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THE SMALLER EMBOLOMEROUS AMPHIBIANS (ANTHRACOSAURIA) FROM THE MIDDLE PENNSYLVANIAN (DESMOINESIAN) LOCALITIES AT LINTON AND FIVE POINTS COAL MINES, OHIO

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ABSTRACT. The remains of small embolomeres (total midline skull length not exceeding 100 mm) from the Middle Pennsylvanian (Desmoinesian) Linton and Five Points coal mines of southeastern Ohio can be distinguished from those of *Leptophractus* found at the same localities by the form and size of the teeth. Its well-ossified condition relative to a comparably sized juvenile specimen of the embolomere *Archeria* indicates a much smaller maximum adult size than that of *Leptophractus*, the other described embolomere from the Linton Coal Mine. Tooth form and count, shape of the squamosal and surangular crest, and stratigraphic occurrence all support tentative placement in the family Archeriidae.

KEY WORDS: North American embolomeres; Middle Pennsylvanian embolomeres; Five Points Coal Mine; Linton

INTRODUCTION

It has been suggested (Romer, 1963) that American Carboniferous embolomerous amphibians sort into two size groups: a group comprising taxa that attained a small body size comparable to that of *Archeria* from the Lower Permian of Texas and a group comprising large-bodied taxa. The anatomy and systematics of the latter group were reviewed by Romer (1963).

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Although numerous embolomere taxa are known from the Carboniferous of Europe (see, e.g., Smithson, 2000), they are relatively rare in North America. Although some of the latter material has been described (e.g., Carroll, 1967; Holmes, 1984; Klembara, 1985; Holmes and Carroll, 2010), significant material collected from the Desmoinesian ("Westphalian D") localities of Linton and Five Points Coal mines in Ohio has not. The Diamond Coal Mine (Hook and Baird, 1986), located near the abandoned town of Linton, is arguably one of the most productive Carboniferous vertebrate fossil localities in North America. A rich assemblage, collected from the cannel below the Upper

Freeport coal of the Allegheny Group, includes nearly 40 genera of fish, amphibians, and reptiles (see Hook and Baird [1986] for a review of this fauna and history of the locality). Aquatic lepospondyls and temnospondyls compose the large majority of the amphibians, whereas embolomeres are poorly represented. A few articulated embolomerous vertebrae and the partial snouts of three large individuals have been described (Cope, 1873, 1875; Romer, 1963), but an account of skeletal elements of a small embolomerous anthracosaur, informally referred to as "Fearon's embolomere" in recognition of R. N. Fearon, who collected the material some time before 1883, has never been published.

More recently, a second fossil assemblage has been discovered approximately 42 km due north at Five Points Coal Mine (Hook and Baird, 1993). Although slightly older (early rather than late Desmoinesian) than the classic Linton locality, the taxonomic composition of the fossil assemblage at Five Points shares many similarities with that from Linton (Hook and Baird, 1993). Disarticulated remains of embolomeres, although uncommon, are preserved. Since embolomere remains are rare, not only at these two sites, but in the North American Carboniferous as a whole, this material warrants description despite its fragmentary and disarticulated condition.

MATERIALS AND METHODS

The specimens described in the paper are held in the collections of the Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania, and Museum of Comparative Zoology (MCZ), Harvard University, Cambridge, Massachusetts.

Specimens examined from the Linton locality

MCZ 2161, articulated vertebrae, thoracic ribs, and a section of articulated ventral armor internal view of a small embolomere exposed ventrally. After acid etching, vertebrae, ribs, and posterior part of a lower jaw and numerous gastralia were also exposed.

MCZ 2293, isolated anterior third of a lower jaw of a small embolomere exposed medially. After acid etching, a latex peal of the lateral aspect was made.

Specimens examined from the Five Points locality

CM 29599, left femur (part and counterpart).

CM 34605, left squamosal and quadrate (part and counterpart).

CM 67188, anterior half of right mandible (part and counterpart).

Although some specimens from Five Points were recovered during surface collecting, most were discovered by splitting cannel coal (see Hook and Baird, 1993). The collecting techniques of R. N. Fearon, who collected the MCZ specimens over 125 years ago, are unknown, but were probably similar. The specimens were acid etched to remove the poorly preserved bone, after which a latex peel was made.

Specimens used for comparison

MCZ 1474, *Archeria crassidisca*. Skull table and disarticulated caudal vertebrae of an immature individual from the Archer City bonebed (Putnam Formation).

DESCRIPTION

Skull. The posterior portion of a lower jaw (MCZ 2161), exposed in medial aspect, is preserved in association with numerous embolomerous centra, ribs, and gastral scales (Figs. 1, 2A). As in other embolomeres, the jaw is deep in the region of the adductor fossa. The dorsal margin of the surangular crest is straight, high, and hori-

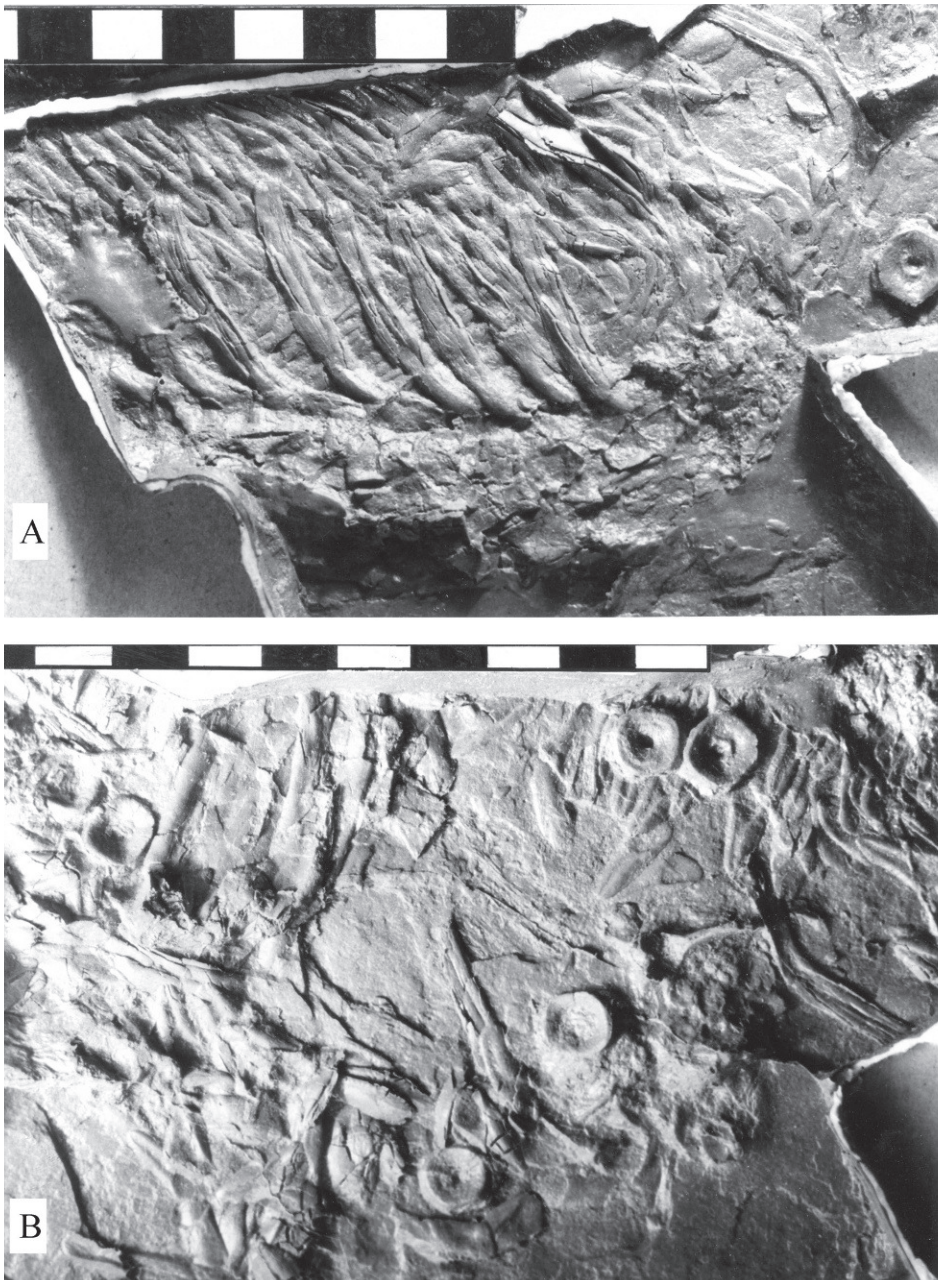

Figure 1. Archeriid. Photographs of latex peal (MCZ 2161) taken after acid etching. A, articulated vertebrae, ribs, and dorsal surface of gastralia. B, disarticulated vertebrae, ribs, gastralia, and posterior portion of mandible in internal view. Scale bars are divided into 1-cm sections.

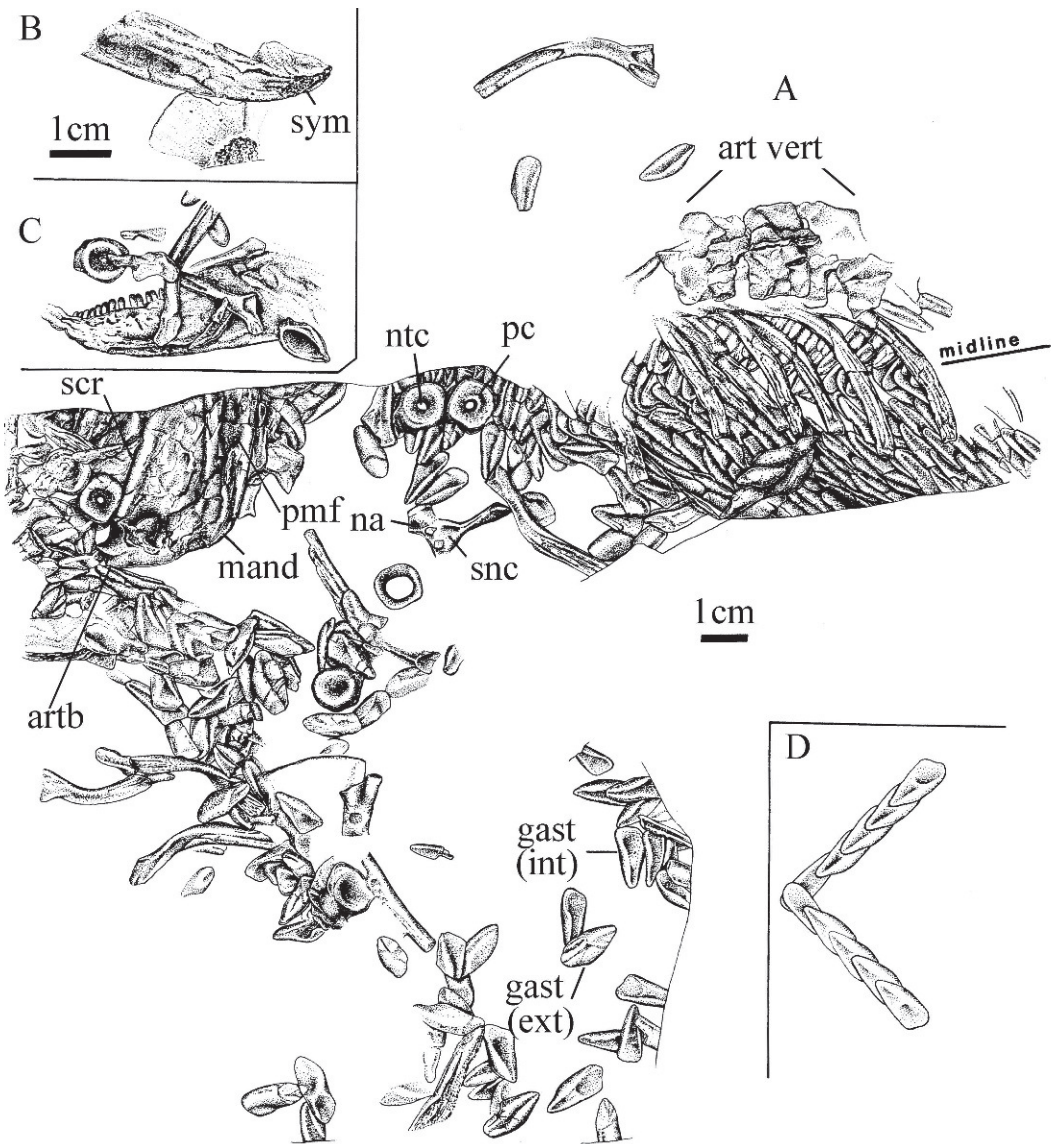

Figure 2. Archeriid. A, drawing of main block (MCZ 2161). B, drawing of anterior end of lower jaw (MCZ 2293), medial aspect. C, drawing of anterior end of lower jaw (MCZ 2293), lateral aspect. D, reconstruction of one rank of gastralia in internal view showing overlap patterns within the row. Abbreviations: artb, boss on articular; gast (ext), gastralia, external surface; gast (int), gastralia, internal surface; mand, mandible; na, neural arch; ntc, notochordal canal; pc, pleurocentrum; pmf, posterior Meckelian fenestra; scr, surangular crest; snc, supraneural canal; sym, symphyseal surface of lower jaw.

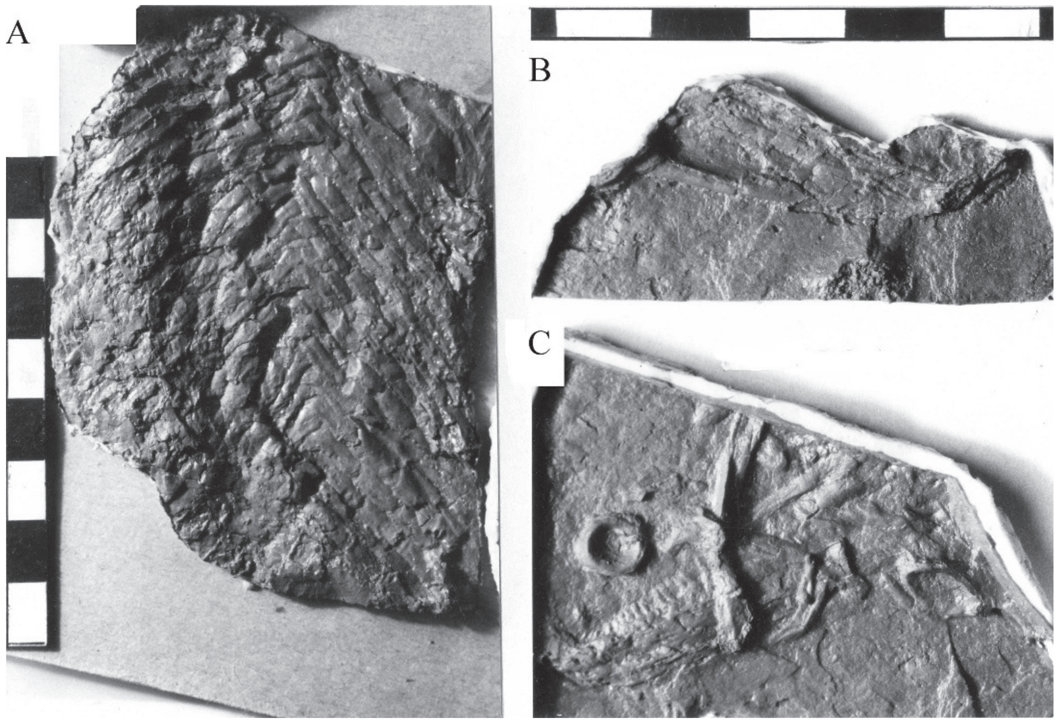

Figure 3. Archeriid. Photographs of latex peals. A, original surface of main block (MCZ 2161) showing ventral surface of gastralia. B, anterior end of lower jaw, medial aspect (MCZ 2293). C, anterior end of lower jaw, lateral aspect, after acid etching (MCZ 2293). Scale bars are divided into 1-cm sections.

zontal, as in *Archeria*. The articular bears a boss posterior to the glenoid, as in *Proterogyrinus* (Holmes, 1984) and *Archeria* (Holmes, 1989). The posterior portion of a large posterior Meckelian fenestra is clearly visible (Figs. 1B, 2A).

The anterior end of a left lower jaw ramus (MCZ 2293) is preserved in both lateral and medial view (Figs. 2B, C, 3B, C). Although not collected with the main block, its small size and association with embolomerous centra suggest that it pertains to the same taxon. It appears to have been from an individual of about the same size as MCZ 2161; the complete jaws would have been no more than 100 mm long. This indicates that the complete skull would have had a midsagittal length (the postparietal length—see Panchen, 1970) of between 85 and 100 mm if skull proportions of embolomeres such as *Proterogyrinus* (Holmes, 1984) or *Archeria* (Holmes, 1989) are assumed. The dermal ornamentation, seen on the lateral surface of the anterior jaw portion (MCZ 2293; Figs. 2C, 3C), is muted as in other embolomeres. The preserved dentary bears 13 small teeth of equal size. As in *Archeria*, the anterior and posterior margins of the teeth are parallel (i.e., the tooth is not tapered), and the blunt terminations appear to be chisel-shaped, although poor preservation precludes more detailed comparisons. This morphology is distinct from that seen in *Leptophractus* (Cope, 1875; Romer, 1963), also found at Linton, in which the teeth show marked variation in size and shape and are

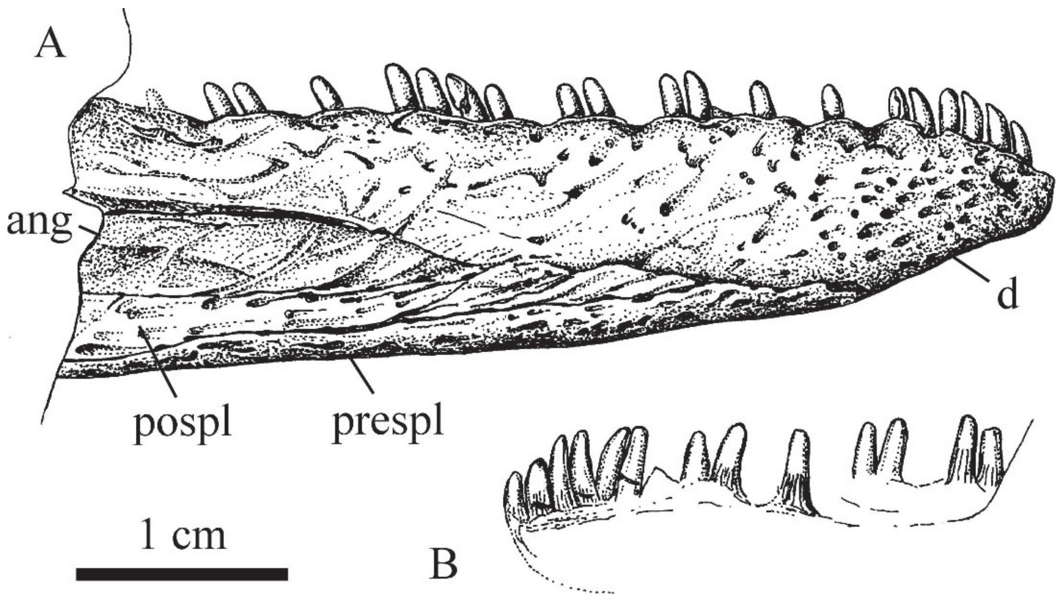

Figure 4. Archeriid. Anterior end of jaw ramus (CM 67188) from Five Points in A, lateral and B, medial views. Abbreviations: ang, angular; d, dentary; pospl, postsplenial; prespl, presplenial.

relatively larger, bullet or cone-shaped, and distinctly recurved.

The anterior half of a right mandible (CM 67188) is preserved at Five Points (Fig. 4). In the region of the symphysis, the lateral surface of the dentary bears closely spaced, round pits. Posterior to this, it bears more widely spaced pits, most of which are extended as shallow grooves. Twenty blunt teeth are preserved in place. Although preservation is imperfect, they are clearly unlike those of *Leptophractus* but resemble those of MCZ 2293 from Linton in being parallel-sided, small, and subequal in size. There is room for at least 15 additional teeth. The dentary tapers posteriorly but still maintains considerable depth at its broken posterior end, suggesting that a significant portion (about one-third) of the tooth row has been lost. If so, a complete dentary would have contained approximately 55 teeth. The coarsely sculptured splenial (presplenial or anterior splenial) has a limited exposure along the ventral edge of the ramus. It terminates directly ventral to the eighth tooth socket. The anterior ends of two additional bones are exposed between the dentary and splenial. The more ventral of the two, presumably the postsplenial, shares a long suture with the splenial and terminates anteriorly directly ventral to the 13th tooth socket. The more dorsal element, presumably the angular, shares horizontal sutures with both the putative postsplenial below and dentary above, tapering to a wedge between these bones immediately ventral to the 21st tooth root. Medial exposure of the jaw is limited to the region of the symphysis and the anterior 13 preserved teeth.

A left squamosal from Five Points (CM 34605) is relatively square in proportions. In contrast to most embolomeres except *Archeria* (Holmes, 1989: text-fig. 2) and *Eoherpeton* (Smithson, 1985, fig. 8), the quadrate lamina of the squamosal is relatively short (Fig. 5), indicating that the quadrate condyle

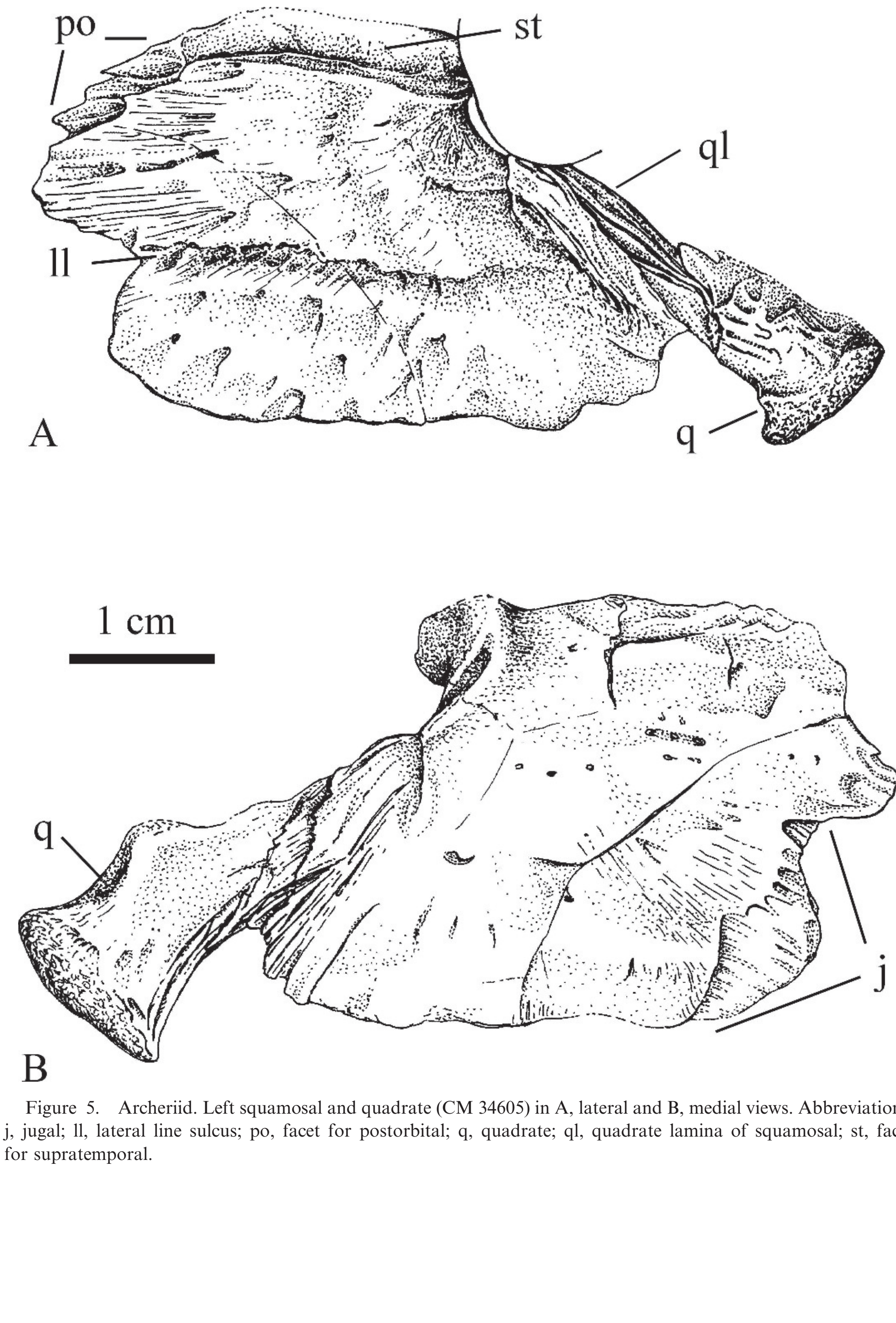

Figure 5. Archeriid. Left squamosal and quadrate (CM 34605) in A, lateral and B, medial views. Abbreviations: j, jugal; ll, lateral line sulcus; po, facet for postorbital; q, quadrate; ql, quadrate lamina of squamosal; st, facet for supratemporal.

would not have projected much posterior to the level of the occiput. Dorsally, the squamosal bears a relatively long, anteroposteriorly oriented trough that articulated with the supratemporal in life. The smooth edges of the trough show no evidence that an interdigitating suture was present. Anterior to the trough, the squamosal bears a fluted facet that underlapped the postorbital. The lateral surface of the squamosal bears a number of pits that radiate from the anterodorsal notch of the squamosal embayment and, at approximately midheight, a distinct, horizontal, continuous lateral line sulcus. The left quadrate remains in articulation with the squamosal, although postmortem rotation about its shaft has exposed the mandibular condyle in anterior view.

Medially, the squamosal bears at its anteroventral corner an overlapping flange for articulation with the jugal. A distinct facet for the quadratojugal is absent. The ventral end of the quadrate is exposed in posterior view. The quadrate condyle is gently saddle shaped, with the medial convexity being better developed than the lateral condyle, as in *Archeria* (Holmes, 1989).

Vertebrae. Six articulated but crushed trunk vertebrae are preserved in dorsolateral aspect in MCZ 2161 (Figs. 1B, 2A). Disarticulated elements from a more anterior portion of the column (on the basis of their proximity to the posterior portion of the mandibular ramus) are exposed in various views. The central elements, which have a notochordal canal of about the same relative size as that in much larger specimens of *Archeria* (Holmes, 1989), are very well ossified considering their small size (about 10 mm in diameter). One neural arch, exposed in anterior view 34 mm behind the mandibular ramus and so presumably from the anterior trunk region, bears a supraneural canal that is relatively smaller than in anterior trunk arches in much larger subadult specimens of *Archeria* from the Geraldine bonebed (Holmes, 1989).

Ribs. Sixteen ribs of varying states of completeness are preserved; several are in close association with the articulated series of vertebrae (Fig. 1A), the rest scattered about the block (Figs. 1B, 2A). Their form, with a well developed capitulum and absence of a flange, is virtually indistinguishable from that of other embolomeres such as *Archeria* and *Proterogyrinus*.

Appendicular Skeleton. A left femur is preserved in part and counterpart at Five Points (CM 29599) in anterodorsal and posteroventral views (Fig. 6). At approximately 50 mm in length, it is about 60% and 65% of the length of the femora illustrated for *Proterogyrinus* (Holmes, 1984) and *Archeria* (Romer, 1957), respectively. Both proximal and distal expansions are well developed, and articular surfaces are clearly set off from the periosteal bone. Neither proximal nor distal ends are as well ossified as in a typical *Proterogyrinus* specimen but are comparable to those described for *Archeria* (Romer, 1957, fig. 8). The adductor crest and rugosities of the internal and fourth trochanters are well developed on its ventral surface. Rugosities for the insertions of the puboischiofemoralis internus and ischiotrochantericus are visible on the dorsal (extensor) surface of the proximal expansion; on the posterodorsal corner of the distal expansion, deep proximodistal grooves mark the origins of the peroneus longus and extensor digitorum longus. On balance, these features suggest that, although CM 29599 is probably not from a fully adult individual, it does not pertain to a juvenile.

Gastral Scales. As originally preserved, MCZ 2161 comprised a section of articulated gastralia from the midtrunk exposed in ventral view (Fig. 3A). Of the approximately 20 ranks exposed, the most complete comprise rows of five elements per side. Each

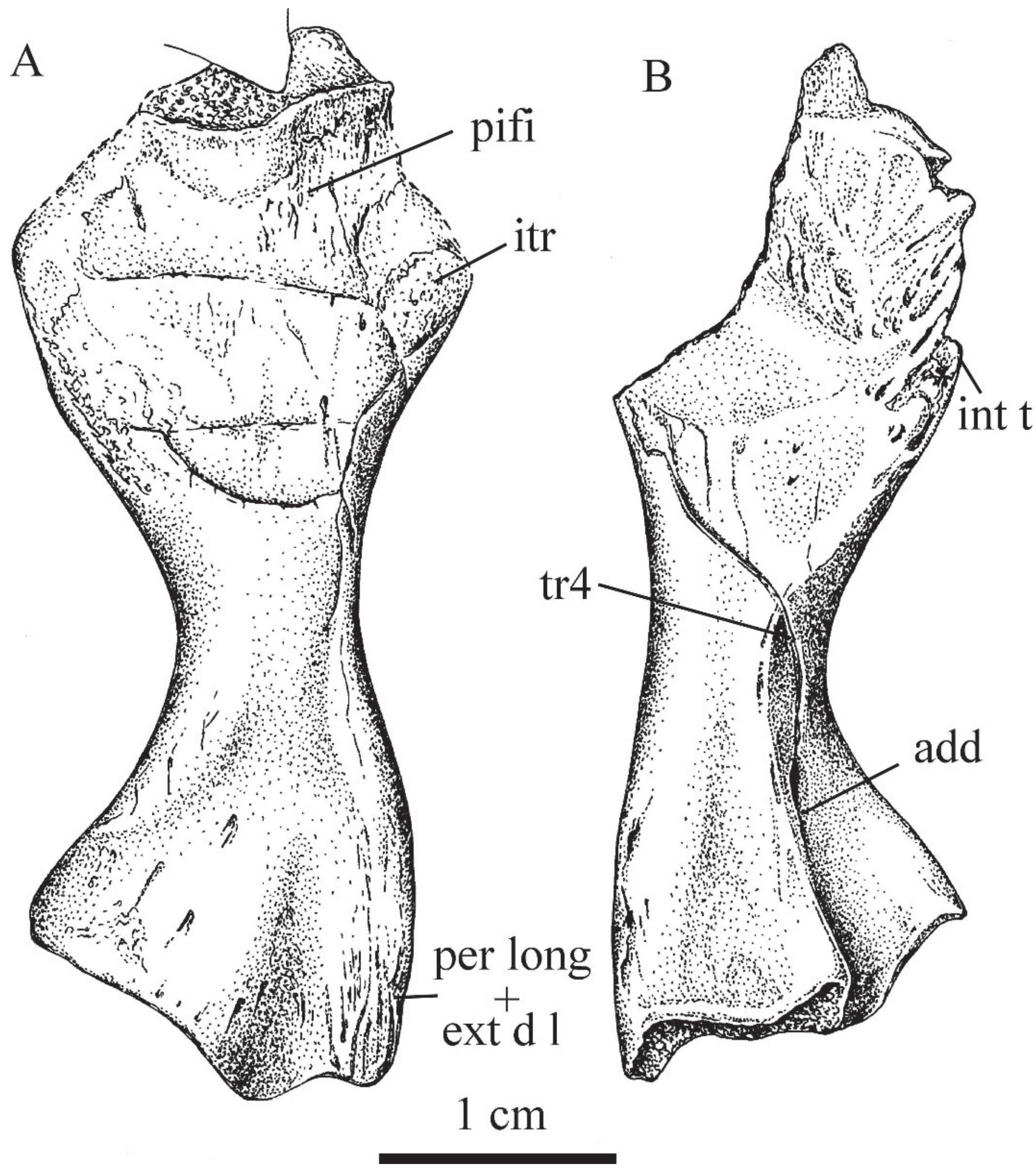

Figure 6. Archeriid. Left femur (CM 29599) in A, anterodorsal and B, posteroventral views. Abbreviations: add, adductor crest; int t, internal trochanter; itr, insertion of the ischiotrochantericus; per long + ext d long, common origin of the peroneus longus and extensor digitorum longus; pifi, insertion of the puboischiofemoralis internus; tr4, fourth trochanter.

rank meets its contralateral counterpart along the midline at an angle of about 90°. Acid etching has subsequently exposed their dorsal surfaces, as well as many isolated gastralia, showing morphology of overlapping surfaces clearly (Figs. 1, 2A). Each element is asymmetrically tear-drop shaped, with the tapered end directed anteromedially. This conforms to the "spindle-shaped" gastral scale morphology common in "labyrinthodonts" (Witzmann, 2007) The smooth, convex ventral (external) surface lacks sculpturing like that seen in the temnospondyl *Greererpeton* (Godfrey, 1989). The dorsal (internal) surface bears a longitudinal groove that broadens at the wider (posterolateral) end to accommodate the ventral surface of the tapered tip of the next lateral scute (Fig. 2D). The posteromedial edge is thicker than the anterolateral edge. A very similar morphology and pattern of overlap is seen in *Greererpeton* (Godfrey, 1989). However, in MCZ 2161, each element is remarkably large, having a length equivalent to at least 25% greater than the diameter of a vertebral centrum. Relatively large gastralia appear to be characteristic of embolomeres. Similar proportions are seen in *Proterogyrinus*, *Archeri*a (Cope and Matthew, 1915), *Pholiderpeton* (Clack, 1987), *Eogyrinus* (Panchen, 1966, 1972) and embolomeres (probably *Calligenethlon*) from Joggins, Nova Scotia (Godfrey *et al.*, 1991; Holmes and Carroll, 2010). In basal tetrapods such as *Greererpeton* (Godfrey, 1989) and *Colosteus* (Hook, 1983), they are little longer than the equivalent of half their respective centrum diameter. They are relatively larger in the temnospondyl *Dendrerpeton* (Carroll, 1967), but still distinctly shorter than the centrum diameter. The paramedian scales have expanded, spoon-shaped medial ends to overlap their counterparts on the opposite side of the median line.

DISCUSSION

Of the 28 and 34 identifiable vertebrate taxa described from the localities of Five Points and Linton, respectively, 21 are common to both localities (Hook and Baird, 1993). Most of the tetrapod taxa at both localities are small lepospondyls; relatively few specimens (a limited number of "labyrinthodonts" and reptiles) are large enough to be included in the same size class as the material described here. None of the elements can be assigned to the Temnosponyli, Baphetoidea (=Loxommatoidea) or to any reptile known to occur at either locality. However, the nature of the dermal sculpturing and shape of the teeth, as well as morphology of the femur and ribs are consistent with what would be expected for an embolomere.

Four embolomere specimens have been described from Linton. Two of these, AMNH 6831 and a "specimen at Columbia University" (see Romer, 1930:127), compose the type material of *Leptophractus obsoletus*. Except for one partial counterpart, both have since been lost (Panchen, 1970). A third skull, originally described as *Leptophractus* and later redescribed as *Anthracosaurus lancifer* (Romer, 1963), is now considered to be a large individual of *L. obsoletus* (Panchen, 1970; Hook and Baird, 1986). A few articulated centra not associated with any of the above are also preserved (Romer, 1963). These specimens indicate that *Leptophractus* was a large embolomere, with a midsagittal skull length estimated to have been between 340 and 355 mm (Panchen, 1977). The Linton material described here pertains to much smaller individuals with a midsagittal skull length of no more than 100 mm. Although it is possible that this material simply pertains to juvenile *Leptophractus* specimens, this is unlikely. The preserved dentary teeth are small, close-set, blunt pegs of uniform size and shape. Up to 55 teeth would have been present in the complete jaw. Teeth in the same region of *Leptophractus* are relatively large, vary considerably in size, and are generally in the form of recurved, pointed cones (Cope, 1875, plates XXXVIII, XXXIX; Romer, 1963, figs. 11, 12). The complete jaw would have held

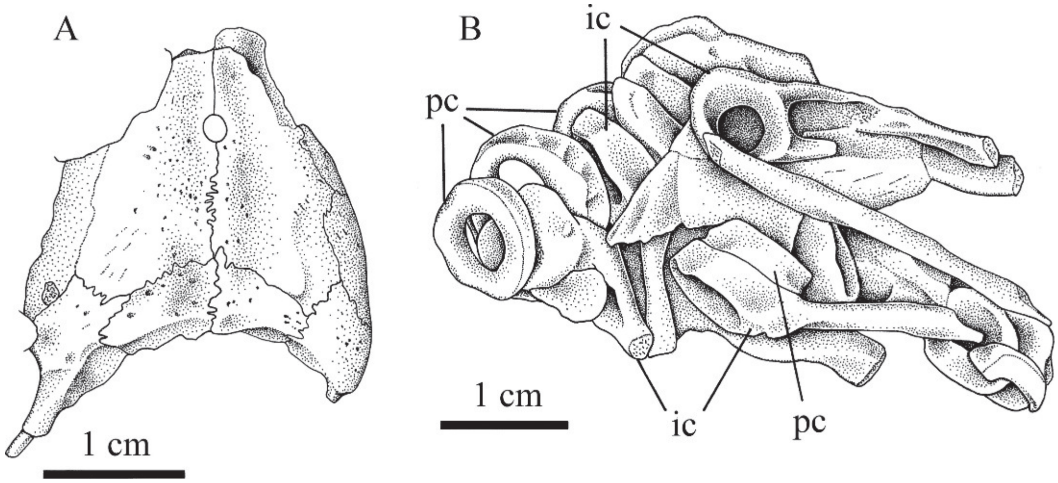

Figure 7. *Archeria crassidisca* (MCZ 1474), an immature individual. A, skull table. B, caudal vertebrae, approximately 30 segments postsacral. Abbreviations: ic, intercentrum; pc, pleurocentrum.

approximately 28 teeth (Romer, 1963). Unless there was a drastic change in form, relative size, and total number of teeth as adult size was approached, the material described here cannot be congeneric with *Leptophractus*. The relatively advanced state of ossification of this material also supports the probability that it represents a taxon distinct from *Leptophractus*. The supraneural canals are small, and vertebral centra are well ossified, restricting the diameter of the notochordal canal. The notochord of embolomeres remains an important structural element in the axial skeleton throughout life. A small notochordal canal persists even in the largest known *Archeria* specimens (centra of 35 mm diameter and skulls of about 300 mm midsagittal length). In subadults with a centrum diameter of about 20 mm and midsagittal skull length of about 170 mm, the canal is slightly larger (Holmes, 1989). However, in one juvenile *Archeria* (MCZ 1474) from the Archer City bone bed, with a midsagittal length of about 85 mm and a caudal centrum diameter of about 9 mm (essentially the same size as the embolomere described here), the osseous centra are thin husks and the notochordal canal accounts for a full half of the diameter (Fig. 7). The centra in MCZ 1474 are clearly embolomerous, with hemal arch-bearing intercentra alternating with archless pleurocentra.

The degree of ossification of the centra of the embolomere described here is more comparable to that in subadult and adult *Archeria*, suggesting that a full-sized adult would have been much smaller than *Leptophractus*. Of the known embolomeres, only *Calligenethlon* has been reported as being smaller, with a midsagittal skull length and centrum diameter of approximately "two to three inches in length" (Carroll, 1967:136) and 5 mm (Carroll, 1967, text-figs. 19, 21), respectively. More recently discovered embolomere material from Joggins, if assignable to *Calligenethlon*, suggests that the type material might pertain to a juvenile individual and that the adult would be somewhat larger, but its skull would not have exceeded 100 mm in midsagittal length (Holmes and Carroll, 2010).

Whether the material from Five Points pertains to the same taxon present at Linton is uncertain. Although the two localities are separated by only 42 km, Five Points is about two million years younger. Nevertheless, it is clear that none of it pertains to *Leptophractus*. Rather, the relatively well ossified material from both localities clearly pertains to more or less adult individuals of an embolomere of small size. Although the dentary from Five Points (CM 34605) is arguably more robust than that from Linton (MCZ 2161), otherwise in cases where the same elements occur in both localities, no differences are apparent, suggesting that the taxa are likely closely related if not conspecific.

Although the embolomere described here is probably not *Leptophractus*, a definitive taxonomic assignment is problematic. The high, straight, horizontal, dorsal margin of the surangular crest and anterior placement of the jaw articulation, as indicated by the short quadrate ramus of the squamosal, are certainly reminiscent of the morphology in *Archeria*. A dentary tooth count of about 55 places this taxon at the high end of the range (from about 24 in *Eoherpeton* [Smithson, 1985] to 55 in *Archeria* [Holmes, 1989]) for embolomeres, and suggests affinities with *Archeria*. However, judging from the estimated maxillary tooth counts, the dentary count in *Proterogyrinus* probably approached 50, suggesting that a high tooth count is not a unique shared character of the Linton/Five Points embolomeres and *Archeria*. Tooth morphology resembles that in *Archeria*, but a similar tooth morphology also occurs in *Proterogyrinus* (Holmes, 1984) and *Pholiderpeton* (Clack, 1987), suggesting the possibility that this tooth morphology is simply plesiomorphic. Although hardly conclusive in itself, it is nevertheless worth noting that the Linton deposits are Desmoinesian—closer in stratigraphic occurrence to the *Archeria* material from the Texas Lower Permian than any other known embolomere. With these caveats, the specimens are assigned provisionally to the family Archeriidae, pending further discoveries.

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