in position. Its termination is unossified. Ridges and fluting, indicating additional insertional area for the puboischiofemoralis internus muscle, cover the ventral surface. A sharp, semicircular ridge sweeps posteriorly from the base of the internal trochanter and describes the distal extremity of the deep intertrochanteric fossa before turning proximally to become continuous with a broadly rounded ridge passing up the posteroventral margin of the femoral head to its proximal termination. This ridge presumably indicates the posterior boundary of the puboischiofemoralis externus muscle. The adductor crest, its proximal end essentially continuous with the base of the internal trochanter, passes diagonally across the ventral surface of the shaft to its termination somewhat posterior to the midpoint of the distal expansion, where it broadens to support the posteroventral portion of the tibial facet of the femur. The anterior and posterior sides of the crest converge to form an angle of much less than 90°, producing a more acuminate ridge than in *Archeria*. Proximally, the base of the ridge broadens somewhat, suggesting the presence of only a weakly developed fourth trochanter, much as in *Archeria*, *Papposaurus*, and the Cowdenbeath and Florence embolomeres, and very distinct from the powerful process seen in the Horton Bluff 'seymouriamorph', *Eryops*, and *Seymouria*. The small size of the process may indicate a relatively small caudifemoralis muscle, or could reflect a different mechanical relation between the muscle and hip joint. The popliteal space, located anterior to the distal end of the adductor crest, bears rugosities and ridges similar to those in *Archeria* for joint ligaments. As in *Papposaurus* and *Archeria*, the restricted ventral surface posterior to the crest terminates in a shallow depression bearing rugosities for the attachment of additional joint ligaments.

The tibia of *Proterogyrinus* (figure 34), although similar in most regards to that of *Archeria* and early tetrapods in general, is very stout. Its maximum length is 53% of the length of the femur. Very similar proportions exist in *Archeria*. Consequently, the crus:femur length ratio is very low relative to those of *Seymouria* and *Gephyrostegus*, in which the tibial lengths are 75% and 63% of the femoral lengths respectively.

The inconspicuous cnemial crest, occupying the mesial part of the proximal extensor surface, is like that of *Archeria*, but is unlike the prominent structure in most early tetrapods in being a broad, low swelling. The proximal articular surface can be divided into two parts. The broad, mesial portion is subcircular rather than convex. The narrower lateral portion is rectangular in outline, and differs from the flat surface of *Archeria* in appearing broadly convex when viewed

from the extensor surface. It begins by facing proximally, but turns to face almost directly laterally as it passes to its lateral termination.

A conspicuous rugose ridge, sweeping mesiolaterally from the base of the cnemial crest, indicates the insertion of the puboischiotibialis muscle. As in *Archeria*, the ridge continues distally along the mesial edge of the bone as a sharp crest before subsiding along the mesial expansion of the tibia. This ridge gives the mesial edge of the bone a convex shape when viewed from the extensor aspect.

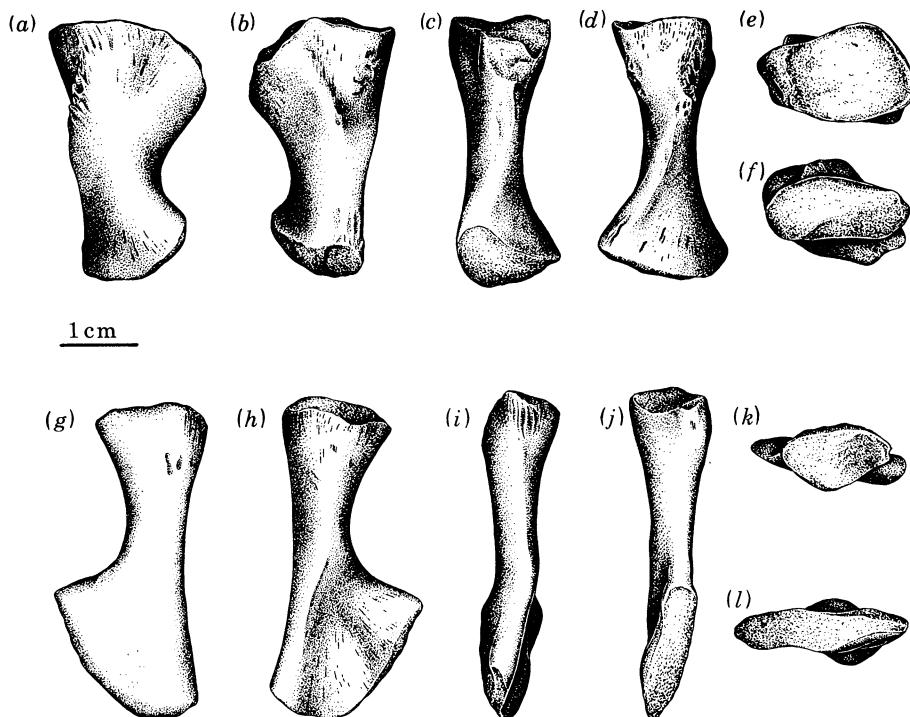


FIGURE 34. *Proterogyrinus scheelei* Romer, CMNH 11091. Rear limb elements. (a)–(f) Left tibia in anterior, posterior, lateral, mesial, proximal and distal views respectively; (g)–(l), left fibula in anterior, posterior, lateral, mesial, proximal and distal views respectively.

The flexor surface of the tibia is very similar to that of *Archeria*. Heavy longitudinal striations, apparently associated with ligament attachment, are evident on the proximal head. A prominent rugose ridge, characteristic of *Archeria* (Romer 1957), is also present in *Proterogyrinus*. The ridge passes diagonally from the centre of the flexor surface of the proximal expansion in a mesiodistal direction, subsiding just distal to the narrowest point of the shaft and probably served as insertional area for shank flexors.

As in *Archeria*, the distal articular surface is oval in outline. The extensor margin is convex in outline, and the flexor margin is essentially straight. The mesial portion of the surface opposing the tibiale and fourth centrale faces directly distally, while the slightly narrower facet for the intermedium faces laterally, forming an angle of approximately 50° with the long axis of the bone as compared with 40° in *Archeria*.

As in *Archeria*, the distal end of the bone is twisted so that its extensor surface faces anteromesially. However, the plane of the distal extensor surface makes an angle of 48° with

the plane of the proximal expansion as compared with 30° for *Archeria*. This approximates the condition seen in more terrestrial early tetrapods such as *Seymouria* or *Eryops*, and allows a more directly anterior orientation of the foot than was possible in *Archeria*.

The fibula (figure 34) is very similar to that of *Archeria* and, unlike the tibia, is not appreciably stouter than its counterpart in that genus. The moderately expanded proximal head bears a terminal articular surface, the shaft is oval in cross section, and the greatly expanded distal head is thin and bears a long distal articular surface rather indistinctly divided into two facets for the fibulare and intermedium. As in *Archeria*, the proximal head of the fibula is twisted so that the flexor surface of the proximal head faces posteromesially. The outlines of the articular surface differ slightly in the two genera and the plane of the proximal flexor surface of the fibula in *Proterogyrinus* makes an angle of approximately 40° with the plane of the distal expansion as compared to 35° in *Archeria*. However, the long axes of the articular surfaces make an angle of about 25° in both genera, indicating that the total amount of 'twisting' is functionally about the same.

Viewed laterally, the fibula has a gentle sigmoidal outline, with the distal end turning slightly outward to meet the more horizontal tarsus, and the proximal end turning inward, causing the concave terminal facet to be tipped slightly mesially to face the fibular facet of the femur as in *Archeria*.

The lateral surfaces of the proximal head and shaft regions of the extensor surface are gently convex. The broad, plate-like distal extensor surface is flat or even slightly concave. Except for rugosities on the lateral portion of the proximal surface for the insertion of the iliofibularis muscle, the extensor surface shows no conspicuous features.

The proximal flexor surface is strongly convex, causing the proximal head to be the thickest part of the bone. The crest of the convexity condenses into a sharp ridge just distal to the narrowest point in the shaft that turns laterally and runs parallel to the lateral margin of the bone, losing prominence distally. As in *Archeria*, this ridge was probably associated with flexor muscles. The distal flexor surface has a complex topography, being essentially concave mesial to the ridge, but having a gently convex portion beginning in the centre of the distal expansion and continuing to its distal termination.

As in *Archeria* and early reptiles, the distal articular surface of the fibula is very long mesiolaterally and very narrow dorsoventrally. The division between the facets for the intermedium and fibulare is indicated by a constriction in the dorsoventral width of the surface. The mesial portion of the fibulare facet is as wide as that for the intermedium. However, the lateral portion becomes much narrower. The thin, distolateral corner of the fibula is not well preserved in any specimen.

Elements of the tarsus are well preserved in CMNH 11067 (figures 16 and 31), CMNH 10938 (figure 35b), and MCZ 4537 (figure 35a), although in none of these specimens is the tarsus complete. Nevertheless, both the dorsal and ventral aspect of the tarsus can be confidently restored with the information from all specimens (figure 36).

The plate-like fibulare, in general similar to that of *Archeria*, is exposed dorsally in CMNH 11067 and ventrally in MCZ 4537. Both dorsal and ventral surfaces are gently concave, as the edges of the bone are raised to increase the articular surface area. It is massive mesially and distally, but thins considerably toward its proximomesial corner. The flat proximal articular surface is wedge-shaped in outline, thickest mesially and thinning laterally. The extensive, rectangular facet for the intermedium is set off at an angle of 105° from the proximal

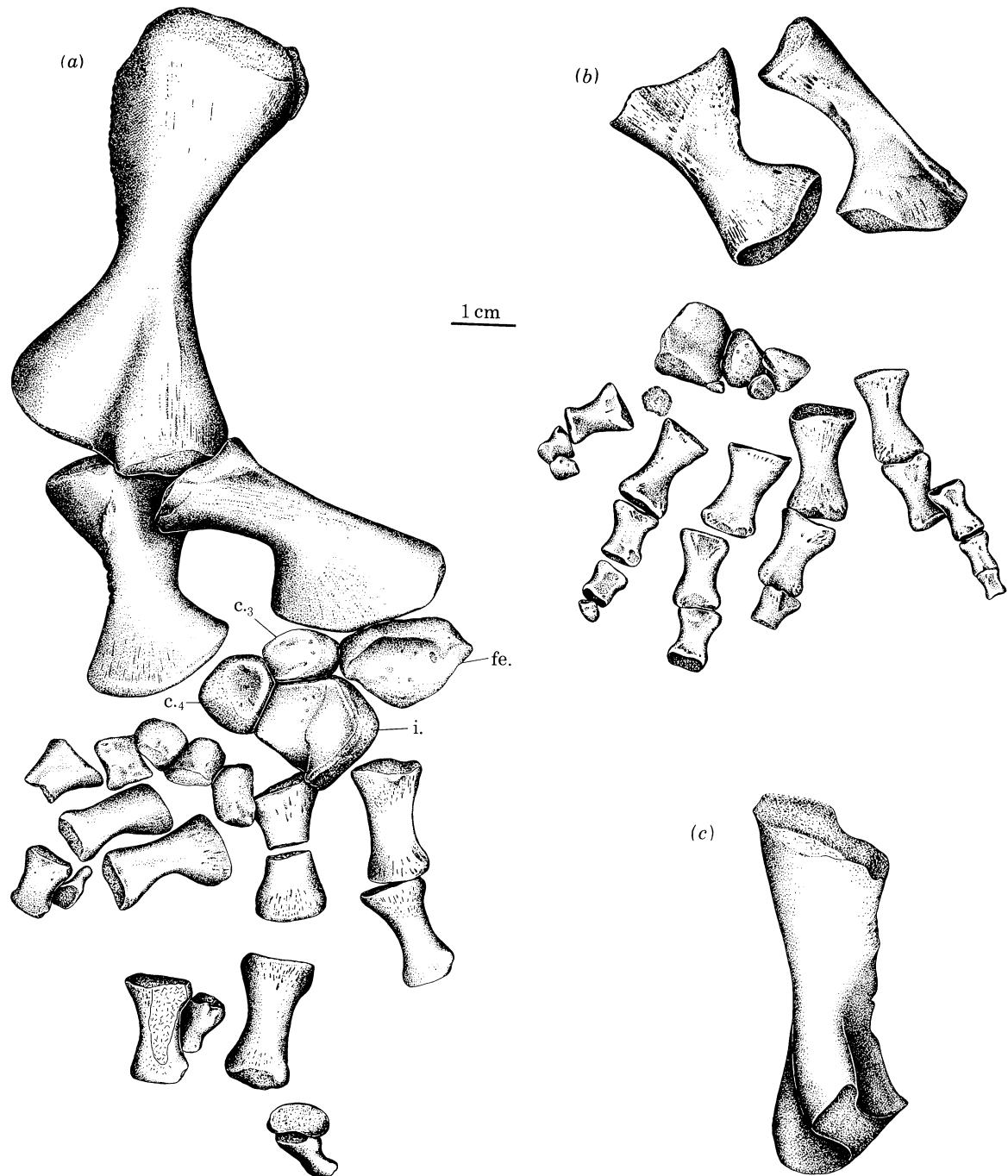


FIGURE 35. *Proterogyrinus scheelei* Romer, rear limb elements. (a) Left rear limb in dorsal view (MCZ 4537); (b) right rear limb, ventral view (CMNH 10938); (c) right femur, anterior view (CMNH 10938).

surface. The facet for the fourth distal tarsal faces mesiodistally and slightly ventrally, and is set off at an angle of 90° to the facet for the intermedium. Dorsally, its raised border is separated from that of the intermedium facet by the channel of the perforating artery that arises from the mesially projecting corner of the fibulare and passes laterally across the dorsal surface of the bone. The fibulare is thickest mesially. The convex facet for the fourth distal tarsal is square

in outline. Although most of this surface engages the fourth distal tarsal, a small portion articulates with the lateral portion of the lateral (third) centrale. This is distinctly different from the condition described for *Archeria* by Romer (1957), in which the surface articulates exclusively with the centrale and the fourth distal tarsal shares a distally directed facet with the fifth distal. Why such a distinct difference should exist between two animals with otherwise similar limbs is puzzling. However, the more poorly preserved tarsus of *Archeria* could easily have been misinterpreted and better material, if discovered, may prove to resemble that of *Proterogyrinus*. The massive, gently convex facet for the fifth distal tarsal faces slightly dorsally and is set off at an angle of about 45° from the facet for the fourth distal. Its dorsal border is conspicuously raised. The rounded lateral border of the fibulare is unfinished, and was presumably continued in cartilage in life.

The dorsal and part of the ventral surfaces of the intermedium are exposed in CMNH 11067. Additional information on the ventral aspect is provided by MCZ 4537. All edges of this massive bone bear wide surfaces for articulation with other tarsal bones except for a short, curved, proximomesially facing notch between the fibular and tibial facets where the bone thins. The angular relations of the articular surfaces and general outline of the bone are closely comparable to those in *Archeria*, the main differences being the shorter distance between fibular and tibial articular surfaces. The dorsal surface is concave, largely because the borders of the facets for the fibulare, tibia, and to a lesser extent, the fibula, are prominently raised. The distomesial articular surfaces appear to have some dorsal exposure, but this could be an artefact of preservation or preparation. Ventrally the borders are not conspicuously raised, and the bone surface is gently concave. The region between the fibular and tibial facets is ‘excavated’ ventrally, causing the bone to be thinner in this region. A distinct groove begins at the distolateral corner and passes diagonally across its ventral surface to become confluent with the ‘excavation’. Blood vessels or nerves, or both, clearly passed from the ventral surface of the crus between the distal ends of the tibia and fibula, crossed the ventral surface of the intermedium, and emerged onto the dorsal surface of the fibular side of the tarsus through the perforating foramen between the fibulare and intermedium.

Although well preserved in CMNH 11067, the tibial side of the tarsus is more difficult to interpret. In that specimen, the distal end of the tibia lateral to the surface for the intermedium articulates with a roughly 8-shaped bone composed of a larger lateral and a smaller mesial component separated by a distinct ‘waist’ where the two parts have incompletely fused. The composite nature of this bone is even more apparent ventrally, where the two subunits are separated by a deep furrow (figure 31). Fusion was clearly incomplete, since in other large individuals (MCZ 4537) the mesial element has been lost (figure 35). This part of the tarsus was poorly represented in *Archeria* and Romer (1957) could tentatively identify a poorly preserved tibiale in only one specimen. Romer’s tibiale probably corresponds to the lateral element in *Proterogyrinus*. Comparison of the tarsus of *Proterogyrinus* with those of temnospondyls suggests that this element represents the fusion of the fourth centrale and tibiale. Where known, the fourth centrale of temnospondyls is large, often almost as large, and in some cases, larger than the tibiale, and in *Trematops* (Schaeffer 1941) and *Archegosaurus* (Zwick 1898) occupies a similar position as the lateral element in *Proterogyrinus* and articulates with the tibia. In *Archegosaurus*, where the fourth centrale is much larger than the tibiale, the two elements were thought by Sewertzoff (1908) to be fused.

Proximally, the surface of the fused tibiale and fourth centrale in *Proterogyrinus* is flattened,

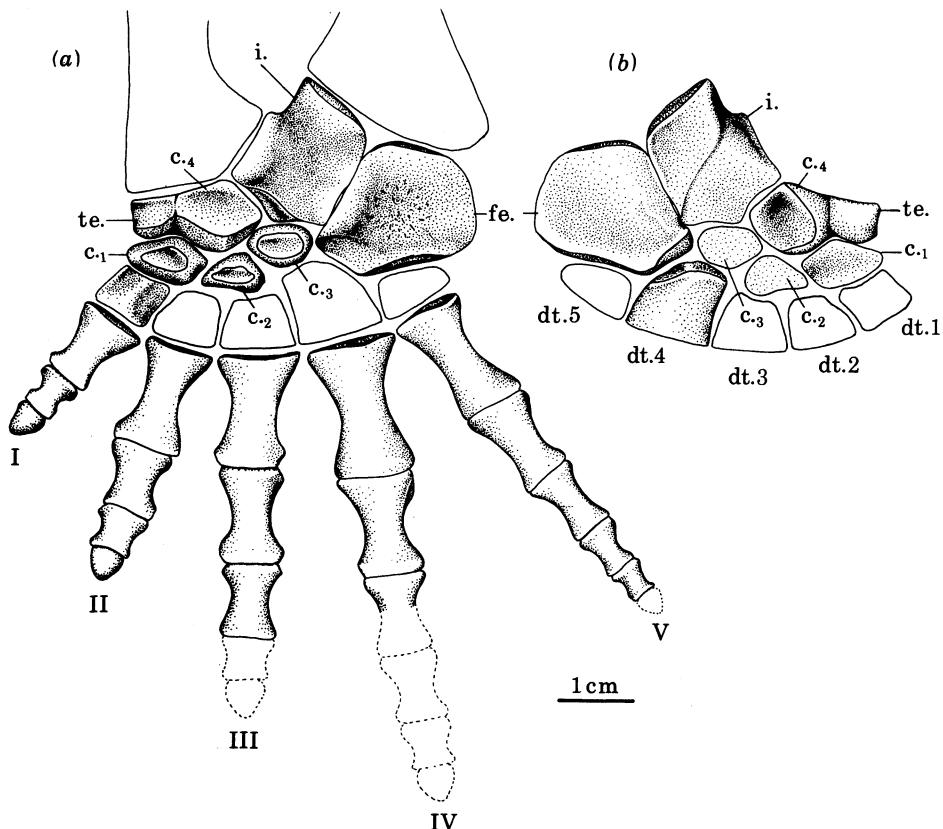


FIGURE 36. *Proterogyrinus scheelei* Romer, restoration of left foot. (a) Dorsal view; (b) ventral view of tarsus.

matching closely the distal surface of the tibia. Distally, the articular surface is convex, with much more of the surface facing dorsally, indicating considerable potential movement between this and more distal elements of the tarsus.

In addition to the large proximal fourth centrale, three distal centralia are preserved in CMNH 11067. All are irregular ovals viewed dorsally (figure 16). They are keystone-shaped, with extensive, flat, ventral-finished surfaces and restricted, concave, dorsal-finished surfaces. As in *Archeria*, the medial centrale (C1) is the largest, C2 is the smallest, and the lateral centrale (C3) is intermediate in size.

Distal tarsals are preserved in CMNH 11067 and MCZ 4537, but except for the first and fourth distals are too poorly ossified to give any information other than their size and general shape. They are consequently represented in figure 36 by unstippled outlines. The first distal, almost as thick dorsoventrally as it is wide mesiolaterally, is rectangular in shape. The large fourth distal, roughly pentagonal in shape, is exposed in ventral view only.

The tarsal structure of *Proterogyrinus* provides some information of the homologies and origin of the reptilian astragalus. The primitive reptilian tarsus, exemplified by *Paleothyris* (Carroll 1969), is composed of the calcaneum (fibulare), astragalus, two centralia (medial and lateral), and five distals. In immature specimens of the primitive reptile *Captorhinus*, the astragalus is composed of three centres of ossification, which Peabody (1951) homologized with the tibiale, intermedium, and proximal centrale of primitive amphibians. This was apparently confirmed by the tarsus of *Gephyrostegus* (Carroll 1970). The astragalus of the microsaur

Tuditanus is also composed of three ossification centres (Carroll & Gaskill 1978). The significance of this fact depends to some extent on whether or not microsaurs are considered to be closely related to reptiles. Regardless of the position taken, *Tuditanus* possesses only one tarsal centrale, indicating that this genus is more derived with respect to this character than primitive reptiles, and certainly more derived than most other Palaeozoic amphibians. This appears to be true of other microsaurs as well. What is known of the tarsus of anthracosaurs and temnospondyls suggests that primitive tetrapods (presumably including reptile ancestors) possessed four centralia and the reduction to three (proximal, lateral and medial) in *Gephyrostegus* is a derived condition. In *Proterogyrinus* the large fourth (proximal) centrale is in the process of fusing with the small tibiale, leaving three distal centralia. This suggests that the incipient astragalus of *Gephyrostegus* was composed of a tibiale–fourth centrale and the intermedium, and that the astragalus of reptiles includes the fourth centrale in addition to the tibiale, intermedium and third ('proximal') centrale. The tibiale–fourth centrale fusion was probably the first event to occur phylogenetically, and was least likely to be preserved in the ontogeny of later tetrapods such as *Gephyrostegus* and *Captorhinus*.

Since preservation of the tarsus is much better in *Proterogyrinus* than in *Archeria*, any reconstructed elements of the tarsus of *Archeria* that differ markedly from corresponding well-preserved elements in the tarsus of *Proterogyrinus* should be suspect. The fibulare and intermedium of both animals are very similar, and this similarity should be extended to the remainder of the tarsus in the absence of contradictory evidence.

The distal articular surface of the tibia is essentially the same length and width as the combined lengths of the corresponding surfaces on the intermedium, fourth centrale and tibiale, indicating that no significant translation was possible. Despite the laterally turning distal head, the joint between the tibia and tarsus was not similar to the free rocking joint in reptiles, as Romer suggested that it was in *Archeria*.

The distal expansion of the fibula and associated structure of the tarsus (particularly the plate-like nature of the fibulare) closely resembles the condition seen in reptiles, although its functional significance is unclear.

Elements of the pes are well preserved in CMNH 11067 (figures 16 and 31), and MCZ 4537 (figure 35a), although the most complete and best articulated foot is shown by CMNH 10938 (figure 35b). In the last specimen, digits one and two are complete, and digit five is probably missing only the ungual. The large size of the most distal-preserved elements in digits three and four suggests that each is missing at least the last few segments. On the basis of these specimens, the phalangeal formula is reconstructed as 2, 3, 4, 5, 5, as in *Archeria* (figure 36). As in *Archeria* the fourth metatarsal is the largest and there is a general reduction in the size of elements towards the mesial side of the pes. Unlike the condition in *Archeria*, but more typical of that seen in early tetrapods generally, the fifth metatarsal is considerably shorter than the fourth. As in the manus, the phalanges of *Proterogyrinus* are more elongated than their counterparts in *Archeria*. This is most pronounced in distal elements. In *Proterogyrinus*, as in early tetrapods generally, the fourth digit is the longest. This is in marked contrast to the condition in *Archeria*, where the phalanges of the fifth digit are longer than those of the fourth, and hence the former is the longest.

A detailed analysis of the mechanics of the pelvic limb is impossible, because the joint surfaces are relatively less well-ossified and defined than those of the pectoral limb. Nevertheless, an attempt has been made to estimate the orientation of the limb at the beginning and end of

each power stroke (figure 37). The preserved structure of the acetabulum suggests no restrictions on movement, but the stride is limited by that of the pectoral limb. A few conclusions can be drawn from the knee joint. The distal articular surfaces of the femur are essentially terminal, with very little ventral exposure. If this approximates the form of the joint surface in life, it would have been necessary to maintain the knee joint considerably below the level of the acetabulum to direct the shank downward. The flat, matching articular surfaces of the knee joint also indicate that little flexion or extension of the shank was possible, although in the absence of any information on the shape of the capping cartilages, these conclusions are equivocal.

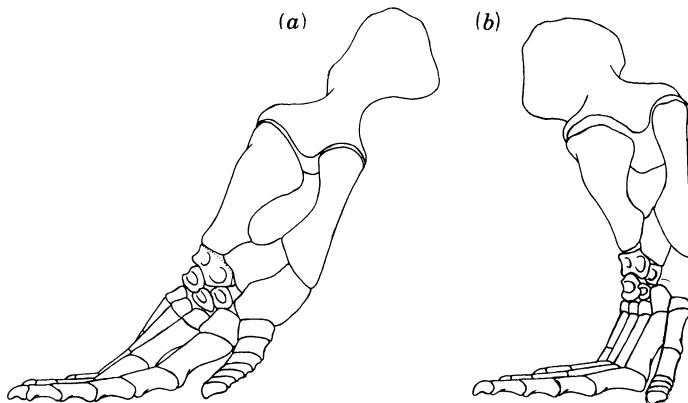


FIGURE 37. *Proterogyrinus scheelei* Romer, two lateral reconstructions of the power stroke of the rear limbs.
(a) Beginning of power stroke; (b) end of power stroke.

PRESERVATION, PALAEOECOLOGY AND LIFE ENVIRONMENT

During the Lower Middle Mississippian, northern West Virginia and southwestern Pennsylvania were covered by an epicontinental sea that deposited the Union Limestone presently underlying the Mauch Chunk. Tectonic activity in the area throughout the latter part of the Mississippian produced a general retreat of the sea to the southwest and subsequently the terrestrial-fluvial-lacustrine deposits characteristic of the Mauch Chunk Group were laid down (Busanus 1974). The Bickett Shale, from which *Proterogyrinus* came, probably represents a fluvio-deltaic sequence deposited to the northwest of the shoreline. Although the Bickett Shale exhibits the most variable lithology of the Mauch Chunk Group, indicating a variety of depositional environments, it was apparently fresh or brackish water in origin. The Bickett Shale includes thin-bedded red or green shales to massive red siltstones or green-grey micaceous channel sandstones with occasional appearances of shaly matrix conglomeratic beds (Busanus 1974).

Vertebrate material is known only from two restricted localities within the Bickett Shale; in the Greer Quarry 10.5 km southeast of Morgantown, West Virginia, and from a second locality in Pennsylvania about 20 km north-northwest of Greer. In both localities, much of the material is disarticulated and fragmentary, forming bone beds. A relatively high energy fluvial environment in which the remains were transported for some distance followed by a lagoonal depositional environment is postulated by Busanus (1974).

All specimens described in this paper were found in a bed immediately above the bone beds

of the Greer locality. The generally well-articulated condition of these specimens indicates that this bed represents a second phase of sedimentation in a lower energy, possibly lagoonal environment. The green-grey matrix varies from a massive, silty shale to a sandstone. The unusually high density of vertebrate remains suggests a sudden mass death for the inhabitants, but the cause is unclear. The absence of mudcracks prompted Busanus to hypothesize that a sudden, temporary influx of salt water from the sea to the southwest may have been responsible.

One additional feature of the Mauch Chunk Group worthy of note is the rarity of coal deposits, indicating that the surface of the deltaic deposits had a sufficient grade to discourage the formation of a coal-swamp environment. This is consistent with the disarticulated and fragmentary nature of most of the vertebrate remains. The bulk of the evidence suggests a changing deltaic environment with a great enough grade to produce streams capable of transporting relatively large bones or whole animals a considerable distance. The development of quiet, temporary lagoonal environments was common. However, these lagoons were regularly subjected to high-energy conditions that probably destroyed or altered them considerably.

In addition to *Proterogyrinus*, the deposits produced a number of specimens of the temnospondyl *Greererpeton*, numerous *Gyracanthus* spines, scales of palaeoniscoids and of crossopterygians, articulated skeletons of the lungfish *Tranodis* and plant fragments (Busanus 1974). It may be inferred from the articulated condition and large numbers of individuals represented that *Greererpeton* and *Tranodis* normally inhabited the environment represented by the deposits. The more fragmentary nature of *Gyracanthus*, palaeoniscoid, and crossopterygian specimens suggests that they may have lived elsewhere, and that their remains were washed in by streams. The rarity of *Proterogyrinus* (relative to the occurrence of *Greererpeton*) may indicate that the lagoon was not its primary habitat, although the generally well-articulated condition of the specimens is evidence that they could not have been transported very far.

The analysis of the mode of life of a Palaeozoic tetrapod based on anatomy and palaeoecology has certain theoretical and practical limitations. Adaptive significance of anatomical structures is assessed by analogy with often only remotely related living animals which introduces considerable possibility for error. Assuming that conclusions concerning palaeoecology are correct, it is often difficult to determine with any degree of certainty that the animal in question actually inhabited that environment or was transported there after death. Nevertheless, with these limitations in mind, a cautious use of the evidence can help to put morphological features and palaeoecological data into perspective.

The well-developed limbs of *Proterogyrinus* make it tempting to hypothesize a terrestrial habitus, especially since as previously pointed out, the large pectoral limbs could not have been retracted against the body, making them an inappropriate adaptation for swimming in open water. However, the presence of lateral line canals, long neural and haemal spines in the caudal region, and the possible presence of a functional spiracle are unlikely features in a terrestrial animal. Nevertheless, unlike *Greererpeton*, which, with its flattened skull, dorsally facing orbits, elongated body, and tiny limbs is clearly adapted to bottom dwelling in relatively quiet water, *Proterogyrinus* appears to have been adapted to a more active existence, perhaps clambering over rocks and debris in the more restricted marginal areas of the lagoons, or perhaps living in one of the streams, using its large limbs to secure itself to objects on the bottom or simply digging into the sand as it negotiated the currents. The well-developed tail was probably, nevertheless, an important swimming organ. The high skull and laterally facing orbits also make it unlikely

that *Proterogyrinus* was restricted to a bottom-dwelling existence. The presence of lateral line canals and possibly a spiracle would not necessarily prevent *Proterogyrinus* from elevating the head above the surface of the water for short periods of time, but make it unlikely that it habitually left the water. A similar cranial anatomy in later embolomeres suggests that this is true of the group in general (one possible exception is the apparently terrestrial carnivore *Anthracosaurus*). Although relatively little is known of the postcranial skeleton of later embolomeres, the trend towards elongation of the presacral column and reduction in the relative size of the limbs, at least in archeriids, may signal an adaptation towards deeper, less turbulent water where limbs are less useful and most locomotion is accomplished by sinusoidal movements of the trunk and tail.

THE RELATION BETWEEN EMBOLOMERES AND SEYMOURIAMORPHS

An evaluation of the relation between embolomeres and seymouriamorphs is not without difficulties because the nature and interrelations of the latter group are far from clear. Romer (1966) considered the suborder Seymouriamorpha to include the following families: Seymouriidae, Kotlassiidae, Discosauriscidae, Chroniosuchidae, Nycteroletteridae, ?Waggoneriidae, ?Lanthanosuchidae, Tseajaiidae, Diadectidae.

The composition of the Seymouriamorpha has most recently been discussed by Heaton (1980). He removed the discosauriscids from the suborder, arguing that they are better considered as gephyrostegid anthracosaurs, dropped the relatively poorly known chroniosuchids, waggoneriids, and lanthanosuchids without comment, and separated the remaining families into two suborders: the primitive Seymouriamorpha comprising the Nycteroletteridae, Seymouriidae, and Kotlassiidae, and the more derived Diadectomorpha, comprising the Limnoscelidae (considered by Romer as primitive reptiles), Tseajaiidae, and Diadectidae.

Although a thorough analysis of the composition and interrelations of the Seymouriamorpha (*sensu* Romer) is beyond the scope of this paper, some commentary is necessary before proceeding. The relatively poorly ossified and paedomorphic discosauriscids, most recently discussed by Ivachnenko (1981), possess a number of primitive features such as the absence of an ectepicondyle and the presence of an anterior flange of the humerus, presence of an intertemporal bone, and closed palate that are shared by nonseymouriamorph batrachosaurs. The tabular-parietal contact, long parasternal process, phalangeal formula, and pleurocentrum-dominated vertebral structure may signify a relation with either seymouriamorphs or embolomeres, but as discussed elsewhere in this paper ('Batrachosaurs and the origin of reptiles'), the taxonomic significance of such characters in Palaeozoic tetrapods is questionable. The very short suspensorium and deep otic notch resemble the seymouriamorph condition, but a similar structure is seen in branchiosauroids, and may simply be paedomorphic. The reduction of the tabular bone and modest ventral reflection of its posterior surface is reminiscent of seymouriamorphs, as is the lozenge-shaped occipital condyle, fusion of the kinetic joint, separate coracoid ossification, and expanded basal plate of the parasphenoid. Unfortunately, no braincases have been described to confirm the presence of laterally placed fenestrae ovales. Although the evidence is not conclusive, the discosauriscids are here considered either as primitive seymouriamorphs, or comprising their plesiomorphic sistergroup. The absence of basal tubera and poorly ossified vertebrae can then be assumed reasonably to be paedomorphic features.

With the possible exception of the form of the otic notch, *Nycteroleteter* and related forms share no secure synapomorphies with seymouriamorphs, and perhaps can be considered more appropriately procolophonid reptiles as proposed by Chudinov (1957).

The chroniosuchids, known largely from the work of Vjuschkov (1957) and Tverdochlebova (1967, 1972, 1975, among other papers) are represented largely by partial skulls and vertebral columns and fragmentary appendicular elements. Despite the apparent loss of the intertemporal, presence of preorbital (? postnasal) vacuities, and dorsal armour attached to the neural spines, the skull and vertebrae share more features with embolomeres than with seymouriamorphs. The parasphenoid does not extend laterally as in seymouriamorphs (Tverdochlebova 1972), nor are the neural arches swollen (Tverdochlebova 1967). The limited information available does not suggest a particularly close relation to seymouriamorphs, and chroniosuchids should probably be considered provisionally as aberrant embolomeres, although the precise relation with the latter group cannot be assessed without more information.

The waggoneriids known from a single, poorly preserved specimen, *Waggoneria knoxensis* (Olson 1951) and a few jaw fragments of '*Helodectes*' (Case 1911) are even more enigmatic. Olson describes a deep, diadected-like otic notch and laterally expanded parasphenoid in *Waggoneria*, but the skull is very poorly preserved, making the precise nature of these morphological features uncertain. Dentition and vertebral structure are very similar to that of a captorhinid reptile. Whatever the affinities of *Waggoneria*, I agree with Heaton in excluding it from the Seymouriamorpha for the time being.

The position of the lanthanosuchids is more problematic. Neither a seymouriamorph otic notch, nor a laterally expanded parasphenoid are present in *Lanthanosuchus watsoni* (Efremov 1946), and the notch of *Lanthanosuchus efremovi* (Ivachnenko 1980) is more comparable to that of a discosauriscid. Although the possession of a short cultriform process and ventrolateral projection of the plate resembling basal tubera may indicate affinities with other seymouriamorphs, the skull is very specialized in many features, and the Lanthanosuchidae must be considered, at most, a very derived seymouriamorph group that provides very little information about the early evolution and interrelations of the suborder.

Tseaiaia shares the widely spaced fenestrae ovales, reduced basioccipital, ventroposterior projections of the paraphenoid that are probably homologues of basal tubera, and a separate coracoid ossification with other seymouriamorphs. The aberrant *Diadectes* appears to share features with *Tseaiaia* (Moss 1972), but its affinities are uncertain.

The long-standing assumption that embolomeres and seymouriamorphs are closely related (Romer 1966) has recently been criticized by Heaton (see 'Batrachosaurs and the origin of reptiles', elsewhere in this paper). The anatomy of primitive batrachosaurs such as *Proterogyrinus*, *Eoherpeton*, and *Crassigyrinus* has helped to re-establish some credibility to Romer's hypothesis. Many of the putative apomorphies that were suggested as excluding embolomeres from relation with the seymouriamorphs, such as ear structure and function and humerus structure, are plesiomorphic. A massively ossified braincase and associated absence of metakinesis are only characteristic of more derived embolomeres. Primitive embolomeres such as *Proterogyrinus* have a 'split' braincase, a plesiomorphy it shares not only with seymouriamorphs, but also reptiles, primitive temnospondyls such as *Greererpeton* and many microsaurs.

The absence of a post-temporal fossa (fossa bridgei) in embolomeres was also used by Heaton to discredit any embolomere-seymouriamorph relation. Examination of the posterior skull table and occiput of *Seymouria* reveals many similarities to embolomeres (figure 38). Although there

seems to be some intraspecific variation in the outline of the posterior skull table as viewed dorsally, in general it is more concave than depicted by White (1939). This was also noted by Case (1911). The sculptured posterolateral corners of the tabulars form modest posterolateral prominences resembling the dorsal (ornamented) portions of the horns of gephyrostegids and *Eoherpeton*. This prominence is clearly set off by a furrow from a large, convex, posteroventrally and laterally turning, unornamented lappet that may be homologous to the unornamented terminal portion of the horn in other batrachosaurs. If this is correct, then *Seymouria* can be considered to possess a reduced tabular horn in which the unornamented portion has been deflected ventrally. As in embolomeres, the large tabulars have considerable occipital exposure, each forming a ventromesial suture with a postparietal and overlying the dorsomesial portion of the opisthotic, the latter bearing large facets for the exoccipital. The exoccipital makes no sutural contact with the postparietal. Of particular significance is the structure of the 'post-temporal fossa'. The tabular and opisthotic make mutual contact at two points: posteromesially and anterolaterally. The 'fossa' lies lateral to the posteromesial contact, where it forms a shallow depression on the occipital surface of the paroccipital process (figure 38). It is important to note that unlike in temnospondyls where the fossa actually 'perforates' the occipital surface at the common junction of the tabular, postparietal and opisthotic bones and passes forward between the skull roof and paroccipital process, the anterior wall of the much shallower pocket of *Seymouria* is formed by the depressed occipital surfaces of the tabular and opisthotic, which remain unbroken except for the *vena capititis dorsalis* foramen that passes between the tabular and opisthotic into the cavum crani. The roof of this channel on the ventral surface of the tabular was figured and labelled (P. T. Fos.) by Watson (1954, figure 30), but not referred to in the text. This configuration, essentially the same as that in embolomeres is distinct from that in temnospondyls (see 'The braincase', above). This highly unusual feature is a convincing synapomorphy between embolomeres and *Seymouria*. A very similar arrangement was described (Watson 1954) in the kotlassiid *Karpinskiosaurus* (figure 38). Paradoxically *Kotlassia*, a close relative, was restored with temnospondyl-like post-temporal fossae (Bystrow 1944). However, as noted by Smithson (1982), a number of specimens were examined by Bystrow, and the presumed composite reconstruction (Bystrow 1944) may have been based in part on one or more temnospondyl fragments. Perhaps significantly, the major difference noted by Watson (1954) between *Karpinskiosaurus* and Bystrow's reconstruction of *Kotlassia* is the form of the post-temporal fossa. These two genera may be synonymous if Smithson's suspicions prove correct. *Limnoscelis* also possesses a reduced post-temporal fossa (Romer 1946). As in embolomeres, *Seymouria* and *Karpinskiosaurus*, the 'fossa' is bounded dorsally and laterally by a large tabular (figure 38). The small postparietal does not contribute to its border. The tabular has a ventral contact with the opisthotic and a dorsal contact dorsomesial to the 'fenestra' with the supraoccipital. Except for the presence of a supraoccipital, this arrangement is the same as in embolomeres, *Seymouria* and *Karpinskiosaurus*. However, Romer equivocated somewhat on the presence of an opisthotic-supraoccipital suture, and it is quite possible that the supraoccipital is actually dorsomesial elaborations of the otic capsule as in embolomeres. Romer does not state whether a foramen passes from the fenestra into the cavum crani, but his figure indicates that it deepens as it turns mesially (figure 38), suggesting the presence of a *vena capititis dorsalis* foramen.

The occiput of *Tseajaia* is generally comparable to that of *Limnoscelis*. Both the large, laterally placed supratemporal and more mesial tabular have considerable occipital exposure, with the

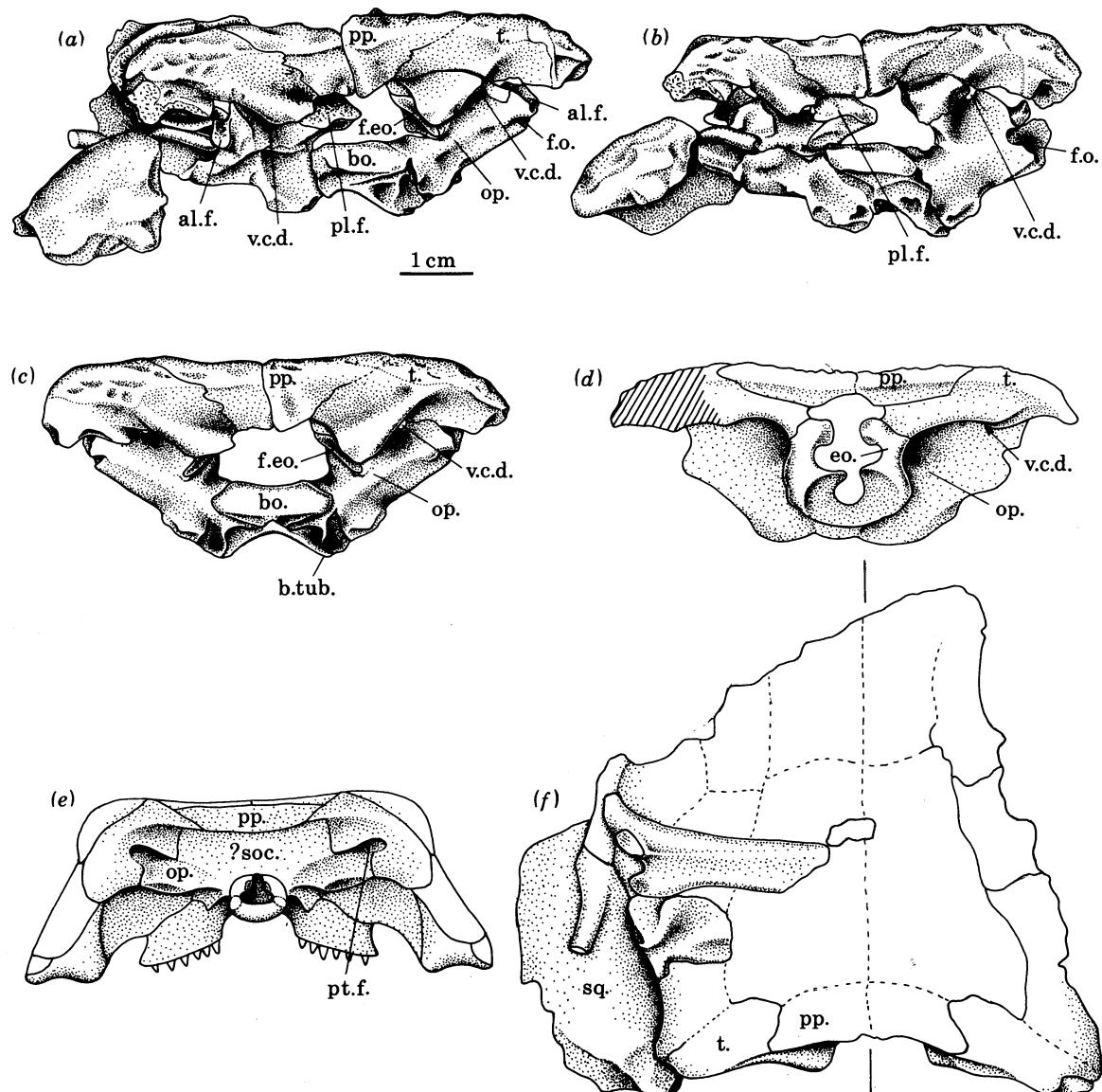


FIGURE 38. The occiputs of some seymouriamorphs. (a) *Seymouria* (MCZ 1086), viewing plane parallel with the transverse plane of the skull. (b) Posterolateral view of MCZ 1086, with the viewing plane forming an angle of 20 degrees with the transverse plane. (c) *Seymouria*, reconstruction based on MCZ 1086. Note that exoccipitals are not restored. (d) *Karpinskiosaurus*, redrawn from Watson 1954. (e) *Limnoscelis*, redrawn from Romer 1946. (f) *Seymouria* (MCZ 1086), dorsal view showing outline of posterior skull margin. Poorly preserved bone surface and intractable matrix renders most of the sutures on skull roof difficult to trace. Scale pertains to (a), (b), (c), and (f) only; (d) and (e) are not drawn to scale.

latter forming a long contact with the occipital plate. As in *Limnoscelis*, no clear supraoccipital-opisthotic suture is visible (Moss 1972). Although the region of the tabular-supraoccipital (?opisthotic) suture is not well preserved, making it impossible to determine the existence of a *vena capitidis dorsalis* foramen, it is clear that a large post-temporal fossa could not have been present. *Lanthanosuchus watsoni* does not have a post-temporal fossa, and there is no evidence that a *vena capitidis dorsalis* foramen was present (Efremov 1946). *Lanthanosuchus efremovi* appears to have a shallow post-temporal fossa somewhat like that of *Seymouria* (Ivachnenko 1980), but

the structure of the occiput is otherwise so divergent that it is difficult to assess its significance to seymouriamorph relations.

Panchen (1980) argued that the skull anatomy of *Eoherpeton* provided evidence of relation between embolomeres and seymouriamorphs. It resembles seymouriamorphs in having widely spaced fenestrae ovales floored by lateral extensions of the parasphenoid, basal tuberae on the parasphenoid, and a similar septomaxilla. Although the tabular horns and otic notch are present, they are both somewhat reduced as compared with those of embolomeres, but closely resemble those of gephyrostegid seymouriamorphs. *Eoherpeton* also possesses the 'split' braincase found in both *Proterogyrinus* and seymouriamorphs. If it also proves to have a vena capititis dorsalis foramen and reduced post-temporal fossae, Panchen's hypothesis would be corroborated. A more complete description of *Eoherpeton*, presently being undertaken by Dr Smithson at Newcastle, should clarify its taxonomic position, but in the meantime it can be considered provisionally a primitive gephyrostegid occupying a position close to the seymouriamorph-embolomere dichotomy (Panchen 1980).

THE AFFINITIES OF *PROTEROGYRINUS* AND THE INTERRELATIONS OF THE BATRACHOSAURIA

Proterogyrinus scheelei, a primitive embolomere-like animal, is the type genus of the family Proterogyrinidae. *Papposaurus* (known only from an isolated femur) an unnamed animal from Cowdenbeath represented by a skull table and a few postcranial elements (Smithson 1980), and the fragmentary '*Pholiderpeton bretonensis*' from Point Edward are here placed in the same family. Although it is possible that these animals are synonymous with *Proterogyrinus*, slight differences in vertebral structure appear to establish the Point Edward animal as a separate taxon, and preliminary examination of the Cowdenbeath specimen reveals apparent differences in limb-skull proportions, but this remains to be confirmed by Dr Smithson's study. *Papposaurus* is more problematic as the only known material is not very diagnostic. When femoral structure becomes better known in the other Scottish proterogyrinids, it may be possible to synonymize this genus with another, but until then it is considered to be a distinct genus.

Only two characters of the family Proterogyrinidae, a skull table morphology showing a raised pineal rim and associated median ridge flanked on each side by a deep depression, and the absence of dentition on the second and third coronoids (the latter confirmed in *Proterogyrinus* only) are known neither to be primitive, nor to occur in later embolomeres. On-going research on more distantly related batrachosaurs, especially *Crassigyrinus* (by Panchen) and *Eoherpeton* (by Smithson) promises to extend our knowledge of the anatomy of the suborder and provide the possibility of identifying further derived characters of the Proterogyrinidae.

Although the unique structure of the skull table and coronoid tooth distribution are sufficient to distinguish *Proterogyrinus* and other proterogyrinids from members of other batrachosaur families, there are no known apomorphies to distinguish *Proterogyrinus* from other members of its own family, making a definitive diagnosis of the genus impossible. Consequently, the diagnosis provided in this paper is by necessity composed only of primitive characters or characters of unknown phylogenetic significance. This anomaly is no doubt due to the paucity of information on the structure of other proterogyrinids. When more becomes known about these animals, comparison will almost certainly reveal some as yet unidentified autapomorphies of *Proterogyrinus*.

The apparent scarcity of apomorphies would be expected to induce an ‘eclectic’ systematist of the Mayr–Simpson school (Mayr 1969; Simpson 1945, 1961) to suggest that the proterogyrinids occupy a phylogenetic position ancestral to later embolomeres. This would be vigorously contested by adherents of the phylogenetic (cladistic) school of systematics who would argue that the search for ancestors is futile because ancestors cannot possess any autapomorphies, and so their definition and recognition is difficult if not impossible (for example, Bonde 1975; Hennig 1966; Patterson 1981). However, Wiley (1981), a cladist, argues that it is possible to test ancestor–descendant hypotheses providing sufficient data are available. Furthermore, Hennig has introduced the concept of the stem group, which readmits a modified form of ‘ancestor’ into a cladistic framework. He defines the stem group as ‘the species which are in direct line of descent of recent species, and also the “side branches” of the phylogenetic tree’ (Hennig 1981, p. 30). It is important to note that he admits the ‘side branches’ (essentially the relicts of the earlier authors) into the stem group.

In the context of the above discussion, the Proterogyrinidae should be considered the stem group of the infraorder Embolomeri. Description of new material pertaining to these groups will no doubt define more precisely the position of *Proterogyrinus* and other proterogyrinids relative to the ‘direct line of descent’ of more derived embolomeres.

A tentative phylogeny of batrachosaurs was recently published by Panchen (1980), a slightly modified version of which is presented in this paper (figure 2). Although not intended as a cladogram, the phylogeny, nevertheless, represents the taxa arranged according to clearly specified synapomorphies. Recently published information on batrachosaurs, in addition to our expanded knowledge of *Proterogyrinus*, permits the construction of a more detailed scheme of character distribution (figure 39) that essentially supports Panchen’s phylogenetic hypothesis. Before the characters included in the distribution are discussed in detail, a few brief comments on methodology are appropriate. As is usually the case in palaeontological research, the choice of characters is limited not only to the skeletal elements and those parts of the soft anatomy directly inferred by them, but also by the completeness and state of preservation of the animals under study. In the case of the Batrachosauria, data are still quite limited, particularly for the postcranium. Description of new material pertaining to other batrachosaurs will hopefully provide new characters with which to test the distribution given here. In some cases it has proved convenient to combine a number of characters that appear to have evolved as a single-character complex in response to the same selective pressures. For instance, *Anthracosaurus* has developed a number of characters, such as massive dentition, reinforced palate, and loss of the kinetic junction that appear to be associated with a change in feeding habits, probably from a piscivorous to a carnivorous diet. Braincase structure, in reality a suite of characters, is another example. To simplify the character distribution, such characters are grouped into a character complex and designated by a single number. This practice creates no difficulties as long as these are characters of terminal taxa, or if characters defining a node are always similarly linked in more derived taxa as well. If new species are subsequently discovered that do not possess a complete set within the complex (that is, the original hypothesis that the characters are linked functionally is refuted), the characters can be separated conveniently since the components of the complex have been clearly specified beforehand. Following generally accepted taxonomic procedures, only those characters considered to be synapomorphies are used in the distribution. Although I agree with Panchen (1982) that the principle of parsimony as used by cladists is not consistent with Popper’s definition of the term (Popper 1959), I nevertheless see no other

objective method for arranging characters once they have been chosen. Although it is tempting to weight characters according to complexity or functional considerations (Hecht & Edwards 1977), it would often be necessary to assume more knowledge of the genetic and developmental basis and functional significance of these characters than we actually possess. In any case, such 'adjustments' would be *a posteriori* despite the intentions of those proposing such a method (Patterson 1982). Although convergence is often easy to differentiate from true homology (synapomorphy) when working with taxa of high rank, convergence and parallelism are less obvious within lower categories. This is probably due to a common epigenetic pattern shared by members of the relatively closely related lineages within the taxon (cf. Alberch 1980). There seems little doubt that these are very common phenomena (Brundin 1968; Cain 1982) but I know of no reliable method of distinguishing these types of characters from true synapomorphies *a priori*, unless one considers similarity and conjunction to be tests. Similarity is hardly a test, as the hypothesis of homology would never have been proposed if there were no similarity between the two structures. Presumably what is meant by the similarity test is a re-examination of the putative homologous structures using ontogenetic evidence or more detailed comparisons of structure and topography to determine whether the structures are really 'the same'. Such an exercise must be approached cautiously in palaeontology, as ontogenetic evidence is usually at best inadequate, and it is often possible to re-interpret other evidence to reconcile with *a priori* bias. In addition, close re-examination of an apparent homology is only likely to occur if it conflicts with the investigator's intuitive taxonomic framework, and so the judgement is in reality *a posteriori* even though the interrelations have not yet been established formally. Conjunction (that is, an hypothesis of homology is refuted if both presumed homologous structures are found on the same organism) is usually not applicable to typically fragmentary fossil material. Consequently, we are left with congruence as the only remaining test of homology (Patterson 1982), but it can only be applied after the most 'parsimonious' character distribution has been generated. It is usually instructive to examine and analyse the apparent convergences (incongruent characters) established by the most 'parsimonious' distribution.

Although the lack of an intrinsic test of homology creates a considerable potential source of error for the practitioners of cladistic methodology, it is no less of a problem for the more traditional eclectic systematists. Despite its many serious shortcomings, I know of no better method. If nothing else, it has the advantage of presenting the author's arguments, opinions and biases in a form that is most easily criticized and perhaps refuted.

Of all the synapomorphies uniting the Batrachosauria (*sensu* Panchen), the most distinctive is the tabular horn (1). It has become modified twice during the group's history; once in the loxommatids it is reduced to 'buttons' (11) and a second time in seymouriamorphs (28) where it is reduced and deflected ventrally. The batrachosaur basal articulation (2), with the main axis of its double articular surface oriented at right angles to the sagittal plane is distinct from that seen in osteolepiform fish, primitive temnospondyls, and microsaurs, suggesting that it is a derived trait (Smithson 1982). A similar arrangement is seen in primitive reptiles (*Captorhinus*, Heaton 1979). The structure of the occiput (3), with a large occipital plate composed of otic capsule only (that is, without a separate supraoccipital ossification), separating the postparietals from the exoccipitals, is a character of less certain polarity. If the osteolepiform occipital plate included a supraoccipital element, character (3) should be considered a synapomorphy of batrachosaurs, as this configuration is not known to occur in other tetrapods. If the osteolepiform occipital plate is composed only of otic capsule as appears to be the case in

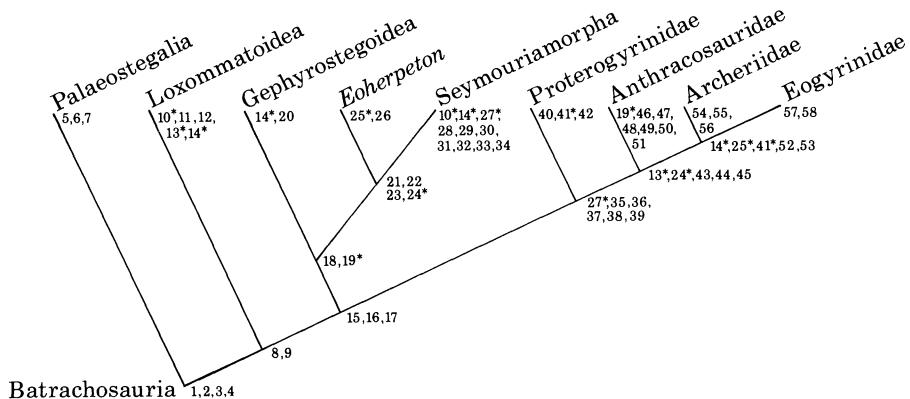


FIGURE 39. A character distribution of batrachosaurs, based in part on information from Panchen 1980. See Appendix I for characters used. Asterisks indicate characters assumed to have evolved independently.

batrachosaurs, its occurrence in the latter would be plesiomorphic (see Batrachosaurs and the origin of reptiles, below). Although evidence is equivocal, the former alternative is provisionally accepted. In any case, this arrangement is quite distinct from the derived condition in temnospondyls, where the occipital portions of the otic capsules are not well-developed mesially, and the exoccipitals make contact with the postparietals (Smithson 1982). Despite the uncertain taxonomic significance of gastrocentrous vertebrae in lower tetrapods, the possession of ventrally continuous pleurocentra (4) appears to be an internally consistent character and is probably a true synapomorphy of batrachosaurs. The structure, particularly in the primitive, highly notochordal batrachosaurs is not really comparable with that seen in reptiles, microsaurs or the temnospondyl *Dolosserpeton* where the well-developed, cylindrical centra all but occlude the notochordal canal, and the neural arches are solidly attached or indistinguishably fused to the neural arches. Although the temnospondyl *Caerorhachis* may represent an early stage in the development of gastrocentrous vertebrae in temnospondyls, its specific relation, if any, to *Dolosserpeton* is unclear, and there is no other evidence that the gastrocentrous structure of these groups went through a stage comparable to that seen in primitive batrachosaurs, indicating that the gastrocentrous structure of batrachosaurs and the other groups may not be strictly homologous.

The first known offshoot of the group, the suborder Palaeostegalia, represented by *Crassigyrinus*, is derived in having a marked interorbital constriction (5), distinctly rhomboidal orbits (6), a shape approached but never attained to such a degree in some more derived batrachosaurs, and a lacrimal excluded from the orbital margin (7) by a thin posterior process of the prefrontal (Panchen 1973). The latter character seems to have originated through a dorsal migration of the orbit away from the lacrimal. Consequently, the lacrimal does not participate in the orbital margin even though the bone extends posteriorly below the orbit to about the midpoint of the opening. This is in marked contrast to the superficially similar loss of the orbital lacrimal in the more derived *Eoherpeton*, eogyrinids, and archeriids (24), where the posterior border of the lacrimal has migrated forward away from the orbit as the snout elongated. The resulting potential gap was bridged by a broad ventral flange of the prefrontal. *Crassigyrinus* retains many primitive (osteolepiform) characters such as the presence of a preopercular bone, a postparietal-supratemporal contact, large postparietals, a possible spiracular cleft, (see

Batrachosaurs and the origin of reptiles, below) long suspensorium, and, despite its relatively large size (skull length, 34 cm), a short preorbital region. A forthcoming complete description of the new Cowdenbeath *Crassigyrinus* material by Dr A. L. Panchen at Newcastle will no doubt further clarify its affinities.

Beyond the palaeostegalian level of organization, the preopercular is lost (8), and the long fish-like suspensorium is considerably shortened (9). The loxommatids, first related to anthracosaurs by Watson (1919, 1926) largely on the basis of stratigraphic occurrence and symplesiomorphies, but later allied with temnospondyls owing to the presence of a postparietal-supratemporal contact (Romer 1947) and the alleged association of rhachitomous vertebrae (Baird 1957), are considered provisionally by Panchen to be primitive batrachosaurs. Although vertebral structure is poorly known there is some evidence that it resembled that in *Crassigyrinus*, and was not rhachitomous (Panchen 1977a, 1980). The postparietal-supratemporal contact, now known to be primitive for batrachosaurs, no longer precludes a relation between the two groups. Although loxommatids share some primitive characters with anthracosaurs such as a closed palate and a high narrow tropibasic skull, Panchen (1980) understandably expressed reservation about his phylogenetic assignment because he could find no distinct synapomorphies except the possession of reduced tabular horns (11). However, the form of the basal articulation (2) is probably also a synapomorphy. The structure of the occipital plate (3) is the same in the two groups, but until the structure and composition of that region of the osteolepiform and primitive tetrapod braincase are better understood, the significance of this character is equivocal. The loxommatids are derived in the possession of preorbital vacuities (12), resembling in some respects the vacuities in the Russian chroniosuchids, absence of the kinetic junction between the cheek and skull table (10) and the development of a highly ossified braincase (13) with fusion of the ethmoid and otico-occipital portions. The latter two features are probably related to a general consolidation and strengthening of the skull. Anthracosaurids, archeriids, and eogyrinids have independently developed a similar braincase structure, while anthracosaurids and to some extent the eogyrinids have also consolidated the cheek-skull table joint. Comparison of the braincase structure of a primitive temnospondyl such as *Greererpeton* with that of the more derived *Edops* or *Eryops* indicates similar trend towards braincase consolidation in that group. The coronoid dentition is completely absent (14) in all known loxommatids. This dentition, certainly an important component in the osteolepiform feeding mechanism, presumably became more or less redundant when this specialized feeding mechanism was abandoned during the fish-amphibian transition. However, coronoid teeth persist (?redevelop) in microsaurs with crushing marginal dentition (for example, *Pantylus*, Carroll & Gaskill 1978), and have a variable occurrence in temnospondyls. Although palaeostegalian batrachosaurs retain a modestly developed set (A. L. Panchen, personal communication) the dentition is suppressed in various ways in more derived genera (42, 45). These dentitions probably have independent evolutionary histories in different Palaeozoic tetrapod groups, and, therefore, specific patterns of coronoid dentition are unreliable for establishing phylogenetic relationships.

The suborder Anthracosauria is characterized by the development of horseshoe-shaped pleurocentra (15) from the primitive, dorsally opened crescents, the tabular-parietal contact (16), and a foramen for vena capitis dorsalis. Although it is possible that the latter is present in loxommatids and therefore developed at an earlier point in batrachosaur phylogeny (see The braincase, above), evidence is weak and at present it is best to consider it a synapomorphy of anthracosaurs only.

The infraorder Seymouriamorpha, one of the two subdivisions of the Anthracosuria, is characterized by an extreme shortening of the suspensorium, with the quadrate advanced almost to the level of the occiput (18). The absence of lateral line sulci (19), clearly a terrestrial adaptation, occurs not only in seymouriamorphs and *Anthracosaurus*, but also in many temnospondyls and, of course, in reptiles, and does not by itself indicate relationship. *Gephyrostegus* (and probably the relatively poorly known *Eoherpeton*) appears to be an early offshoot from this assemblage, although at least *Gephyrostegus* is clearly distinguishable from other seymouriamorphs by the unique pustular ornamentation on the dermal skull roof (20). As in some other batrachosaurs, the coronoid dentition is entirely absent (14).

All other seymouriamorphs (including *Eoherpeton*) have a laterally positioned fenestra ovalis (21), basal tubera on the parasphenoid (22), and a reduced tooth count (23), although this trend seems to be reversed in some later seymouriamorphs (for example, *Kotlassia*). Because tooth count shows no well-documented pattern of variation in early tetrapods, the latter character is included with some hesitation. With the exception of *Gephyrostegus* no seymouriamorph has a parasymphysial tusk. Although absent in all known microsaurs (Carroll & Gaskill 1978), it occurs very consistently in temnospondyls, making its loss in seymouriamorphs potentially significant.

Eoherpeton is distinguished from other seymouriamorphs by a large pineal foramen (26) and the exclusion of the lacrimal from the orbit (25). The latter character, approached but not quite attained in *Gephyrostegus*, can be correlated to the elongation of the preorbital region, and is, therefore, not considered to be homologous to the exclusion of the lacrimal from the orbital margin in *Crassigyrinus* (7). The remaining seymouriamorphs, here characterized primarily on the basis of the relatively well-known *Seymouria*, are typified by a suite of distinctive characters such as a reduced, lozenge-shaped basioccipital (28), absence of nasolabial groove (30), impedance-matching stapes (32), swollen neural arches with disc-shaped pleurocentra fused to the arches (33) and absence of the anterior flange of the humerus and associated development of an ectepicondyle (34). They are convergent with a number of other batrachosaur groups in the absence of the kinetic junction between cheek and palate (10) and the absence of coronoid teeth (14). They are also apparently convergent with embolomeres in the loss of the fossa bridgei (see The relation between seymouriamorphs and embolomeres, above). However, the occipital region of *Gephyrostegus* is poorly known, and until Dr Smithson's redescription of *Eoherpeton* is completed, little is known of the details of the 'post-temporal fossa' in the latter genus. If it proves to be a shallow, blind pocket of the type seen *Seymouria*, it is probable that the loss of the fossa bridgei is a synapomorphy of all anthracosaurs, and not developed independently by seymouriamorphs and embolomeres.

Other features, although characteristic of *Seymouria*, are variable in occurrence or precise form in other seymouriamorphs. The reduced, ventrally deflected tabular horn (29) can also be seen in *Kotlassia* and *Karpinskiosaurus*. In *Limnoscelis*, the tabular horn is completely absent, and the supratemporal has sent a thin posterior projection to sheath the down-turned tabular laterally. The horn of *Tseajaia*, composed mostly of supratemporal with a modest contribution from the tabular mesially, can be derived from the condition seen in *Limnoscelis*. The 'supratemporal horn' of *Tseajaia* is therefore not homologous with the tabular horn of earlier seymouriamorphs such as *Gephyrostegus* and *Eoherpeton*. The nature of the otic notch structure (31) is clearly related to the fate of the tabular horn.

The other major group of anthracosaurs, the infraorder Embolomeri, is characterized by the absence of vomerine fangs (35), the development of a separate ventral ramus of the tabular

horn (36), a large surangular crest (37), a processus alaris of the jugal making contact with the pterygoid (38), and large Meckelian fenestrae (39). As discussed above, it is uncertain whether the loss of the fossa bridgei is a synapomorphy of embolomeres and seymouriamorphs, or whether it occurred independently. However, in all known embolomeres, even the shallow pockets have been lost, and the lateral tabular-opisthotic contact has migrated anteriorly, causing the vestibule of the vena capititis dorsalis to face more laterally. If the shallow, non-perforating post-temporal fossa proves to be a consistent character in primitive seymouriamorphs, then the complete absence of any pocket and reorientation of the lateral tabular opisthotic facet seen in embolomeres should be distinguished from the condition seen in seymouriamorphs and established as another synapomorphy of the group.

The family Proterogyrinidae is characterized by a unique rimmed pineal, and median ridge flanked on either side by a depression on the postparietals (40). The jugal is exposed on the ventral margin of the skull (41). In *Crassigyrinus* and other primitive batrachosaurs, the large quadratojugal and long maxilla form an unbroken ventral skull border below the jugal. With the reduction of the quadratojugal associated with the shortening of the suspensorium and the anterior migration of the maxilla connected with the elongation of the preorbital region, these elements lose their primitive contact. This is approached but not quite accomplished in *Gephyrostegus*. Although not characteristic of loxommatids, it occurs in one species (*Baphetes kirkbyi*), and also in both archeriids and eogyrinids. Since shortening of the suspensorium and elongation of the snout is a general trend in batrachosaurs, the independent development of this character would not be surprising. The general trend towards reduction of coronoid dentition is also exhibited (42), although the specific combination (present on coronoid 1, absent on coronoids 2 and 3) is unique for batrachosaurs.

The remaining embolomere families (Anthracosauridae, Archeriidae, and Eogyrinidae) have evolved (independently from loxommatids) a co-ossified braincase (13), and lack parasymphysial tusks (24), the latter condition convergent with all seymouriamorphs except *Gephyrostegus*. The intercentrum is ossified to form a complete disc (43), and the dorsal suture on the pleurocentrum is absent (44). None of these taxa possess teeth on the first or second coronoids (45) and this is assumed to be the primitive condition for the three family clade.

The family Anthracosauridae (*Anthracosaurus*) possesses several distinctive characters including a single large Meckelian fenestra (46), presumably produced by the loss of the bar between the two fenestrae present in other embolomeres, and a small fenestra on the squamosal-jugal suture (47). The absence of lateral-line canals (19) developed independently from seymouriamorphs, and widely spaced, laterally facing orbits (48) probably indicate a terrestrial habitus. A number of features such as a massive dentition, reinforced palate, loss of the kinetic junction between cheek and skull table, and the dorsal migration of the external naris, presumably to permit consolidation of the maxilla-premaxilla contact (and resulting reduction in the nasolabial groove), all appear to be associated with a carnivorous diet (49). The massive development of the marginal palatal bones appears to have concealed or caused the elimination of the processus alaris. The very shallow suspensorium in *Anthracosaurus* may be correlated with a reorganization of jaw adductor muscles, increasing the static pressure exerted and allowing the use of the massive dentition on large prey (Panchen 1981). The shallow subtemporal fossa cannot accommodate a well-developed surangular crest, which consequently is reduced in height.

Members of the families Archeriidae and Eogyrinidae both lack a coronoid dentition (14), have a lacrimal excluded from the orbit (24) and a jugal exposed along the ventral margin

of the skull (41). These characters, convergent with some other batrachosaurs, have already been discussed. They also possess a very distinctive, deep lower jaw (52) and have lost the ventral ramus of the tabular horn (53) seen in proterogyrinids and anthracosaurids.

Archeriids have emphasized the chisel-shaped tooth shape (54) that is approached in some maxillary teeth of *Proterogyrinus*. They have an elongated snout (55), indicative of a piscivorous diet, and an elongated presacral vertebral column (56), presumably associated with aquatic locomotion.

In the eogyrinids, the intertemporal has become sutured to the postorbital (56), but the supratemporal-squamosal contact remains unfused. The supraneural canal of the neural arches is closed (57).

BATRACHOSAURS AND THE ORIGIN OF REPTILES

The Anthracosuria (*sensu* Romer) has generally been considered ancestral to reptiles since publication of Watson's classic works on the subject (Watson 1919, 1926), despite attempts to relate reptiles and microsaurs (Vaughn 1962; Brough & Brough 1967). Carroll (1970) in his description of *Gephyrostegus* summarized the characteristics possessed by this primitive anthracosaur that he believed indicated the group's position as reptile ancestors:

- (i) general proportions of the skull and palate, despite the presence of an otic notch, resemble those of the romeriid captorhinomorphs;
- (ii) some details of skull structure, such as the tabular-parietal contact, small interpterygoid vacuities, and suture patterns of the preorbital region of the skull roof also resemble romeriid captorhinomorphs;
- (iii) the intertemporal bone is superficial 'resting on extensive ventral lappets from surrounding bones' (p. 271). Carroll took this as an indication that the bone was being reduced;
- (iv) absence of lateral-line canals;
- (v) pleurocentrum-dominated (gastrocentrous) vertebral centrum;
- (vi) long parasternal process of interclavicle;
- (vii) phalangeal count of manus 2, 3, 4, 5, 3;
- (viii) presence of incipient astragalus, in which the tibiale and intermedium are fused, but the proximal centrale is still a discrete element;
- (ix) wheat-shaped ventral scales and absence of dorsal (epidermal) scales.

The anthracosaur ancestry of reptiles has more recently been discussed by Panchen (1972b, 1975, 1977a). He argued that many of the characters used to establish this relation are of questionable phylogenetic significance. The tabular-parietal contact, long considered to be a synapomorphy of the two groups, probably evolved independently (Panchen 1972b). Also damaging to the theory was the demolition of Romer's theory of the evolution of the 'labyrinthodont' vertebral centrum (Holmes & Carroll 1977; Panchen 1977a). As a consequence, the phylogenetic significance of gastrocentrous vertebrae within Palaeozoic amphibians is ambiguous. This vertebral pattern appears not only in batrachosaurs, but also in some temnospondyls (Bolt 1969; Holmes & Carroll 1977), and lepospondyls, inducing Panchen to regard 'the possession of an essentially diplospondylous gastrocentrous vertebra as a primitive character of unknown taxonomic extent in early tetrapods', and therefore not useful for establishing relations (Panchen 1977a, p. 313).

The astragalus is not a character unique to reptiles and gephyrostegids (Panchen 1972b),

but has evolved separately in at least two microsaur genera (Carroll & Gaskill 1978) and is therefore an unreliable indicator of relationships. The same argument can be applied to a long parasternal process, which also occurs in microsaurs (Carroll & Gaskill 1978) and ichthyostegids (Jarvik 1980).

The absence of lateral-line canal grooves, although suggestive of terrestrial habits, does not indicate affinity with reptiles. Most microsaurs and some temnospondyls, notably the primitive *Dendrerpeton* (Carroll 1967) also lack them, but are clearly not related to reptiles.

The intertemporal of *Gephyrostegus*, whether or not superficial, is still a large element. No other anthracosaur shows any tendency to approach a reptilian condition by reducing that bone. Nor is the five-toed manus unique to reptiles and anthracosaurs. Five digits occur in the manus of primitive nectridians, although the phalangeal count is slightly lower (Bossy 1976). Although no known microsaur has more than four digits in the manus, some forms show evidence that this was derived from a primitive five-toed condition (Carroll & Gaskill 1978). Several microsaurs possess a pes with the reptilian 2, 3, 4, 5, 3 phalangeal count. Although anthracosaurs and reptiles both appear to possess ventral scales that are vaguely wheat-shaped while lacking dorsal scales, too little is known about the scales of Palaeozoic tetrapods to be certain of the taxonomic significance of these characters. In any case, these characters alone hardly justify relating the two groups. Most of the characters traditionally used to associate anthracosaurs and reptiles are therefore either primitive for tetrapods or have evolved independently in other groups and are not useful in establishing relationships.

Heaton (1980), in addressing the problem of the origin of reptiles has taken a novel approach to amphibian-reptilian relations. He argued in favour of recognizing a subclass of amphibians, the Batrachosauria, to include the order Cotylosauria, composed of the reptile-like seymouri-amorphs and diadectomorphs, and specifically excluding the Anthracosauria (embolomeres and gephyrostegids), thus redefining the term Batrachosauria as used by Panchen (1980). His argument comprises three approaches:

- (i) he agrees with Panchen (1972b), that the traditionally accepted synapomorphies of anthracosaurs (embolomeres) and reptiles are plesiomorphic, convergent, or spurious;
- (ii) he identifies what he considers to be apomorphies of anthracosaurs (embolomeres) that preclude close relationships with reptiles or 'batrachosaurs';
- (iii) he enumerates a number of apparent synapomorphies of cotylosaurs and reptiles.

Although he used a number of characters to relate cotylosaurs and reptiles, it was mainly differences in braincase structure that were used to exclude embolomeres from their classical position as reptile relatives. He first suggested that the similarities between the braincase of reptiles and cotylosaurs represented derived characters indicating a common origin. These are:

- (i) a general reduction in ossification over the ancestral (osteolepiform fish) condition;
- (ii) a loss of the osseous roof in the sphenethmoid and development of a simple V- or Y-shaped cross section. The cavity for the passage of nerves is undivided by osseous partitions;
- (iii) a distinct separation of sphenethmoid and otic-occipital elements;
- (iv) a loss of tectum synoticum, leaving the anterior part of the otic-occipital region unroofed, but retention of the tectum posterior (supraoccipital).

According to Heaton, these specializations, particularly the reduction of dorsal ossifications, provided the potential for dorsoventral flexion of the braincase and allowed batrachosaurs and primitive reptiles to develop metakinesis, with the contact between the supraoccipital and skull roof acting as an axis around which the otic-occipital unit rotates. Anthracosaurs (embolomeres),

loxommatids and temnospondyls, because they retained the highly ossified condition of osteolepiform fish never developed metakinesis and became akinetic after the loss of the ancestral neurokinetic condition (Heaton 1980) making it impossible to derive the reptilian or batrachosaurian condition from that seen in any of these groups.

There seems little doubt that more derived Palaeozoic batrachosaurs (or temnospondyls) could not have been metakinetic. It is also unlikely that the cotylosaur braincase could have been derived from the structure seen in such animals. However, in neither the more primitive *Proterogyrinus* nor the distantly related *Greererpeton* is there development of an ossified roof in the otic-occipital (that is, neither the embryonic tectum synoticum nor the tectum posterior, if present at all, ossified) nor is there an ossified sphenethmoid roof in *Proterogyrinus*. The otic-occipital and unpartitioned sphenethmoid subunits are widely separated in both animals. The osteolepiform fish *Eusthenopteron* (Jarvik 1954, figure 6a) has an unpartitioned sphenethmoid (a unit corresponding to both the tetrapod sphenethmoid and basisphenoid), suggesting that this may be primitive for tetrapods. That incomplete ossification in *Proterogyrinus* and *Greererpeton* is due to immaturity is unlikely, as the larger specimens of both animals are otherwise well ossified and give every indication of being adults. Although the supra-occipital appears to be absent, the otic-occipital is attached to the skull roof only posteriorly, in a manner analogous to the attachment between the supraoccipital and the skull roof of batrachosaurs (*sensu* Heaton). Whether a metakinetic joint was present is uncertain.

It appears likely that many braincase characters such as the separation of the sphenethmoid and otic-occipital, and reduced dorsal ossification that are presumably prerequisites for metakinesis (designated as shared, derived characters of 'batrachosaurs' and reptiles by Heaton) actually arose at an earlier stage in tetrapod evolution and had a much wider distribution than Heaton realized (even some microsaurs appear to show them). These characters presumably evolved soon after the ichthyostegid level of organization in which the braincase appears to be essentially like that of osteolepiform fish, but before the divergence of batrachosaurs, temnospondyls or microsaurs from this ancestral condition. Various groups (including embolomeres) later convergently reossified the braincase and co-ossified the sphenethmoid and otic-occipital divisions.

Heaton further argued that the structure of the otic-occipital of the anthracosaurian braincase specifically excluded the group from relationship to reptiles and the reptile-like batrachosaur amphibians. According to Heaton, the common ancestor of 'batrachosaurs' and reptiles reduced the tectum synoticum, but retained the tectum posterior (supraoccipital), whereas anthracosaurs (embolomeres and gephyrostegids) reduced the tectum posterior but retained the tectum synoticum. The structure of *Proterogyrinus* contributes little to the resolution of this particular issue, as the dorsal portion of the otic-occipital remained completely unossified. Although it is possible that an unossified tectum posterior (supraoccipital) occupied the gap between the opisthotics dorsal to the foramen magnum, the condition in *Archeria* in which the more extensively ossified opisthotics are separated on the occipital plate only by a gap of about 1 mm (R. Holmes, personal observation) indicates that the dorsal space in *Proterogyrinus* was occupied in life by mesial cartilagenous extensions of the opisthotics. The 'supraoccipitals' of *Palaeoherpeton* (Panchen 1964) and *Eoherpeton* (Panchen 1975) are apparently artifacts (A. L. Panchen, personal communication) and no other known anthracosaurs possess a supraoccipital exposed on the occipital surface. However, Heaton's argument assumes that the possession of both tectum synoticum and tectum posterior ossification is a primitive tetrapod

condition. The neurocranial anatomy of fish cannot confirm this, since although the otic-occipitals of the presumed ancestral osteolepiform braincases are roofed in bone, they bear no sutures to delineate separate ossifications (Jarvik 1954; Romer 1937). Nor are separate ossifications evident in the neurocrania of primitive actinopterygians (Patterson 1975) and Devonian diploans (Miles 1977), inducing the latter author to suggest that primitive sarcopterygians (from which tetrapods presumably evolved) 'did not share a fixed pattern of ossification centres with primitive actinopterygians' (Miles 1977, p. 26). Consequently, the ubiquitous distribution of a 'supraoccipital' in teleosts and many more primitive actinopterygians cannot be used as evidence that this bone in a primitive tetrapod character, since there is no way to be sure that the bone is homologous with the supraoccipital of tetrapods. Although no extant vertebrates possess a well-developed tectum synoticum as defined by Heaton, at least the tectum posterior, commonly derived initially as paired condensations from the occipital arch (Goodrich 1930) appears to be a common, and possibly primitive feature in the embryology of gnathostomes. However, its ossification to form a distinct supraoccipital has a variable occurrence in primitive tetrapods. Temnospondyls and primitive batrachosaurs do not show it presumably because early in development the paired embryonic condensations were incorporated into neighbouring elements, probably the otic capsules to which they became indistinguishably fused. Among Palaeozoic amphibians, only the microsaurs appear to have a distinct supraoccipital. De Beer (1937) in noting the sporadic and apparently random occurrence of a well-developed chondrocranial roof in vertebrate phylogeny argued that the degree of its development is of no taxonomic significance. Nevertheless, if Heaton is correct in his assumption that a separate supraoccipital ossification is a primitive tetrapod character, then he is justified in using its absence in anthracosaurs (and presumably their more primitive relatives) to assert that neither the reptilian nor the 'batrachosaur' braincase can be derived from any known batrachosaur (*sensu* Panchen). It should be noted here, however, that not all of Heaton's 'batrachosaurs' possess a supraoccipital. This is certainly true of *Seymouria*, probably true of the kotlassiids, and may be true of *Limnocalis* and *Tseajaia*. The apparent absence of this element in more primitive seymouriamorphs indicates that the supraoccipital may be a synapomorphy of the more advanced groups only. A redescription of the very primitive batrachosaur *Crassigyrinus*, now being undertaken by Dr Panchen at Newcastle, may provide new information on the structure and constituency of the primitive batrachosaur occiput.

The absence of a post-temporal fossa (fossa bridgei) in anthracosaurs (embolomeres) has also been identified as an apomorphy barring a close relationship between that group and reptiles (Heaton 1980). This fossa, well developed in osteolepiform fish and retained in a number of primitive tetrapod groups including reptiles, is thought to have been eliminated in anthracosaurs by a dorsal migration of the paroccipital process. Although the fossa is absent in embolomeres, it may be present in more primitive batrachosaurs such as *Eoherpeton* and *Crassigyrinus*. It is hoped that more complete descriptions of these two animals, now being completed by Dr Smithson and Dr Panchen, respectively, will resolve this question.

Another major controversy associated with the question of batrachosaur-reptile relations centres around the structure of the stapes, middle ear cavity, and otic notch in primitive tetrapods. Evidence from classical embryological studies strongly indicates that the stapes and middle ear cavity of tetrapods are homologous with the hyomandibular bone and spiracular diverticulum of fish (Goodrich 1930). The tympanum was once thought to have been derived from the operculum, but this now seems highly unlikely (Lombard & Bolt 1979).

The tympanum, forming part of an impedance-matching system, is supported by a bony notch in most extant reptiles and anuran amphibians, and when a notch at the back of the skull was first described in Palaeozoic amphibians, it was assumed to have performed the same function (Romer 1947). It was also tacitly assumed that the conversion from hyomandibular to stapes was completed during the fish-tetrapod transition, and that the earliest amphibians therefore had a middle-ear structure broadly comparable to that of modern tetrapods complete with tympanum. Lower Permian temnospondyls and batrachosaurs (for example, *Eryops*, *Edops*, *Seymouria*), among the first of these groups to be well known, supported these conclusions in having a lightly built stapes that was directed toward the dorsally located notch. This hypothesis is not without difficulties, however. Microsaurian amphibians all lack an otic notch, and the stapes, although variable in size and degree of ossification, appears to have been a substantial element that was directed ventrolaterally. Carroll & Gaskill (1978) suggested that vibrations were probably transmitted by the stapes to the inner ear directly from the substrate, and implied that no tympanum was present. Primitive Palaeozoic reptiles, presumed to have been derived from notch-bearing amphibians, have a stout, ventrolaterally directed stapes and did not have an otic notch. Watson (1954) suggested that these animals lacked a tympanum, and Hotton (1959) estimated that such a stapes would have been insensitive to all but very low frequency vibrations. Reisz (1981) argued that the ear of Palaeozoic reptiles was insensitive to airborne sound, and by implication, no tympanum was present. Carroll (1970) hypothesized that the stapes of primitive reptiles could have been derived from the type of stapes typical of then known Palaeozoic batrachosaurs by a ventrolateral migration of its distal end as a result of decreased body size associated with the amphibian-reptilian transition. However, there is no evidence that such a character reversal occurred, and he has since changed his mind (Carroll 1980). Some early temnospondyls without an 'otic' notch have recently been described (Carroll 1980; Holmes & Carroll 1977; Smithson 1982), making the presence of a tympanum in at least some primitive amphibians questionable. Furthermore, the temnospondyl *Greererpeton*, in addition to lacking a notch, has a large stapes which appears to have supported the braincase against the cheek (Smithson 1982). The picture is further complicated by the discovery of a similar stapes in the primitive temnospondyl *Dendrerpeton* despite the presence of a well-developed notch (Clack 1983).

The absence of any evidence for a tympanum in most Palaeozoic tetrapods, and particularly the common occurrence of a large, heavy stapes with at best limited auditory capabilities suggests that the conversion from structural brace to impedance-matching ear ossicle of the type seen in mammals, anuran amphibians, and most reptiles did not occur until after the fish-amphibian transition, and that the impedance-matching stapes has evolved independently several times. Lombard & Bolt (1979), in a detailed analysis of the comparative anatomy of the ear structure of both recent and fossil tetrapods have concluded that the tympanum and tympanic processes of the stapes of recent mammals, reptiles (including birds), and frogs are not homologous. More specifically, the amphibian tympanic membrane, including that of 'labyrinthodonts' (presumably anthracosaurs) is not ancestral to that of amniotes, and that such notch-bearing Palaeozoic amphibians are not suitable amniote ancestors. Panchen (1972b) reached the latter conclusion based on fossil evidence and there seems little doubt that it is correct. However, implicit in the argument is the assumption that a notch necessarily indicates the existence of a tympanum and impedance-matching stapes.

All known batrachosaurs possess a well-developed notch. The slender dorsolaterally directed

stapes of *Seymouria* reinforced the idea that this notch held a tympanum in all genera. However, Clack (1983) has broken with this tradition by pointing out that the notch in the eogyrinid embolomeres *Pholiderpeton scutigerum* and *Palaeoherpeton decorus* are not of a sufficient size or suitable shape to support a functioning tympanum. She further suggests that the embolomere notch may simply have been a by-product of the posterior expansions of both the tabular horn and the suspensorium, and has no functional significance. However, in *Proterogyrinus*, the notch cannot be accounted for by posterior elongation of the tabular, since the notch extends well forward of the tabular-supratemporal suture, and in all other batrachosaurs (including loxommatids) it extends to at least the level of that suture. A survey of batrachosaurs and temnospondyls reveals no simple correlation between extent of posterior development of the tabular and suspensorium and the occurrence of a notch. In *Gephyrostegus*, the quadrate lies in approximately the same transverse plane as the occiput, yet the notch is well developed. In *Greererpeton*, on the other hand, the quadrate lies considerably posterior to the level of the occiput, but there is no trace of a notch. The temnospondyl *Dendrerpeton* possesses a well-developed notch despite the absence of either tabular horns or a posteriorly extended suspensorium. Although these observations bring us no closer to establishing the significance of the notch, they do suggest that it is not simply an artefact of allometry. It is probably most economical to hypothesize that the notch in batrachosaurs (and perhaps in some temnospondyls as well) is a persistent spiracular cleft inherited from the fish condition (Smithson 1982), as Clack inferred but did not state explicitly. Such an explanation would seem less appropriate for the terrestrial *Dendrerpeton*, unless it is assumed that the spiracle was non-functional.

The absence of a tympanum in *Pholiderpeton* and *Palaeoherpeton* is also indicated by the occurrence in both genera of a large, heavily built stapes similar to that in *Greererpeton* (Clack 1983). Smithson (1982) argued that the stapes of *Greererpeton* almost certainly took no part in the transmission of airborne sound from a tympanum to the inner ear, but rather suggested that the element acted as a mechanical brace that prevented the weakly attached braincase from being pulled ventrally away from the skull roof during contraction of the hypaxial musculature. Clack (1983) in noting the firm nature of the opisthotic-skull roof contact in embolomeres considered such a support role in *Pholiderpeton* and *Palaeoherpeton* unnecessary, and instead proposed that the stapes in these genera functioned as a transmitter of low frequency vibrations to the fenestra ovalis. Research on living tetrapods shows that reception of low frequency (below 1 kHz) airborne sound can be accomplished without a tympanum. In snakes, pressure waves that pass unimpeded through the skin and muscles of the head vibrate the large quadrate and are passed through the attached stapes to the fenestra ovalis (Wever 1978). Amphisbaenids use loose facial skin to pick up vibrations, which are passed by way of an extracolumella and stapes to the fenestra ovalis (Wever 1978). A heavy stapes with a large footplate, although incapable of being driven effectively by a tympanum, actually transmits low frequency vibrations more efficiently than does a lightweight stapes. This principle is used by many living amphibians, in which the opercularis system is employed to augment reception of low-frequency vibrations by functionally increasing the surface area and mass of the footplate (Lombard & Staughton 1974). Although a variety of methods are used to receive and convey airborne sound to the stapes, as far as I am able to determine, the footplate is in all cases suspended within the fenestra ovalis by an annular ligament that allows it to vibrate freely in a piston-like or rocking motion. Without the ability of the stapes to 'float' in the fenestra ovalis, it would be, in principle, no more use in transmitting vibrations to the inner ear than any other

skull bone that makes contact with the otic capsule. The stapes of captorhinid reptiles (Heaton 1979), and probably all other primitive reptiles is sutured immovably to the lateral surface of the braincase and could not have moved in the fenestra ovalis. Extensive overlap between the footplate and lateral wall of the braincase in *Greererpeton* indicates that such movement was also impossible in that genus. Although the structure of the fenestra ovalis in *Pholidoperdon* is unknown, the great similarity in the structure of the stapes to that of *Greererpeton*, particularly the presence of a greatly expanded footplate, makes its auditory function questionable. Although the margin of the fenestra ovalis is imperfectly preserved in *Palaeoherpeton*, the preserved bone surface on the lateral aspect of the braincase dictates its maximum size, which could not have been significantly greater than that depicted in the reconstruction (Panchen 1964, figure 6). However, the footplate of the stapes as preserved in the type (Panchen 1964, figure 14; Clack 1983, figure 2) is much larger, almost twice the diameter of the reconstructed fenestra ovalis, indicating that the footplate could not have been inserted into the fenestra but must have overlapped the lateral wall of the braincase as in *Greererpeton*. Nevertheless, even if the stapes of embolomeres was incapable of moving freely in the fenestra ovalis and was therefore, in principle, no more effective in transmitting airborne sound than the tabular, it still may have transmitted some groundborne vibrations picked up by the lower jaw, although the commonly held belief that this form of hearing is important in snakes has been disproved (Wever 1978) and may not be a practical form of sound reception in any tetrapods.

As in *Greererpeton*, the wing-shaped, laterally directed plate probably rested against the pterygoid–epipterygoid complex in embolomeres, but as correctly pointed out by Clack (1983), the well-consolidated contact between the braincase and skull table made it unnecessary to hypothesize that the element functioned to prevent disarticulation of the braincase from the dermal roof. However, the lack of any sutural connection between the suspensorium and either the skull table or braincase posterior to the orbits in most batrachosaurs indicates that the ventrolaterally directed stapes may have served as a tension–compression member, damping ventrolateral–dorsomesial movements of the suspensorium during feeding, thus preventing excessive excursions of joint surfaces at the basal articulations. It should be noted that the only batrachosaurs known to possess a lightly built, potentially impedance-matching stapes (seymouriamorphs) have fused the kinetic junction.

In addition to the hypothesis that the stapes of Palaeozoic tetrapods functioned as transmitters of low-frequency vibrations, a number of different mechanical functions have been proposed in the various groups. Since none of these mechanical hypotheses closely resembles that proposed for osteolepiforms (Thomson 1969) it is difficult to know which, if any, represents the primitive tetrapod condition. However, if one accepts the plausible hypothesis that batrachosaurs represent the primitive tetrapod skull structure in which the mesokinetic junction is lost, but the kinetic line between the table and cheek is retained, then a tension–compression function of the stapes may also be primitive for tetrapods. Once the dorsal kinetic junction was lost in other tetrapod groups, the stapes became free to perform other mechanical functions, such as a braincase support in the metakinetic skull of primitive reptile (Heaton 1980) or a brace to prevent ventral movement of the braincase in primitive temnospondyls (Smithson 1982), and in some cases to serve as an impedance-matching stapes.

In summary, many of the synapomorphies used by Heaton to infer a sister-group relationship between his ‘Batrachosauria’ and reptiles and to exclude ‘anthracosaurs’ (embolomeres) from relationship with either of the above now appear to be false or equivocal. Of particular

significance is the revelation that in primitive batrachosaurs, not only is the 'otic' notch unlikely to have held a tympanum, but that in all known cases other than the derived seymouriamorphs the stapes closely resembles that of primitive temnospondyls (at least *Greererpeton* and *Dendrerpeton*) and may represent the primitive tetrapod pattern (Clack 1983). Although there is some evidence that embolomeres and seymouriamorphs, together with loxommatids and the extremely primitive *Crassigyrinus* form a monophyletic group termed the Batrachosauria (see The relationship between embolomeres and seymouriamorphs, and The affinities of *Proterogyrinus* and the interrelations of the Batrachosauria, elsewhere in this paper), the lack of any secure synapomorphies between reptiles and batrachosaurs or any other amphibian group renders amphibian-reptilian interrelations ambiguous despite recent attempts to resolve the problem (Gaffney 1979; Gardiner 1982, 1983). Two promising characters, the form of the basal articulation and the course of the vena capitis dorsalis, may be synapomorphies of batrachosaurs and reptiles, but too little is known about the distribution of these characters in primitive tetrapods to be very confident about proposing a sister-group relationship on this basis alone. Nevertheless, the Batrachosauria is the most primitive known group of amphibians, certainly showing far fewer derived characters than do temnospondyls or microsaurs and other 'lepospondyls', and in a number of features is more primitive than the enigmatic ichthyostegids. The anatomy of *Proterogyrinus*, as well as related forms such as *Eoherpeton* and *Crassigyrinus* indicate that they belong to a very conservative assemblage, the most primitive members of which structurally are not very divergent from the prototetrapod morphotype from which all known tetrapod groups can be derived.

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ABBREVIATIONS USED IN THE FIGURES

| | | | |
|----------|---|-------------|--|
| al.f. | anterolateral facet of opisthotic for articulation with tabular | f.ob. | obturator foramen |
| ang. | angular | f.m. | foramen magnum |
| ant.cor. | anterior coronoid | f.o. | fenestra ovalis |
| ant.m.f. | anterior Meckelian fenestra | hum. | humerus |
| art. | articular | i. | intermedium |
| at.ar. | atlas arch | ic. | intercentrum |
| ax. rot. | axis of rotation | icl. | interclavicle |
| b. | body of centrum | il. | ilium |
| b.art. | basal articulation | il.(po.pr.) | posterior process of ilium |
| b.o. | basioccipital | isc. | ischium |
| bsph. | basisphenoid | it. | intertemporal |
| b.tub. | basal tuber | j. | jugal |
| c.1 | 1st centrale | k.j. | kinetic junction |
| c.2 | 2nd centrale | l. | lacrimal |
| c.3 | 3rd centrale | lt. | left |
| c.4 | 4th centrale | max. | maxilla |
| cl. | clavicle | n. | nasal |
| clei. | cleithrum | n.a. | neural arch |
| cor. | coracoid | n.c. | neural canal |
| cor.t. | coronoid tooth | nt.c. | notochordal canal |
| c.r. | caudal ribs | nut.c. | nutrient canals |
| d. | dentary | op. | opisthotic |
| d.ram. | dorsal ramus of tabular horn | os. | abnormal bony growth on acetabulum |
| d.t. | distal tarsal | p. | parietal |
| ect. | ectopterygoid | p.cor. | posterior coronoid |
| eo. | exoccipital | pal. | palatine |
| epi. | epipterygoid | par. | parasphenoid |
| f. | frontal | part. | prearticular |
| fe. | fibulare | pat. | facet on exoccipital for proatlas |
| fem. | femur | pc. | pleurocentrum |
| fib. | fibula | pin. | pineal foramen |
| f.eo. | facet on opisthotic for articulation with exoccipital | pl.f. | posterolateral facet of opisthotic for articulation with |
| f.il. | foramen piercing mesial surface of ilium | pm. | tabular premaxilla |

| | | | |
|---------|------------------------------|------------|---------------------------------------|
| po. | postorbital | sa.cr. | surangular crest |
| pof. | postfrontal | sc. | scapulocoracoid |
| po.m.f. | posterior Meckelian fenestra | sn.c. | supraneural canal |
| pos. | postsplenial | soc. | supraoccipital |
| pp. | postparietal | sph. | sphenethmoid |
| pr.al. | processus alaris | sq. | squamosal |
| prf. | prefrontal | st. | supratemporal |
| pro. | pro-otic | sym. | symphysis |
| prs. | presplenial | t. | tabular |
| pt. | pterygoid | te. | tibiale |
| pt.f. | post-temporal fossa | tib. | tibia |
| psym. | parasymphyseal tusk | tr.pr.sac. | transverse process of sacral vertebra |
| pub. | pubis | v? | vomer? |
| q. | quadrate | v.c.d. | groove for vena capititis dorsalis |
| qj. | quadratojugal | v.ram. | ventral ramus of tabular horn |
| rt. | right | | |
| sa. | surangular | | |
| sac. | sacrum | | |

APPENDIX 1

Characters used in figure 39

- (1) tabular horns
- (2) two-faceted basal articulation with axis in transverse plane
- (3) opisthotics fused medially to form occipital plate (no separate supraoccipital) dorsal to the foramen magnum
- (4) pleurocentrum complete ventrally
- (5) interorbital constriction
- (6) rhomboidal orbits
- (7) loss of orbital lacrimal through dorsal migration of orbit
- (8) absence of preopercular
- (9) moderately shortened suspensorium
- (10) complete absence of kinetic junction between cheek and skull table
- (11) tabular horns reduced to small 'buttons'
- (12) preorbital vacuities
- (13) braincase with co-ossified sphenethmoid and otic-occipital portions, both with ossified rooves and sphenethmoid partitioned by bony septa
- (14) dentition on all three coronoids absent
- (15) horseshoe-shaped pleurocentrum
- (16) tabular-parietal contact
- (17) vena capititis dorsalis foramen
- (18) quadrate advanced almost to the level of the occiput
- (19) absence of lateral line canals
- (20) pustular ornamentation on skull

- (21) laterally positioned fenestra ovalis with short, broad parasphenoid
- (22) basal tubera
- (23) reduced tooth count (less than 25 maxillary teeth)
- (24) absence of parasymphysial tusk
- (25) loss of orbital lacrimal due to snout elongation
- (26) large pineal
- (27) absence of perforating post-temporal fossa (fossa bridgei)
- (28) reduction of subcircular basioccipital cotyle to lozenge-shape
- (29) reduced and ventrally deflected tabular horn
- (30) absence of naso-labial groove
- (31) squamosal forming part of dorsal border of notch
- (32) impedance-matching stapes
- (33) swollen neural arch fused to disc-shaped pleurocentrum
- (34) absence of anterior flange and presence of an ectepicondyle
- (35) absence of vomerine fangs
- (36) ventral ramus of tabular horn
- (37) large surangular crest
- (38) processus alaris of jugal contacting pterygoid
- (39) large Meckelian fenestrae
- (40) rimmed pineal and median ridge flanked on either side by depressions on the postparietals
- (41) jugal exposed at ventral margin of skull
- (42) dentition absent on coronoids two and three
- (43) intercentrum ossified dorsally to form a complete disc
- (44) dorsal suture absent on pleurocentrum
- (45) dentition absent on coronoids one and two
- (46) single large Meckelian fenestra
- (47) fenestra on squamosal-jugal suture
- (48) widely spaced, laterally facing orbits
- (49) carnivorous adaptations:
 - massive dentition and reinforced palate
 - loss of kinetic junction
 - reduced surangular crest
 - loss of processus alaris
 - dorsal nostril and reduced nasolabial groove
- (50) dorsally expanded quadrate
- (51) centrum with occluded notochordal canal
- (52) jaw deep at angle
- (53) loss of distinct ventral ramus of tabular horn
- (54) predominance of chisel-shaped teeth
- (55) long snout
- (56) elongated presacral column
- (57) intertemporal sutured to the postorbital
- (58) loss of supraneural canal