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CAPTORHINOMORPH "STEM" REPTILES FROM THE PENNSYLVANIAN COAL-SWAMP DEPOSIT OF LINTON, OHIO

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ABSTRACT

Two new specimens, plus one previously misidentified as an adelospondylous amphibian bring to four the known captorhinomorph reptile remains in the classic Linton fauna. The skull and jaw specimens are clearly assignable to the Mazon Creek genus *Cephalerpeton*, although specifically distinct from *C. ventriarmatum*; the postcranial specimen conforms to the Linton species *Anthracodromeus longipes*. As the question of possible synonymy between these two nominal genera cannot be resolved on the evidence available, both names are retained *sub judice*. The Linton species designated *Cephalerpeton* aff. *C. ventriarmatum* (of late Westphalian D age) may have been derived from the Mazon Creek species (early Westphalian D) through enlargement of the mandibular teeth and resultant reduction of the dental formula. These agile, lizard-like small reptiles occur as rare erratics in the Linton deposit.

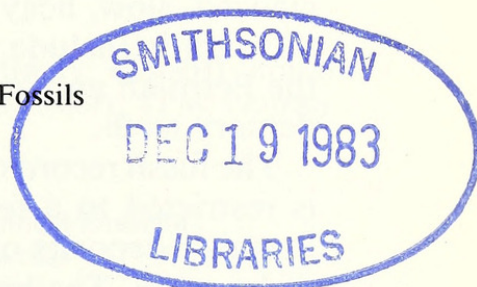
INTRODUCTION

The suborder Captorhinomorpha occupies a unique position in the early evolution of reptiles. The fossil record of this group extends from the Lower Pennsylvanian into the Upper Permian, forming one of the longest reptilian phylogenies within the Paleozoic. The Captorhinomorpha include the oldest known true reptiles (Eureptilia) and are

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closely related to the important synapsid (pelycosaur and therapsid) and diapsid (eosuchian, lepidosaur, and archosaur) lineages. The suborder can be divided into two families, the Protorothyrididae and the Captorhinidae. The protorothyridid genera were formerly included in the family Romeriidae (Carroll and Baird, 1972), but with the removal of the type genus *Romeria* to the Captorhinidae (Heaton, 1979) the family name Protorothyrididae Price, 1937 (emend. Gregory, 1950) becomes the correct designation for this group (Reisz, 1980).

Members of the more advanced captorhinomorph family, the Captorhinidae, occur in large numbers in terrestrial strata of Early to Late Permian age from the equatorial Laurasian land mass (Olson, 1952, 1954, 1962; Olson and Beerbower, 1953; Konzhukova, 1956; Heaton, 1979) and have also been found recently on the Gondwana land mass (Taquet, 1969; Kutty, 1972; Gaffney and McKenna, 1979). The captorhinids form a compact group of structurally similar, relatively specialized, slow, heavy-set reptiles. The structural changes that occur in this family include an approximately five-fold increase in size during the Permian and an increase in the numbers of rows of maxillary and dentary teeth.

The fossil record of the more primitive family, the Protorothyrididae, is restricted to a few specimens from the Pennsylvanian and Lower Permian deposits on the North American and European land masses of Laurasia. The known members of this family also form a compact group of structurally similar animals, but, in strong contrast to the captorhinids, the protorothyridids are relatively generalized, small, agile reptiles. Our current understanding of the Protorothyrididae is based primarily on the studies by Carroll (1964, 1969), Carroll and Baird (1972), and Clark and Carroll (1973).

The Pennsylvanian fossil record of this phylogenetically important group of reptiles appears to be restricted in variety and numbers by their preference for dry ground, away from the environments typically preserved during this period. Only as a result of preservation under unusual circumstances are we able to study a few remains of early protorothyridids. Specimens of *Hylonomus lyelli* and *Paleothyris acadiana* have been recovered from inside *Sigillaria* tree stumps that were preserved in standing position near Joggins and Florence, Nova Scotia, respectively (Carroll, 1964, 1969). A single skeleton of *Cephalerpeton ventriarmatum* has been found in an ironstone nodule from Mazon Creek, Illinois (Gregory, 1948, 1950; Carroll and Baird, 1972). Single, nearly complete skeletons of *Coelostegus prothales* and *Brouffia orientalis* from Nýřany, Czechoslovakia, and a poorly preserved, immature skeleton of *Anthracodromeus longipes* from Linton, Ohio, constitute the only protorothyridid material hitherto known from these famous coal-swamp deposits (Carroll and Baird, 1972). Although the coal-swamp faunas of Linton and Nýřany have been studied for more

than a century, and thousands of specimens representing scores of fish and amphibian genera have been collected, only seven specimens of fully terrestrial reptiles have been found. These animals were probably erratics rather than customary members of the aquatic communities with which their remains are associated. The ecologies of the Westphalian coal-swamp deposits in which reptiles occur have been discussed by Westoll (1944), Rayner (1971), and most recently by Milner (1980). A revised list of the tetrapods present at Linton has been published by Hook (1981).

The purpose of this paper is to describe two additional specimens of protorothyridid reptiles that were recently collected at the Linton mine dump by Dr. Richard Lund, together with a previously misidentified specimen in the British Museum collection. Our study was based on high-fidelity latex casts (Baird, 1955) of skeletons preserved as natural molds in carbonaceous shale (Linton) or sideritic mudstone (Mazon Creek).

Abbreviations.—AMNH, American Museum of Natural History; BM(NH), British Museum (Natural History); CM, Carnegie Museum of Natural History; YPM, Peabody Museum of Natural History, Yale University.

Key to abbreviations used in the figures:

a = astragalus	p for = parapineal foramen
ang = angular	pmx = premaxilla
c = calcaneum	po = postorbital
ch = chevron	pp = postparietal
cr = caudal rib	prf = prefrontal
d = dentary	prv = presacral vertebra
f = frontal	ptf = posttemporal fenestra
fib = fibula	q = quadrate
il = ilium	qj = quadratojugal
is = ischium	sa = surangular
j = jugal	scl = sclerotic plate
l = lacrimal	sp = splenial
mt = metatarsal	sq = squamosal
mx = maxilla	st = supratemporal
p = parietal	t = tabular
pf = postfrontal	tib = tibia
	v = vomer

SYSTEMATIC PALEONTOLOGY

Class Reptilia Linnaeus, 1758

Subclass Eureptilia Olson, 1947

Order Captorhina Olson, 1947

Suborder Captorhinomorpha Watson, 1917

Family Protorothyrididae Price, 1937

Cephalerpeton Moodie, 1912

Figured specimens.—CM 23055 (Fig. 1), a crushed, distorted skull; the left premaxilla, maxillae and lacrimals, right frontal and parietal,

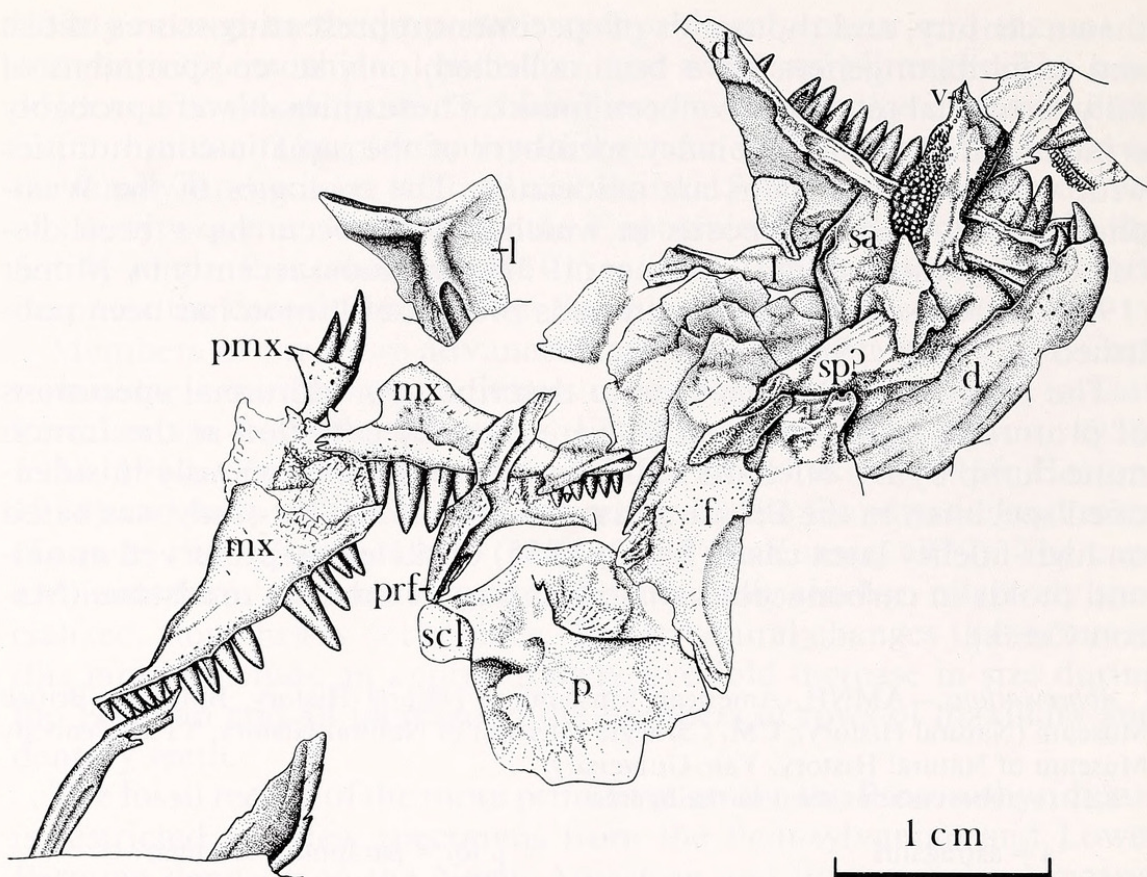


Fig. 1.—*Cephalerpeton* aff. *C. ventriarmatum*, CM 23055, a partial, disarticulated skull.

left prefrontal, right vomer, and a sclerotic plate are identifiable. The mandibles are represented by the dentaries, left surangular, and possibly right splenial. Other skull bones are present but are too badly fragmented for precise identification.

BM(NH) R.2667 (Fig. 2), the anterior part of a right mandible in lingual aspect (purchased as part of the J.W. Davies Collection, 1895). This specimen was mentioned by Steen (1931:885) as the "lower jaw of an *Adelospondyl*."

Description

Skull.—The identifiable portion of the skull CM 23055 resembles the type specimen of *Cephalerpeton ventriarmatum* (YPM 796) in a number of significant features. As in the type specimen, the maxillary process of the premaxilla is short, with places for only three teeth. Although Carroll and Baird (1972) reconstructed YPM 796 with a long maxillary process of the premaxilla, as is the case in other primitive captorhinomorphs, restudy of the premaxilla reveals that only three teeth can be accommodated on this bone. A three-toothed premaxilla

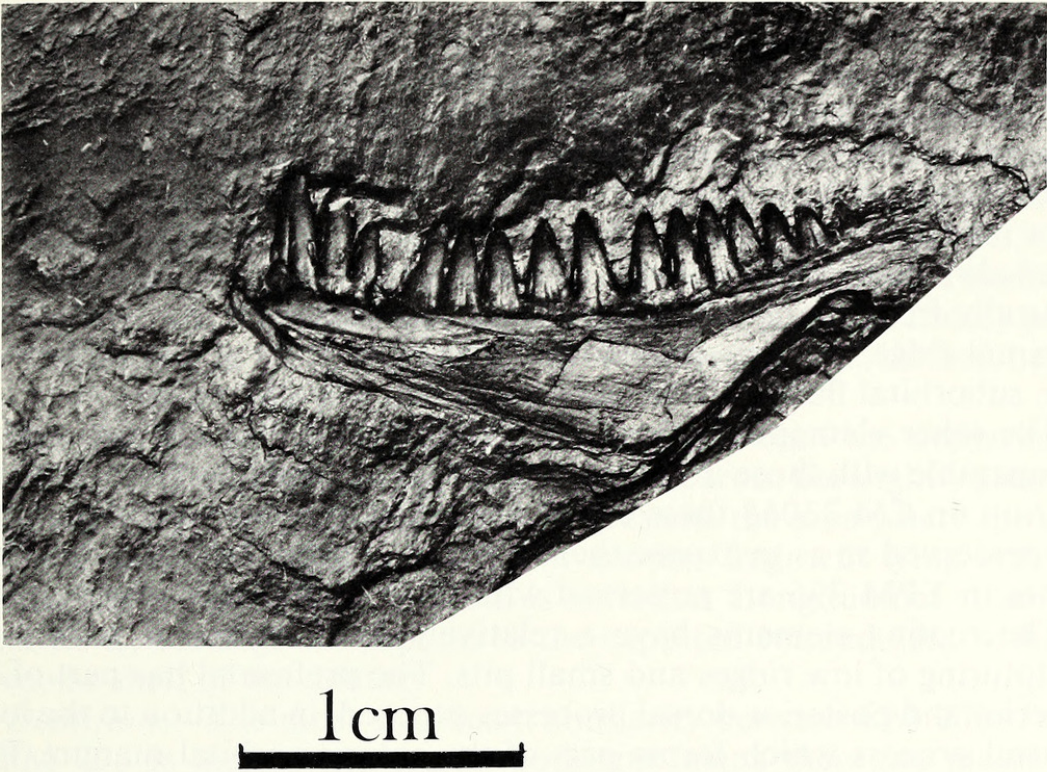


Fig. 2.—*Cephalerpeton* aff. *C. ventriarmatum*, BM(NH) R.2667, right dentary exposed in medial view.

was shown in earlier reconstructions by Gregory (1948, Fig. 2) and Baird (1965, Fig. 6).

The fact that the maxillae are exposed in lateral view in CM 23055, but in partial medial view in YPM 796, makes direct comparisons difficult. In CM 23055 the maxilla, completely separated from the other skull elements, has a large dorsal expansion above the caniniform teeth. The dorsally directed plate of bone is large enough to have extended dorsally to meet the nasal and to have covered the anterior process of the lacrimal that may have extended to the narial opening. In the type specimen of *Cephalerpeton ventriarmatum* the maxillae and lacrimals, exposed in medial view, have remained in articulation so that the external relationship of these bones cannot be established.

The similarity between the left lacrimals in the two specimens, both exposed in medial view, is striking. In YPM 796 the lacrimal duct opens to the interior near the mediodorsal margin of the maxilla and just anterior to the midpoint between the orbit and the external naris. The open groove for the lacrimal duct extends anteroventrally and its ventral margin forms a narrow ridge above the mediodorsal margin of the maxilla. The posterior part of the lacrimal has a long suborbital flange that may have excluded the maxilla from the orbit; much of the

orbital margin of the lacrimal is covered medially by a long ventral process of the prefrontal. The same condition occurs in CM 23055. In this specimen the lacrimal duct is only partly covered by bone. A striated region on the medial surface of the lacrimal just ventral to the open region of the lacrimal duct indicates that this area was covered by a medial shelf of the maxilla to give the same arrangement as in *Cephalerpeton ventriarmatum*. A long groove in CM 23055 extends ventrally from the dorsal tip of the orbital margin to the level of the lacrimal ridge; this groove held the ventral process of the prefrontal. The suborbital flange of the lacrimal is also well developed.

The other elements of the skull roof in CM 23055 are not readily comparable with those in the type specimen of *Cephalerpeton ventriarmatum*. In CM 23055 these elements (prefrontal, frontal and parietal) are preserved so as to expose their external surfaces, whereas the same bones in YPM 796 are preserved with their medial surfaces exposed.

The roofing elements have a relatively well developed pattern of sculpturing of low ridges and small pits. The prefrontal has part of its anterior and posterior dorsal processes exposed, in addition to the long ventral process which forms part of the anterior orbital margin. The frontal has a pair of well developed, long grooves along its lateral margin for the attachment of the prefrontal and postfrontal. Between these grooves the frontal has a short, laterally directed process that forms part of the dorsal orbital margin. The medial margin of the badly crushed right parietal is overlapped by the frontal; its features are analyzed in detail in a subsequent section. Overlapping the postero-lateral corner of the parietal is a sclerotic plate that is similar to those preserved in YPM 796; it is a thin, subrectangular bone with a bevelled edge.

Mandible.—Parts of the mandibles preserved in CM 23055 include both dentaries and fragments of the right surangular and splenial. Although both dentaries are partially covered by surrounding elements, sufficiently large portions of the left medial and right lateral surfaces are exposed to describe this element. The dentary is unusually deep dorsoventrally throughout its length. In association with this unusual depth, the anterior portion of the dentary near the symphysis is somewhat more massive than in other protorothyridids of similar size; more significantly, the dentary is twice as deep dorsoventrally at the level of the twelfth tooth than at the third. Although all skull elements are severely crushed, preservation cannot account for the unusual proportions of the dentary. The dorsal edge of the dentary is concave in lateral view, providing additional evidence of the unusual depth of the mandible in the posterior half of the dentary, and probably in the rest of the mandible. The alveolar shelf is also unusually large, as exposed on the left dentary, and its sutural surface with the splenial is extensive.

Only the left dentary is sufficiently exposed to indicate that it had places for 17 or 18 teeth. The thirteenth tooth of this dentary has been figured by Currie (1979, Fig. 13b), greatly magnified, to illustrate the pattern of vertical lingual striations on teeth of most Paleozoic reptiles. A nearly complete right dentary is exposed in medial view in BM(NH) R.2667 (Fig. 2). This element is identical to the left dentary of CM 23055, showing the typically deep subalveolar expanse of bone, and the large teeth with infolding of the enamel. As in CM 23055, there is only place on the dentary of BM(NH) R.2667 for seventeen teeth. Unfortunately the symphysis is not preserved.

The right surangular is partially exposed between the dentaries of CM 23055. Gentle striae on its surface radiate from the slightly grooved dorsal margin; the groove probably represents the area where the coronoid attached. The identification of another fragment lying between the dentaries as the right splenial is tentative. Longitudinal striations near its dorsal edge correspond to the expected sutured area with the alveolar shelf of the dentary.

Dentition.—The most significant similarity between CM 23055 and YPM 796 is their dentition. In both specimens there are places for three premaxillary and 16 maxillary teeth. This is far below the number in other primitive captorhinomorphs—*Hylonomus* has a dental formula of $5 + 36$, *Paleothyris* has $6 + 35$, and *Protorthyris* has $5 + 30$ (Carroll and Baird, 1972; Clark and Carroll, 1973). In both specimens the first premaxillary tooth is large, roughly equal to the caniniform tooth on the maxilla, and much larger than in other primitive captorhinomorphs. The larger teeth show some infolding of the enamel. The palatal dentition is also quite similar in the two specimens, with closely packed small denticles covering most of the vomers.

Discussion

Similarities between CM 23055 and BM(NH) R.2667 from the Middle Pennsylvanian (late Westphalian D) deposit at Linton, Ohio, and YPM 796 from a slightly older horizon (early Westphalian D) at Mazon Creek, Illinois, indicate that these reptiles can be placed in the same genus. There are, however, some significant features that distinguish the Linton specimens from *Cephalerpeton ventriarmatum*. The preserved portion of the dentaries in CM 23055 and BM(NH) R.2667 demonstrates that the lower jaw was deeper dorsoventrally than the corresponding portions of the lower jaw in *C. ventriarmatum*. The teeth on the lower jaws of the Linton specimens are also larger and fewer in number than those of *C. ventriarmatum*. In the latter species the teeth on the dentaries are not substantially different from those in other protorothyridids, but there are places for only 21 or 22 teeth on the dentary, a much lower number than in other genera (Carroll and Baird,

1972). The dentaries of the skull from Linton (CM 23055) have places for no more than 18 large teeth (the exact number is uncertain), whereas the British Museum dentary has 17 (with possibly one more concealed at the posterior end). In these features the Linton specimen appears even more advanced than *C. ventriarmatum*. These differences are compatible with a postulated ancestor-descendant relationship in which the geologically older species is understandably more primitive in certain osteological features.

Anthracodromeus Carroll and Baird, 1972

Figured specimen.—CM 25282 (Fig. 3), consisting of one dorsal and ten caudal vertebrae, caudal ribs, chevron bone, scattered ventral scales, and parts of the pelvic girdle and hind limbs.

Description

CM 25282 includes a single posterior dorsal vertebra which has the general proportions characteristic of all protorothyridid captorhinomorphs. The centrum is a relatively long, low cylinder, pinched in at the middle. The neural arch is not swollen, and the neural spine is relatively tall and blade-like. The shape of the neural spine is remarkably similar to those of the dorsal vertebrae in the type specimen of *Anthracodromeus longipes* (AMNH 6940). As shown by Carroll and Baird (1972), neural spines of the dorsal vertebrae are hatchet-shaped, expanding anteroposteriorly from normal-sized bases to wide summits. This feature of the neural spines distinguishes *Anthracodromeus* from all other protorothyridids.

The lateral surfaces of the neural spines in the type specimen of *Anthracodromeus longipes* have a peculiarly “sculptured” or “hammered” appearance. In our opinion this very unusual feature can be accounted for by the poor ossification and manner of preservation of the type skeleton (which is obviously that of a very immature animal). In such a juvenile individual the perichondral bone sheathing the neural spines would be so thin that, when subjected to severe compression (as is typical in Linton material), it would become imprinted with the spongy texture of the interior. CM 25282 is nearly twice as large as the type specimen and is well ossified, so crushing during preservation has not produced the same appearance on its neural spines.

Seven anterior caudal vertebrae are preserved in nearly perfect articulation. Although they are incomplete, significant osteological features can be determined: The ratio of the length to posterior height of the centrum is almost 2:1. The centra have diminished in diameter, indicating that the tail was probably long and slender. The neural arches are long, narrow structures with slender zygapophyses and relatively tall neural spines. The best preserved neural spine, seen on the sixth

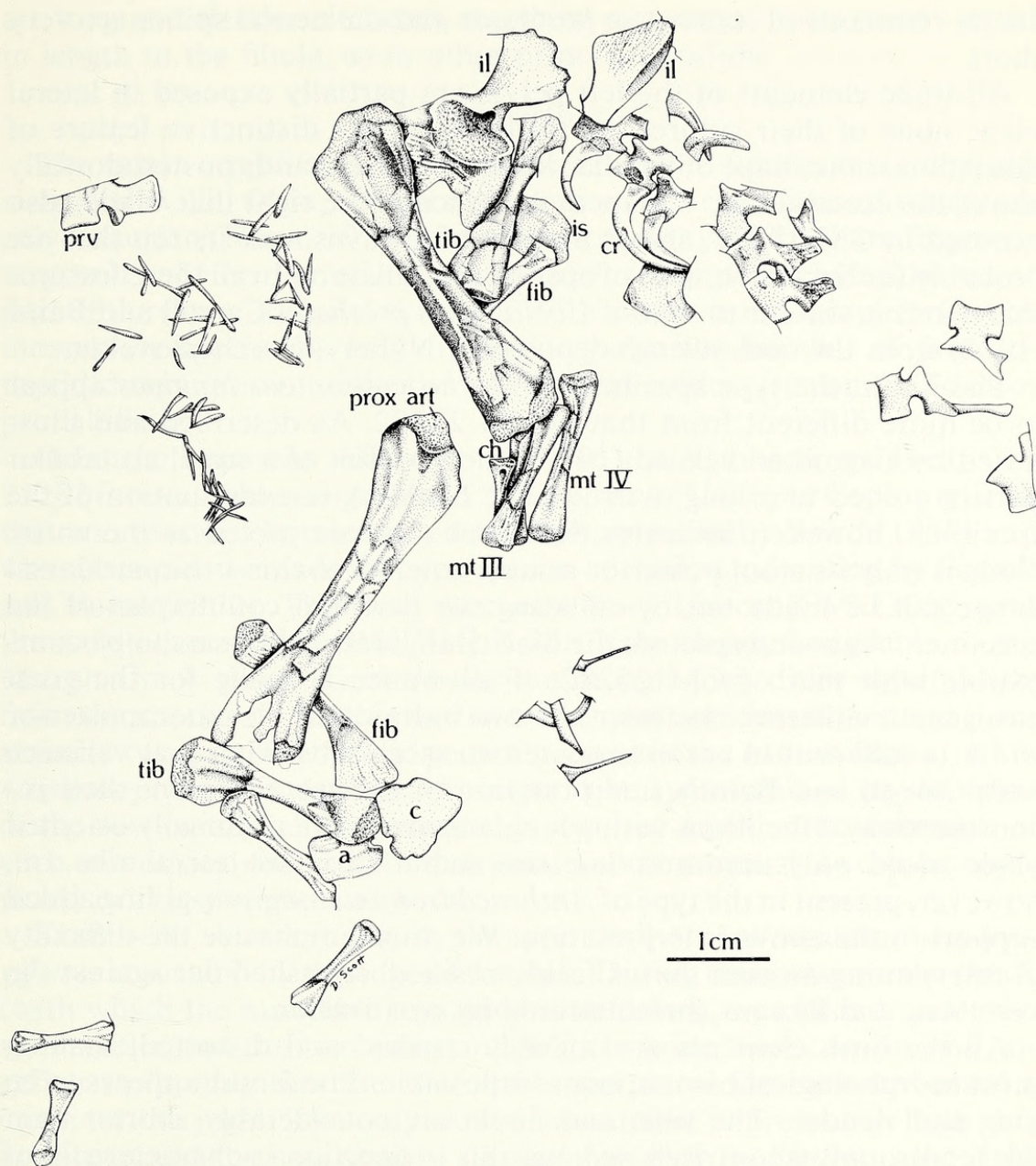


Fig. 3.—*Anthracodromeus longipes*, CM 25282, scattered vertebrae, pelvis, hind limbs, and scattered ventral scales.

vertebra of the series, has the same height as that of the isolated dorsal vertebra, but its profile tapers upward so that its summit is less than half as expanded as that of the dorsal vertebra. The three most anterior vertebrae of the series have well developed transverse processes for the posteriorly curved caudal ribs. The two most posterior vertebrae have short, small lateral stumps on the centra which probably represent transverse processes. Three isolated caudal vertebrae are probably from the mid-portion of the tail; their centra are still quite long, but there

are no remnants of transverse processes and the neural spines are very short.

All three elements of the left pelvis are partially exposed in lateral view; none of their sutures is visible. The only distinctive feature of this pelvis is the shape of the iliac blade, which expands posterodorsally above the acetabulum. The medial surface of the right iliac blade, also exposed in CM 25282, shows a series of grooves near its top that are probably for the attachment of epaxial musculature. In all these features this pelvis is similar to that of *Coelostegus prothales* Carroll and Baird (1972) from the coal-swamp deposits of Nýřany, Czechoslovakia.

The ilia in the type specimen of *Anthracodromeus longipes* appear to be quite different from that of CM 25282. As described and illustrated by Carroll and Baird (1972), they consist of a small acetabular portion joined to a long, narrow iliac blade. A re-examination of the specimen, however, indicates that what was interpreted as the entire blade is only its stout posterior ramus; anterior to this a thinner dorsal flange can be made out by collating the part and counterpart of the specimen. As re-interpreted, the iliac configuration appears to be compatible with that of CM 25282, if allowance is made for the great ontogenetic difference between the two individuals; its anteroposterior width is sufficient to accommodate two sacral ribs. This is at variance with Carroll and Baird's interpretation of the sacral region; their reconstruction of the ilium with a long, narrow, posterodorsally oriented blade could only accommodate one sacral rib. Two sacral ribs are, however, present in the type of *Anthracodromeus longipes*, giving added support to the above interpretation. We must emphasize the difficulty of interpreting an area that is feebly ossified, squashed flat against the vertebrae and femora, and obscured by pyritization.

All the limb elements are strongly crushed and distorted, making most morphological comparisons impossible. The femur appears to be long and slender. The tibia and fibula are considerably shorter than the femur, only about 56% as long; this proportion is characteristic of protorothyridids. The tibia has a wide proximal head and a slightly narrower distal end. The proximal end of the fibula appears narrow, whereas the distal end is broad and blade-like. The calcaneum, as in *Paleothyris*, (Carroll, 1969) is distinctive in having a distolateral notch. This notch, not found in other primitive reptiles, separates the distal surface of articulation with the fourth and fifth distal tarsals from the lateral edge of the calcaneum. The astragalus is partially obscured by the tibia, but it was undoubtedly L-shaped. The size of the distal end of the fibula indicates that the proximal fibular articulation of the astragalus was smaller than the tibio-astragalar articulation and that the neck of the astragalus was narrow, as in *Paleothyris*. The metatarsals

are long and slender elements, the third metatarsal being nearly equal in length to the fibula, as in other protorothyridids.

Comparisons

The total eureptilian sample known from the Linton mine deposit, near Wellsville, Ohio, consists of seven specimens, three of which are pelycosaurian (Reisz, 1975) and four protorothyridid; all are fragmentary, and only the type of *Anthracodromeus longipes* includes the major part of the (very juvenile) skeleton. With such a small sample and such incomplete specimens it is difficult to judge the number of protorothyridid taxa present, either on anatomical evidence or on the basis of probabilities.

Once the apparent difference between ilia has been resolved, CM 25282 is reasonably assignable to "*Sauropleuria*" *longipes* Cope, a species that was tentatively transferred to *Cephalerpeton* by Baird (1958) and was subsequently made the type species of *Anthracodromeus* by Carroll and Baird (1972). The skull specimen from Linton (CM 23055) and the isolated mandible (BM[NH] R.2667) are clearly assignable to the Mazon Creek genus *Cephalerpeton* although they differ significantly from the species *C. ventriarmatum*. The question thus arises: are there actually two protorothyridid genera present in the Linton fauna, or are *Cephalerpeton* and *Anthracodromeus* to be synonymized on the basis of the new evidence? To answer this requires a further examination of such anatomical features, both cranial and postcranial, as can be compared in the specimens at hand.

Skull.—As shown in Fig. 4, the type skull of *Anthracodromeus longipes* is truncated by the edge of the slab. During compression the cheek (with which the mandible remained articulated), was folded under the skull table, and the two sheets of delicate bone were compressed together so forcibly that the rim of the parapineal foramen embossed a circle on the jugal. The only skull element that is present in both this specimen and the new skull of *Cephalerpeton* from Linton is the right parietal.

In the latter specimen (Fig. 1), the disarticulated parietal lies with its dorsal surface uppermost and its anteroposterior axis pointing toward five o'clock; its medial margin is overlapped by the frontal so that only part of the heavily-rimmed parapineal foramen is exposed. The posterior margin of the parietal, which faces the prefrontal as the specimen lies, has its sculptured surface rabbeted by two semicircular embayments for the articulation of overlapping elements. These rabbets are floored by a posterior continuation of the parietal, as is indicated by the way the striations radiate from the center of ossification. This posterior configuration of the parietal is similar to that seen in *An-*

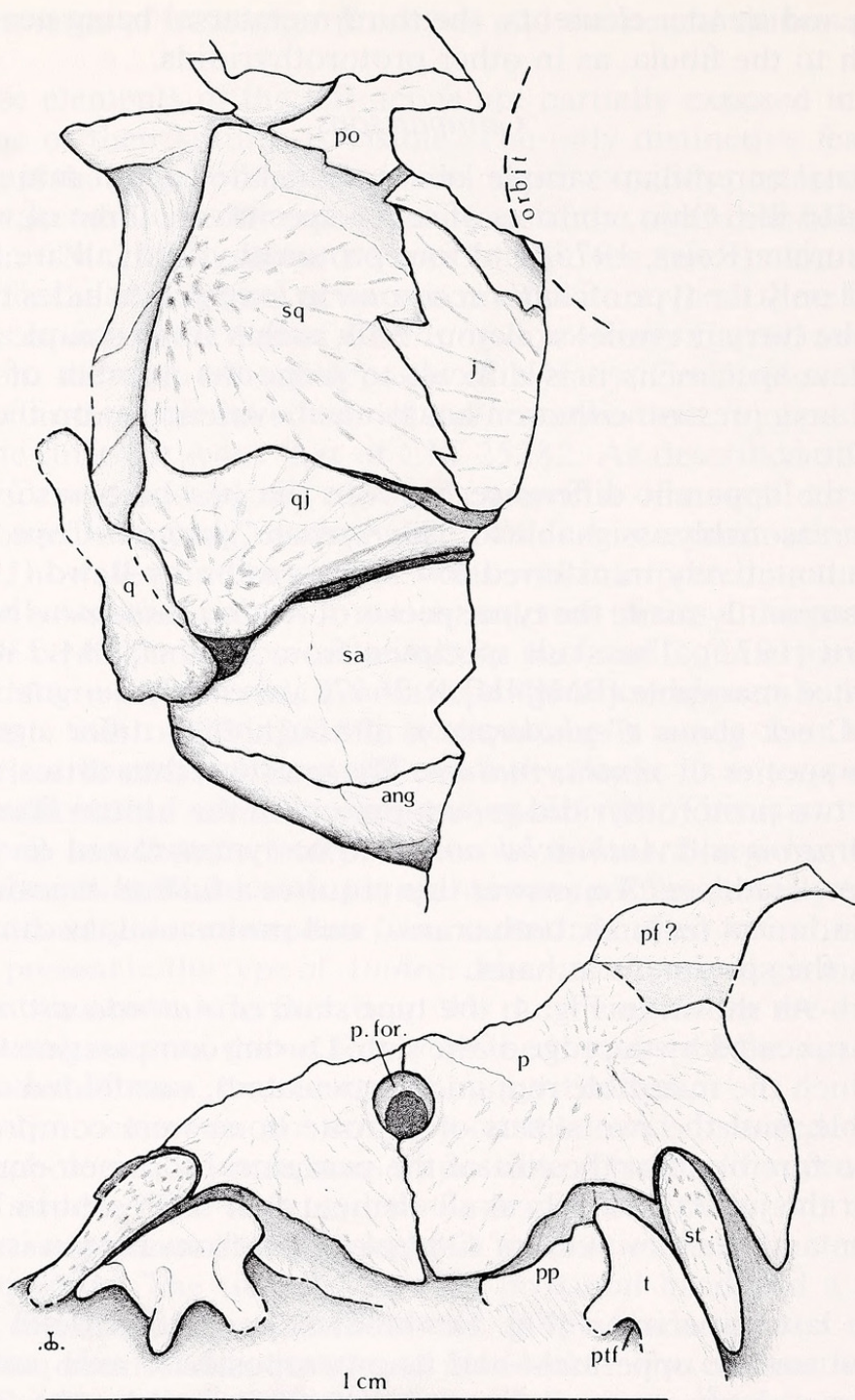


Fig. 4.—*Anthracodromeus longipes*, AMNH 6940, partial skull from holotype skeleton, part and counterpart.

thracodromeus longipes (Fig. 4), where the more lateral embayment accommodates the supratemporal, while the more medial one, which is doubly curved, accommodates both the postparietal and the dorsal process of the tabular. On the anterior margin of the parietal, in CM

23055, are shallow articular facets for the overlapping frontal and post-frontal, and on the anterolateral corner is one for the postorbital. The long parietal lappet seen in *A. longipes* is not in evidence in CM 23055, but this area is concealed by a sclerotic plate.

The parietal of CM 23055 has all the landmarks of the corresponding elements in the protorothyridid genera *Hylonomus*, *Brouffia*, *Coelostegus* and *Paleothyris*, although it differs significantly from them in proportions, being conspicuously short relative to its width. In the type of *C. ventriarmatum* the shape of the parietal has had to be reconstructed from the configuration of the surrounding elements (Carroll and Baird 1972, Fig. 2). The restoration shows it as broader than it is long; but a reconsideration of the palate indicates that the skull has been made too wide in this region. Thus the true proportions of the parietal in *C. ventriarmatum* are too conjectural for valid comparisons to be made. Similarly, in the type of *A. longipes* the parietal has been reconstructed as broad and short (Carroll and Baird 1972, Fig. 5); but as the anterior part of the bone is missing, its actual proportions remain uncertain. Thus the parietal, the only cranial element that permits the two skulls from Linton to be compared with the one from Mazon Creek, is too incompletely preserved to provide a sound basis for taxonomic judgement.

The cheek region is similar in the type specimens of *C. ventriarmatum* and *A. longipes*. It differs from the cheeks of other Pennsylvanian protorothyridids in being short anteroposteriorly. This shortening of the cheek would be consistent with a shortening of the skull table (for which, as noted above, direct evidence is lacking).

Mandible.—The only part of the mandible that can be compared directly in CM 23055 and the type of *A. longipes* is the posterodorsal area of the surangular. In both these specimens the mandible appears to be slightly deeper than in other protorothyridids. Given the incomplete nature of the cranial remains of these specimens little reliance can be placed on small proportional differences. In the type of *Cephalerpeton ventriarmatum* the lower jaw does not appear to be deeper than in other protorothyridids; this condition corresponds to the relatively unspecialized mandibular dentition present in this species.

Vertebrae.—As *Anthracodromeus* has been said to differ from *Cephalerpeton* in having hatchet-shaped neural spines and elongate limbs, these postcranial characters require reexamination. In the type specimen of *C. ventriarmatum* the neural spines are preserved only on the axis and the seven succeeding vertebrae, so our comparisons must be restricted to this region. Only in vertebrae 7 through 9 are the profiles of the neural spines clearly recorded: here the summits of the spines are *not* expanded anteroposteriorly. In the more anterior cervicals the situation is less clear. In the corresponding region of the type specimen

of *A. longipes* the neural spines are irregular and their summits expanded, but to a lesser extent than those of the more posterior vertebrae (compare Figs. 1 and 4A in Carroll and Baird 1972). Thus the difference, though real, is not great, and it may be accentuated by the fact that the first specimen is three-dimensionally preserved while the second is crushed paper thin.

Forelimb.—In the type of *A. longipes* the humerus is 8 trunk-centra long; it articulates closely with a radius and ulna that are at least 5 trunk-centra long. The ends of all these elements are convexly rounded. In *C. ventriarmatum* an impression of the fleshy forelimb surrounds the bones, so their relative positions are probably close to natural. The humerus is 6.7 trunk-centra long; it is separated by a gap from a radius and ulna that are 4.7 trunk-centra long, and these in turn are widely separated from the metacarpals. The gaps between the bones are plain evidence of incomplete ossification. The ends of the limb bones are concave, indicating that the type of *C. ventriarmatum* may have been even more immature than the type individual of *A. longipes*. This difference in levels of ossification may account for the differences in limb proportions. On the other hand, the vertebrae of *A. longipes* appear to be more severely compressed than those of *C. ventriarmatum*. This difference in crushing would tend to impart greater apparent length to the centra of *A. longipes*, giving a falsely low limb to vertebral length ratio of this long limbed form. These probable differences in levels of ossification, preservation and compression, make comparisons between limb to central length ratios difficult.

The foregoing comparisons lead us to conclude that, although there are similarities between the type species of the nominal genera *Cephalerpeton* and *Anthracodromeus*, the evidence to justify a positive statement of synonymy or non-synonymy is either lacking or ambiguous. This is partly because the Protorothyrididae are inadequately represented in the fossil record, the morphological variation of particular taxa is unknown, and the known specimens are difficult to compare as a result of their fragmentary nature. It is not possible, therefore, to differentiate the morphological similarities that are indicative of relationships at the familial level from those that are indicative of relationships at generic or specific levels. In such a doubtful case the taxonomically *parsimonious* course would be to opt for a tentative synonymy, while the *conservative* course would be to retain both generic names until further evidence is forthcoming. Lacking strong convictions either way, we choose the second course. Rare though these reptiles are, their source localities are still yielding specimens to diligent collectors; so we may reasonably hope that future finds will clarify the issue.

In the preceding pages we have demonstrated the presence at Linton of a reptile that is unquestionably assignable to *Cephalerpeton* although it differs from *C. ventriarmatum* in species-level characters. In view of the possibility that this species may prove to be Cope's "*Sauropleura*" *longipes* we refrain from proposing a new specific name, but merely designate it as *Cephalerpeton* aff. *C. ventriarmatum* to indicate its distinctness from the type species.

REVISED DIAGNOSES

Cephalerpeton Moodie, 1912

Type species.—*Cephalerpeton ventriarmatum* Moodie, 1912

Diagnosis.—Protorothyridid captorhinomorph reptile characterized by short cheek, dorsally enlarged maxilla, very large marginal teeth with plicate enamel, reduced dental formula of three premaxillary and 16 maxillary teeth, heavily denticulated vomer, and long limbs.

Cephalerpeton ventriarmatum Moodie, 1912

Diagnosis.—Mandibular dentition relatively unspecialized; mandible shallower, with 21 or 22 teeth.

Horizon.—Ironstone nodules of Francis Creek Shale overlying Number 2 (Wilmington or Colchester) Coal, Carbondale Formation, Allegheny Group, Middle Pennsylvanian (early Westphalian D).

Locality.—Banks of Mazon Creek, Grundy County, Illinois.

Cephalerpeton aff. *C. ventriarmatum*

Diagnosis.—Shorter maxillary enclosure of lacrimal duct than in *C. ventriarmatum*; dentition more specialized with relatively larger teeth; dentary deeper, with place for 17 teeth.

Horizon.—Carbonaceous shale underlying Upper Freeport Coal, Freeport Formation, Allegheny Group, Middle Pennsylvanian (late Westphalian D).

Locality.—Diamond Mine (Linton) near Wellsville, west bank near mouth of Yellow Creek, Saline Township, Jefferson County, Ohio: NE corner Sect. 13, T9N, R2W.

Anthracodromeus Carroll and Baird, 1972

Type species (monotypic).—*Sauropleura longipes* Cope, 1874.

Diagnosis.—Protorothyridid captorhinomorph reptile characterized by short cheek, hatchet-shaped dorsal neural spines, and very long limbs and feet.

Horizon and locality.—As for *Cephalerpeton* aff. *C. ventriarmatum*.

LIFE HABITS

Protorothyridid captorhinomorphs are considered to have been small, agile, terrestrial animals that fed largely on arthropods (Carroll, 1969; Carroll and Baird, 1972). Their gracile bodies, long limbs and high degree of ossification of the skeleton in the better known genera imply that protorothyridids were agile runners and tree climbers like the extant small, terrestrial and arboreal lizards. A terrestrial habitat is also suggested by the occurrence of the Pennsylvanian protorothyridids *Hylonomus* and *Paleothyris* in the hollows of upright *Sigillaria* stumps at Joggins and Florence, Nova Scotia. Too much should not be made of this point, however, for the same trees contain skeletons of evidently amphibious or aquatic labyrinthodonts—the edopoid *Dendrerpeton* and the embolomere *Calligenethlon* at Joggins, the edopoid *Cochleosaurus* and an unnamed embolomere at Florence (Museum of Comparative Zoology material).

Dietary habits of Paleozoic reptiles are difficult to establish in the absence of direct evidence, such as stomach contents. Speculations on preferred diets are generally based upon the known contemporaneous faunas as well as the skeletal morphology and dental patterns of the forms in question. It is generally assumed that the protorothyridids were insectivorous, although comparisons with modern lizards indicate that they were probably capable of preying on a variety of small terrestrial animals, including tetrapods. The marginal dentition seen in *Cephalerpeton* is considerably larger and more robust than those of other protorothyridids or of modern insectivorous lizards. The size and morphology of its skull and dentition indicate that *Cephalerpeton* was able to feed not only on arthropods, but also upon smaller terrestrial vertebrates, such as some of the lepospondyl amphibians, or young individuals of protorothyridids. An appropriate menu of insects occurs in association with the reptiles in the Mazon Creek and Nýřany deposits. At Linton, however, insect remains are absent, although the fauna includes infrequent specimens of more heavily sclerotized arthropods, such as diplopod myriapods (Baird, 1958a; Hoffman, 1963), and a pygocephalomorph crustacean (Brooks, 1962:199). It seems likely that the robust dentition of *Cephalerpeton* was able to deal with relatively hard-shelled arthropods of this sort. Myriapods are among the more common terrestrial arthropods in the Braidwood fauna of Mazon Creek, and many of them, such as *Euphoberia* and *Acantherpestes*, have spinescent exoskeletons that presumably developed as a defense against predation (Rolfe, 1980; Hannibal and Feldmann, 1981). The number of terrestrial predators against which such defenses might have evolved is limited, but it includes the dissorophid labyrinthodonts (Carroll, 1964), terrestrial microsaurs such as *Tuditanus* (Carroll and Baird, 1968), the smaller pelycosaurs (Reisz, 1972, 1975), and the protorothyridids.

On the other hand, millipedes are notoriously deliberate pedestrians, probably requiring little speed or agility to catch. As *Anthracodromeus* obviously had both a slender, lightly built body and long limbs it was able to capture agile invertebrates such as the fleet and nimble cockroaches (Blattaria) that abounded in fossil localities of Westphalian age. Although not preserved at Linton, cockroaches are plentiful in the Mazon Creek sediments where they constitute 21% of the insect fauna (Richardson, 1956). It seems most likely that these specialized prothorothyridids had evolved their long limbs more as adaptations for predation than as a means to escape from predation. Their potential predators, primarily the haptodontine and ophiacodont pelycosaurs, were evidently much less agile than *Anthracodromeus*.

In addition to long legs, *Anthracodromeus* had feet that are remarkable for their length and areal extent when compared to its slight body weight. Both manus and pes are almost completely represented in the type specimen and have been reconstructed by Carroll and Baird (1972: Fig. 5). Although in life the feet would have been more compact laterally and the metapodials less splayed-out than they appear in that reconstruction, the reptile was doubtless able to scamper over boggy or muddy surfaces where other tetrapods would have become mired.

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