A NEW LIMBLESS VERTEBRATE FROM THE PENNSYLVANIAN OF MAZON CREEK, ILLINOIS

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ABSTRACT. A well preserved aistopod skeleton is described from the Pennsylvania shale of Mazon Creek, Illinois. Noteworthy features are the extensive fenestration of the skull roof in the temporal region, highly ossified braincase, large orbits with narrow interorbital septum, forwardly placed jaw articulation, broad epipterygoid, relatively large otic capsules, large stapedial plate, and differentiated cervical vertebrae. Phlegethonitia was probably snake-like in habits rather than fossorial or aquatic. The Aistopoda are regarded as Reptilia rather than Amphibia, and are placed in the Microsauria as a specialized suborder.

A HITHERTO undescribed dolichosomid in the Lacoe collection of Mazon Creek nodules in the United States National Museum was brought to my attention by Dr. David Dunkle, who generously placed it at my disposal for study and description. Details of skull structure preserved in this specimen throw new light on the affinities and probable habits of the Aistopoda. Dr. E. H. Colbert and Mrs. Rachel H. Nichols have kindly assisted in this study by permitting me to examine Cope's types from Linton, Ohio, in the American Museum of Natural History. Dr. Karl M. Waagé kindly read the manuscript. Drawings of the vertebrae and the restoration of the skull were made by Miss Shirley Glaser.

Class Reptilia
Infraclass Captorhina
Order Microsauria
Suborder Aistopoda
Family Dolichosomidae
Genus Phlegethonitia Cope 1871

Phlegethonitia mazonesis n. sp.


Type locality: Mazon Creek, near Morris, Grundy County, Illinois.

Horizon: Roof shales of the Morris, or No. 2, or Colchester Coal which forms the base of the Carbondale formation, Alleghany series, Pennsylvanian system, in Illinois. It lies at the base of the Neuropteris flexuosa zone, Floral zone H of Dix, equivalent to the Westphalian D of western Europe.

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Diagnosis: Smaller than *P. linearis* Cope. Vertebrae more elongate and slender. Orbit relatively larger.

**DESCRIPTION**

Skull and articulated skeleton of this small, snake-like animal are preserved as almost uncrushed molds filled with remains of the bone and finely crystalline white kaolinite.¹

Text-Fig. 1. *Phlegathonia mazonensis* n. sp., lateral views of skull as preserved, drawn from photographs of latex casts, x 5. A, left side, including anterior dorsal vertebrae and hyoid. B, right side. I1 optic foramen. V trigeminal foramen. EP epipterygoid. FR frontal. H hyoid. JU jugal. LA lacrimal. M, mandible. MX maxillary. PA parietal. PAS parasphenoid. PF postfrontal. PRF prefrontal. PT pterygoid. PX premaxillary. Q quadrate. QJ quadratojugal. SPE sphenethmoid. ST stapes. The left maxillary and jugal are visible in both views.

An impression of the soft tissues surrounds the skeleton. The preserved specimen is about 156 mm. long along the curve of the backbone, and may have been slightly longer in life as the end of the tail is not preserved. There are no traces whatever of limbs or limb girdles. The animal has the highly ossified braincase and forward jaw suspensorium characteristic of

¹Prof. Horace Winchell kindly determined the composition of the white powder which fills the cavities in the Mazon Creek fossils from a sample taken from this specimen. An X-ray powder reflection pattern diagnostic of Kaolinite was obtained. The index of refraction is 1.56 with very low birefringence.
burrowing reptiles and amphibians, but retains large eyes and has a slender, snakelike lower jaw.

**SKULL**

The skull (Text-Figs. 2, 3) is elongate and narrow. Its roof is of nearly uniform width from the most anterior point preserved back to the otic region where it rapidly widens. The dorsal profile is gently convex over the orbit and nasal region, flat above the braincase, and rises slightly at the posterior end to a strong transverse crest which separates the skull roof and occiput. Side walls of the braincase are as fully

![Diagram of skull](image)

Text-Fig. 2. *Phlegetontia mazonensis* n. sp. Restoration of skull, x 10. A, dorsal aspect, B, palatal aspect. Abbreviations as in fig. 1.

ossified as in snakes, and there appears to have been extensive reduction of the skull roof in the temporal region. The orbits lie slightly anterior to the center of the skull and contained large eyeballs protected by sclerotic plates.

The short lower jaw articulates with the skull anterior to
the otic region, so that it is narrower than the head. The rami of the jaw are slender throughout and bear conical teeth anteriorly. Small teeth are also present on the maxillae. As the anterior end is not exposed, the length cannot be stated;

from front of nasal to parietal crest the length is 7.2 mm.; width between orbits 0.7 mm.; width across otic capsule 3.1 mm.
Roofing bones: No median suture can be observed on nasals and frontals, which are separated by a straight transverse suture above the front edge of the orbit. These bones are of equal width, are slightly curved longitudinally and flat transversely, and are confined to the roof of the skull. Above the orbits the frontals narrow to slightly less than the width of the nasals; posteriorly they widen slightly to a weak postorbital process and then gradually narrow to the cordate posterior termination above the middle of the braincase. Distinct temporal ridges converge posteriorly from the postorbital processes, lateral to these the frontal curves away toward the side of the braincase; anterior to the ridges the surface of the frontal bears ornamentation of short, longitudinal ridges. This pattern extends onto the nasals. A distinct groove lies above each orbit, close and parallel to its margin.

Behind the frontoparietal suture the braincase consists of a single bone whose component ossifications no longer can be distinguished. There is no pineal foramen. The parietals curve smoothly downward around the braincase. This curved wall extends forward lateral to the frontals to a point beneath the postorbital process and then turns inward. Its anterior extent is concealed by the sclerotic plates; ventrally it is continuous with the ossified interorbital septum. In the temporal region the side walls continue downward to the basicranium. Posteriorly they curve outward to include the relatively enormous otic region.

The skull roof is bounded posteriorly by an abrupt occipital crest which runs outward from its median apex at right angles to the axis of the skull. It curves back slightly upon reaching the auditory capsules, following the contour of the back of the skull for a short distance, and then continues directly outward to the edge of the skull above the paroccipital processes.

Circumorbital series: Dorsally, the frontal borders the orbit extensively. A small prefrontal has very little orbital exposure. Below it lies a larger lacrimal which, on the right side, can be observed to extend downward nearly if not entirely to the lower limit of the orbit, and to curve back beneath its anterolateral border. The large three-pronged jugal bounds the orbit behind and below and has a low process reaching backward toward the quadrate. Its surface is lightly sculptured. Above
its postorbital process there are indications of bones connecting with the postorbital process of the frontal (Text-Fig. 1), but the extent of these is not determinable without destroying important portions of the specimen. It is not known whether both postorbital and postfrontal were present, or but one of them. Such evidence as could be obtained by probing the cavity at the back of the orbit suggests that the orbit was bounded posteriorly by only a slender rod of bone.

**Temporal region:** On the left side of the specimen crushed fragments of a slender quadratojugal extend from the zygomatic process of the jugal to the quadrate. The squamosal is represented by fragments of a plate extending upward outside of the quadrate from its condyle nearly to the level of the top of the otic capsule. These obviously extended farther, but the extent to which the cheek region was covered by bone remains unknown. The nature of the parietal surface definitely precludes a completely roofed skull such as is found in normal stegocephalians or cotylosaurs. The opening for the temporal muscles lies above jugal and squamosal and below the frontals and parietals; it has homologous boundaries with that of advanced synapsids, or certain cryptodire turtles, or possibly with that of the Euryapsid reptiles (Proterosauria, Sauropterygia). In all probability it is a convergent, independent, development.

**Braincase:** Almost no sutures are present between the bones of the neurocranium. In the following description names of ossifications normally present will be used sometimes to designate the area where their development would be expected, rather than to signify that such elements have actually been identified in the specimen.

The occipital surface (Text-Fig. 4) presents a deep central pit within which lies the foramen magnum, flanked on either side by the backwardly projecting otic capsules. These project below the level of the basicranium as rounded swellings on the ventral surface in a fashion suggestive of mammalian bullae. Otherwise the outline, seen from behind, is roughly triangular, much broader at the base than in altitude.

The small basioccipital, bearing a deep, conical notochordal pit 0.3 mm. in diameter, joins the ventral margins of the otic blocks. Dorsally, the occipital crest likewise connects these structures. No details are visible in the median pit; presence
of supraoccipital and extent of exoccipitals, if distinct, are unknown. Rounded ridges covering the posterior and horizontal semicircular canals run forward from their junction at the most posterior point of the skull, directly lateral to the condyle. The former rises and passes forward to its junction with the occipital crest; the latter is directed outward toward the paroccipital process which marks the outer angle of the triangle. A shallow fossa lies above and lateral to these ridges, behind the occipital crest.

Text-Fig. 4. *Phlegethontia mazonensis* n. sp. Restoration of skull, x 10. Occipital aspect. FM foramen magnum. C condylar pit. POP paroccipital process. TU tubera basisphenoidalis (?). Other abbreviations as in fig. 1.

Dorsally the otic capsule is confluent with the parietal roof of the braincase in a smooth reëntrant depression which runs backward and slightly inward from near the head of the epipterygoid toward the apex of the occiput. The thin occipital crest (Text-Fig. 5, OCC.) crosses its top, and a conspicuous rounded ridge (AC) marks the course of the anterior canal; in front of this the surface curves downward behind the pterygoid. Laterally, the ridge covering the external semicircular canal (Text-Fig. 5, LC.) projects sharply in line with the occipital crest, and turns down at a strong angle in front, toward the quadrate. This ridge separates the dorsal and ventral surfaces of the capsule, the lower sloping up toward it much as the upper does. The ventral profile is rounded, projecting somewhat below the level of the palate, its lowest point just in front of the fenestra ovalis.

The ventral surface of the capsule is occupied largely by a relatively enormous fenestra ovalis which is directed slightly outward and backward, and completely filled by the stapedial foot (Text-Fig. 2B, ST.). It is rounded pentagonal in outline, with the posterior border longest and nearly straight, transverse to the skull axis. The medial border extends slightly
farther anteriorly than the lateral before curving around to the anterior point. The anteromedian side extends ventrally to the lowest point of the otic capsule. The transverse width of the fenestra is 0.85 mm.

The stapes consists of a large foot plate which completely fills the fenestra ovalis and conforms to its outline, and a central thickening which may be regarded as the base of the columellar shaft. There is no indication of a stapedial foramen. The stapes is relatively larger and more ventrally directed than in the amphisbaenids, Gymnophiona, or *Lysorophus*. *Lysorophus* and the amphisbaenids resemble *Phlegethontia* in having large stapedial plates which suggests a possible adaptive significance rather than relationship.

Two pairs of small processes extend ventrally from the anterior border of the otic region. The lateral pair correspond to paroccipital processes in function, giving support to the quadrates. They are situated at the anterolateral angle of the capsules. Details of their form and relationship with the quadrates and pterygoid are obscure. Medial to the paroccipital processes, occupying about half of the space between them and the midline, are a pair of transversely elongate processes (Text-Fig 4, TU.) which project downward just behind the transverse portion of the pterygoid. Perhaps they correspond to the tubera basisphenoidales, although their lateral position is most peculiar for those structures.

A large parasphenoid covers the entire ventral surface of the braincase and spreads laterally beneath the otic capsules.
to the medial border of the fenestra ovalis. Anteriorly its cultriform process (Text-Fig. 2, PAS.) extends to in front of the orbit. Its posterior end is concave, continuing the arc of the posterior surfaces of the otic capsules. On each side, commencing just lateral to the notochordal pit, sutures run outward and slightly forward to the fenestra ovalis, separating the basioccipital-parasphenoid from the exoccipital (?) and opisthotics. If the plane of the palate and cultriform process of the parasphenoid be considered horizontal, the posterior portion of the basicranial axis, from condyle to in front of the otic capsules, slopes slightly downward to the front. Between the fenestrae ovales its transverse section is concave, turning downward on either side of the midline to cover the bulging vestibular chamber. Parasphenoid forms the medial and most if not all of the anterior border of the fenestra ovalis, its boundary with the proötic being concealed. Likewise, no anterior boundary between the parasphenoid and anterodorsal wall of the otic capsule can be distinguished.

Between the quadrates the parasphenoid abruptly narrows into a long, tapering, needle-like cultriform process which extends forward to contact with the prevomers beneath the anterior part of the orbit. Just ahead of the base of this process the small, cylindrical basipterygoid processes diverge forward and downward to their contact with the pterygoids. A median ridge arises slightly posterior to the base of the anterior process, and continues forward as its ventral margin.

Ossification of the orbitotemporal walls of the braincase is complete (unless there were unossified areas covered by the ascending process of the epipterygoid) from parasphenoid to skull roof and from otic capsules forward to the posterior margin of the orbit, in the region of the pila antotica. The smoothly curved surface of the parietal sweeps downward and converges to the narrow basicranial axis. Two large foramina are visible, low on the side of the braincase; the trigeminal foramen (which in this form may have also carried at least the palatine and facial branches of the Facial nerve), situated just in front of the expanded otic region, visible behind the ascending process of the epipterygoid; and the optic foramen, just behind the orbit (Text-Fig 5). The interorbital septum is ossified from the optic foramen forward to the posterior edge of the orbit. Here the ossification ends along a vertical
line. Only the needle-like parasphenoid rostrum continues anteriorly.2

Above the optic foramen the narrow interorbital septum widens and merges with the forward end of the parietal in an ossification of the planum supraseptale. The tubular anterior portion of the braincase so formed rapidly rises to just beneath the skull roof and narrows to a small part of the interorbital width of the frontals. A portion of this structure is concealed beneath the displaced sclerotic plates, but on the left side (Text-Fig. 1A, SPE.) the sphenethmoid ossification can be seen to extend back nearly to the posterior edge of the orbit, and so close to the rest of the braincase that a gap is unlikely.

In the front of the orbit a falcate bone descends from the frontals, where it is continuous with the aforementioned trough supporting the olfactory bulbs, to the base of the orbit, close to but not in contact with the tip of the parasphenoid process. Except for the extreme dorsal portion, this sphenethmoid appears to be a thin median ossification. Its anterior edge is nearly vertical and somewhat irregular, either from breakage or where the ethmoid cartilages adjoined it. Dorsally the bone forks and forms a narrow V-shaped tube which extends back the entire length of the orbit, as described above. It is separated from the frontals by suture, hence the tube must be regarded as part of the sphenethmoid rather than formed by ventral projections of the frontals, as is the analogous structure in snakes.

Palate: Premaxillaries are concealed in matrix at the anterior end of the specimen in such a depth that development is not feasible. A thin cross section of a bone terminating 1.9 mm. in front of the main portion of the skull (Text-Fig. 1B, PX.) may represent the ascending process of one of them; if so, the snout was acute rather than blunt. A portion of the left maxillary extends forward from its contact with the jugal beneath the orbit and bears about 10 small, pointed, conical teeth along its inner margin. The low facial portion

2In preparing the specimen a fragment of matrix which bridged the parasphenoid dorsally just anterior to the end of the ossified septum was removed and examined. Although the rubber cast prepared subsequently suggests a gradually tapering dorsal surface to the rostrum anterior to the optic foramen, close examination of it also reveals the line between bone and matrix, and microscopic examination of the specimen will confirm the structure here described.
of the bone rises outward and upward from the tooth row. Anteriorly its height is unknown; at the posterior end it is extremely low and may touch the orbit for a short distance between lacrimal and jugal.

Prevomers are indicated by impressions of crushed bone uniting the anterior ends of the pterygoids with the tip of the parasphenoid. No teeth are visible on them. A thin slip of bone runs posteriorly from these close inside the maxillary, tapering to a point well anterior to the back of the maxillary bone, (It is visible on the left side, from above); presumably this is the palatine. It is uncertain whether there was contact between palatine and pterygoid, although this is reasonable. The left side of the palate is displaced downward below the orbit, partly destroying the relationships of elements, but fortunately exposing some which otherwise would remain concealed.

The pterygoids (Text-Fig. 2B, PT.) are elongate bones extending back from beneath the anterior half of the orbit to the basipterygoid articulation, and then turning outward in front of the otic capsules to the quadrate. The anterior portion in life must have lain horizontally beneath the orbit. Its medial edge is straight, and lay closely paralleling the anterior process of the parasphenoid, so that the interpterygoid vacuities were extremely narrow and slender. Its widest point is at the rear of the orbit proper, whence it tapers to a point in front, and also tapers posteriorly to a slender band which extends from beneath the optic foramen back to slightly behind the basipterygoid articulation where the ventral edge becomes a little thickened and turns slightly downward and outward to a posterior terminal knob. From this knob, and also from a point on the lateral surface of the bone opposite the basipterygoid process, the quadrate ramus of the pterygoid extends laterally and slightly posterior along the front of the otic capsule to the quadrate; in this region also the bone is a vertical ribbon. It is possible that part of the quadrate ramus is formed by the epipterygoid.

The epipterygoid (Text-Fig. 5, EP.) rises as a broad ascending process above the pterygoid, extending forward from above the basipterygoid articulation half the distance to the orbit. Its posterior border rises vertically from the quadrate ramus (which may be either pterygoid or epipterygoid, as no sutures can be distinguished) and curves back slightly above the trigeminal foramen. The posterodorsal point
is gently rounded into the slightly curved dorsal border which slopes forward slightly from about the level of the top of the otic capsule toward the optic foramen. The anterior border drops steeply and then curves gently into the dorsal surface of the pterygoid. No suture is visible between the two elements. The dorsal surface of the ascending process is close to the side of the parietal wall of the braincase, but there is no indication of suture between them.

Conditions in the Cynodontia (Olson, 1944, p. 111, fig. 25) are suggested by the extensive development of the ascending process of the epipterygoid; however, the sutural contact with the skull roof and periotic characteristic of the mammal-like reptiles is lacking. Development of this element in Phlegethontia may be an adaptation to fossorial habits, like the extensive ossification of the braincase, or may merely serve to protect the structures of the cavum epipitericum from pressure of the enlarged temporal muscle. Amphibiaenids (Cope, 1892, p. 190) and snakes (Williston, 1925, p. 72) entirely lack the epipterygoid; in the Gymnophiona (De Beer, 1937, pl. 73) the ascending process in larvae is slender. Among vertebrates with similar habitus, Lysorophus alone has well-developed epipterygoids (the "posterior pillars" of Sollas, 1920, Figs. 5-7, pp. 488, 500-502); they reach the parietals and show definite anteroposterior elongation, although far less than Phlegethontia.

The articular surface of the quadratojugal consists of a rounded transverse hemicylinder projecting downward and forward from the anteroventral-lateral angle of the otic capsule and quadratojugal ramus of the pterygoid. Immediately behind it, on the ventral surface of the skull, is a small transverse wedge-shaped process, possibly the tuber basisphenoidalis. Dorsally, the quadratojugal blends indistinguishably with the pterygoid. Externally it is covered by the squamosal, which binds it to the paroccipital process, and by the quadratojugal. Its form is imperfectly revealed by the rubber casts from the specimen.

The anterior position of the jaw articulation is analogous to that found in the amphibiaenids, Gymnophiona, and Lysorophus, and may be regarded as a habitus character of limbless, burrowing vertebrates.

Lower jaw: On the left side the structure of the jaw is revealed. A posterior element which suggests the angular of frogs, but which, from its well developed cotylus for the quadratojugal must also include a fused articular, forms the post-
terior portion of the jaw and extends forward as a vertical plate medial to the dentary. The articular surface is a transverse, hollow cylindrical area directed upward and backward. There is no retroarticular process. Anterior to the angular the dorsal surface is slightly grooved, as in the Salientia, suggesting the course of Meckel's cartilage above the bone. A weak coronoid process is present rising from the medial dorsal border. The anterior extent cannot be determined.

The posterior end of the dentary is a thin, vertical plate. A number of minute teeth are present along the upper edge of the short visible section. As with the upper jaw, the form of the anterior portion remains unknown.

_Sclerotic plates_: Eight overlapping plates are visible in the posterior part of the left orbit, and nine similar plates in the right. Each is convex outward, and measures 1.0 mm. transversely by 0.1 mm. across. The direction of overlap is counterclockwise in the preserved section of each ring.

_Hyoïd_: A slender curved ossification of one of the hyoid cornua extends backward from a short distance behind the lower jaw to beneath the fourth vertebra. A shorter rod lies parallel to it extending forward and downward from the third vertebra. It is not evident whether this is the same element of the opposite side or an additional ossified ceratobranchial. If the structure be compared with the hyoid of lizards, the ossification is the first ceratobranchial (middle cornu of hyoid) which, according to Cope (1892, p. 191), is the only constantly ossified hyoid element in that group.

**VERTEBRAL COLUMN**

Ninety-nine vertebrae are preserved; the column was somewhat, but probably not much, longer. There are 8 cervicals, 67 rib-bearing dorsals, and 24 preserved caudals. All are lepospondylos with typical hour-glass constriction of the notochordal space; Many of the vertebrae are broken through the centra in such a way that the kaolinite filling of the notochordal cavity is exposed. Neural arches extend the entire length of the vertebrae, completely enclosing the neural canal. There are no neural spines and the zygapophyses are not developed laterally, but transverse processes are conspicuous.

The first two vertebrae (Text-Fig. 1) (technically the second and third of the column) lack movable ribs. Their transverse
Pl. 1. *Phlegethontia mazonensis* n. sp. Type specimen, U. S. N. M. Div. Vert. Paleont. No. 17897. Figure 1. Nodule containing entire skeleton, x 1. Figure 2. Counterpart showing skull and anterior part body, x 1. Figure 3. Counterpart showing posterior vertebrae, x 1. Figure 4. Portion of counterpart showing skull and gastralia, x 5.
processes are relatively stout, and directed more at right angles to the vertebrae and more downward than those of succeeding vertebrae, and their neural canals are greatly enlarged, so their diameters are greater than the centra, giving the neural arches a swollen appearance. Like the dorsal vertebrae, the neural spines are represented only by faint ridges, along the dorsal surfaces of the arches.

The axis has a large odontoid process extending forward toward the occipital condyle. Its neural arches are slightly shorter than those of the following vertebra, and differ in form from them only in the absence of prezygapophyses. A ventral median keel rises below the odontoid and continues back to the middle of the centrum. There is a nutrient foramen just in front of the transverse process. Presumably the odontoid process includes both the atlantal centrum and axial intercentrum, if any. If any arches were developed on the atlas, there is now no trace of them. The backwardly projecting otic capsules protect the atlantal region from external pressure. Apparently the craniovertebral joint was loose, that is, there was no close fit of the bony parts. It seems probable from the large size of the neural canal in the anterior vertebrae, that the foramen magnum was large, perhaps occupying most or all of the deep pit between the otic capsules. The vertebrae were connected to the skull by ligaments and membranes attaching to the posterointernal margin of the otic capsules, and the dorsal musculature had more lateral insertion on the otic region. Such an arrangement would provide protection to the spinal cord combined with flexibility of the head upon the neck. The lateral position of the dorsal musculature would increase its leverage for moving the head against a resistant medium, which would agree with other adaptations for fossorial habits.

The form of the axis is extremely suggestive of that of *Amphisbaena* (Zangerl, 1945, fig. 1), although differing in details attributable to the lacertilian ancestry of that genus. Similarity to the cervicals of *Lysorophus* is confined chiefly to the enlarged neural canal. The close-fitting neural arches of the atlas are absent, and the vertebrae are relatively much longer.

The second cervical vertebra is somewhat like the first, with large neural canal, centrum somewhat flattened above and
narrower than the arches, downwardly projecting stout transverse processes from the base of the arch.

Commencing with the third vertebra the ribs are movable. Cervical ribs (the first six) are shorter and somewhat stouter than those of the trunk, probably in relation to strong cervical musculature. The neural arches of the vertebrae gradually decrease in size until the neural canal of the first dorsal is somewhat smaller than the centrum. Preservation of this section of the vertebral column did not justify further preparation to determine the exact form, which does not appear to have differed materially from typical dorsals farther back.

![Diagrams](image)

Text-Fig. 6. *Phlegethontia mazonensis* n. sp. Mid-dorsal vertebrae, x 10. A dorsal, B lateral, C ventral aspect. Anterior caudal vertebra, x 10. D dorsal, E ventral aspect.

The presence of two ribless cervicals in *Phlegethontia* resembles the Amphibia, but the definitely recognizable posterior cervical ribs which are shorter and stouter than those of the body are a reptilian feature. The body form of *Phlegethontia*, which had no constriction at the neck, tended toward equalization of rib length. Consequently, the cervical region is less conspicuous than in normal reptiles, just as it is lost in snakes.

Mid-dorsal vertebrae have centra with circular ends but considerable constriction of the sides so that in ventral aspect they appear narrow-waisted. The median ventral ridge is slightly concave downward. Deep conical pits at each end of the centra meet so that the notochordal space was continuous. The ends of adjacent centra fit closely, and there is no trace of an intercentral element. Transverse processes (Text-Fig. 6, A-C.) are given off just above the center of the cen-
trum in the anterior half of the vertebra. The posterior edge of the process is a round pillar which extends forward from the center of the vertebra, at an angle of forty-five degrees. At its end is a hollow facet, which may have had cartilaginous extension. Connecting this process with the anterior part of the centrum is a sheet of bone whose anterior edge runs forward to the top of the anterior end of the centrum. Above the level of the diapophyses the sides of the neural arch rise vertically along the entire length of the vertebra. They curve inward over the neural canal and are surmounted in the dorsal midline by a low ridge. The zygapophyses slope inward and do not project laterally beyond the sides of the neural arches. The openings for spinal nerves are inconspicuous spaces below the zygapophyses.

Vertebrae decrease in diameter slightly posteriorly, so that the caudals average smaller than the dorsals, but the change is gradual and imperceptible. In the posterior dorsal region and caudal region the single median ventral ridge on the centrum is replaced by a pair of fine longitudinal ridges on either side of the base of the centrum. In this posterior region the centra are slightly less constricted medially than farther forward; between the ventral ridges the bottom of the centrum is essentially flat, and the sides rise abruptly and vertically from the lateral ridges. The point of transition to this type of structure was not ascertained.

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<th>Measurements of Vertebrae</th>
<th>mm.</th>
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<tr>
<td>Axis, total length centrum</td>
<td>1.80</td>
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<tr>
<td>Axis, length odontoid process</td>
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<tr>
<td>Axis, height from base centrum to top spine</td>
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<td>Mid dorsal, length from tips of zygapophyses</td>
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<tr>
<td>Mid dorsal, length base of centrum</td>
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<td>Mid dorsal, width across postzygapophyses</td>
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<td>Mid dorsal, width across diapophyses</td>
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<td>Mid dorsal, horizontal diameter end of centrum</td>
<td>0.73</td>
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<tr>
<td>Caudal vertebra, length base of centrum</td>
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The ribs of the 75th vertebra are similar in length and other respects to those farther forward; the 76th vertebra lacks ribs but otherwise appears closely similar to those preceding it. The transverse processes of the caudal vertebrae
are similarly located to those of the dorsal vertebrae, and differ only in being essentially thin, flat processes without the posterior thickening found where ribs are present. The posterolateral border is slightly convex instead of straight.

No evidence is available concerning the presence of chevrons in the tail.

**Ribs:** Beginning with the third vertebra, ribs extend back to the seventy-fifth. The first six ribs (cervicals) are somewhat shorter and stouter than the remainder. Presumably they are double headed, although this cannot be determined in this region as the heads of the ribs are concealed beneath the vertebrae. The diameter of the shaft of the first rib, which is typical of this group, is 0.11 mm.; its length 1.42 mm. The following ribs are slightly longer, 1.55 to 1.75 mm. At the tips the shafts are slightly expanded and rounded. The curvature is slight.

The ninth and succeeding dorsal vertebrae have more slender ribs which are definitely double headed and curved. The tuberculum articulates with the end of the stout posterior portion of the transverse process, the head appears to have articulated with the side of the anterior edge of the centrum, but no facet is observable for it. Dorsal ribs are about 3.3 mm. long. They continue without appreciable change to the 75th vertebra. None are present on the 76th. There is no suggestion of either enlargement of a sacral rib nor of the bifurcate tips of ribs in the cloacal region found in snakes and reported by Zangerl (1945, p. 767) in some amphibiaenids.

**Gastrolia:** Extending from immediately behind the skull to the 13th vertebra, along the ventral surface of the body is a series of fine gastralia. The individual bones are extremely fine, being about 0.03 mm. in diameter and 1.23 mm. long. They have a somewhat chevron arrangement, with the apex directed forward, but the arrangement is loose, and individual elements are in general separated by many times their diameter. Details of the arrangement may be observed in the accompanying photograph (Plate 1, Fig. 4).

**HABITS**

*Dolichosoma* and *Ophiderpeton* have been reconstructed as elongate, limbless, somewhat wormlike amphibians. It is generally conceded from their occurrence in coal deposits that
they inhabited the pools of the coal-swamps. Fritsch, believing that they had internal gills, was the more certain that they were aquatic.

The skull of Phlegeonthontia presents analogies with those of the fossorial amphibiaenids and coelilians, and with snakes. Interpretation of this form either as a burrowing animal or as a subaerial snake-like creature does not preclude its living about the edges of the coal-swamp pools, so that the rather infrequent occurrence of aistopod remains in these deposits may be explained. There is insufficient basis for assuming that they were aquatic. The urocordylids, of similar body form, differ markedly from the aistopods in the strong development of neural spines and haemal processes of the caudal vertebrae. Such development of the tail is known in various aquatic vertebrates and is accompanied by transverse flattening of the tail to form a more efficient swimming organ. The round tail of the aistopods shows no such adaptation.

Fossorial habit is suggested by four features of Phlegeonthontia: 1) the high degree of ossification of the braincase; 2) the forward position of the lower jaw articulation; 3) the large otic capsules and large stapedial foot; and 4) the absence of limbs. Of these, the first and fourth are equally characteristic of snakes, which are limbless and possess one of the most completely ossified braincases found among reptiles. The enormous otic capsules and large stapedial plate unquestionably have their closest analogues in the burrowing amphibiaenians, but may in part be attributable to a primitive heritage. The otic region of fish and amphibians is relatively large, and reduction of body diameter in aistopods might accentuate their proportional size. The large stapedial foot is also found in the primitive reptile Captorhinus, and may be regarded as a primitive feature. The anterior position of the quadrates and short lower jaw of Phlegeonthontia agree with the fossorial forms and contrast strongly with the elongate jaws and posteriorly placed quadrates of snakes.

But there is an important difference between Phlegeonthontia and the burrowers in the form of the jaw. For in amphibiaenids and in Lysorephus the angular region of the jaw is deep, whereas in Phlegeonthontia and the snakes it is exceedingly slender. It may be noted that Dolichosoma agrees with Phlegeonthontia in this respect, whereas Ophiderpeton has a deeper jaw,
more suggestive of the fossorial types; this coincides with the reduction of the orbit in that genus.

The well developed eyes of the dolichosomids contrast strongly with all known burrowing animals; cocciilians, amphibiaenids, other burrowing lizards, typhlopid snakes, not to mention the burrowing mammals, all tend markedly toward blindness and reduction of the eyes. In this respect *Phlegethontia* is more like the snakes, a group which resembles the burrowing forms in most of the characters in which *Phlegethontia* resembles them. Like snakes, *Phlegethontia* probably depended upon visual stimuli for location of prey and enemies. This suggests that it was, at least to a considerable extent, a subaerial animal.

Adaptational significance of the broad ascending process of the epipterygoid is uncertain. Obviously, this structure served to protect the organs of the cavum epiptericum from pressure of the enlarged temporal muscle. But it has no analogue either in the snakes or amphibiaenids, both of which completely lack the epipterygoid. Camp (1923, p. 393) notes that among lizards the epipterygoid is always lost in burrowing forms. As its development in the dolichosomids is unique, it is best regarded as a specialization of that group with adaptive function analogous to the highly ossified braincase.

The peculiar combination of characters cited here suggests 1) that *Phlegethontia* was derived from some partly fossorial animal which had lost its limbs and developed an anterior position to the jaw articulation, bony braincase, and large stapes in adaptation to fossorial life, but had retained fairly well developed eyes. *Ophiderpeton* represents a continued adaptation of this line to subterranean existence. 2) That *Phlegethontia* had become more strictly subaerial (in contrast to subterranean), had lost the heavy fossorial jaw and become adapted to snapping up active prey, most probably small insects. The great development of the temporal muscle suggests snapping habits. It continued the development of protecting walls of its braincase, possibly as protection against the struggles of its active prey. Among living forms, its closest analogues are the snakes rather than the burrowing lizards.

**Relationship**

*Comparison with Pennsylvania genera:* Snake-like, limbless or nearly limbless tetrapods of the late Pennsylvanian and
early Permian include the nectridians *Urocreryx*, *Sauropleura*, and their allies; the aistopods *Ophiderpeton*, *Dolichosoma*, and *Phlegethontia*; and *Lysorophus* and *Cocytinus*, lepospondyls (or adelospondyls) whose relationships have been much debated. Nectridians may be summarily excluded from consideration as near relatives of *Phlegethontia mazonensis* by the structure of the caudal vertebrae with enlarged neural and haemal processes, and by their normally roofed skulls.

Relationship of *Ophiderpeton* to *Dolichosoma* is by no means certainly established; their skull structure is widely different, and the similarity of their vertebrae is no greater than that produced by convergence of adaptive habits in amphisbaenids and coelacians. Presence of a peculiar process from the shaft of the ribs adjacent to the head may signify relationship, but maintenance of separate families is probably justifiable.

That *Phlegethontia mazonensis* is not closely allied to *Ophiderpeton* is easily established by the following differences:

1. Orbit large with indication of large eye.
2. Quadrates forward of posterior margin of skull.
3. Posterior end of lower jaw slender and shallow.
4. Ribs without auxiliary process near head.
5. Vertebrae with transverse processes of different form, although low; zygapophyses much closer to midline.
6. Fine, needle-like gastralia and no ventral armor of wheat-shaped scales.
7. No trace of limbs or girdles.

Numerous similarities between *Phlegethontia mazonensis* and *Dolichosoma longissimum* Fritsch suggest relationship. Close study of galvanotypes of the Nyran specimens in conjunction with Fritsch’s figures (1883, esp. pls. 18 and 22) have suggested modifications in the interpretation of the skull of *Dolichosoma*. The bone called pterygoid by Fritsch and squamosal by Steen (1938, p. 223, fig. 12) is the jugal. The Nyran specimens are plainly broken off through the pineal foramen and lack the posterior portion of the braincase. Hence the rapid widening of the skull roof in the otic region is not observable on them. The position of the jaw articulation is thus seen to lie not at the rear of the skull, as suggested in earlier reconstructions, but forward of the otic region, just
about opposite the pineal foramen, exactly as in Phlegethon-
tia mazonensis. The constriction of the skull roof behind the
postorbital process is exactly similar to that in the Mazon
Creek specimen and indicates a temporal opening through
which the upper end of the epipterygoid (squamosal of
Fritsch) is visible. The forked distal end of ribs appear to
be crushed ribs of normal shape. With these considerations
in mind, the following characters are identical in the two
genera:

1. Skull roof with upper temporal opening.
2. Forward quadrate suspensorium.
3. Slender lower jaw with conical teeth in anterior por-
tion, and extremely similar form of articular.
4. Similar form of frontals, parietals, circumorbital
series, maxillaries, epipterygoid.
5. Scierotic plates.
6. Large orbit.
7. Anterior cervical vertebrae of specimen in Fritsch's
Pl. 18, fig. 1, have heavy downwardly directed trans-
verse processes.
8. Dorsal vertebrae with extremely similar transverse
processes (See pl. 18, fig. 3).
9. Cervical ribs heavier than those of body region.
10. Needle like gastralia confined to anterior part of body.
11. No limbs.

The principal differences between the Mazon Creek and
Nyran aistopods are:

1. Wider nasals in American form ( ?).
2. Vertebrae relatively longer and with less expanded
zygapophyses in P. mazonensis.
3. No trace of the cross bar near the head of the ribs
in Phlegethon'ia. Ribs of Dolichosoma are relatively
more slender and more sharply bent near the head.
4. No pineal foramen in Phlegethon'ia.

None of these features are of sufficient magnitude to be
regarded as a bar to close relationship. The skull of Dolicho-
soma longissimum is sharply pointed with long slender pre-
maxillaries. This feature is not visible in the Mazon Creek
form, but it has been pointed out (p. 645) that faint indica-
tions of bone in front of the well preserved part of the skull
suggest long premaxillaries. Moreover, the skull of *Phlegethontia linearis* Cope from Linton is slender and pointed like that of *Dolichosoma*.

Fritsch (1883, p. 107) and Romer (1930, p. 86) have pointed out that *Phlegethontia* Cope from Linton, Ohio, is similar to *Dolichosoma* Huxley (and especially to *D. longissimum* Fritsch) in form of skull and general characters of the vertebrae, and in possessing exceedingly slender ribs. It also appears to have been limbless. Through the kindness of Dr. E. H. Colbert, I have been able to examine specimens of *Phlegethontia linearis* at the American Museum of Natural History. Interpretation of the type is difficult, yet it seems probable that it belongs to an animal closely related to the Mazon Creek aistopod. The following pertinent features were observed:

1. In the type of *P. linearis*, A. M. No. 6886, the vertebrae are of a far larger individual than *P. mazonensis*, being about 2.8 mm. long. The transverse processes are directed forward from the middle of the vertebra in a similar fashion, but the vertebrae are considerably wider in proportion to their length. How much of this is the result of distortion cannot be determined.

2. In specimen no. 6966 (Cope 1875, pl. xliii, fig. 1), the roofing bones of the skull show ornamentation of irregular, longitudinal ridges and pitting, similar to that of the Mazon Creek form.

3. This skull is probably exposed on the right side, with the lower jaw nearest the edge of the block. If so, there is sculpture on the lateral surface of the jaw, a difference from the Mazon Creek specimen which could be attributed to size. Only one orbit can be distinguished, which supports this interpretation.

4. Like the Nyran specimens of *Dolichosoma*, the otic region of the skull seems to have been broken away. No indication of the temporal fenestra could be observed, but the specimen is badly crushed so that there is no proof of its absence.

5. The orbit appears slightly smaller relative to the size of the skull than in the Mazon Creek form.

Positive identification with material of this nature is extremely difficult. The form of the vertebrae suggests affinity,
and there are no other known forms save Ophiderpeton, which already has been excluded, with which confusion is possible. Both the Mazon Creek and Linton specimens show special resemblance to Dolichosoma longissimum, although in different characters. In view of the environmental similarity and close relationship of other faunal elements of the Linton and Mazon Creek deposits (Westoll, 1944, pp. 103-108) it seems highly probable that Phlegethontia mazonensis was closely related to if not identical with P. linearis. The new specific name is given in recognition of the slight difference in age and locality, and to designate this far better preserved specimen. No adequate basis is available for evaluating the slight morphological distinctions (used in the "diagnosis") in terms of a genetic species concept. It is quite possible that P. mazonensis belonged to a population which included the actual ancestors of P. linearis.

Cocytinus and Lysorophius have been considered related by most recent students. They present many similarities in the ossified branchial arches and form of skull. Comparisons are here made with Lysorophius as the better known representative of the group. Phlegethontia mazonensis resembles Lysorophius in:

1. Large orbit.
2. Anterior position of quadrate (more extreme in Lysorophius).
3. Well ossified lateral walls of braincase.
4. Wide epipterygoid.
5. Large stapedial foot, short columella.
6. Reduction of roof over postorbital region.
7. Absence of pineal foramen.

Lysorophius differs importantly from Phlegethontia in:

1. Deep angle of jaw.
2. Toothed prevomers.
3. Peculiar process connecting prefrontal and maxillary.
4. Ossified branchial arches.
5. Vertebrae bearing transverse processes high on neural arch instead of low on centrum.

It may be safely concluded that these differences in structure are more fundamental than the resemblances, which are largely in habitus features. There is no evidence of close relationship of the aistopods and lysorophids.
Relationship to Coecilians: Although the modern coecilians (Apoda, or Gymnophiona) resemble Phlegethontia in several features such as the general form of the vertebrae, well ossified skull, and forwardly placed suspensorium, there is strong evidence against relationship of these groups.

1. The gymnophonan skull is platybasic whereas that of Phlegethontia is strongly tropibasic.
2. Gymnophonans have dentigerous prevomers.
3. The gymnophonan skull is completely roofed; this however, is regarded as secondarily derived from a condition with open temporal region (Goodrich, 1930, 322).
4. The stapes is far smaller and laterally placed in coecilians.
5. The coecilian lower jaw has a long retroarticular process.

Other differences are the greatly reduced eyes of the modern form (with which the platybasic cranium is possibly associated), and the extremely short ribs, which may be attributed to the general evolutionary tendency toward non-ossification known to exist in the Amphibia. Nevertheless, the differences in skull plan are so fundamental that relationship must be extremely remote.

Relationship to Amphisbaenids: The limbless burrowing lizard family Amphisbaenidae present a remarkable number of resemblances to Phlegethontia and other aistopods in skull structure. Zangerl (1945, 1944) has argued that the many amphibian resemblances in this group separate them from both snakes and lizards, and doubts the propriety of their reference to the Squamata. Against such a view it must be pointed out that the procoelous vertebrae, which have taken on some of the characters of the other genera of burrowing reptiles and amphibians, still plainly show the imprint of lacertilian origin. Furthermore Camp (1923, p. 372) has shown that the musculature has the characteristic plan of lizards of the section Autarchoglossa.

The amphisbaenids are introduced here, not to question their place among the lizards, but to show how similar are the adaptive features of these families.

Resemblances of Phlegethontia mazonensis to the amphisbaenids include:
1. Extensive ossification of the lateral walls of the braincase.
2. Forward position of quadrate, jaw short relative to skull length.
3. A lacertilian type of chondrocranium, extremely tropibasic, modified by large otic capsules. The embryology of the amphibiaenids is not known, but presumably is of lacertilian type.
4. Parasphenoid broad posteriorly, but with basicranial elements narrowing in orbitotemporal region.
5. Large round stapedial foot.

*Phlegethontia* differs from the amphibiaenids in
1. Notochordal vertebrae.
2. No vestige of limbs or girdles.
3. Slender lower jaw.
4. Large orbit.
5. Parasphenoid rostrum extending forward to near front of palate.
6. Well developed epipterygoid.
7. More ventral position of fenestra ovalis.

It may safely be concluded that there is no close relationship between these families, but merely some adaptive convergence.

*Are Aistopods reptiles?* Since their description by Huxley in 1871, the aistopods have been regarded as highly specialized but primitive amphibians. Huxley adduced no arguments in favor of his view, but the early age, and the resemblance of the lepospondylyous vertebrae to those of caudate amphibians seemed ample justification.

*Phlegethontia* possesses the following characteristics which are generally held to be reptilian rather than amphibian.
1. Tropibasic neurocranium with high interorbital septum.
2. Broad ascending process of epipterygoid.
3. Beginning of the differentiation of a series of 7 cervical vertebrae. (The first six ribs are different from those posterior to them). This condition in *Phlegethontia*, indeed, suggests derivation from a form with a better developed neck; such an ancestor would probably have been a reptile.
In addition the following features are developed in a fashion characteristic of reptiles or anthracosaurs:

1. Basipterygoid processes.
2. Narrow interpterygoid vacuities.
4. Amphisbaenid-like stapes.

Of distinctive amphibian features, there are only two, the lepospondylous vertebrae and extremely large otic capsule. Neither of these is critical. Vertebrae of such primitive reptiles as the pelycosaurs have lepospondylous centra very similar to those in question; modern caudates retain an extremely primitive type of vertebrae, which in the late paleozoic was not confined to amphibians. As has been pointed out in a previous article (Gregory, 1948), the lepospondylous microsau res are in all probability reptiles. Aistopods may be limbless derivatives of the microsaurs. The large otic capsule is indeed a primitive character. It also has adaptive significance, as is testified by the hypertrophy of these structures in the amphibiaenids, and the analogous enlargement of the auditory bulla in fossorial rodents. In Phlegethon ita both factors may have been operating; the ancestral type may have possessed large otic capsules, which became accentuated in proportion to the size of the skull with development of an otherwise narrow body and head. Further, if the large stapes and forward suspensorium are really indicative of fossorial ancestry, the same factors which lead to production of large capsules in the amphibiaenids may have operated.

Phlegethon ita possesses none of the diagnostic characters of the Amphibia, and has an extremely reptilian braincase. It seems most reasonable therefore, to place it in the latter Class.

The lepospondylous vertebrae of aistopods suggest that their closest relatives among the reptiles are the microsaurs, a contemporary Pennsylvanian group. In spite of the advanced development of a temporal fossa in the aistopod skull, which may be regarded as an adaptive specialization analogous to the loss of limbs, it is suggested that at least for the present they should be associated with the normal microsaurs under the Infraclasse Captorhina. The high number of presacral vertebræ in microsaurs shows the beginning of the trend toward lengthening the body carried to an extreme in the aistopods.
SYNOPSIS OF CLASSIFICATION

Class Reptilia
  Subclass Parareptilia
  Subclass Eureptilia
  Infraclass Captorhina
    Primitive Eureptilia usually with completely roofed temporal region of skull, notochordal vertebrae with crescentic intercentra usually present throughout column.

Order Captorhinomorpha
  Genera with swollen neural arches, 23-26 presacral vertebrae. Small to large size, limbs normal, primitive; dentition durophagous except in Linnoscelis.

Order Microsauria
  Small genera with normal neural arches. Intercentra not always ossified throughout dorsal region. Number of presacral vertebrae increased.

Suborder Microsauria vera
  Microsaurs with lizard-like bodies, triangular skulls, well-developed limbs, scales; 30-40 presacral vertebrae.

Suborder Aistopoda
  Microsaurs with elongate, snake-like bodies, limbless or nearly so: vertebrae extremely numerous, lacking neural spines, neural arches ossified entire length of centra, ribs long and slender; skulls elongate with incompletely roofed temporal region, highly ossified braincases, relatively large otic capsules, generally forwardly directed suspensorium. Pennsylvanian.

Family Ophiderpetontidae
  Aistopods with small orbit, relatively heavy lower jaw, scales on back, and thick set of wheat shaped scales on belly. Small to large size.


Family Dolichosomidae
  Aistopods with narrow pointed skull and slender lower jaws; large orbit; a temporal fenestra bounded by parietals, squamosals, and postorbitals; stapes very large, quadrates situated anterior to otic capsules; transverse processes of vertebrae low on centrum and directed forwardly; minute needle like gastralia in anterior part of body; no scales.
Genera: *Dolichosoma* Huxley—Jarrow, Nyrany.
Ribs more slender, with accessory cross bar near head. Pineal foramen present.

*Phlegethontia* Cope—Linton, Mazon Creek.
Ribs somewhat stouter, lacking cross bar. Pineal foramen absent.

**References**


**Peabody Museum**

**Yale University, New Haven, Conn.**