

THE BRAINCASE OF THE ANTHRACOSAUR *ARCHERIA CRASSIDISCA* WITH COMMENTS ON THE INTERRELATIONSHIPS OF PRIMITIVE TETRAPODS

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ABSTRACT. The braincase of the embolomere *Archeria crassidisca* from the Lower Permian of Texas is described, and provides much new detail about a primitive tetrapod braincase. It is a solidly ossified unit as in other embolomeres and like them has no separate dorsal ossification of the occipital arch (supraoccipital). It retains evidence of primitive braincase characters (ventral cranial and lateral otic fissures) found in the embryonic stages of recent jawed vertebrates, and seen in the adult stages of primitive fish groups. A survey of the braincases in early tetrapods shows that no taxonomic weight can be accorded to the degree to which they are ossified. Certain characters (parasphenoidal tubera for the insertion of subvertebral (hypaxial) muscles, and a median retractor pit in the basisphenoid) resemble those in *Seymouria*. The latter is also seen in the anthracosaur *Eoherpeton* and the reptile *Eocaptorhinus*, and is proposed as a shared derived character uniting a reptiliomorph ramus of tetrapods. Another character which this group also shares (true synovial basal articulation) may represent a further derived character. However, the condition of both these characters is unknown in some of the earliest tetrapods (e.g. *Crassigyrinus* and the loxommatids), and so may be primitive for all tetrapods.

ANTHRACOSAURIAN amphibians, known from the Carboniferous and Permian of Europe and North America, have generally been considered close to the ancestry of reptiles since Watson's pioneering works on Palaeozoic amphibians (Watson 1926). Consequently, members of the group have attracted much attention despite their relative rarity in the fossil record (Watson 1926; Panchen 1964, 1966, 1970, 1972a, 1975, 1977, 1980; Romer 1963; Carroll 1967; Clack 1983, 1987; Holmes 1984; Klembara 1985; Smithson 1985). However, the generally fragmentary condition of this material has made it difficult to evaluate this hypothesized relationship, and it has recently been criticized (Panchen 1972b, 1975, 1977; Heaton 1980).

The most common and by far the best preserved anthracosaur is *Archeria crassidisca* (Cope 1884), from the Texas Permian. However, despite the pivotal position in tetrapod evolution attributed to the Anthracosauria, little other than an excellent description of the appendicular skeleton (Romer 1957) has been published on *Archeria* since material pertaining to this form was described by Cope (1878, as *Cricotus heteroclitus*). The paucity of published descriptions of *Archeria* is disappointing. It is conceivable that its relatively young age (Lower Permian, in contrast with the Carboniferous ages assigned to the other North American and European genera) and apparent aquatic specializations blunted the interest of those investigators largely concerned with the reputed relationships between earlier (and presumably more primitive) anthracosaurs and reptiles.

The vertebrate braincase is a complex structure showing many characters that are potentially useful in establishing relationships. Although the braincase has been described in a few anthracosaurs (Panchen 1964, 1972a; Holmes 1984; Clack 1987), the material has been poorly preserved or incomplete, leaving serious gaps in our knowledge. Abundant, well-preserved material of *Archeria* permits a virtually complete, detailed description of the braincase that can serve as a standard for comparison with other anthracosaurs and other primitive tetrapods.

Throughout this paper, the terms 'anthracosaur' and 'Anthracosauria' are used in the sense

of Panchen (1975) to include only the Embolomeri (*sensu* Holmes 1980) plus the families Gephyrostegidae and Eoherpetontidae.

MATERIALS AND METHODS

All specimens (except one, see below) of *Archeria* referred to in this paper are from the collections of the Museum of Comparative Zoology of Harvard University, and were catalogued as *Archeria* (or '*Cricotus*'), presumably on the advice of A. S. Romer. The authors have no reason to disagree with this. There is no doubt that they all belong to the same genus, and probably to the same species, for which *crassidisca* is considered the valid name, but the taxonomy is in need of revision (see Panchen 1970 for the most recent review). The rest of the skull of this form has not been described before, though this is currently being undertaken by one of us (R. H.).

The following *Archeria* material was excavated from the Geraldine Bonebed of Archer County, Texas, over several field seasons beginning in 1939. This deposit (referred to as 'obviously a bog deposit' by Romer and Price 1940), is of Lower Admiral (Lower Permian) age, and has also yielded many specimens of *Edaphosaurus*, *Eryops*, and *Dimetrodon*. The matrix, a soft grey clay with high organic content, is easily separated from the black bone using a mounted needle. Although most specimens have suffered some compression, preservation is otherwise excellent (see Romer 1957 for details). The stratigraphy is discussed in Romer and Price (1940) and Romer (1958).

The following specimens of *Archeria* were used in this study:

MCZ 2052: Nearly complete, although slightly disturbed braincase in articulation with skull roof.

MCZ 2072: Nearly complete otic-occipital-parasphenoid complex in association with skull roof.

MCZ 2121: Parasphenoid-basisphenoid-basioccipital complex and partial sphenethmoid. A skull roof bearing the same specimen number was presumably found in association with these elements, but was apparently separated during preparation.

MCZ 6985: Isolated basisphenoid.

MCZ 8935: Isolated parasphenoid-basisphenoid complex.

Also studied:

MCZ 2505: Plaster cast of braincase (original, specimen FMNH UC 871, Field Museum of Natural History, Chicago) (Williston 1918) (Briar Creek Bonebed, Archer County, Texas. Admiral Formation, Wichita Group).

DESCRIPTION

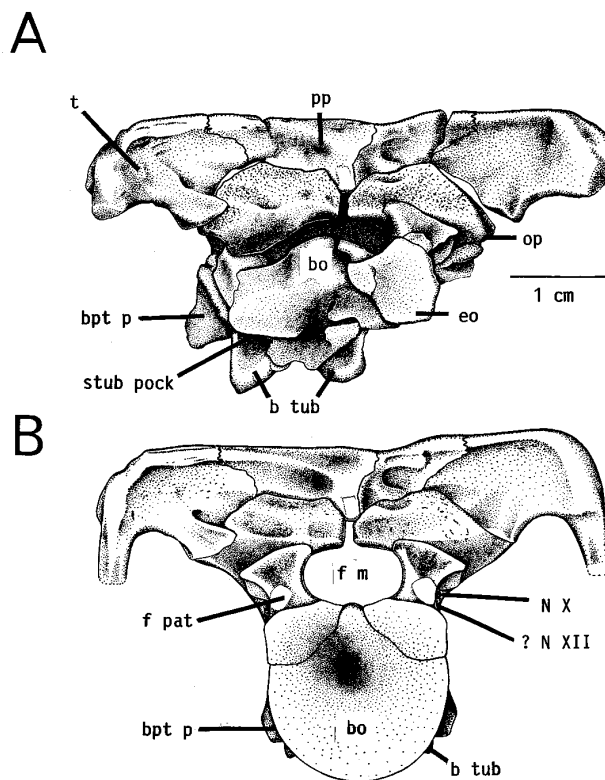
The braincase of *Archeria* is essentially similar to those of the British embolomeres in being a massively ossified structure composed of a posterior otic-occipital housing the brain and vestibular apparatus, and an anterior sphenethmoid through which the branches of the olfactory nerves passed. The co-ossified otic-occipital and sphenethmoid were firmly sutured to the underside of the dermal roofing elements throughout most of their length and as potential structural members of the skull, would have been particularly effective at resisting dorsoventral compression. Since the braincase is intimately associated with elements of the overlying dermal roof, relevant aspects of the latter will be considered here.

Associated Dermal Elements

The extensive occipital exposure of each postparietal slopes posteroventrally at an angle of 45° and reaches a maximum depth of approximately 5.5 mm below the level of the skull roof measured half-way between the midline of the skull and its contact with the tabular in MCZ 2052. Each postparietal contributes to a ventroposterior process that projects between the opisthotics (text-fig. 1). A deep pocket with slightly roughened margins marks the insertion of the epaxial musculature. The ridged margin of each of these pockets sweeps dorsolaterally from the midline, approaching the dorsal rim of the skull as it nears the postparietal-tabular suture. The ridge continues on to the tabular, where it runs parallel to the dorsal surface of the tabular as it turns posterolaterally on to the tabular horn.

Contact between the postparietal and opisthotic is continuous from the midline to the former's suture with the tabular. The occipital sheet of the postparietal is relatively thin however, at most 1 mm thick at its contact with the opisthotics. This sheet is preserved only in MCZ 2052, in which the dorsal

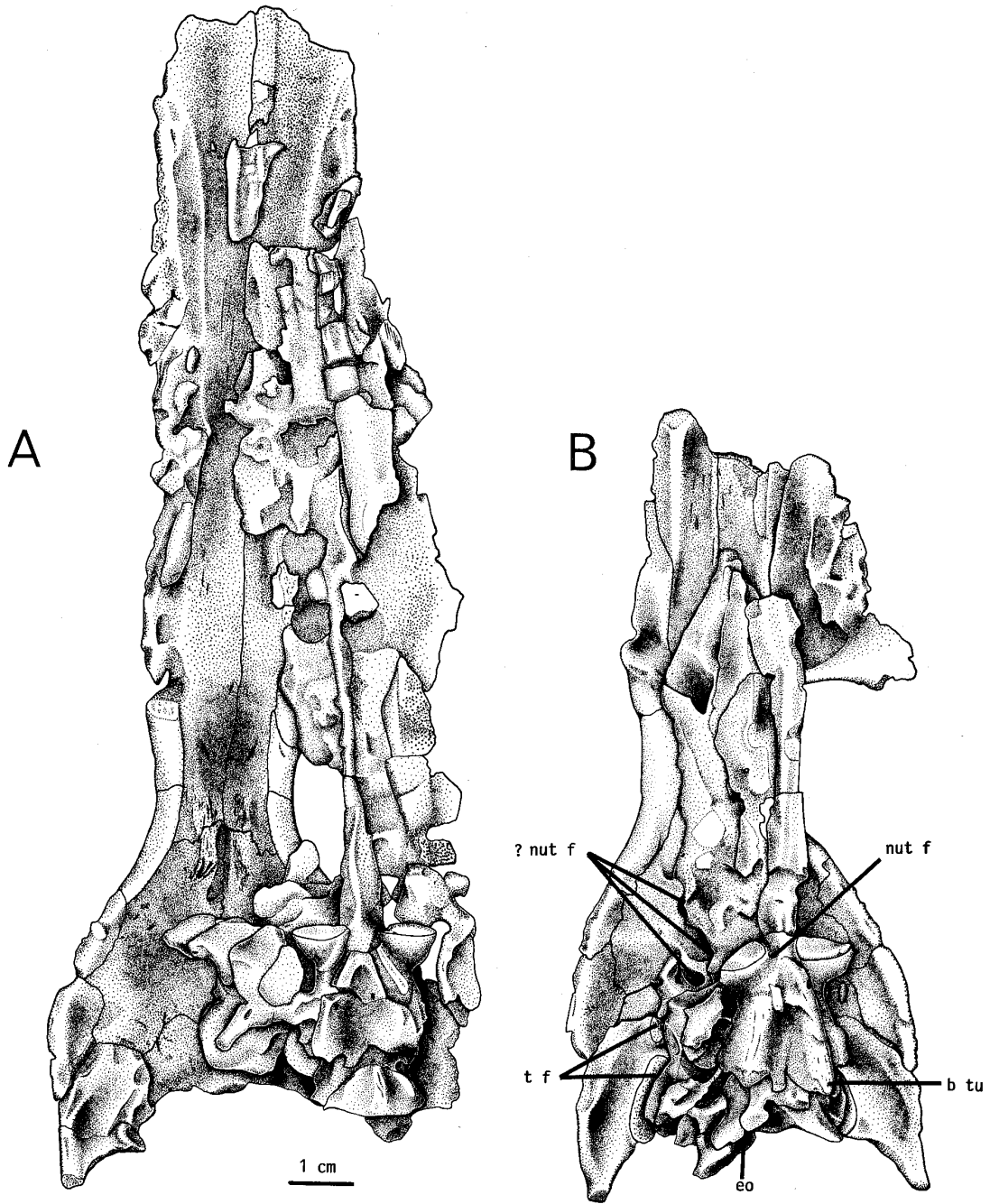
TEXT-FIG. 1. *Archeria crassidisca* (Cope). Occipital views of braincase. A, MCZ 2052. B, reconstruction.



part of the occiput is little disturbed. The postparietal-opisthotic suture is clearly not the primary area of attachment between the skull roof and otic region.

The extensive and complex contact between the tabular and opisthotic provides a firm attachment between the occipital margin of the braincase and the skull roof. As in *Palaeoherpeton* (Panchen 1964) and *Pholiderpeton* (Clack 1987), there are two separate facets on the ventral surface of the tabular for attachment of the opisthotic. In MCZ 2052 the slightly displaced right opisthotic exposes these facets (text-fig. 2B). The more posterior, ventromedially facing facet is relatively much longer than the equivalent facet in *Palaeoherpeton*. The long axis of the facet makes an angle of approximately 10° with the anteroposterior axis of the skull. The posterior border of the facet is manifest in occipital view as the long curved contact between the opisthotic and tabular (text-fig. 1). Immediately anterior to the facet is a small channel that appears to be homologous to the deep groove located lateral to the posteromedial tabular facet of *Palaeoherpeton*, *Pholiderpeton*, and *Proterogyrinus* (Holmes 1984; Smithson 1986). However, the channel, probably admitting the vena capitis dorsalis into the cranial cavity, faces laterally rather than posterolaterally.

Another much smaller facet, homologous to the anterolateral facet of *Palaeoherpeton*, *Pholiderpeton*, and *Proterogyrinus* is located anterior to the channel. However, the facet occupies a more anteromedial position. An elongate depression located on the underside of the tabular lateral to the opisthotic facets may be homologous to a similar depression in *Palaeoherpeton* identified by Panchen as the course of the stapes. This interpretation assumed the then generally accepted hypothesis that the stapes of embolomeres was directed dorsolaterally toward the 'otic notch'. This has recently been



TEXT-FIG. 2. *Archeria crassidisca* (Cope). Ventral views of braincase. A, MCZ 2072. B, MCZ 2052.

challenged (Clack 1983), and it now seems unlikely that this groove was associated with the stapes in either genus.

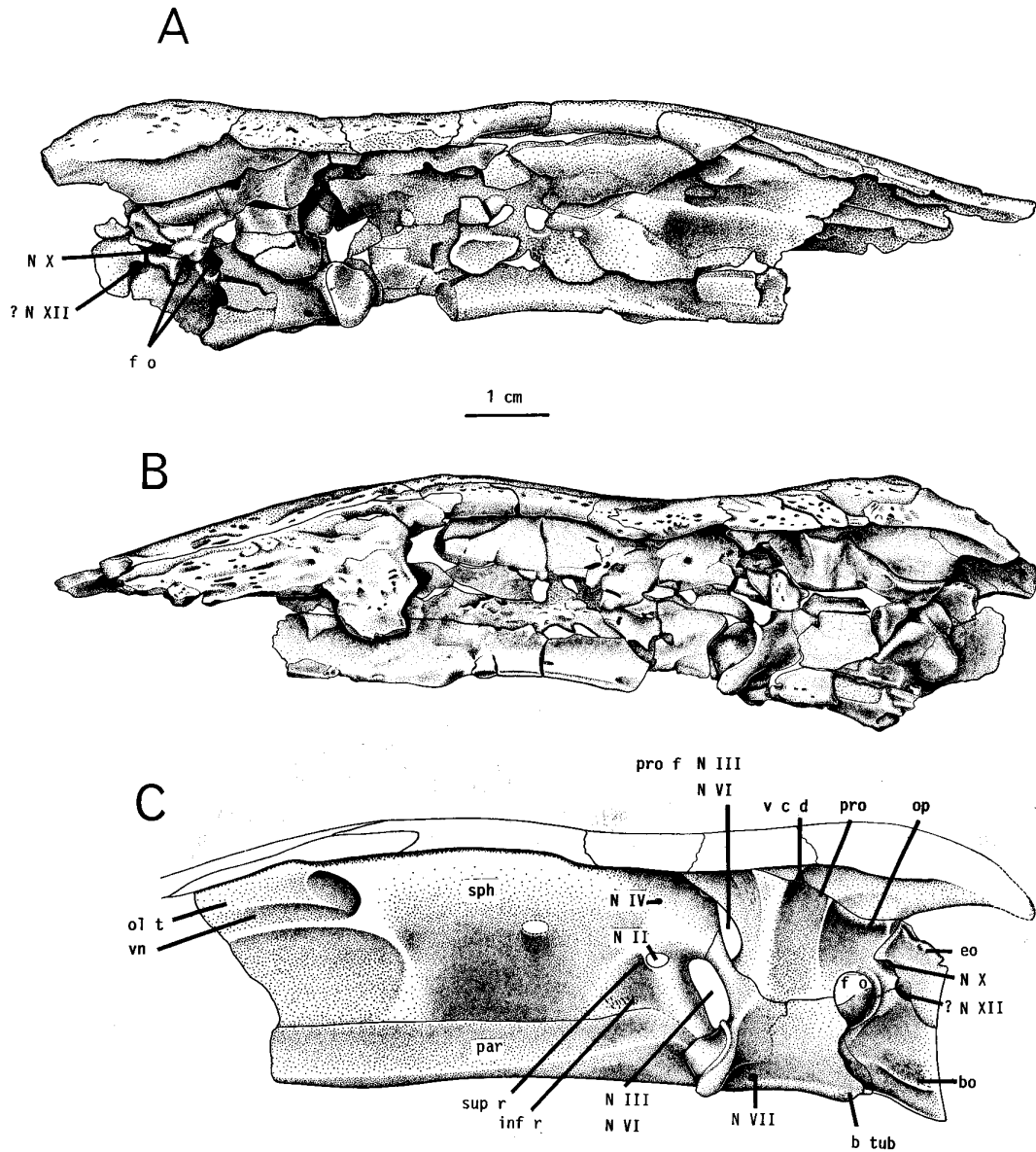
The considerable occipital exposure of the tabular begins medially at its suture with the postparietal and opisthotic. As it sweeps laterally, it turns increasingly posteriorly, and terminates as the medial surface of the tabular horn (text-fig. 1). As in other embolomeres, and unlike the condition in temnospondyls, the tabulars extend far medially, restricting the occipital exposure of the postparietals. Each tabular is separated from its corresponding postparietal by a ventromedially orientated suture, causing the tabular to be even wider ventrally than it is dorsally.

Posterior to the pineal opening, each parietal is thickened in the region of its connection with the braincase. In MCZ 2052, a series of five foramina set in pockets along the anterior portion of the lateral edge of this thickening passes into the substance of the bone. The posterior three foramina face in an anterolateral direction, and the anterior two face in a posterolateral direction (text-fig. 2B). The foramina seem too conspicuous for nutrient canals, and although their function is uncertain, Clack (1987) suggested that one might have received the columella cranii. Immediately anterior to the pineal extends a narrow excavation (2 mm wide and 14 mm long in MCZ 2072) indicating a median gap in the contact between the braincase and skull roof (text-fig. 2A) as in *Palaeoherpeton* (Panchen 1964). Lateral to this, a band of extremely rugose bone on each parietal indicates firm attachment. These bands extend anteriorly on to the frontals where they become less conspicuous and therefore less well demarcated from the gently striated surface between them.

Neurocranial elements

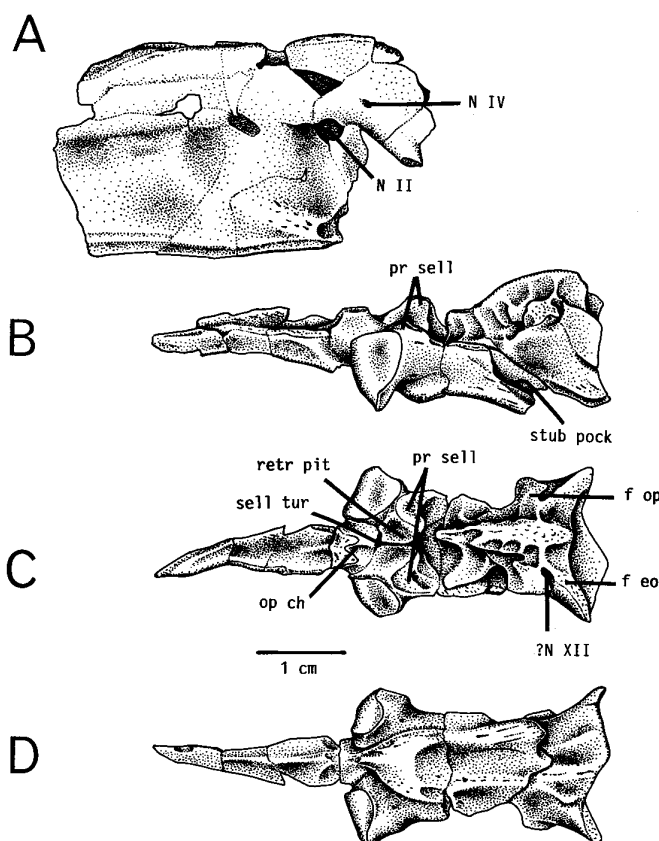
Several specimens show aspects of the braincase structure. In MCZ 2052 (text-figs. 1, 2B, 3A), it is well preserved, although it has been dorsoventrally compressed causing some damage to the lateral walls of the otic-occipital region and partial occlusion of the foramen magnum. The sphenethmoid region is essentially complete, although similarly compressed and having its ventral portion rotated to the left about the longitudinal axis passing between the braincase and skull roof (text-figs. 2 and 3). Except for minor dislocations of the opisthotic and tabulars and narrow gaps between dermal and endochondral elements, the articulating facets of the braincase are still closely associated with those of the skull roof, to which they must have been firmly attached in life. In MCZ 2072 (text-fig. 2A) the otic-occipital region, although more disrupted than in MCZ 2052, is essentially complete except for the exoccipitals. The sphenethmoid region is poorly preserved. In MCZ 2121 the ventral part of the otic-occipital region and the back of the sphenethmoid are preserved (text-fig. 4). Additional information on the structure of the parasphenoid and basisphenoid is obtained from MCZ 6985 and 8935.

Occipital elements. The unfinished occipital surface of the massive opisthotic slopes posteroventrally at an angle of about 37° from the frontal plane. As preserved, the opisthotics are separated at the midline by the midventral projection formed by the two postparietals, and ventral to this by a gap of about 1 mm that was probably filled with cartilage in life. This 'widow's peak' of the postparietals also occurs in *Proterogyrinus*, *Palaeoherpeton*, and *Pholiderpeton*, and may be characteristic of embolomeres. *Pholiderpeton* has recently been shown to be the senior synonym of *Eogyrinus* (Clack 1987). Dorsally, each opisthotic is attached to the postparietal by a dorsolaterally orientated suture. The suture between the opisthotic and the tabular curves smoothly ventrally as it passes posterolaterally. At the posteroventral termination of this suture the tabular hooks medially around the posterolateral corner of the opisthotic. In no specimen is the opisthotic-tabular suture fused. Ventrally, each opisthotic forms part of the curved dorsal rim of the foramen magnum; lateral to this each bears a rough triangular facet for articulation with the exoccipital. Poor preservation of the ventrolateral wall of the opisthotics in all specimens makes it impossible to determine whether *Archeria* possessed a digitiform process. This process, described in *Palaeoherpeton* (Panchen 1964), *Anthracosaurus* (Panchen 1977), and *Pholiderpeton* (Clack 1987), was originally considered to be part of an interlocking mechanism between the tabular and opisthotic (Panchen 1964). Recent evidence indicates that the process did not contact the tabular, but may have contacted the exoccipital (Clack 1987), although in all cases, crushing makes it difficult to be sure. A similar, probably homologous



TEXT-FIG. 3. *Archeria crassidisca* (Cope). Lateral views of braincase. A, MCZ 2052, right lateral view. B, MCZ 2052, left lateral view; C, reconstruction.

process is present in an undistorted opisthotic of *Proterogyrinus scheeli*. It clearly does not make contact with either of the above bones, but may have articulated with the dorsal process of the stapes (Holmes 1984). This may be a plausible functional interpretation of the digitiform process in other embolomeres as well.



TEXT-FIG. 4. *Archeria crassidisca* (Cope), MCZ 2121. A, B, left lateral view of braincase, sphenethmoid (A) displaced dorsally to expose matching surfaces with cultriform process. C, dorsal view of parasphenoid-basisphenoid-basioccipital. D, ventral view of parasphenoid-basisphenoid-basioccipital.

There is no evidence for the existence of a separate supraoccipital. The position which it occupies in early reptiles is occupied by the posterodorsal portion of the opisthotics. This agrees with the condition in other anthracosaurs such as *Eoherpeton* (Panchen 1980; Smithson 1985), *Anthracosaurus* (Panchen 1977), *Pholiderpeton* (Clack 1987), and also *Seymouria* (White 1939). Panchen now believes (pers. comm.) that the suture between the 'supraoccipital' and the postparietals of *Palaeoherpeton* (Panchen 1964) is an artefact of preservation, and that the supraoccipital did not exist as a separate ossification. Although *Gephyrostegus* has been reconstructed with a supraoccipital (Carroll 1970), it is unlikely that it possessed this element (Holmes 1984). As in other anthracosaurs, *Archeria* is derived in having lost the fossa bridgei.

The lightly built exoccipital is expanded at both ends. Its dorsal expansion bears a triangular facet for attachment to the opisthotic. The exoccipital does not extend to the dermal skull roof. This is a primitive feature shared by all batrachosaurs (*sensu* Panchen 1975). The medial concave surface forms the lateral wall of the foramen magnum. The lateral surface of the exoccipital is also concave, giving the bone a distinct 'waist'. There appears to be a convex facet for articulation with the proatlas arch in this region, but broken bone surface makes it impossible to determine detailed structure. The ventral expansion of the exoccipital bears a posteromedially facing facet that contributes to the dorsolateral

part of the occipital condyle. (As in most Palaeozoic tetrapods, it is technically a cotyle, but as it is universally referred to as a 'condyle' we will not break with tradition.)

The basioccipital is roughly cone-shaped with a dorsally offset apex. Viewed dorsally, there is a wing-shaped process on either side of the apex (text-fig. 4C). Unlike advanced temnospondyl amphibians such as *Eryops*, but like the primitive loxomatids and other batrachosaurs as far as known, the basioccipital forms the bulk of the deeply concave occipital condyle. The notochordal pit is placed so that it is centrally located in the complete condyle. Dorsally, the basioccipital bears two dorsolaterally facing concavities to receive the ventral expansions of the exoccipitals. Immediately anterior to each facet, a deep furrow floored by finished bone can be seen to terminate medially in a pit. The channel may represent the course of the hypoglossal nerve (see below), although the nerve clearly would have had to pierce the cranial cavity dorsal to the pit. Anterior to the channel is an ill-defined facet for the opisthotic.

The unfinished dorsal surface is extremely complex. A massive median ridge runs from the occipital surface forward, its crest horizontal at first, and then sweeps anteroventrally to an attenuated termination just posterior to the dorsum sellae. The vertical walls of the central ridge bear numerous irregular transverse ridges and grooves which drop down to the level of the floor of the cranial cavity. These ridges are also seen in *Palaeoherpeton*. In ventral view the anterior portion of the basioccipital is unfinished and bears deep longitudinal grooves for suture with the parasphenoid. Posteriorly, the finished surface bears three longitudinal striated ridges (text-figs. 2 and 6). A median ridge is continuous with that on the parasphenoid. Two ventrolateral ridges, in line with those forming the basal tubera, terminate in blunt points just anterior to the condylar rim. Laterally, the basioccipital contributes to the posteroventral margin of the fenestra ovalis. The rim is sharply raised, particularly ventrally. At the base of this rim the bone is pierced by a small nutrient foramen.

Other aspects of the otic-occipital region. Both otic capsules, still associated with their corresponding tabulars, are well preserved in MCZ 2052 (text-fig. 1). Although the braincase has undergone dorsoventral compression, forcing the parasphenoid-basisphenoid-basioccipital complex upward relative to the skull roof and causing considerable damage to the ventral portions of the otic capsules in the region of the fenestra ovalis, restoration of this area is possible with little chance of serious error (text-fig. 3C). Between the two dorsal facets for the reception of the attachment surfaces on the tabular is a shallow notch which, in conjunction with the previously described channel between the anterior and posterior articular surfaces of the tabular, forms a small foramen passing into the dorsal cranial cavity. The foramen, described also in *Palaeoherpeton* (Panchen 1964), *Proterogyrinus scheeli* (Holmes 1984), and *Seymouria* (Holmes 1984), was identified by Panchen (1964) as the passage for the vena capitis lateralis, but based on comparison with living vertebrates, more likely admitted the vena capitis dorsalis into the cranial cavity (Holmes 1984). However, in *Archeria* the foramen faces more laterally than in any of the above genera because of a reorientation of the facets of the double tabular-opisthotic contact.

The region of the fenestra ovalis is disturbed, but can be restored using information from both sides of MCZ 2052. Most of the posterodorsal part of its margin, born by the opisthotic, is preserved on both sides, although in both cases that section of the bone is dislocated. On the left side, that part of the opisthotic bearing the rim has broken away from the main body during dorsoventral compression of the braincase and now rests in the fenestra (text-fig. 3B). The ventral part of the left otic capsule (formed from the prootic with possibly some contribution from the opisthotic posteriorly) has been sheared off and pushed into the brain cavity, but is otherwise intact. Its unfinished surface bears the poorly defined anterior margin of the fenestra. The fenestra clearly perforated the otic capsule. Watson (1926) described an unperforated 'pseudo-fenestra ovalis' in '*Palaeogyrinus*' (= *Palaeoherpeton* Panchen, 1970) and *Pholiderpeton*, and argued that this represented a primitive tetrapod condition. Reinterpretation of the specimens (Panchen 1964) reveals that the fenestra, as in *Archeria* actually perforated the capsule wall.

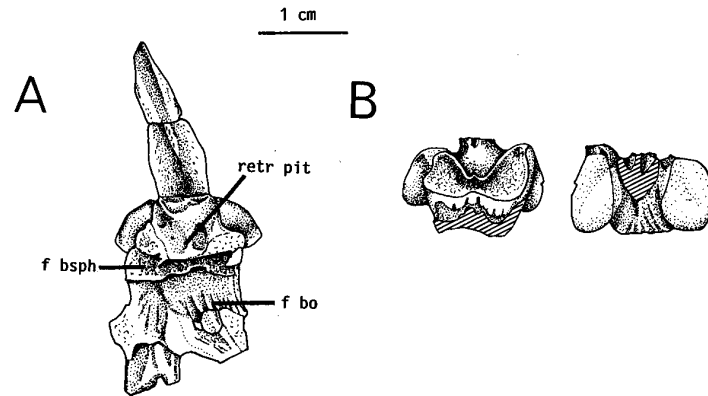
The vagus foramen (X), passing between the exoccipital and posteroventral extension of the opisthotic, is clearly visible. Ventral to this, an embayment of the exoccipital at its common

intersection with the opisthotic and basioccipital probably marks the passage of the hypoglossal nerve (text-fig. 3A). A deep furrow on the dorsal surface of the basioccipital (see above) may have served as the floor of this foramen. As far as it is known in other Palaeozoic tetrapods, this foramen pierces the body of the exoccipital. However, in the presumed ancestral (osteolepiform) condition where the occipital bones cannot be recognized as separate ossifications, branches of the hypoglossal nerve exit through foramina in the lateral wall of the occipital region ventral and posterior to the vagus foramen (Romer 1937; Jarvik 1954), in a position roughly equivalent to the foramen in *Archeria*.

The basisphenoid and parasphenoid. The basipterygoid processes of the basisphenoid are well preserved in MCZ 2052, 2072, and 2121, leaving no doubt as to their morphology. The articular surfaces are not saddle-shaped as they are shown in the restorations of *Palaeoherpeton* and '*Eogyrinus*' (Panchen 1964, 1972a) but, as in *Proterogyrinus scheeli* and *Pholiderpeton* (Clack 1987) bear two facets, one anterodorsal in orientation, the other anteroventral. The planes are not separated by a sharp ridge as in loxomatids (Beaumont 1977), but round gently into one another. In MCZ 2121 and 6985, the junction forms a gently convex profile, although in a braincase described by Williston (1918), it is somewhat concave. The anteroventral face is the smaller, forming the lower third of a circle, and has a convex surface. The anterodorsal face is approximately triangular, the longest side formed anteriorly where the two faces of the articular surface meet. The surface forms a concave depression posteriorly, where it reaches upwards almost to the base of the processus sellaris, but becomes convex anteriorly where it meets the junction with the anteroventral face. In anterior view, the junction between the two faces slopes down from the braincase at an angle of about 45°, while in lateral view it slopes posteriorly at an angle of about 23°. These angles, however, are not consistent among other braincase specimens, for example in MCZ 2052 and 2072 in which they are smaller. The articular surface is well preserved in several specimens and is finely sculptured in a way suggestive of a synovial joint. It is clearly differentiated from the smooth periosteal bone surrounding it. As in *Proterogyrinus scheeli* the basal articulation might have allowed ventrolateral movement of the suspensorium along a transverse axis (inclined 23° from the frontal plane in *Archeria*), or perhaps slight rotation about this axis, but would have precluded rotation around a dorsoventral axis (see also Clack 1987).

Dorsal to the bases of the basipterygoid processes the basisphenoid on each side sends a stout, curved process anterodorsally to attach to the sphenethmoid. This process, derived from the pila antotica and termed the processus sellaris in *Eocaptorhinus* (Heaton 1979), is the thickened anterolateral margin of the dorsum sellae, which separates the cavum cranii from the sella turcica. Dorsally, the processus sellaris forms the anteroventral margin of the prootic foramen, and ventrally forms the anteroventral margin of an elongated foramen, here called the interorbital fenestra, that probably marks the exit of nerves III and VI (see below). A more anterior pair of processes of the basipterygoid, no doubt derived from the embryonic pila metoptica, form part of the anterior margin of the latter foramen, and meet the sphenethmoid more anteriorly. The position of the suture is not visible. On the dorsal surface of the basisphenoid between the bases of these processes is a median longitudinal groove that was occupied in life by either the pituitary body or the optic chiasma. Between the bases of the processus sellares and ventral to the sella turcica is a well-developed median retractor pit for the origins of the retractor bulbi and bursalis muscles as described in *Eoherpeton* (Smithson, 1985) and the reptile *Eocaptorhinus* (Heaton 1979).

The parasphenoid sheaths the external surface of the basisphenoid and the anterior portion of the basioccipital. The basal plate is unusually short, leaving a large expanse of basioccipital exposed posteriorly. The parasphenoid and basisphenoid are indistinguishably fused except dorsally, where a distinct suture can be seen immediately posterior to the bases of the processus sellares in MCZ 2121 and 6985 (text-figs. 4c and 5b). In MCZ 8935 (text-fig. 5A), an isolated parasphenoid in which all but the anterior part of the basisphenoid has been lost, the well-defined rugose facet for the posterior part of the basisphenoid is clearly exposed. The basioccipital is entirely absent, revealing its extensive, heavily fluted attachment area. Between the two facets is a strip of finished bone surface, indicating that the basioccipital and basisphenoid did not co-ossify in adult *Archeria*, and the persistent ventral fissure of the endochondral braincase was closed only by the parasphenoid.

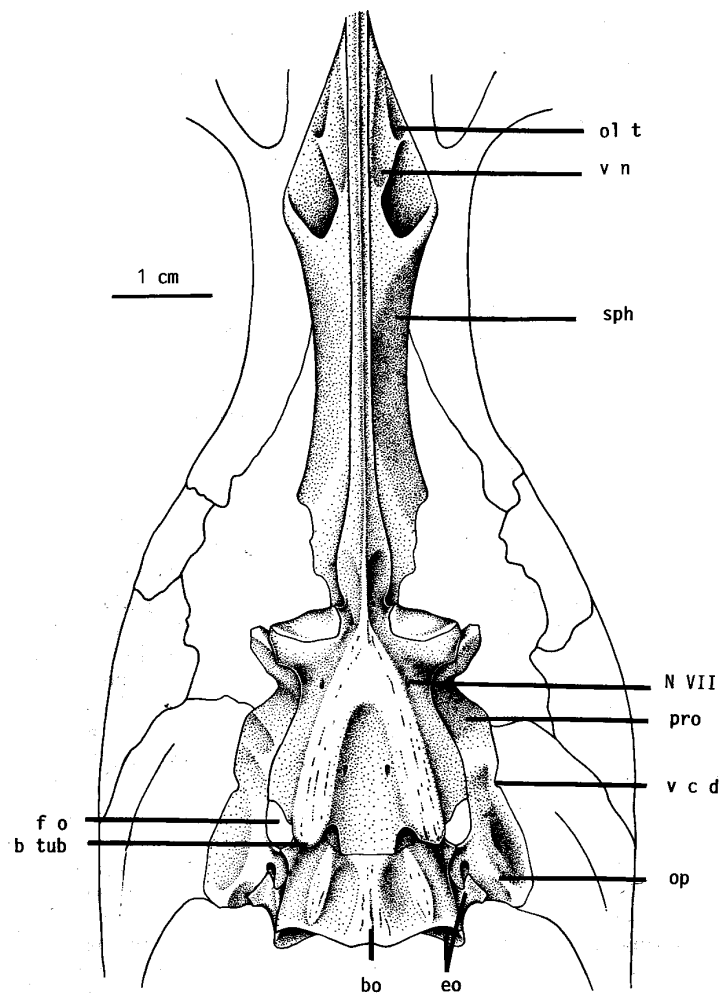


TEXT-FIG. 5. *Archeria crassidisca* (Cope). A, MCZ 8935, dorsal view of parasphenoid showing basisphenoid and basioccipital articular facets. B, MCZ 6985, posterior and anterior views of basisphenoid.

During embryological development the braincase is formed first by chondrification of anterior trabecular and posterior basal plates. These fuse in many cases to form a complete floor to the braincase, for example in elasmobranchs, dipnoans, and modern amphibians. However, in other gnathostomes, these elements remain separate, joined ventrally only by the dermal parasphenoid (Goodrich 1930). Although it remains possible that the braincase floor of *Archeria* was completed by cartilage, it seems that the ossifications reflect the embryological gap between the anterior and posterior elements of the braincase. Such a gap is seen in fossil gnathostomes such as acanthodians (Miles 1973) and palaeoniscids (Gardiner 1973), where it is known as the ventral otic or ventral cranial fissure. An unossified gap in this position is recorded by Romer and Witter in *Edops* (1942), who note that it is characteristic of skulls as far removed as crossopterygians and pelycosaurs. This condition also occurs in *Captorhinus* (Price 1935), *Eocaptorhinus* (Heaton 1979), and *Procolophon* (Carroll and Lindsay 1985). A ventral otic fissure is also noted by Jarvik in *Eusthenopteron* (1954, 1980), though whether this is strictly homologous with that of palaeoniscids is doubted by Gardiner and Bartram (1977). They regard the ventral part of the intracranial joint of rhipidistians to be the homologue of the ventral otic fissure of palaeoniscids.

Laterally, the parasphenoid sheaths the posterior part of the basisphenoid and anterior part of the basioccipital, and participates in the anteroventral margin of the fenestra ovalis. Near the ventral margin of the lateral surface, immediately posterior to the basipterygoid process is a small foramen for the passage of the palatine branch of the seventh cranial nerve.

The triangular basal plate of the parasphenoid (text-fig. 6) is remarkably *Seymouria*-like in some of its features. Its strongly raised ventrolateral margins, bearing longitudinal striations, diverge posteriorly from their common origin between the basipterygoid processes as in all embolomeres. Posteriorly, each ridge terminates in a prominent, posteroventrally projecting 'basal tuber', a feature generally considered to be diagnostic of seymouriamorphs. Unlike *Seymouria*, however, the rugose terminations of the 'basal tubera' are well ossified. Anterodorsal to each tuber is a deep, conical pocket (text-fig. 1) whose anteriorly directed apex reaches almost to the level of the basipterygoid process. Although the disarticulated braincase of *Proterogyrinus scheeli* is less well preserved, the raised ventrolateral margins of the parasphenoid diverge from the basioccipital (Holmes 1984), indicating the presence of similar pockets. *Pholiderpeton* (Clack 1987) is similar, but in other embolomeres preservation is too poor to establish the morphology of this region. In MCZ 2121 the right basal tuber and ventral wall of its associated pocket have been broken away, showing clearly that the parasphenoid sheathed the ventrolateral wall of the basioccipital in this area and therefore completely



TEXT-FIG. 6. *Archeria crassidisca* (Cope). Reconstruction of braincase, ventral view.

encased the supratuberal pocket (text-fig. 4). The opisthotic does not contribute to the wall of the pocket, as it does in *Seymouria* (White 1939), making the homologies of the pocket less certain. The parasphenoid terminates posteriorly in a blunt, median projection of variable form (compare text-figs. 2 and 4), again approaching the structure in *Seymouria*.

Between the diverging ridges of the basal plate is a central depression bearing a pair of foramina identified by Panchen (1964) as channels for minor branches of the internal carotid in *Palaeoherpeton*. As in *Palaeoherpeton*, there is a distinct groove passing around the base of the basipterygoid processes for the passage of the internal carotid and the palatine branch of the seventh cranial nerve. A foramen, at first thought to be the carotid foramen, pierces the base of the right basipterygoid process in MCZ 2052 (text-fig. 2B). However, although the corresponding area of the left process is well preserved, no

foramen could be identified, nor could it be seen in MCZ 2072 or 2121. This variable occurrence indicates that it was a nutrient foramen rather than for a major artery and that the carotid passed with the nerve around the front of the base of the process and then posterodorsally into the cavum cranii, as in *Pholiderpeton* (Clack 1987). Unlike *Eryops*, however, the artery did not pass through its own foramen in the floor of the sella turcica, but must have passed through the ventral part of the large foramen for the retractor bulbi and cranial nerves III and VI. Apart from those reported by Panchen (1972a) in the lectotype of '*Eogyrinus*', no carotid foramina have been described in anthracosaurs, seymouriamorphs, or reptiles.

The cultriform process, V-shaped in cross-section, is high and narrow. It expands laterally immediately anterior to the basiptyergoid articulations. Ventrally, it bears an acuminate ridge that begins posteriorly at the junction of the two ridges on the body of the parasphenoid, passes forward between the bases of the basiptyergoid processes and on to the cultriform itself. Anterior to the basiptyergoid process is a distinct depression on each lateral surface that is confluent with the carotid groove. Its significance is unknown, but it may have provided an area of attachment for eye muscles. The dorsal surface of the cultriform process exhibits striations except for an area of about 6 mm in length immediately in front of the basiptyergoid processes where the sphenethmoid does not make contact with the parasphenoid. This area is occupied by two pockets of uncertain significance separated by a median ridge (text-figs. 4B and 5A). Although these pockets may have contained the anterior foramen for the internal carotid as in *Eocaptorhinus*, poor bone surface makes this uncertain. The cultriform process is incomplete anteriorly in all specimens.

Sphenethmoid. An essentially complete although crushed sphenethmoid is preserved in MCZ 2052 (text-figs. 2B and 3). Additional information is obtained from MCZ 2121 (text-fig. 4). Both specimens are unitary structures rather than being composed of a dorsal ossification bearing lateral tectal processes and a ventral ossification as described in *Palaeoherpeton* (Panchen 1964) and *Pholiderpeton* (Clack 1987). The sphenethmoid of *Archeria* forms a thin interorbital septum ventrally, and expands dorsally to accommodate the forebrain and olfactory tracts.

Posteriorly, the sphenethmoid forms the anterior walls of the prootic foramen and the more ventral interorbital fenestra. It makes contact with the basisphenoid at two points: dorsally between the two foramina where it fuses with the processi sellares and ventrally below the interorbital fenestra. Immediately anterior to the ventral foramen, a distinct swelling in the sphenethmoid wall indicates the presence of a laterally compressed channel at the midline that carried the optic (II) nerves from the optic chiasma anterodorsally through the sphenethmoid to an optic foramen on each lateral surface (text-figs. 3 and 4A). Panchen (1972a) described in the same position a thickening of the interorbital septum in '*Eogyrinus*' that is probably evidence for the presence of this channel. A depression immediately anterior to the optic foramen probably marks the origin of the anterior rectus, and more ventrally an elongated roughened area provided attachment sites for the inferior and posterior recti muscles. There is no evidence for the origin of the superior rectus, but it must have attached to the sphenethmoid dorsal to the optic foramen.

Archeria is unlike *Palaeoherpeton* and more like *Pholiderpeton* in having a separate foramen for nerve II. It is impossible to determine with certainty whether nerve III existed independently as in *Pholiderpeton* or with nerve VI as in *Palaeoherpeton*, since all specimens are crushed or otherwise poorly preserved in the expected position of the foramen. However, since no foramen borders can be identified in any of the specimens, it is assumed that nerve III left the cavum cranii through a common opening with nerve VI. About 6 mm directly dorsal to the foramen for nerve II is a small foramen for the passage of nerve IV.

Ventrally, the sphenethmoid thickens slightly and is bevelled to fit into the V-shaped trough of the cultriform process, to which it is firmly attached except for the posterior 6 mm.

Anterior to the cavum cranii proper, the dorsal expansion of the sphenethmoid contained the olfactory tracts and vomeronasal nerves. Unlike *Palaeoherpeton*, in which Panchen (1964) interpreted two pairs of longitudinal canals within the sphenethmoid, the equivalent canal in *Archeria* has no ossified divisions. MCZ 2121 shows a median ridge on the floor of the canal, suggesting that a

membranous partition divided the cavity into bilateral halves, but unlike *Palaeoherpeton*, there is no evidence that each was subdivided into separate channels for an olfactory tract and a vomeronasal nerve. In *Pholiderpeton* (Clack 1987) a single midline septum divides the sphenethmoid cavity anteriorly. An undivided condition is seen in loxommatids (Beaumont 1977). However, as in the latter group, the shape of the anterior opening of the canal marks the separate paths of the nerve and nerve tract. A distinct horizontal channel passes anteriorly across the lateral surface of the sphenethmoid from the ventral part of the opening indicating the probable course of the vomeronasal nerve, while the anterolaterally facing dorsal portion provided passage for the olfactory tract. This is in agreement with the spatial relationship between these two nerves in *Eryops* (Sawin 1941). Unlike *Pholiderpeton* and *Palaeoherpeton*, there is no evidence for the passage of the profundus branch of the fifth nerve. The sphenethmoid thins anteriorly and terminates in an unfinished margin about 15 mm anterior to the foramina for nerve I.

Midway between the foramina for nerves I and II the interorbital septum is very thin and is perforated immediately below the longitudinal canal in all specimens showing this area. However, the bone surface is always broken and it is not possible to confirm with any certainty the presence of a fenestra to allow communication of orbital blood sinuses as in the lectotype of '*Eogyrinus*'.

DISCUSSION

Degree of braincase ossification

The highly ossified, unitary braincase of the type often found in embolomeres, temnospondyls such as *Edops* (Romer and Witter 1942) and *Eryops* (Sawin 1941), and the loxommatids has long been considered a primitive feature of early tetrapods. This is largely because primitive members of all known fish groups, including the osteolepiforms most commonly considered to be 'ancestral' to tetrapods, also have highly ossified braincases. The earliest and in many ways most primitive known tetrapod *Ichthyostega* is also interpreted in this way (Jarvik 1952). Since the first described temnospondyls, anthracosaurs, and loxommatids all had similarly highly ossified, sutureless braincases, it was assumed to be a universal condition in the 'Labyrinthodontia' (Romer 1947). It was considered to be a plesiomorphic trait inherited directly from the fish condition (Heaton 1980). As our knowledge of Palaeozoic tetrapods has increased, it has become clear that this picture is not entirely accurate.

Some members of a wide variety of distantly related groups such as anthracosaurs (Holmes 1984; Smithson 1985), temnospondyls (Smithson 1982), and microsaur (Carroll and Gaskill 1978) possess less well-ossified braincases in which the otic-occipital and sphenethmoid regions are separated by a distinct gap, in a manner at least superficially resembling that in reptiles such as the early *Eocaptorhinus* (Heaton 1979) and many reptiliomorph 'amphibians' (Heaton 1980). This prompted Holmes (1984) to suggest that the poorly ossified condition may be primitive for tetrapods (at least above the ichthyostegid level) and that the highly ossified structures seen in later members of most early tetrapod groups is convergent. This interpretation was put forward not only to account for the widespread occurrence of this 'reptiliomorph' braincase in Palaeozoic tetrapods, but also to answer Heaton's (1980) assertion that the reptilian braincase could not have been derived from the highly ossified, unitary structure he assumed to be characteristic of all 'labyrinthodonts'. Holmes pointed out that some of these primitive tetrapods exhibited a braincase structure much more similar to that of reptiles.

This approach was probably overly simplistic, however. Other than being less well ossified, the braincase anatomy of these forms was probably not significantly different from that of their better ossified relatives. Although it is still possible that there were consistent phylogenetic trends in the degree of ossification of the braincase among different lineages of Palaeozoic tetrapods, functional and/or structural considerations were also likely to have been important as determining factors. Failure to ossify the braincase is found most commonly in animals which are small or in those which are aquatic, in particular flat-headed forms. In these cases, the support function of the braincase would

have been less important. Thus, poorly ossified braincases are seen in the small temnospondyls *Dendroherpeton* (Carroll 1967) and *Tersomius* (Carroll 1964), aquatic temnospondyls such as *Dvinosaurus* (Bystrow 1938), the metoposaurs (Wilson 1941), the colosteid *Greerherpeton* (Smithson 1982), the small anthracosaur *Eoherpeton* (Smithson 1985), the seymouriamorph *Seymouria* (White 1939), and the early reptile *Eocaptorhinus* (Heaton 1979). Full ossification is achieved (or maintained) in large-skulled animals such as loxommatids, *Edops*, *Eryops*, and eogyrinids.

Unfortunately, these correlations are not entirely consistent. Although the embolomeres *Proterogyrinus*, *Palaeoherpeton*, and *Archeria* are all of moderate size (their skulls, measured from the posterior tip of the postparietal to the tip of the snout are approximately 110, 150, and 170 mm respectively), both *Palaeoherpeton* and *Archeria* show full ossification while in *Proterogyrinus* it is very incomplete. Of the three, *Proterogyrinus* is the smallest, but is less conspicuously adapted to an aquatic environment. Nevertheless, the ossified portions in *Proterogyrinus* follow the basic embolomere pattern, and there is no evidence from the articulating surfaces of the dermatocranium that this was not also true of the unpreserved (cartilaginous) portions. The unitary braincase of later embolomeres could easily have been derived from such a structure by developing (?redeveloping) the potential for complete ossification of the cartilaginous regions.

In contrast, the more derived tetrapod groups such as seymouriamorphs and reptiles appear to have lost the potential for full ossification. Why this should have occurred is unknown, but the reduced ossification and retention of distinct sutures between elements is reminiscent of the condition in more derived actinopterygians. It is generally agreed that the primitive actinopterygian braincase was a fully ossified, sutureless structure (Patterson 1975; Gardiner 1984). Since this is also the case for all well-known primitive sarcopterygians, it may well be a primitive osteichthyan character. In more advanced actinopterygian groups, braincase ossification is reduced, and sutures tend not to co-ossify, permitting continuous growth. The same trend is repeated in actinistians and dipnoans. It could have occurred in tetrapods as a consequence of small size or aquatic adaptations.

If very small size was associated with the transition from amphibian to reptilian status as Carroll (1970) has suggested, it might have been possible in principle to derive the reptilian-type braincase from the poorly ossified structure of a small anthracosaur despite Heaton's (1980) arguments to the contrary. Nevertheless, the braincase of reptiles and anthracosaurs show no undisputed synapomorphies (but see below) and a few apparent apomorphies of the latter make such a derivation problematic (Holmes 1984).

The variability of braincase ossification not only within monophyletic groups but also across a broad range of primitive tetrapod groups indicate that it is unreliable as a taxonomic character, with the polarity of the degree of ossification not determinable. If the potential for full ossification is primitive, its appearance cannot be used to define any tetrapod group. A group with poor ossification of the braincase (e.g. reptiles) could still have been derived from a group with a primitive, highly ossified braincase. If full ossification is derived rather than primitive, it probably arose for structural reasons and therefore could quite possibly have convergent origins in different groups.

Fate of the embryonic braincase fissures, and parasphenoid development

Embolomeres, of which the best preserved braincases are those of *Archeria*, retain clear evidence of the primitive lateral otic (embryonic metotic) and ventral cranial fissures. The dorsal part of the lateral otic fissure is represented in the large foramina for nerves X and XII between the exoccipital and opisthotic, and in the weak association of the exoccipital with the otic capsule. The connection is made only by a cartilage-lined facet and the exoccipitals are frequently found detached from the skull. The condition is surely primitive but is retained in other early tetrapods including loxommatids and *Seymouria*. The primitive condition for actinopterygians and presumably also for osteichthyans in general is also to have the lateral otic fissure perichondrally lined (Patterson 1975). In later actinopterygians the fissure was either cartilage-filled or completely obliterated. In some, the dorsal part of the occipital arch became incorporated into the otic capsules, in a way analogous to that seen in temnospondyls. In reptiles it is the supraoccipital which serves this purpose, assuming the supraoccipital to be a derivative of the occipital arch. In *Eocaptorhinus* the junction between the

exoccipital and opisthotic was still of the 'articular' kind, with a cartilage-finished surface as seen in embolomeres (Heaton 1979).

The more ventral parts of the lateral otic fissure are represented by the weak ossification between the otic capsule and the basioccipital, which results in the frequent disruption of the embolomere braincase along this line. The margins of the fenestra ovalis in the same region are frequently damaged in consequence.

The ventral cranial fissure is represented by the gap described above between the basisphenoid and basioccipital. The same region is often poorly ossified in early tetrapods showing that the ventral cranial fissure is only sealed in places by the backwards growth of the parasphenoid. An analogous situation is found in actinopterygians. Here, the position of the fissure shifts backwards as a result of the increase in area for the origin of the eye muscles, the myodome (Patterson 1975; Gardiner and Bartram 1977). The parasphenoid grows backwards to cover the fissure. Clearly in tetrapods the condition has arisen for quite different reasons.

Ichthyostega is notable for a number of unusual characters one of which is that the backwards growth of the parasphenoid had not occurred, thus the ventral cranial fissure was still exposed. However, in all other known tetrapods there has been some sealing of this fissure; it must, therefore, have been subject to a strong selective pressure to do so rapidly.

It is possible that sealing of the fissure in primitive tetrapods was partly a response to the need for a stable insertional area for ventral cervical musculature on the base of the braincase. Muscles inserting on a weakly attached basisphenoid might have tended to dislocate it, especially in forms with a poorly ossified neurocranium. Consequently, in all known primitive tetrapods except *Ichthyostega*, there is a posterior elaboration of the parasphenoid that bridges the ventral cranial fissure and braced the basioccipital on the remainder of the braincase, usually forming a ventral basal plate.

In the very primitive *Crassigyrinus*, only the lateral walls of the parasphenoid extend posterior to the fissure, and in the only known specimen showing this region the basioccipital was found separated from the skull (Panchen 1985). In *Eoherpeton*, although the parasphenoid plate is better developed ventrally, the basioccipital is similarly weakly attached (Smithson 1985). Although this may be a primitive feature of anthracosaurs, the weak contact between the basioccipital and parasphenoid is probably also related to the development of a pair of posteriorly facing pockets between the basioccipital and parasphenoid (see below). This effectively reduced the contact area between these two elements and considerably weakened the joint between the basioccipital and the rest of the skull. In *Archeria* the joint has been reinforced by the development of an inner lamina of the parasphenoid that sheaths the basioccipital and forms the medial wall of the pocket (see Occipital elements above).

Occasionally, the basal plate of primitive tetrapods bears a bilateral pair of depressions (loxommatids, Beaumont 1977; *Micraroter*, Carroll and Gaskill 1978; *Greererpeton*, Smithson 1982), sometimes incorrectly termed the '*tubera basisphenoidales*' (Romer 1930; Smithson 1982). These have been identified as insertional areas for cervical muscles (Smithson 1982). The posterolateral margins of the plate are produced into rounded eminences in some forms. These eminences, most properly termed *tubera parasphenoidales* have also been proposed as attachment sites for ventral axial musculature (Watson 1926; Romer and Witter 1942; Beaumont 1977).

Among anthracosaurs, specimens of *Archeria*, *Proterogyrinus*, and *Pholiderpeton* show parasphenoid plates with a well-preserved posterior margin. In these cases, both the diverging raised lateral borders, bearing longitudinal striations, and the *tubera parasphenoidales* are extremely well developed. Other genera in which the parasphenoid plate is at least partially preserved clearly show similarly raised lateral margins that almost certainly must have terminated in tubera. Why the lateral ridges and tubera are so well developed in anthracosaurs is uncertain, but it may be related to the form of the basioccipital condyle in which the rounded ventral rim swings well ventral to the general level of the parasphenoid plate. Without the ventral elaboration of the tubera and ridge system, the subvertebral muscles would have had to make a sharp dorsal turn after clearing the rim of the condyle in order to insert on the parasphenoid.

Another conspicuous feature of the parasphenoid in *Archeria* is the development of a pair of pockets enclosed within the parasphenoid dorsal to the tubera. *Pholiderpeton* was apparently similar

(Clack 1987). Although the disarticulated braincase of *Proterogyrinus* is less well preserved, the parasphenoid plate is much wider than the overlying basioccipital, making it almost certain that similar pockets were present in this genus as well.

The parasphenoid of *Crassigyrynus* (Panchen 1985) is extremely similar to those of *Archeria* and *P. scheeli*, the most conspicuous difference being the absence of a thin bony lamina between the posteriorly diverging ridges of the basal plate that leaves the basioccipital exposed ventrally. In his description of the basioccipital, Panchen noted that 'the lateral overlap areas' (i.e. the surface which would contact the diverging arms of the parasphenoid) 'are not distinguishable in texture from the exposed ventral ones' (Panchen 1985, p. 518). This suggests the absence of a bony connection between the lateral walls of the basioccipital and the medial surface of the parasphenoid and implies the presence of pockets as in anthracosaurs. However, the diverging arms of the parasphenoid show striated surface internally. This could indicate muscular or ligamentous tissue attachments or alternatively could indicate the presence of a sutural connection with an unpreserved part of the basioccipital. The matter remains unresolved.

Characters of the basisphenoid and their significance

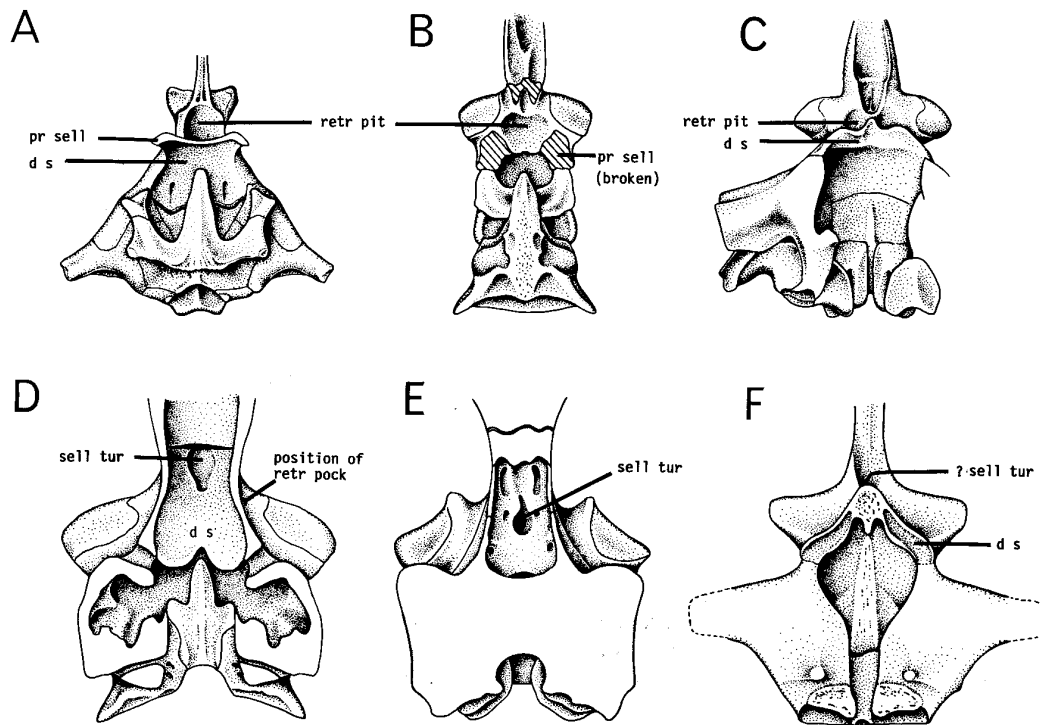
The unusually good preservation of the basisphenoid in *Archeria* allows detailed comparison with the basisphenoid of other tetrapods. Between the basipterygoid processes, on its dorsal surface, lies a conspicuous bowl-shaped depression lined with perichondrium. Although it bears a faint median ridge, it is otherwise undivided. *Eoherpeton* (Smithson 1985) and *Seymouria* (White 1939) possess similar depressions in the same position, although the median ridge on the anterior face of the dorsum sellae is better developed in the latter. The braincases of other embolomeres are too poorly preserved to determine the anatomy of this region (text-figs. 4c and 7b, c).

The anatomy and position of this depression in anthracosaurs and seymouriamorphs are strikingly similar to those of the retractor pit of early reptiles such as *Eocaptorhinus* (Heaton 1979) (text-fig. 7A), pelycosaur (Romer and Price 1940) and the extant reptiles *Sphenodon*, *Lacerta*, *Varanus* (Säve-Söderbergh 1946), and *Ctenosaura* (Oelrich 1956). Moss (1972) also described a concave depression here in *Tseajaia*, though does not figure it. The region is not described in *Diadectes*, but *Limnoscelis*, recently restudied by Fracasso (1983), also possesses a similar retractor pit. In the extant forms above the retractor pit serves as the origin of the retractor bulbi and bursalis muscles. These muscles pass anterolaterally and dorsally from their common origin through a gap in the lateral braincase wall (equivalent to the interorbital fenestra of anthracosaurs) with nerves III and VI. The metoptic membrane, which surrounds the more dorsally positioned pituitary body, fuses immediately below the latter and attaches to the median ridge of the pit.

What little is known of the braincase anatomy of other early tetrapod groups indicates that their basisphenoid anatomy is generally quite different. In the temnospondyl *Edops* (Romer and Witter 1942), nerves III and VI emerge separately from the highly ossified orbitosphenoid, and although a distinct transverse channel for the interorbital vein was present, it was not only too small to have admitted musculature into the braincase but was also located too far posterior to the pituitary fossa to be considered homologous with the retractor pit. It seems most likely that the retractor muscles never gained access to a central cavity ventroposterior to the pituitary body as in anthracosaurs and reptiles, but originated bilaterally from the surface of the braincase as in sarcopterygian fish such as *Eusthenopteron* (Jarvik 1980). This is probably the primitive tetrapod condition. In all microsaur in which braincase structure is well known, the lateral walls dorsal to the basisphenoid are almost completely ossified, thus restricting the retractor musculature to an external attachment as in *Edops*, but the homologies of these bony sheets are uncertain (Carroll and Gaskill 1978) and it is difficult to determine if this condition is primitive or derived (text-fig. 7D, E).

Reliable information on braincase structure of other temnospondyls is limited to a few genera. In *Greererpeton* the dorsum sellae forms a forwardly directed wedge between the basipterygoid processes (Smithson 1982), and although the braincase is not ossified immediately anterior to this point, there is no evidence of a retractor pit of the type seen in anthracosaurs and reptiles (text-fig. 7F). The retractor musculature presumably originated from the anterolaterally facing walls of the dorsum sellae or more

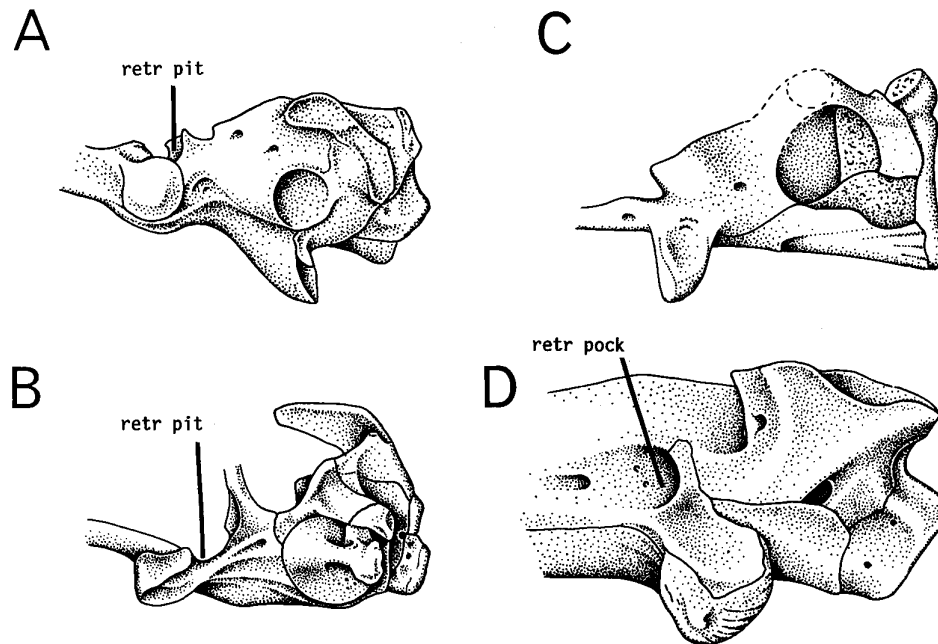
posteriorly on the basisphenoid. Smithson (1982) also noted a rugose area on the sphenethmoid which might have represented the site of origin of some of the eye musculature. In the more 'tropibasic' skulls of eryopoid temnospondyls, the retractor muscles originated from paramedian pockets. However, these retractor pockets in *Eryops* cannot be considered homologous to the retractor pit of reptiles and anthracosaurs because they are located posteroventral to the dorsum sellae (text-fig. 8) rather than immediately below the sella turcica anterior to the dorsum sellae (Sawin 1941, especially pl. 7*b, c*). A similar morphology is seen in some less well-preserved eryopoids such as '*Actinodon*' (Boy 1971), and dissorophids (Carroll 1964).



TEXT-FIG. 7. Tetrapod braincases in dorsal view. A, the reptile *Eocaptorhinus* (after Heaton 1979). B, the anthracosaur *Archeria*. C, the reptiliomorph tetrapod *Seymouria* (after White 1939). D, the temnospondyl *Eryops*, depicted in frontal section to expose cavities of auditory capsules, cavum cranii, and sphenethmoid (after Sawin 1941). E, the temnospondyl *Edops* (after Romer and Witter 1942). F, the colosteid *Greererpeton* (after Smithson 1982).

A parallel phenomenon is exhibited by the development of the myodome in actinopterygians. However, the central myodome developed from anterior bilateral pockets to accommodate the greatly lengthened recti muscles (Goodrich 1930; Patterson 1975) unlike the tetrapod condition, where only the retractor group is involved (Säve-Söderbergh 1946).

Whether the presence of a retractor pit in anthracosaurs, seymouriamorphs, and reptiles represents a true synapomorphy is uncertain. The detailed correspondence in structure is striking, although parallel developments of similar structure in some temnospondyls and teleostome fish may mean that its presence is simply related to how 'tropibasic' the braincase is. Its distribution among other early tetrapods, notably loxommatids and *Crassigyrinus*, remains unknown.



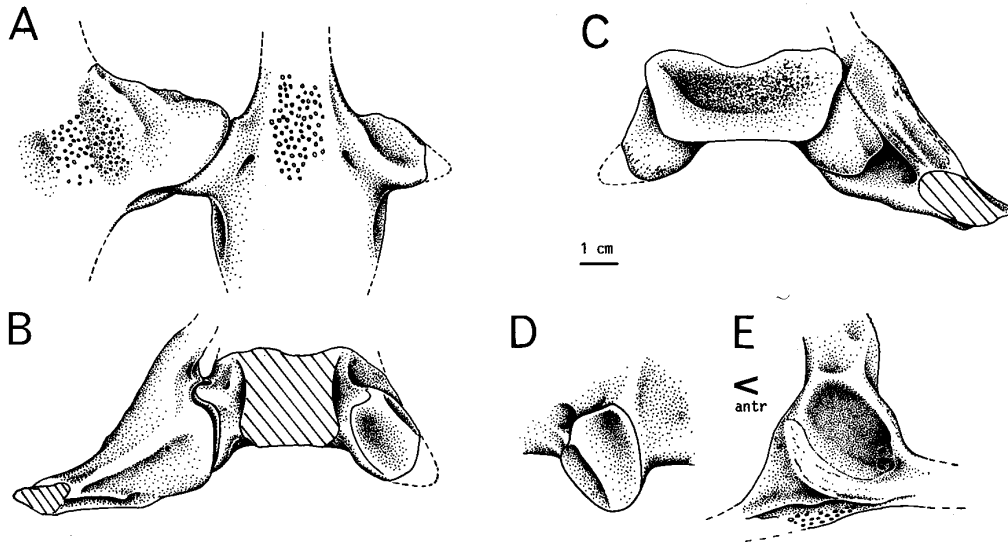
TEXT-FIG. 8. Tetrapod braincases in lateral view (posterior portion only). A, the reptiliomorph tetrapod *Seymouria* (after White 1939). B, the reptile *Eocaptorhinus* (after Heaton 1979). C, the colosteid *Greererpeton* (after Smithson 1982). D, the temnospondyl *Eryops* (after Sawin 1941).

Basal articulation

It has recently been pointed out (Smithson 1982) that the morphology of the basicranial articulation is very similar in anthracosaurs, loxommatids, and primitive reptiles. In all of these forms, a complex, double-faceted articular surface on the basiptyergoid process is received by a matching surface (the conical recess) of the epiptyergoid. The morphology of both surfaces indicates that the joint was probably synovial, possibly functioning as a pivot during kinetic movements of the skull (Panchen 1964; Beaumont 1977; Heaton 1980). Because this structure is distinct from the probably immobile 'peg and socket' basal articulation common in temnospondyls with unfused basal articulations and microsaurians as far as known, and is also clearly derived with respect to the rhipidistian condition, Smithson (1982) proposed it as a synapomorphy of at least anthracosaurs and loxommatids, although the polarity of this character is uncertain.

As is often the case with Palaeozoic tetrapods, the shortage of reliable data makes it difficult to evaluate this hypothesis. Certainly the structure of the articulation in more intensively studied forms such as the temnospondyl *Greererpeton* (Smithson 1982) and the microsaur *Pantylus* (Romer 1969) support Smithson's position. In *Trimerorhachis* the matching surfaces of the parasphenoid and epiptyergoid, although clearly not coossified, bear striations that indicate an essentially immobile joint (pers. obs.). However, *Edops* (Romer and Witter 1942), an undisputed temnospondyl, has a basicranial articulation resembling that of anthracosaurs and loxommatids in several respects. Specimen MCZ 1235 is illustrated in text-fig. 9. This is from Pagett, Young County, Texas, Moran Formation, Lower Permian.

The basiptyergoid process of the basisphenoid bears two elongate concave articular facets separated by a prominent, rounded ridge orientated about 50° to both the transverse and frontal planes. The upper facet faces dorsolaterally and slightly anteriorly, and the lower facet, antero-



TEXT-FIG. 9. *Edops craigi* Romer, details of basicranial articulation. Based on MCZ 1235. A, ventral view. B, anterior view. C, posterior view. D, lateral view of left basipterygoid process. E, medial view of right conical recess.

ventrally and slightly laterally. The basipterygoid articulation was clearly not coossified, as the surface of the process, unlike the formless termination seen in *Eryops* (Sawin 1941), has distinct structure and is circumscribed by a thickened lip, suggesting the existence of a synovial joint. Its tapered distal termination appears to have been extended in cartilage.

The conical recess is in the form of a half cone with the free edges 'rolled outward' to make the surfaces slightly convex toward its two long margins. The tip of the cone forms a distinct pit in the substance of the epipterygoid that must have received the pointed cartilaginous termination of the basipterygoid process. Whether movement occurred at this joint is, of course, unknown. The tight fit of the concave basipterygoid facets against the convex surface of the conical recess seems to preclude any rotation about the ventroposteriorly directed axis of the joint, and the insertion of the tip of the process into a pocket at the apex of the recess must have restricted longitudinal translation. The basal articulation of *Edops* resembles most closely that of loxommatids and *Crassigyrinus* (Panchen 1985), suggesting that this general form may be primitive for tetrapods.

General conclusions

Although no other anthracosaur possesses a braincase as well preserved as that of *Archeria*, sufficient information is available to indicate that the structure shows remarkably little change from the base of the Upper Carboniferous (Namurian) to the Lower Permian, a span of approximately 30 million years. As one of us (R. H.) intends to show in a future publication on the anatomy of *Archeria*, this conservatism is also found in much of the rest of the skeleton. Anthracosaurs as a whole, unlike reptiles with which they share some characters, are a remarkably conservative lineage. However, the origin of reptiles is associated with the invasion of the rigorous terrestrial environment that prompted an extensive adaptive radiation (Carroll 1982), whereas anthracosaurs with few exceptions appear to have been restricted to a relatively stable aquatic environment in which there was little selective pressure for directional evolution.

Seymouriamorphs have traditionally been considered to be anthracosaur (s.s.) derivatives (e.g. Romer 1966), although Heaton (1980) has recently argued that they belong to entirely

different amphibian groups. *Eoherpeton*, an anthracosaur that initially appeared to show several seymouriamorph-like characters and therefore to be morphologically intermediate between the two groups (Panchen 1975, 1980; Holmes 1984) has since been shown to have none of the structural peculiarities of seymouriamorphs (Smithson 1985) and does not support a close relationship between the two groups. Furthermore, anthracosaurs and the archaic tetrapod *Crassigyrinus* share a number of characters, which if synapomorphies (Panchen 1985) would exclude seymouriamorphs from direct relationship with anthracosaurs. Yet anthracosaurs and seymouriamorphs do share several features of the braincase which may indicate some level of relationship, specifically the possession of basal tubera and supratuberal pockets, median retractor pit, mobile basal articulation, and a foramen for the vena capitis dorsalis, although the last character may be open to interpretation (Holmes 1984).

Anthracosaurs also share many characters with reptiles, and as a result have often been proposed as reptile ancestors (Carroll 1970; Romer 1966). This view has been challenged (Panchen 1972*b*, 1975, 1977; Heaton 1980), by arguing that these similarities are plesiomorphic for tetrapods, convergent, or spurious (see Holmes 1984 for a review of the problem). Nevertheless, the hypothesis of some form of relationship has not lapsed completely. Panchen has recently suggested that a true (i.e. moveable) basal articulation characterizes a 'reptiliomorph' ramus of early tetrapods that includes *Crassigyrinus*, anthracosaurs, seymouriamorphs, probably diadectomorphs, and reptiles (Panchen 1985). This is a plausible suggestion, considering that the basal articulation does not resemble any known fish condition or that in temnospondyls or 'lepospondyls'. We propose that a median retractor pit may characterize the same group, although until the distribution of these characters is more completely known in lower tetrapods, a more specific hypothesis of interrelationship cannot be proposed.

CONCLUSIONS

The braincase of *A. crassidisca* is described from well-preserved specimens from the Geraldine Bonebed (Admiral Formation, Lower Permian, Texas).

It is a solidly ossified box, like those of most other embolomeres, but the distribution of either solidly or incompletely ossified braincases among early tetrapods suggests that this is not a character of taxonomic significance. It probably has more to do with structural or functional considerations such as size and degree of terrestriality of the animal.

Remnants of the embryonic lateral otic and ventral cranial fissures, found also in the ossified braincases of some primitive fish, are seen in that of *Archeria*. The ventral cranial fissure was sealed only by the dermal parasphenoid. The development of the parasphenoid in tetrapods was possibly connected with the need to incorporate the basioccipital more firmly into the braincase to accommodate neck musculature.

A retractor pit in the basisphenoid housed the origin of some of the eye retractor muscles. This structure is very similar to that seen in early reptiles and seymouriamorphs, and may be a synapomorphy uniting these groups. Unfortunately, this character is not known in the primitive tetrapod group *Loxommatidae* nor in *Crassigyrinus*. If it were found there also, it may unite these with the former into a reptiliomorph ramus of tetrapods, which would also be characterized by a true mobile basal articulation.

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ABBREVIATIONS

antr	anterior
bo	basioccipital
bpt p	basipterygoid process
bsph	basisphenoid
b tub	basal tuber
d s	dorsum sellae
eo	exoccipital
f bo	facet on parasphenoid for the basioccipital
f bsph	facet on parasphenoid for the basisphenoid
f eo	facet on basioccipital for the exoccipital
f m	foramen magnum
f o	fenestra ovalis
f op	facet on the basioccipital for the opisthotic
f pat	facet on the exoccipital for the proatlas
inf r	scar for the inferior rectus muscle
N II	optic foramen
N III	passage for the oculomotor nerve
N IV	trochlear foramen
N VI	passage for the abducens nerve
N VII	facial nerve foramen (palatine branch)
N X	vagus foramen
N XII	hypoglossal foramen
nut f	nutrient foramen
ol t	groove for the olfactory tract
op	opisthotic
op ch	optic chiasma
par	parasphenoid
pp	postparietal
pro	prootic
pro f	prootic foramen
pr sell	processes sellares
retr pit	retractor pit
retr pock	retractor pocket
sell tur	sella turcica
sph	sphenethmoid
stub pock	supratuberal pocket
sup r	scar for the superior rectus muscle
t	tabular
t f	facet of the tabular for articulation with the opisthotic
v c d	foramen for the vena capitis dorsalis
vn	groove for the vomeronasal nerve

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