

TAXONOMIC REVISION
OF THE LYSOROPHIA,
PERMO-CARBONIFEROUS
LEPOSPONDYL AMPHIBIANS

CARL F. WELLSTEAD

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ABSTRACT

The Lysorophia is an order of small, but extremely elongate and tiny-limbed aquatic lepospondyl amphibians known from the Middle Pennsylvanian through the Lower Permian periods, primarily in North America. The order comprises one family, Cocytinidae, with three recognized species: *Brachydectes newberryi* (= *Cocytinus gyrinoides*), *B. elongatus* (= *Lysorophus tricarinatus*, *partim*), and *Pleuroptyx clavatus*. Other named species are considered Lysorophia, *incertae sedis*. Members of the Lysorophia are distinguished by their fenestrate skulls, anteriorly

sloping suspensoria, short mandibles (each bearing a lateral mandibular fenestra), and extensive, well-ossified hyobranchial skeletons. Presacral vertebrae are holospondylous and number between 69 (*B. newberryi*) and 97 (*B. elongatus*). Neural arch halves are sutured at their midlines and to their centra.

While closely similar to one another, lysorophoid species are highly derived relative to other Paleozoic amphibians. They are most closely related to microsaur, judged principally through the morphology of the craniovertebral articulation.

INTRODUCTION

A renewed paleontological interest in lepospondyls has resulted in relatively recent completion of reviews of nectrideans (Bossy, 1976; A. C. Milner, 1980) and microsaur (Carroll and Gaskill, 1978). A third group of lepospondyls which has also been poorly understood is the Lysorophia (lysorophoids), an order of elongate, tiny-limbed and primarily aquatic amphibians, ranging in length from a very few cm to roughly 1.5 m (figs. 1, 26D). Their presacral vertebral counts are high and their skulls are remarkable in bearing large orbitotemporal fenestrae (figs. 2, 3). Fossils representing the Lysorophia were first discovered in Upper Carboniferous rocks of eastern Ohio (Wyman, 1857, 1858) and, since then, have been reported from the Upper Carboniferous of the British Isles and from the Lower Permian of the North American midcontinent and southwest.

Understanding of the Lysorophia has been confused and incomplete due, in part, to factors inherent in the fossil material. For example, specimens of Upper Carboniferous lysorophoids tend to be incomplete and often extremely fragmentary (figs. 6, 7, 25), because their source is frequently the roughly handled waste rock accumulated during the mining of coal in the 19th and early 20th centuries. The shattered nature of this rock is particularly devastating to elongate specimens, which naturally seem to break into more, dissociable fragments than do compact forms.

These same specimens are preserved as dorsoventrally flattened parts and counterparts, exposed along fracture planes which pass irregularly through the skeletons and reveal them as arrays of sectioned bones. Scant detail of the skeleton or of individual bones is decipherable from such preservation. Not infrequently, the bone material itself may be destroyed by oxidation of iron sulfides. As a result, adequate preparation of the specimens has been impossible until recently (Baird, 1955; Heaton, 1980). Thus, fragmentary material and the ineffective preparations of earlier workers has severely hampered proper description of lysorophoids.

In addition to difficulties presented by fossil preservation, hindsight has shown that in several cases earlier workers have been premature in erecting lysorophoid species, since later discoveries have shown the type specimens to be nondiagnostic. This is particularly the case for several lysorophoid species based on vertebral centrum morphologies, now known to be very generalized within the order.

Moreover, the study of lysorophoids has suffered from careless taxonomic procedures. A classic example among the lysorophoids is the citation by Moodie (1916) of a single specimen as the holotype of distinct species in two genera. The specimen is actually the type of neither species. A difficulty such as this is aggravated by the fact that earlier

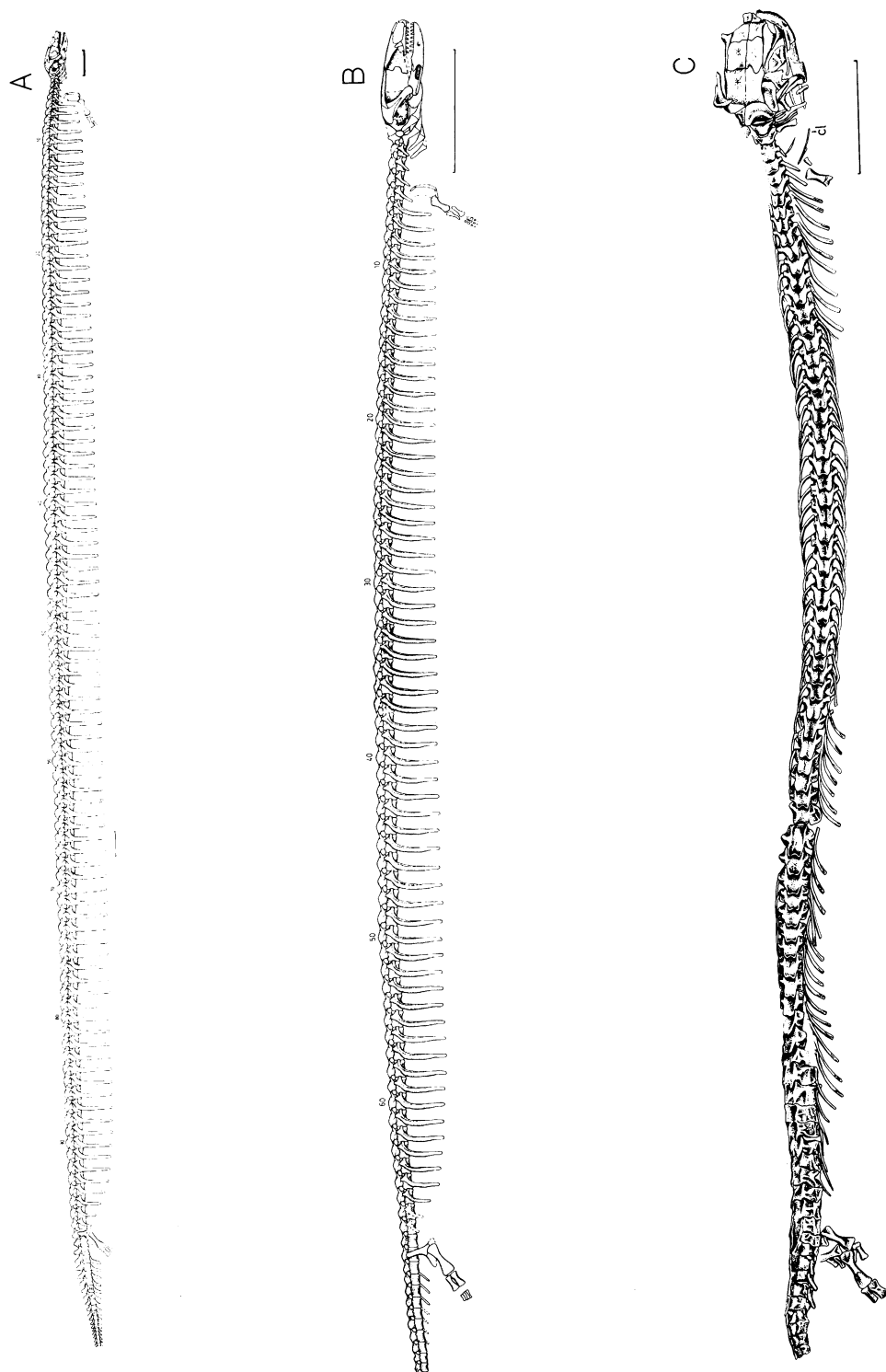


Fig. 1. *Brachydectes*. **A**, *B. elongatus*, reconstruction, based principally on UCLA-VP 2802 and AMNH 6172; **B**, *B. newberryi*, reconstruction, based principally on BM(NH) R.2544; **C**, *B. newberryi*, BM(NH) R.2544. Bar scale = 1 cm.

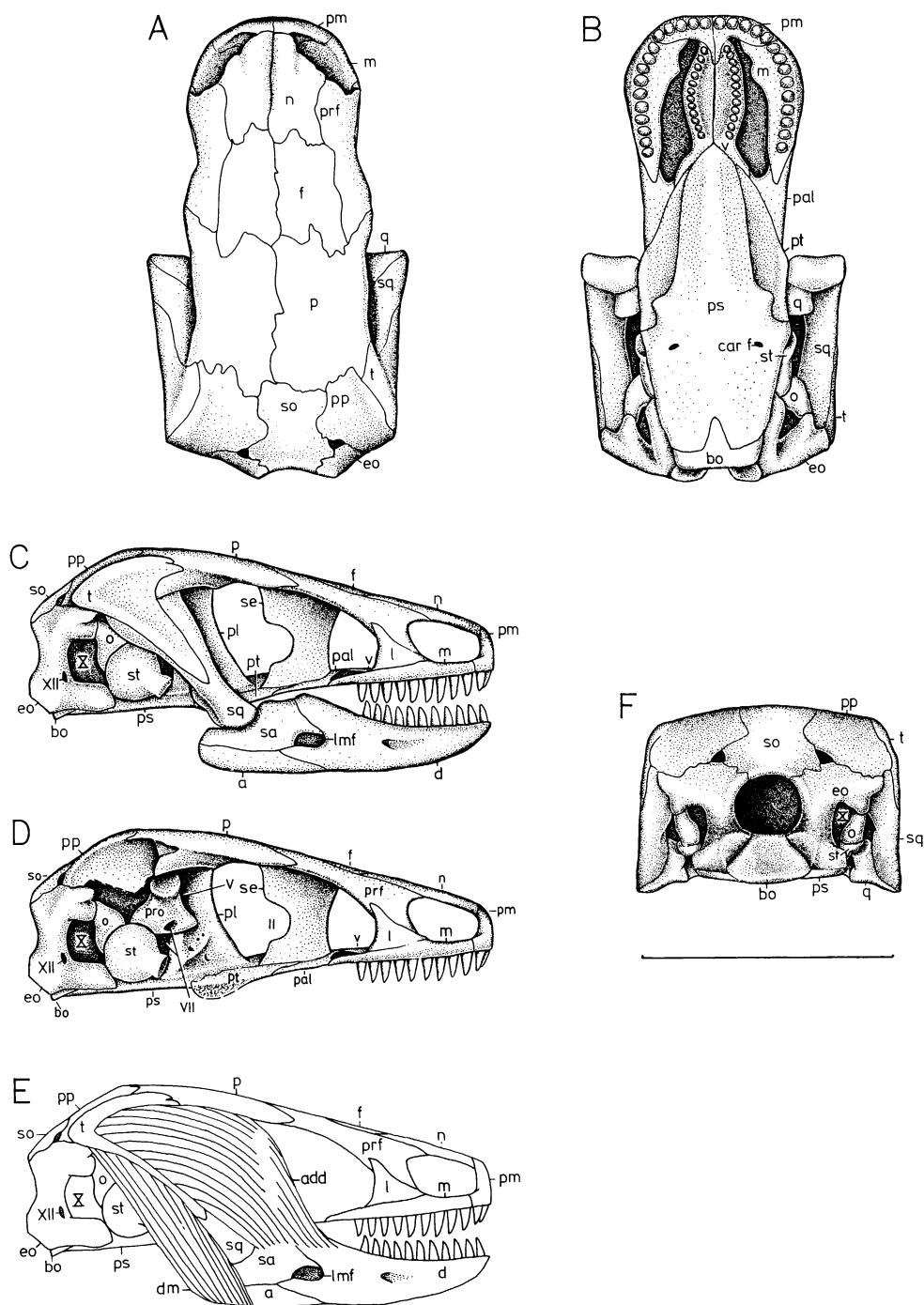


Fig. 2. Skull reconstructions, *Brachydictes elongatus*. A, dorsal view; B, ventral view; C, right lateral view; D, right lateral view, showing braincase; E, general reconstruction of adductor mandibulae and depressor mandibulae; F, posterior view. Bar scale = 1 cm.

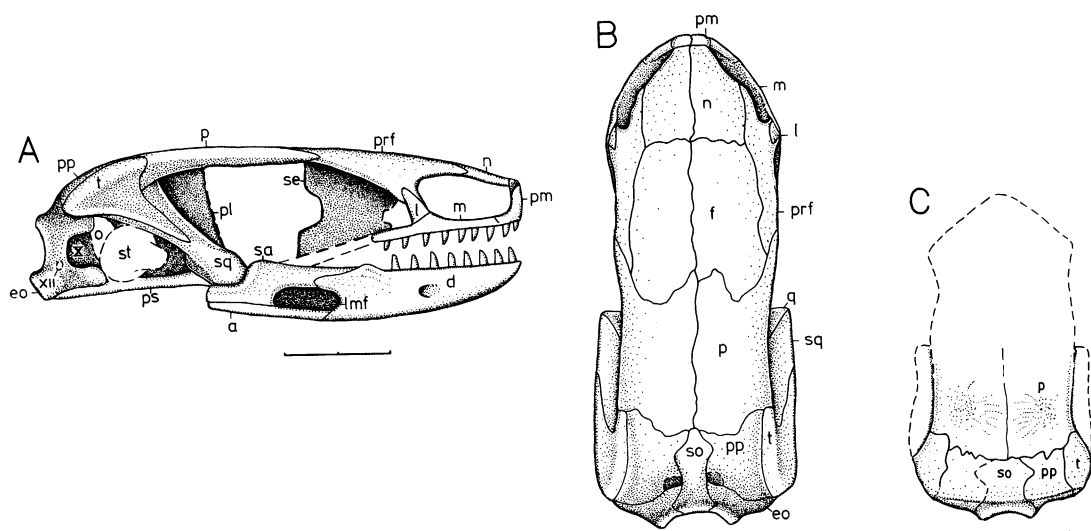


Fig. 3. Skull reconstructions. A, B, *Brachydedetes newberryi*, lateral and dorsal views, respectively. Bar scale = 2 mm. C, *Pleuroptyx clavatus*, incomplete, based on MCZ 2303. Bar scale = 1 cm.

workers illustrated only a minimum of specimens and, then, frequently by little more than sketches.

This review is intended to correct the woefully inadequate knowledge of the anatomy of lysorophoids and the confusion over their systematics. Such a study is necessary to assess their position among the Amphibia. A reexamination of this group will allow comparison with modern elongate forms of both burrowing and aquatic habitus and will further illustrate the diversity of vertebrate life in the Upper Paleozoic.

ACKNOWLEDGMENTS

Because of the great stratigraphic and geographic range involved and large number of specimens concerned, this project could not have been completed without the fossil material furnished by many individuals and institutions. Foremost among these is Dr. Donald Baird, who supplied a series of latex casts of nearly all significant lysorophoid specimens from Linton. David Hamilla, Greg McComas, Richard Seltin, and Dwayne D. Stone also kindly supplied specimens in their care. Other critical material was loaned by the following institutions: American Museum of Natural History, British Museum

(Natural History), Carnegie Museum of Natural History, Field Museum of Natural History, University of Kansas Museum of Natural History, Museum of Comparative Zoology, United States National Museum, University of Michigan Museum of Paleontology, and the University of Wyoming Department of Geology.

The project benefited from advice, encouragement, and a variety of assistance received from Donald Baird, David Berman, John Bolt, J. Clay Bruner, Robert L. Carroll, William Dougherty, Daniel K. Emmett, M. A. Fields, Stephen Godfrey, Robert B. Holmes, Robert W. Hook, H. Jaeger, Larry D. Martin, A. C. Milner, D. E. Nodine-Zeller, E. C. Olson, H.-P. Schultze, T. R. Smithson, J. P. Sousa, H.-D. Sues, H. Tyson, P. P. Vaughn, Denis Walsh, F. Westphal, and the Leroy L. Wade Computer Center at Creighton University in Omaha.

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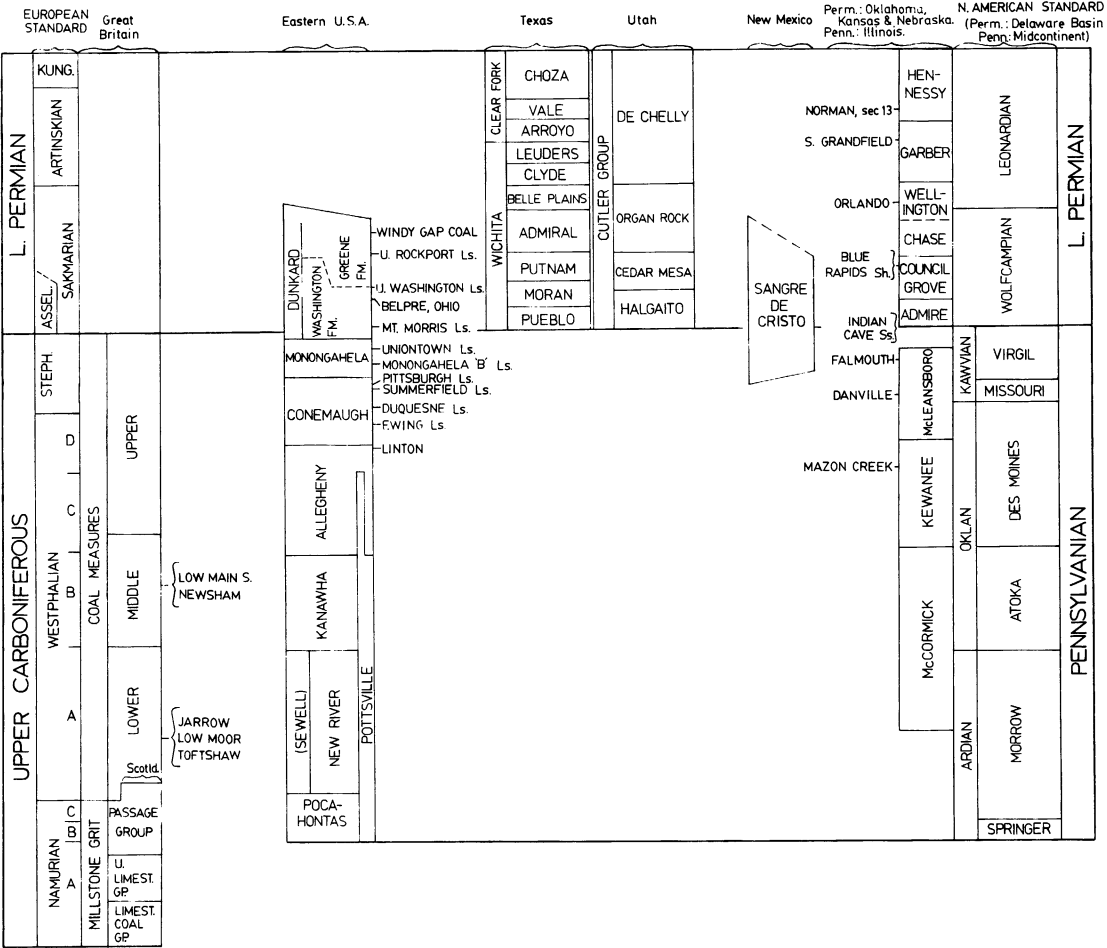


Fig. 4. Stratigraphic correlation of lysorophoid producing localities. Principally after Panchen (1970), modified after Armstrong et al. (1979), Baars (1962), Barlow (1975), Brill (1952), Moran (1952), Romer (1974), Vaughn (1965, 1969b), and Simpson (1979).

to R. L. Carroll. Other direct financial support was received from a Sigma Xi Grant in Aid of Research. Mr. Meyer Oknine of Montreal provided considerable indirect assistance during my doctoral studies at McGill.

ABBREVIATIONS

Institutional Abbreviations

- AMNH American Museum of Natural History, New York
- BM(NH) British Museum (Natural History), London

- ČGH National Museum, Prague
- CM Carnegie Museum of Natural History, Pittsburgh
- DSH private collection of David S. Hamilla
- FMNH Field Museum of Natural History, Chicago
- (UC, UR, PR) G Hancock Museum
- GPIT Institut für Geologie und Paläontologie, Tübingen
- MB. Am Humboldt Museum, Berlin
- KU University of Kansas

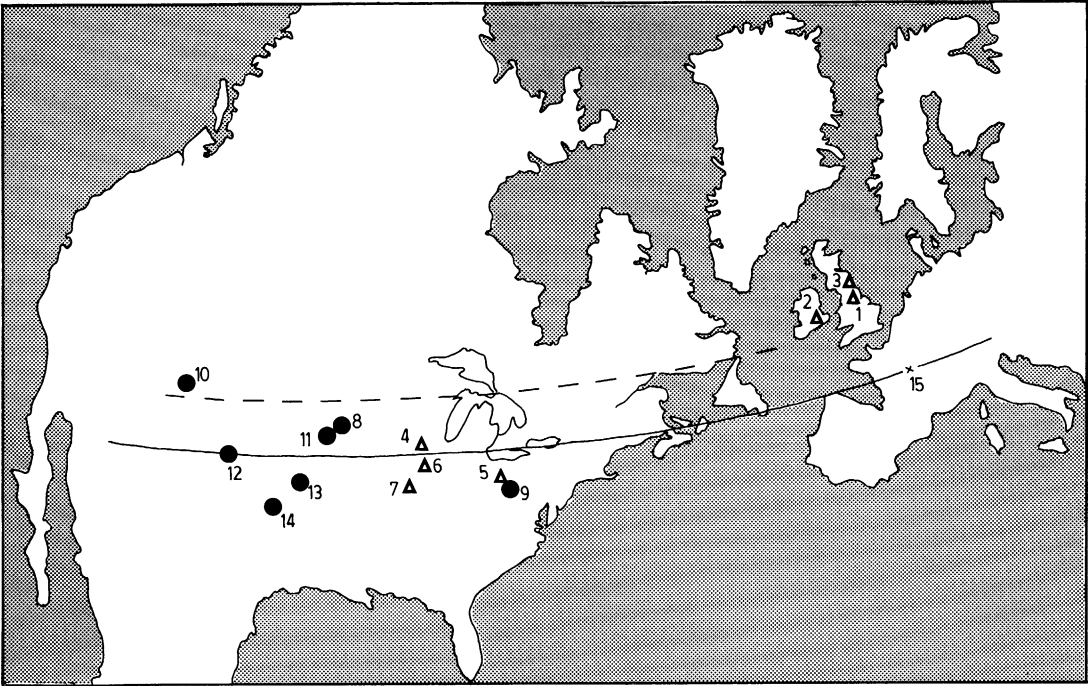


Fig. 5. Geographic distribution of lysorophoids plotted in relation to Carboniferous (broken curve) and Permian (solid curve) equators, after Panchen (1970) and authors cited therein. See also Scotese et al. (1979). 1, Toftshaw-Low Moore; 2, Jarrow; 3, Newsham; 4, Mazon Creek; 5, Linton and other Upper Pennsylvanian localities in Ohio, West Virginia and Pennsylvania; 6, Danville, Illinois; 7, Falmouth, Illinois; 8, Peru, Nebraska; 9, Dunkard sites, Ohio and West Virginia; 10, Lisbon Valley, Utah; 11, Westmoreland, Kansas; 12, San Miguel County, New Mexico; 13, Hennessey and Wellington formations, Oklahoma; 14, Leuders Formation and Clear Fork Group, north-central, Texas; 15, Nièvre, France. Triangles: Pennsylvanian (Upper Carboniferous) sites. Solid circles: Permian sites. X, doubtful lysorophoid.

	Museum of Natural History, Lawrence				University of Wyoming, Laramie
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts	Anatomical			
PU	Princeton University Museum of Natural History, Princeton		a	angular	
RM	Redpath Museum, Montreal		ac	"accessory bone"	
UCLA-VP	University of California, Los Angeles		add	adductor mandibulae	
UMMP	University of Michigan Museum of Paleontology, Ann Arbor		art	articular	
USNM	United States National Museum, Washington, D.C.		bo	basioccipital	
UW	Department of Geology,		bs pt pr	basipterygoid process	
			car f	carotid foramen	
			cb	ceratobranchial	
			ch	ceratohyal	
			cl	clavicle	
			clth	cleithrum	
			dm	depressor mandibulae	
			d	dentary	
			delt	deltpectoral crest	
			eb	epibranchial	

eo	exoccipital
f	frontal
fe	femur
fi	fibula
fib	fibulare
h	humerus
hh	hypohyal
hyob	hyobranchial elements
icl	interclavicle
int f	intertrochantic foramen
int tr	internal trochanter
il	ilium
isch	ischium
l	lacrimal
lmf	lateral mandibular fenestra
m	mandible
met	metapodials
n	nasal
na	neural arch
o	opisthotic
p	parietal
pal	palatine
pl	pleurospenoid
pm	premaxilla
pp	postparietal
prf	prefrontal
pro	prootic
pro at	proatlas
ps	parasphenoid
pt	pterygoid
ptf	posttemporal fossa
q	quadrate
r	radius
sa	surangular
sc	scapulocoracoid
se	sphenethmoid
so	supraoccipital
sp	splenial
sq	squamosal
st	stapes
t	tabular
ti	tibia
tib	tibiale

u	ulna
v	vomer
I-XII	cranial nerves

METHODS

As noted, fossil vertebrates from the Upper Carboniferous Linton locality are preserved in a manner which makes them difficult to study. The latex casting technique described by Baird (D., 1955) has solved this problem by allowing high-fidelity positive casts of the Linton fossils to be made. Specimens used in this study from Linton and also from Mazon Creek were prepared using this technique and in most cases the preparations were made by Dr. Baird. Several others were prepared by Bob Hook, Ingrid Birker, Greg McComas, David Hamilla, and the author. Specimens from other localities were more effectively prepared mechanically using a fine needle.

Dorsoventral crushing of skulls in specimens from Linton prevents direct measurement of skull lengths and widths, but does leave the skull roof relatively intact anterior to the parietal-postparietal suture. Therefore, comparisons of skull proportions between *Brachydectes newberryi* and *B. elongatus* are made on the basis of skull roof length, estimated from parietal-postparietal suture to snout tip, and skull roof width, estimated at the level of the parietal-postparietal suture.

Measurements reported in the text were made using a binocular microscope equipped with a grid ocular.

In this work, the terminal elements of the posthyoid visceral arches have been identified as epibranchials in presumed homology with similar elements in urodeles. The reader should be aware that the homologies of these elements in urodeles have been questioned (e.g., Rosen et al., 1981; Duellman and Trueb, 1986).

SYNOPSIS OF PREVIOUS WORK

A lysorophoid specimen (MCZ 2157, fig. 6) was one of the first fossil tetrapods to be announced from Upper Carboniferous rocks at the now-famous Linton site in eastern Ohio (Wyman, 1857). Fossil collections made at

Linton by J. S. Newberry and Charles M. Wheatley and those from a site near Danville, Illinois, made by Wm. Gurley provided E. D. Cope with the material for naming and briefly describing between 1868 and 1877 all

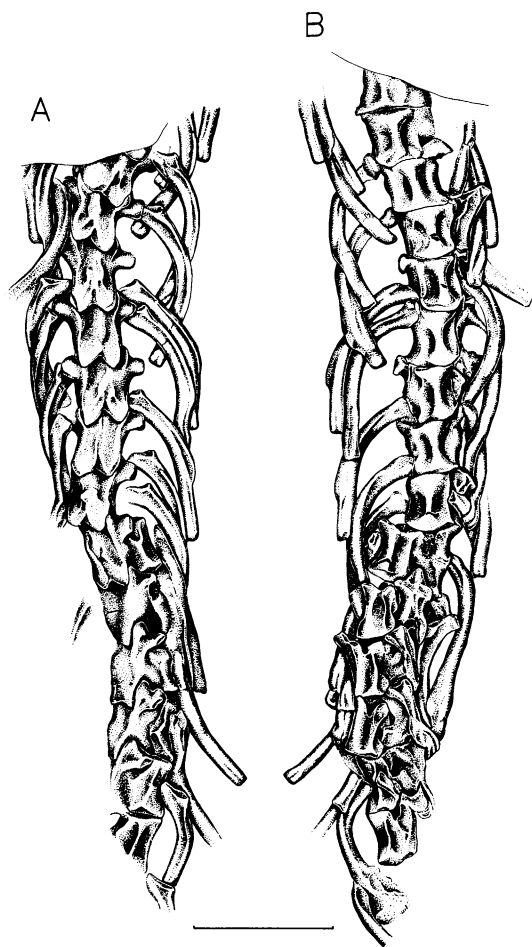


Fig. 6. *Brachydectes newberryi*, MCZ 2157. Part and counterpart. Bar scale = 1 cm.

but one of the lysorophoid species recognized in this work.

From 1875 until 1929, lysorophoid genera from Linton, comprising *Brachydectes*, *Cocylinus*, *Molgophis*, and *Pleuroptyx* were considered to represent a wide and varying range of extinct and modern amphibian groups, including microsaur (e.g., Cope, 1868, 1869, 1888, 1898; Huene, 1913c; Moodie, 1916), aïstopods (Fritsch, 1883; Nicholson and Lydekker, 1889; Lydekker, 1890; Zittel and Eastman, 1902; Jaekel, 1909; Huene, 1913c; Zittel et al., 1923; Moodie, 1911; Gregory, 1917), nectrideans (Zittel et al., 1911, 1923), and urodeles (Cope, 1875a, 1875b; Moodie, 1912a, 1912b, 1916).

Lysorophus tricarinatus is the only Upper Carboniferous lysorophoid not represented at Linton. The species (Cope, 1877) was based on a few vertebral centra discovered at the Danville site. A notable feature of these centra was that the neural arches had clearly been sutured, rather than fused, to the centra (fig. 28A–N). Cope (1881, 1888) considered *L. tricarinatus* to be a pelycosaur presumably because certain pelycosaurs were known to exhibit a similar condition.

No more of the genus was reported from Danville, or elsewhere until Case (1902a, 1902b) discovered a series of vertebrae with centra similar to those of *L. tricarinatus* in the collection of Texas Permian vertebrates at the University of Chicago (now in the Field Museum of Natural History). The red matrix holding the specimen accentuated not only the neurocentral suture, but also a suture along the midline between left and right neural arch halves. Impressed with the similarity, Case referred this material to *L. tricarinatus*. He further noted that a skull found in the vicinity of the vertebrae was similar to that of *Isodectes*. This association may either be accidental or the identification of the skull incorrect, because *Isodectes* is a temnospondyl labyrinthodont similar to *Saurerpeton* (Carroll and Gaskill, 1978: 148). This skull has not been relocated and its identity cannot be confirmed.

Broili (1904a; see also 1904b) published the first description of a skull confidently associated with vertebrae of the Texas Permian lysorophoid. He considered it to be a rhynchocephalian reptile and made *Lysorophus* the type genus of the Paterosauridae, which he felt represented a line of reptiles rising directly from fish. Broili's interpretation grew in part from his misidentification of lysorophoid hyobranchial elements as "gular plates" and from the perceived similarity of the vertebral centra to those of fish, specifically carp. Williston later recognized that the name of Broili's new family was technically unavailable and substituted "Lysorophidae" for "Paterosauridae" (Williston, 1908a).

Williston (1908a) and Case (1908) published further descriptions of the skull of the Texas Permian lysorophoid, claiming it to be an amphibian. Williston went so far as to

suggest that it was a urodele and offered descriptions of postcranial material, making the first notice of limbs and caudal skeleton. Later that same year, Williston (1908b) suggested implicitly that *Lysorophus* warranted the erection of a new amphibian order, but failed to name it. Jaekel (1911), perhaps acting upon this suggestion, included an “?Order Lysorophi” in his summary of living and fossil amphibians without further comment.

The debate over the amphibian or reptilian status of *Lysorophus*, based on the Texas material, continued into the 1920s, as Broili (1908a, 1908b, 1913) and supporters (Zittel et al., 1911) continued to maintain its reptilian status, and as Williston (1910a, 1910b, 1912, 1916) and supporters (e.g., Abel, 1919, 1920; Broom, 1910, 1918; Case, 1911, 1915; Huene, 1913a, 1913b, 1913c; Jaekel, 1911; Moodie, 1909b, 1911; Sollas, 1918; Stromer, 1912; Watson, 1917) considered it an amphibian, possibly with urodelan or apodan (Moodie, 1909b) affinities.

The differences of opinion over the taxonomic status of *Lysorophus* centered around interpretations of the hyobranchial skeleton and occipital condyle. Broili (1904a) published the first description of the four branchial arches in *Lysorophus*, but, as noted above, considered its hypohyals to be fishlike gular plates (Broili, 1904a, 1904b, 1908a, 1913). Williston disputed this identification, first confusing the hypohyals with displaced proatlas elements (Williston, 1908a), but finally recognizing them to be hyobranchial elements (Williston, 1912).

Broili (1908a) correctly described the occipital condyle as tripartite, composed of portions of both exoccipitals and part of the basioccipital. However, he failed to note that not only reptiles, but many Paleozoic amphibians including labyrinthodonts and microsaurs, possess occipital condyles of a similar composition. On the other hand, Williston (1908a, 1912) and Case (1908) erred in considering the occipital articulation to be similar to that of modern amphibians, consisting only of two exoccipital condyles. Huene (1913a, 1913b) resolved the situation, noting that, indeed, exoccipitals and basioccipital constitute the condyle, but also that, rather than being a strict condyle, the articular sur-

face is concave with the basioccipital portion being recessed between the more prominent exoccipital portions.

While Zittel et al. (1923) kept *Lysorophus* among the Reptilia in their textbook, Sollas (1920), convinced of its amphibian status, seems to have ended the argument with a detailed description of *Lysorophus* based on serial sections.

The modern concept of a taxonomic group uniting Upper Carboniferous and Lower Permian lysorophoids originated with Watson (1929), who recognized the similarity between the Linton lysorophoid *Cocytinus gyrinoides* and “*Lysorophus tricarinatus*” of the Permian redbeds of the midcontinental United States. On the basis of the shared presence of a neurocentral suture, Watson grouped them with adelogyrinids in his order Adelospondyli. However, he did not address other taxa now considered to be lysorophoids. A year later, Romer (1930) also noted similarities between *C. gyrinoides* and “*L. tricarinatus*” and based the Lysorophia on them. Romer also correctly suggested synonymies of Linton species *Brachydectes newberryi*, *Cocytinus gyrinoides*, and *Molgophis wheatleyi*, but referred segments of vertebral column representing Linton lysorophoids *Pleuroptyx* and *Molgophis* to colosteid labyrinthodonts.

Since 1930, most authors have placed the lysorophoids either in Watson’s Adelospondyli (e.g., Steen, 1931; Case, 1946) or in Romer’s Lysorophia (Romer, 1933; Tatarinov, 1964; Kuhn, 1965, 1968, 1970; Carroll, 1988). However the Adelospondyli are no longer recognized, because of the relatively widespread occurrence of the supposedly diagnostic neurocentral suture (Romer, 1950; Westoll, 1942, 1943). Now identified as a well-circumscribed group, the lysorophoids appear to be most closely related to microsaurs (Romer, 1950, 1966; D. Baird, 1965; Brough and Brough, 1967).

This summary condenses the rather chaotic taxonomic history of the lysorophoids. Interested parties are encouraged to refer to the original literature for first-hand exposure to the matter.

Comparisons made in the present study have resulted in the following taxonomic resolution:

ORDER LYSOROPHIA

Brachydectes newberryi (= *Cocytinus gyrinoides*, *Molgophis wheatleyi*).

B. elongatus n. sp. (= *Lysorophus tricarinatus*, partim), representing that Permian redbed material of the North American midcontinent and southwest classically recognized as "*Lysorophus*" in contrast to the type *L. tricarinatus* material of the Pennsylvanian Danville, Illinois, locality.

Brachydectes sp. (= *Lysorophus minutus*).

Pleuroptyx clavatus, type and referred material of

P. clavatus and *Molgophis brevicostatus* (partim, Schwartz, 1908).

Lysorophia, incertae sedis.

Lysorophus tricarinatus Cope, 1877, all type and originally referred material.

Lysorophus dunkardensis Romer, 1952, all type and originally referred material.

Lysorophus sp., nondiagnostic material referred to the genus by various authors.

Molgophis macrurus (= *M. brevicostatus*), all type and originally referred material.

SYSTEMATIC PALEONTOLOGY

CLASS AMPHIBIA

ORDER LYSOROPHIA ROMER, 1930

REVISED DIAGNOSIS: Extremely elongate, tiny-limbed amphibians with skull possessing large orbitotemporal fenestrae. Lacrimal and prefrontal are the only remaining circumorbital bones. Postparietals effect a sloping or arched transition from skull roof to occiput. Tabular, squamosal, and quadrate form a tapering rod, slanting anteroventrally to support a craniomandibular articulation well anterior to occiput. A broad parasphenoid is the principal element in the ventral surface of the skull. It separates the reduced pterygoids and contacts the vomers. There are no interpterygoid vacuities. The palatal dentition consists of a vomerine arcade of teeth smaller than those of the marginal dentition, but concentric to them in array. Ossifications of the braincase include paired pleurosphenoids and strutlike sphenethmoids. The supraoccipital passes between postparietals to contact the parietals. Mandible lacks coronoid bone and is roughly 0.6 times the length of the skull. It bears one mental foramen in the dentary and a large lateral mandibular fenestra bordered by dentary, angular, and surangular. The hyobranchial apparatus is well developed, possessing hypohyal and ceratohyal pairs and four paired branchial arches consisting of ceratobranchial and epibranchial elements. Presacral vertebral counts range among species from 69 to nearly 100. Presacral vertebrae are holospondylous, notochordal, and trussed by sev-

eral carinae. Neural arches are sutured to the centra and are paired, left and right halves being sutured to one another at the midline. The tail is short and possesses hemal arches sutured to the centra. Dermal and endochondral elements of girdles are present, but reduced in size. Scapulocoracoid lacks ossified glenoid. No distinct coracoid is present. Manus possesses no more than four digits. Pes possesses four, possibly five digits. There is no evidence of bony scales or gastralia along the body.

FAMILY COCYTINIDAE

COPE, 1875b: 12

Molgophidae (Cope, 1875a: 357, partim). Romer, 1966: 363, partim.

Lysorophidae (Williston, 1908a: 237, partim). Romer, 1966: 363, partim.

TYPE GENUS: *Cocytinus* Cope, 1871: 177 (= *Brachydectes* Cope, 1868: 214).

REVISED DIAGNOSIS: Same as order. The *Cocytinidae* is the sole family in the order.

STRATIGRAPHIC RANGE: Westphalian A (Lower Pennsylvanian) through Leonardian (Lower Permian).

GENERAL ANATOMY OF THE COCYTINIDAE

SKULL

DERMAL ROOF: The lysorophoid skull (figs. 7C, D, 13) is notable for its extreme orbitotemporal fenestration and for the position of the craniomandibular articulation, well ahead

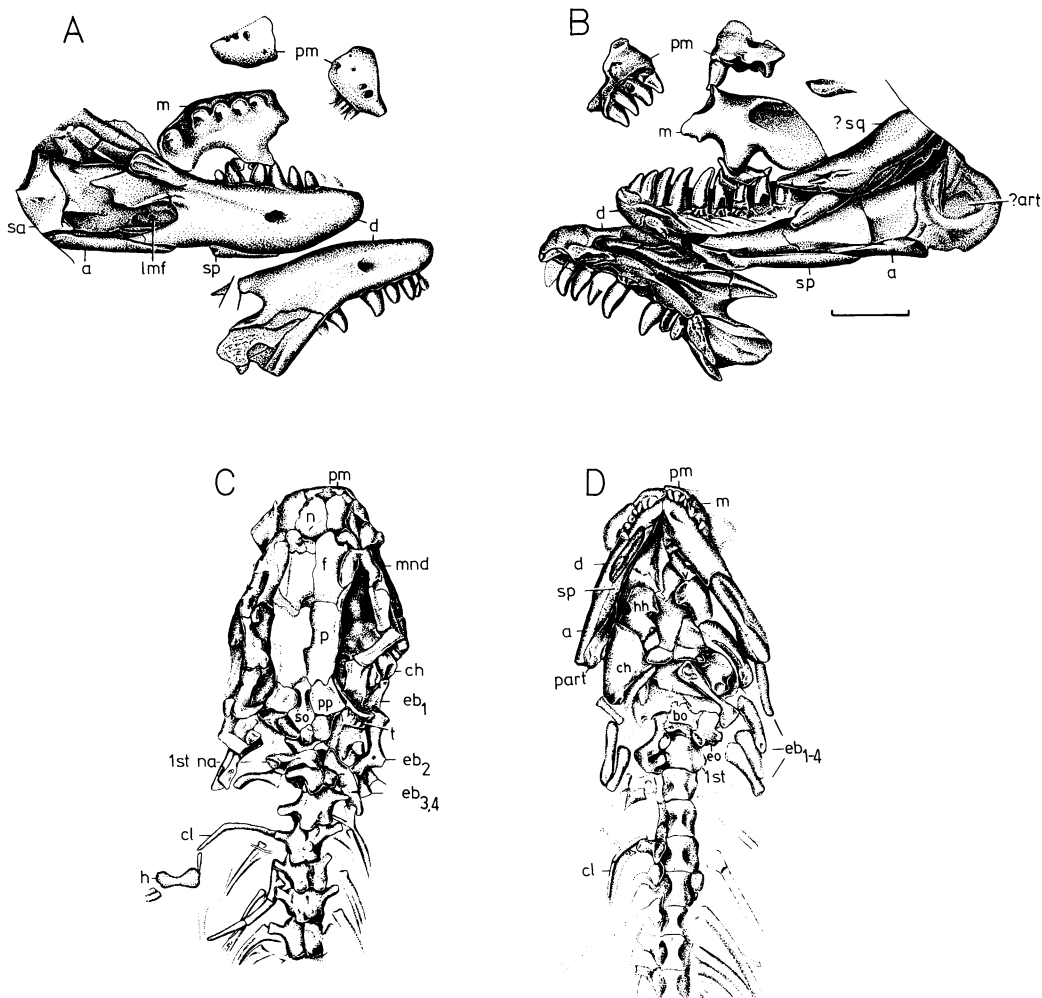


Fig. 7. *Brachyectes newberryi*. A, B, Holotype, AMNH 6941. Part and counterpart. Bar scale = 0.5 cm. C, D, AMNH 6925. Part and counterpart, holotype of "*Cocyttinus gyrinoides*." Bar scale = 1 cm.

of the occiput. The large nares are separated from the orbitotemporal region only by a slim lacrimal. Distinct intertemporal, supratemporal, postfrontal, jugal, and quadratojugal bones are absent, as is the parietal foramen. There are no indications of lateral line canals. Well-developed dermal sculpture is present only in relatively large individuals.

Bone tissue in the skull, as well as in the hyobranchial apparatus, ribs, and appendicular skeleton is almost entirely compact. Spongiosa is present primarily in the carinae of the vertebral centra.

The skull roof has relatively straight lateral edges and is composed primarily of a median

series of paired, irregularly rectangular postparietal, parietal, frontal, and nasal bones. The dorsal surface of the skull roof is gently convex along both the longitudinal and transverse axes. Transverse sutures are distinctly serrate and exhibit substantial overlap. Longitudinal sutures may be either sinuous or serrate.

The following general description of the lysorophoid skull is based primarily on specimens of *Brachyectes elongatus* because of their essentially three-dimensional state of preservation. Except where noted, the skulls of *B. newberryi* and *Pleuroptyx* are similar.

The parietals are the largest of the roofing

bones, predominating the skull roof between the orbitotemporal fenestrae. A broad process of each parietal extends anteriorly to underlap as much as one-third the length of the frontal bones (figs. 14F, 15A, D). This process bears two longitudinal ridges, one of which is visible as the anterolateralmost serration of the parietal and was described by Sollas (1920). The other cannot be viewed when the frontal and prefrontal are in place, but wedges between them at depth as figured by Bolt and Wassersug (1975, fig. 11) and as seen in figures 14F and 15A in which frontals and prefrontals have been displaced. In the region of the frontoparietal overlap, the skull roof may be noticeably thicker than elsewhere (Bolt and Wassersug, 1975).

Sollas noted two additional processes of the parietal in *B. elongatus*, one of which he called the posterolateral process (cf. fig. 13E, F). It was described as bifurcate, sending one ramus between the postparietal and tabular and a more ventral ramus to the tabular and prootic. To the contrary, what Sollas interpreted as separate rami are actually the edges of a groove in which rests the anterior process of the tabular. This region, however, does expand ventrally and bifurcates into two other processes, one which is held between prootic and squamosal and another which laps onto the dorsal edge of the squamosal (fig. 16B). Sollas' second parietal process is a stud on the ventral surface of the parietal (fig. 15E), which inserts into the sheathlike dorsal end of the pleurosphenoid.

Posteriorly, the parietals contact the postparietals and supraoccipitals. Laterally, they assist the postparietals in supporting the tabular and squamosal bones.

While the longitudinal sutures tend to be sinuous in lysorophoid skulls, that between the two parietals in *B. elongatus* is distinctly serrate.

Behind the parietals lie the postparietals. These bones are approximately half the size of the parietals, and are kept from meeting at the midline by the intervening supraoccipital. This separation may, in part, explain why earlier workers identified the postparietals as either epiotics, supratemporals, squamosals, or tabulars (Bolt and Wassersug, 1975; Sollas, 1920, and references therein).

With the supraoccipital, the postparietals

effect an arched transition from the skull roof to the occiput in *Brachydectes*. The transition is more angular in *Pleuroptyx* and is marked by a transverse ridge across the posterior skull roof (fig. 26A). In specimen AMNH 7558 (fig. 15A, *B. elongatus*), in which bones surrounding the postparietals have been displaced, the postparietal is seen to have a stout anterior process which extends under the parietal, as Sollas (1920: 494) first noted. He also commented on the presence of an appropriate groove in the parietal to accommodate this process. Therefore, not only is the parietal-postparietal suture serrate, as seen in plan view, but also extensively overlapping.

At its lateral edge, the postparietal sends down a broad flange (figs. 13F, 15D) to support the tabular and squamosal.

The postparietal-exoccipital suture is bevelled, as the postparietal laps onto the exoccipital (figs. 13F, 14E, 16E). The postparietals border foramina in the approximate position of posttemporal fenestrae.

The frontals and nasals are approximately equal in length, but are roughly 25 percent shorter than the parietals. The frontal pair is about three-quarters the width of the parietal pair, while the nasal is only two-thirds this width, effecting a gradual tapering of the median series anterior to the frontoparietal suture.

Anterior to the overlap with the parietal, a slim lateral ledge of each frontal is produced to support the bordering prefrontal. This ledge continues forward to become the process of the frontal which underlaps the nasal (fig. 14B). Sollas (1920: fig. 16) and Bolt and Wassersug (1975: fig. 10) showed that this process tapers sharply toward the midline and to be half the length of nasal.

Bolt and Wassersug (1975: 326) described the nasal-prefrontal suture as a simple butt joint, but commented that the prefrontal underlaps the nasal in the posterior portion of their contact. Among the specimens available, the nasal-prefrontal suture can be either sinuous or serrate (fig. 13B). The prefrontal fails to underlap the nasal anterior to the level of the lacrimal rim of the nares. Anterior to the nasal-prefrontal contact, the nasals form a large portion of the bony dorsal rim of each naris.

Anteriorly, each nasal bears a median

trough directed toward the premaxilla and a lateral process described as bifurcate (Bolt and Wassersug, 1975: 326). The median trough is partially preserved in the left nasal of AMNH 6172, but is far narrower than that reconstructed by Bolt and Wassersug (1975: fig. 4). According to these authors, the floor of the trough disappears anteriorly to create a large fenestra bordered laterally by the dorsolateral process of the premaxilla. This process, they suggested, articulates with the bifurcate lateral process of the nasal. Unfortunately, the material available does not preserve the region well enough for comment on either the bifurcate nature of the lateral process of the nasal or the purpose of this fenestra.

The main body of the premaxilla may be irregularly rectangular as in *B. elongatus* or triangular as in *B. newberryi* (fig. 7A, B), perhaps due to individual variation or to differential ossification among species. The anterior face of the premaxilla may be planar or somewhat undulate (as reconstructed by Bolt and Wassersug, 1975). It may bear one or several small foramina or fossae and possesses nasal, palatal, and maxillary processes. In the available material there is only one nasal process, which rises from the dorso-medial region of the premaxilla to contact the nasal. Perhaps due to poor ossification or to breakage, there is no distinct dorsolateral process of the premaxilla as described by Bolt and Wassersug (1975). The palatal process is situated ventral to the anterior extreme of the vomer, contacting it in an overlapping suture (fig. 14D). The maxillary process butts against the anterior extremity of the maxilla and sends a short, horizontal lappet onto its dorsal surface (cf. Bolt and Wassersug, 1975). Four teeth are present in the premaxilla of *B. newberryi* (AMNH 6941, fig. 7B). The premaxillary tooth count is uncertain in *B. elongatus*. Sollas (1920) reconstructed five simple conical teeth in the bone while Bolt and Wassersug (1975) recognized seven.

The prefrontals are slim bones which border the frontals and posterior portions of the nasals and pass posteriorly to contact the parietals. In doing so, the prefrontal appears to fill some portion of the space occupied by the postfrontal in other early tetrapods and possibly that of the postorbital as well. A ven-

trolateral process of the prefrontal supports the lacrimal in a distinct groove (fig. 14D).

Williston (1912) found no distinct lacrimal in the skull of *B. elongatus*. Sollas (1920) interpreted the lacrimal as an ascending process of the maxilla, even though neither of the specimens of *B. elongatus* available to him exhibited the process in continuity with the body of the maxilla. Bolt and Wassersug (1975) correctly interpreted this "process" as a distinct lacrimal bone. It is a triangular element with a long apex which rests in the groove of the ventral process of the prefrontal. The lacrimal is bowed outward and forms a portion of the rim of both the naris and the orbitotemporal fenestra. Its expanded base bears a broad, triangular, shallowly recessed facet in which rests the facial process of the maxilla. The bone bears no indication of a lacrimal canal.

The maxilla extends for one-third the skull's length. It has a very low profile and a broad palatal shelf (figs. 7A, B, 13A, C, 14D), bearing a medial process at midlength which is directed toward the vomer. The anterior extreme of the maxilla is overlapped by a lappet of the maxillary process of the premaxilla. A very modest facial process of the maxilla rises to contact the lacrimal. Posteriorly, the maxilla shares a long overlapping suture with the thin anterior process of the palatine. As frequently happens (e.g., Sollas, 1920: 506), this relationship is disrupted in the specimen illustrated in figure 14D. Maxillary teeth are simple, pointed cones as in the premaxilla. They may be slightly recurved. The estimated tooth count in each maxilla is ten.

The suspensorium is a tapered rod composed of two bones descending from the skull roof to support the quadrate. The more dorsal of these two bones lies lateral to the postparietals at the edge of the skull roof and is interpreted as the tabular by analogy with similarly placed bones in labyrinthodonts, nectrideans, aïstopods, and in acceptance of such an interpretation of these elements in microsaur and adelogyrinids (Carroll and Gaskill, 1978; Panchen, 1972). The dorsal portion of the tabular has a broad contact with the ventral flange of the postparietal and overlaps both the postparietal-squamosal contact and a portion of the parietal-postparietal contact. The anterior process of the

tabular lies in a groove in the posterolateral process of the parietal, while its ventral process lies in a long groove in the lateral surface of the squamosal.

Although the tabular is characterized in other amphibians as an element supporting the braincase through contact with opisthotic or exoccipital (e.g., Panchen, 1972), the tabular in lysorophoids appears to be screened from such contact by extensive overlap with the squamosal. Contact between tabular and the tabular lobe of the exoccipital, which was reported but not illustrated by Sollas (1920: 505), is not evident in the available material. The tabular and exoccipital do approach each other closely, however, and contact may have been made in cartilage.

Earlier workers have identified the tabular as either the squamosal (Huene, 1913b, 1913c; Williston, 1908a, 1912) or as the supratemporal (Sollas, 1920; Gregory et al., 1956; Thomson and Bossy, 1970; Bolt and Wassersug, 1975). The confusion between tabular and squamosal seems to have been caused by misinterpretation of sutures as fractures. On the other hand, the possibility does exist that the lysorophoid tabular represents a fusion of the tabular and supratemporal, as has also been suggested for microsaurs and adelogyrinids (Carroll and Gaskill, 1978; Romer, 1969; Thomson and Bossy, 1970). This consideration seems reasonable, since in overlapping the squamosal, the tapered process of the tabular extends into the region normally held by the supratemporal.

The squamosal is a thick, wedge-shaped bone, dorsally held between the ventral processes of the parietal and postparietal and the under surface of the tabular. The squamosal tapers from the skull roof but flares medially into a broad process (alar process of Sollas) which extensively overlaps the quadrate, effectively concealing it from lateral view. The lateral surface of the squamosal bears a long, slender groove which receives the ventral process of the tabular. The dorsolateral process of the prootic supports the squamosal medially (cf. figs. 2C, D, 15B).

The quadrate is an irregularly rectangular prism whose long axis parallels that of the squamosal-tabular unit. Enveloped laterally by the squamosal, the quadrate contacts the pterygoid medially (fig. 14A, C). The squa-

mosal-quadrate sutural contact is oblique to the sagittal plane, so that as the quadrate broadens ventrally to form its two, modest condyles, the squamosal tapers in a complementary fashion. This tapering, beveled surface of the squamosal is seen in figures 8A, 16A. Superficially, the pterygoquadrate suture appears to be a concavo-convex surface (fig. 16B); however, a transverse section of this region (Bolt and Wassersug, 1975, fig. 12) shows the suture to be serrate. Williston (1908a) noted a foramen in this region of the quadrate, but none was found in this study. Dorsally, the quadrate ends abruptly in a blunt surface (fig. 16A), which may have been continued dorsally in the palatoquadrate cartilage.

PALATE: Figure 14C, D demonstrates the relationships of pterygoid, palatine, and vomer in specimen UMMP V3036. The palate is derived relative to that in most primitive amphibians in the wide separation of the pterygoids, but also by the apparent elimination of interpterygoid vacuities by the broad parasphenoid. Superficially, the pterygoid and vomer appear to butt against the parasphenoid, but Bolt and Wassersug (1975: 318) have demonstrated that these bones share a bevelled suture. The palatine clearly spans the overlapping suture of the pterygoid and vomer. It sends a long anterolateral process to contact the dorsal surface of the maxilla. Bolt and Wassersug (1975: fig. 5) illustrated a posterolateral process of the palatine which has not been found in the material at hand.

The pterygoid is a flat, narrow bone. Its palatal surface faces ventromedially at a shallow angle. Its "upper" surface thus faces dorsolaterally but steepens to be nearly vertical at the quadrate. Gaps between the pterygoid and parasphenoid in AMNH 6172 (fig. 13C) may have been filled by cartilage as Bolt and Wassersug (1975: 328) suggested. Similar gaps in specimen UMMP 3036 (fig. 14C) are artifacts of preparation. There are no obvious facets marking the pterygoid portion of the basipterygoid joint. There is no distinct epipterygoid.

The vomers have relatively straight medial edges (fig. 14A) and probably contact one another in straight sutures. Their outer edges are curved and each bears an arcade of roughly a dozen teeth which are noticeably smaller

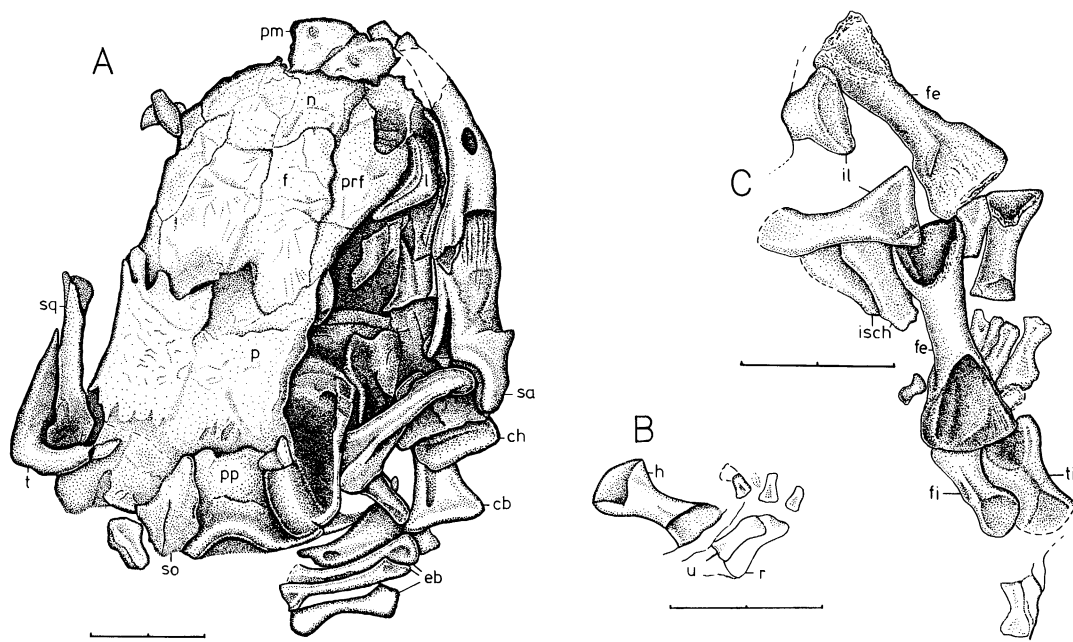


Fig. 8. *Brachydesmus newberryi*, BM(NH) R.2544. A, Skull detail; B, forelimb detail; C, hindlimb detail. Bar scale = 2 mm.

than those of the marginal dentition. At its anterior extreme, each vomer possesses a tapered process which contacts the palatal process of the premaxilla. Posteriorly, the separation of the pterygoids allows the vomers to contact the parasphenoid.

BRAINCASE: Ossified portions of the braincase in *B. newberryi* and *B. elongatus* include the parasphenoid, supraoccipital, and basioccipital bones, as well as the sphenethmoid, pleurosphenoid, and exoccipital pairs (figs. 2, 14B, 15A–D). Otic bones and stapes have been identified with confidence only in *B. elongatus*. Much of the braincase was completed in cartilage, especially anterior to the otic region.

The broad parasphenoid (figs. 13C, 14C) is the largest bone in the skull. In ventral view, its outline conforms to the perimeter of the braincase, except where it is deeply embayed for the ventral process of the basioccipital. The parasphenoid widens gradually as it approaches the pterygoids, supporting the exoccipitals and, probably, the stapes. At the posterior extremity of the pterygoid-parasphenoid contact, the parasphenoid is abruptly constricted. In front of this constrict-

tion in AMNH 6172 (fig. 13C) are small projections which may be the basipterygoid processes. However, there are no obvious facets which might mark a mobile basipterygoid articulation. The edges of the parasphenoid continue forward for a short distance roughly parallel to one another and then quickly converge toward the midline. Here the short cultriform process of the parasphenoid is wedged between the vomers. Visible posterior to the basipterygoid region in AMNH 4696 (fig. 14A) and AMNH 6172 are two foramina, presumably for carotid arteries.

The palatal surface of the parasphenoid is essentially flat but may bear broad, shallow depressions on either side of the basioccipital embayment and on either side of the midline at its anterior end, as noted by Sollas (1920: 497). Dorsally, the parasphenoid contacts the pleurosphenoid without visible suture (fig. 15B). Anterior to the pleurosphenoid the dorsal surface of the parasphenoid is gently concave (fig. 15E).

The basisphenoid is not present as a distinct element in lysorophids, but, as in many early tetrapods, may be fused with the parasphenoid. A fracture coursing between inter-

nal carotid foramina in the parasphenoid of AMNH 4696 (fig. 14A of this paper; Huene, 1913a: fig. 10B; Case, 1908: fig. 1) may mark a weakness indicating the boundary between embryonic anlagen of the parasphenoid and basisphenoid as Zangerl (1944) found in young amphisbaenids. Otherwise, the basisphenoid may be represented in the basal portion of the pleurosphenoid (discussed below).

The supraoccipital may be similar to the postparietals in size and shape as in AMNH 6172 (fig. 13B) or it may be severely constricted at midlength as in AMNH 4701 (fig. 13E). The bone passes between the postparietals to contact the parietals. The supraoccipital bears serrate sutures with the postparietals and exoccipitals. It forms the dorsal portion of the rim of the foramen magnum and portions of the rims of small openings which may be homologous with the posttemporal fenestrae. The dorsal surface of the supraoccipital may be flush with the postparietals or raised, perhaps through distortion, to resemble a "sagittal crest," as Huene (1913a) termed it.

In figure 15A, the parted suture between the supraoccipital and parietals reveals a broad process of the supraoccipital which underlaps portions of the parietals anteriorly and of the postparietals laterally. This process is also evident in figure 13a and plate 70 of Sollas (1920).

The exoccipitals constitute a large portion of the occiput and form the greater portion of the protruding rim of the foramen magnum. Each exoccipital is broadly expanded dorsally and ventrally and is severely constricted at midheight by embayments for the foramen magnum and the tenth (vagus) nerve. Near the rim of the vagal foramen, where the ventral anterior process of the exoccipital becomes distinct, is a small foramen through which probably passed the twelfth cranial nerve.

The dorsal expansion of the exoccipital shares overlapping sutures with the supraoccipital and postparietal and forms part of the rim of the (?)posttemporal fenestra. This dorsal expansion sends a process anteriorly, which in *B. elongatus* (fig. 13A, D) can be seen to bifurcate, maintaining the exoccipi-

tal-postparietal suture on one hand and sending a ventral ramus to support the opisthotic, on the other. Ventrally, the exoccipital bears a long, lateral process and a shorter, stout, posteromedial process. The long, lateral process rests on the edge of the parasphenoid and follows it anteriorly toward the otic region where it supports the stapes (fig. 15B, C). The stout medial process bears a shallow, posteromedially directed facet which is the exoccipital portion of the occipital articulation. These facet-bearing processes of the exoccipitals rest on the parasphenoid and on the lateral surfaces of the basioccipital.

In this paper several references have been made to the pair of foramina in the lysorophoid occiput bounded by exoccipital, supraoccipital, and postparietal. These are in the approximate positions of the posttemporal fenestrae (or possibly fossa Bridgei; Holmes, 1984) of temnospondyl amphibians and rhipidistian fish. However, the posttemporal fenestrae in temnospondyls are rimmed by the tabulars, postparietals, and paroccipital processes of the opisthotics, which suggests that they may not be strictly homologous with the foramina in lysorophoids. Moreover, the open nature of the lysorophoid skull makes it impossible to ascertain where these foramina lead, if not directly into the cranial cavity. They seem too small to be the site of epaxial muscular insertion as possibly were the posttemporal fenestrae in temnospondyls and rhipidistian fish; they may have carried blood vessels draining the neck and head region as Holmes (1984) and O'Donoghue (1921) have suggested.

The basioccipital is thick and bluntly wedge-shaped in lateral view (fig. 15D). Most of the bone rests on the parasphenoid. However, a portion extends posteriorly beyond the parasphenoid to contribute a shallow, median cotyle to the occipital articulation. This cotyle receives the "odontoid" process of the first vertebra. On the ventral surface of the basioccipital is a V-shaped process which, in effect, forms a coarsely serrate suture with the parasphenoid (e.g., fig. 13C). The ventral surface of this process is flush with the ventral surface of the parasphenoid.

In dorsal view the basioccipital would seem to be a rounded pentangular prism whose apex

is directed anteriorly. Each anterolateral facet of the prism bears a large fossa of unknown purpose.

The opisthotic (figs. 2C, D, 14B) is an irregularly pear-shaped bone, the smaller end of which contacts the dorsal, anterior process of the exoccipital. The broad expansion of the opisthotic supports the stapes and may have served to complete the vagal foramen. In none of the available material is the opisthotic fused to the exoccipital (contra Huene, 1913a, 1913b).

The prootic is a stout bone having processes directed toward the parietal, squamosal, pleurosphenoid, and stapes. The two broad basal processes contact the posterior process of the pleurosphenoid and support the stapes. These two processes diverge around a foramen through which may have proceeded a branch of the seventh nerve. Dorsally the prootic is somewhat constricted and expands again into an irregularly oval, dorsolaterally directed surface. The more medial half of this surface contacts the posterolateral portion of the parietal. The lateral portion is set off from the medial portion by a slight flexure and contacts the squamosal.

The stapes possesses a broad, circular footplate supported by pro- and opisthotic and by a process of the exoccipital. In some of the specimens examined, the posterodorsal portion of the perimeter of the footplate bears a substantial notch which may be an artifact of preparation or may have been finished in cartilage. The short columella is offset from the axis of the footplate and is directed anterolaterally toward the suspensorium, but never contacts it in the specimens examined, although a cartilaginous connection may have existed. The distal end of the columella expands into an oval concavity in the largest available specimen, FMNH PR 1456 (fig. 16A).

The pleurosphenoid and sphenethmoid, respectively, the posterior and anterior pillars of Sollas (1920), are laterally compressed struts of bone arising from the dorsal surface of the palate to contact the underside of the skull roof. By its contact with the prootic, the pleurosphenoid (epipterygoid of Case, 1908; Broom, 1918; and Gregory, 1948) seems to have incorporated the otherwise indistin-

guishable basisphenoid. As noted above, there is no visible line of suture between the pleurosphenoid and the parasphenoid (fig. 15B, E). Its base is long, but narrow, extending posteriorly beyond the level of the stapes and medial to it. As they rise, the concave anterior and posterior edges of the pleurosphenoid approach each other to form a stout column which is rounded on its posterior surface but comes to an edge anteriorly. The column is cylindrically hollow to receive the ventral process of the parietal (figs. 14B, 15E). The posterolateral aspect of the pleurosphenoid is developed into a stout process with a flat, dorsal surface upon which rests the anterior ventral process of the prootic. At the base of this process are three small, (?) nutrient foramina. The internal surface of the pleurosphenoid is very shallowly concave to conform with the tall, oval cross section of the braincase. The pleurosphenoid and prootic together form the rim of the foramen for the fifth nerve. Ventrally these two bones and the stapes rim the foramen for the seventh nerve.

The sphenethmoids are narrow struts of bone comprising the anteriormost ossifications of the braincase (figs. 10A, 14B). They contact the dermal roof near the frontal-prefrontal suture and contact the palate in the vicinity of the parasphenoid-palatine suture. The exact arrangement of these sutures is uncertain (cf. Bolt and Wassersug, 1975).

PROPORTIONAL DISTINCTIONS BETWEEN THE SKULLS OF *B. NEWBERRYI*, *B. ELONGATUS*, AND *PLEUROPTYX CLAVATUS*

While the skulls of different lysorophoid species have very similar bone configurations, the skulls of *B. elongatus* and *B. newberryi* are distinguishable through the length-to-width proportions of their skull roofs (see Methods section). This ratio in *B. newberryi* is roughly 2.6:1, while that in *B. elongatus* is approximately 1.8:1 (table 1). Regression analysis has shown the plots of estimated skull roof length versus width for these two species (fig. 23) to be statistically distinct beyond the 0.95 probability level.

The sole skull known of *Pleuroptyx clavatus* is too incomplete for this comparison

TABLE 1
Skull Roof Proportions in *Brachydictes*

Specimen	Estimated roof length (mm)	Estimated roof width (mm)	L/W
<i>B. newberryi</i>			
AMNH 2156	7.2	2.6	2.77
AMNH 6861	9.8	4.0	2.45
AMNH 6925	12.8	4.4	2.91
BM(NH) R.2544	7.6	3.2	2.38
		\bar{x} =	2.64
<i>B. elongatus</i>			
AMNH 4698	14.8	9.2	1.61
AMNH 4699	11.7	5.8	2.10
AMNH 4700	13.6	8.0	1.70
AMNH 4761	15.4	8.4	1.84
AMNH 4762a	10.4	6.8	1.53
AMNH 4884	9.4	5.8	1.62
AMNH 6172	14.3	7.8	1.83
AMNH 21910	11.6	7.2	1.61
Sollas' spec. 2 ^a	14.4	6.2	2.32
UMMP 3036	13.5	7.5	1.80
USNM 8892	10.8	6.4	1.69
		\bar{x} =	1.79

^a (Sollas, 1920, fig. 1).

to be made. However, a comparison of width-to-length ratios of the parietal pair (among all three species, table 2) shows the proportions of the bone pair in *B. newberryi* (\bar{x} = 1.03, N = 5) and *B. elongatus* (\bar{x} = 1.32, N = 13) to be significantly distinct from that in *P. clavatus* (\bar{x} = 1.60) at a probability level beyond 0.95. This distinction is supported by the overlapping ranges of these values in *B. newberryi* and *B. elongatus*, in contrast to the gap existing between them and that in *Pleuroptyx*. The biological significance of the difference in parietal pair width-to-length ratios between *Brachydictes* and *Pleuroptyx* is unknown, but it supports both a subjective impression of a broader skull in *P. clavatus* and the taxonomic distinction made between these two lysorophoid genera based on other characters.

MANDIBLE

As exemplified by *Brachydictes* (figs. 7, 13), the stout mandible is approximately 0.6 the length of the skull. Posteriorly, it bears a dis-

TABLE 2
Width-to-Length Ratios of Parietal Pair in *Brachydictes* and *Pleuroptyx*

Specimen	Estimated width (mm)	Estimated length (mm)	W/L
<i>B. newberryi</i>			
AMNH 2156	2.8	3.0	0.93
AMNH 6861	4.0	4.4	0.91
AMNH 6925	4.4	5.2	0.85
BM(NH)R 2544	3.2	3.2	1.00
PU 20391	19.0	13.0	1.46
		\bar{x} =	1.03
<i>B. elongatus</i>			
AMNH 4698	9.2	6.4	1.44
AMNH 4699	5.8	5.6	1.04
AMNH 4700	8.0	5.6	1.43
AMNH 4701	7.4	5.8	1.28
AMNH 4761	8.4	6.0	1.40
AMNH 4762a	6.8	4.8	1.42
AMNH 4884	5.8	4.6	1.26
AMNH 6172	7.8	6.6	1.18
AMNH 21910	7.2	5.8	1.24
FMNH PR 1456	14.0	9.9	1.42
Sollas' spec. 2 ^a	6.2	5.6	1.45
UMMP 3036	7.5	5.3	1.40
USNM 8892	6.4	5.4	1.19
		\bar{x} =	1.32
<i>Pleuroptyx clavatus</i>			
MCZ 2303	9.6	6.0	1.60

^a (Sollas, 1920, fig. 1).

tinct articular notch and a modest retroarticular process. At midlength the dentary and surangular together form a low, rounded coronoid process, which may bear ridgelike scars marking jaw adductor insertion. Laterally, a large oval mandibular fenestra is rimmed by dentary, surangular, and angular. Anterior to the coronoid process, the mandible tapers gradually toward the symphysis. While unobstructed medial views of complete mandibles are unavailable, various views in a number of specimens suggest the absence of mandibular fossae or Meckelian fenestrae. Distinct coronoid or other nondentary, tooth bearing bones are absent from the mandible.

Viewed laterally, the dentary is a wedge-shaped bone (fig. 7A), which comprises the anterior two-thirds of the lateral mandibular surface. Its two distinct posterior processes rim a large portion of the lateral mandibular

fenestra and share extensive overlap with the angular and surangular. At its midlength the dentary bears a lone mental foramen. A shallow, but distinct, groove proceeds anteriorly from it. Medially, the Meckelian groove is covered by the splenial and prearticular (fig. 7B). The existence of a small Meckelian foramen near the symphysis is possible but uncertain, because the region is obscured or disrupted in the specimens examined. The ridged internal surface of the dorsal posterior process of the left dentary in *B. newberryi* (fig. 7B) demonstrates the extensive nature of its overlap with the anterior process of the surangular. The dentary may hold as many as a dozen, pointed conical teeth, although the mandible in AMNH 6941 (*B. newberryi*, fig. 7A, B) bears only nine. These teeth may be slightly recurved, but lack any labyrinthine plications.

The surangular is an irregularly sigmoidal bone whose stout central portion and anterodorsal process rim a portion of the lateral mandibular fenestra. The anterodorsal process is broadly overlapped by the dorsal posterior process of the dentary. The posteroventral process of the surangular forms the lateral rim of the articular notch and participates in the retroarticular process with the articular, prearticular, and angular. Between the dentary and articular notch, the surangular forms the dorsal surface of the mandible and contacts the prearticular medially.

The angular is a long wedge of bone which forms the posterior portion of the ventral surface of the mandible in both lateral and medial views. Along with the surangular and prearticular, the angular supports the articular. The anterior portion of the angular is bound by overlapping sutures shared with the splenial and the dentary.

The prearticular sheaths a major portion of the medial surface of the mandible, extending from its participation in the retroarticular process to the symphyseal region. The bone assists in supporting the articular and mirrors the surangular in bearing a distinct articular notch. The prearticular shares long sutures with the angular and splenial ventrally and with the surangular and dentary dorsally. The prearticular and dentary envelope the overlapping suture shared between the splenial and angular.

The splenial is a slender, elongate bone which overlaps the angular posteriorly and shares long sutures with the dentary ventrally and prearticular dorsally. The splenial extends almost, if not quite, to the symphysis and bears no obvious foramina.

The lysorophoid lateral mandibular fenestra, unique among amphibians, may be homoplastic with a similar opening, the external mandibular fenestra, in archosaurs, the rhynchosaurid *Mesosuchus* (Romer, 1956), the pelycosaur *Ophiacodon* (Romer, 1966), and in dicynodont and therocephalian therapsids (Kemp, 1972, 1982). As discussed by Kemp (1972) and Bramble (1978), this opening in therapsids lies in a zone of neutral stress and may exist due to resultant nondeposition of bone. This explanation may also apply in the case of *Brachydictes*, since the lateral mandibular fenestra occurs at the juncture of three bones (dentary, angular, and surangular), which Frazzetta (1968) discussed as appropriate for fenestration resulting from reduced stress.

HYOBRANCHIAL SKELETON

The hyobranchial skeleton of *Brachydictes* consists of the hyoid arch and four branchial arches (figs. 7C, D, 16C, D, F). That of *Pleuroptyx* is incompletely known. Lysorophoid hyobranchial elements are generally stout, cylindrical bones, each gradually constricted at midlength. Contrary to a claim by Sollas (1920), the posterior elements are not much more gracile than the more anterior elements. However, in *Brachydictes* the hypohyals and ceratohyals are distinct from the more typical elements. The hypohyals are flat, relatively thick bones, equally as long as wide and waisted at midlength. They are approximately half as long as the ceratohyals. The ceratohyals are broadly similar to the common hyobranchial elements, but each possesses a broad, medial flange. From their articulation with the hypohyals, the ceratohyals curve posterodorsally, passing medially to the retroarticular process of the mandible.

As preserved, epibranchial 1 in both species of *Brachydictes* is conical (figs. 7C, 16D). However, this condition may be due to breakage or poor ossification, particularly in *B. elongatus*, described later. The second epi-

branchials in the Carboniferous species *B. newberryi* and *P. clavatus* are distinct in bifurcating distally into short processes which may have served as points of hyobranchial muscle attachment (figs. 7C, 26A). Epibranchial 2 of the Permian species *B. elongatus* lacks this bifurcation (fig. 16A).

Cope (1874, 1875a), Moodie (1916), and Sollas (1920) described basibranchials in the lysorophoid hyobranchial skeleton. No such medial elements were found in this study.

Although lysorophoids have been described as perennibranchiate (Cope, 1872; Pompeckj, 1912; Case, 1915; Abel, 1919, 1920; Huene, 1948, 1956; Kuhn, 1965), they exhibit no evidence of either external or internal gills. Their epibranchials bear no grooves or facets, which in perennibranchiate *Necturus* mark the course of afferent branchial arteries and which, in part, suggest the presence of external gills in *Dvinosaurus* (Bystrow, 1939); nor does the matrix enclosing lysorophoid specimens bear carbonaceous film indicating the presence of external gill rami as found associated with *Branchiosaurus* of the Upper Carboniferous and Permian of Europe (Bulman and Whittard, 1926; Watson, 1963; Boy, 1974) and possibly of North America (Romer, 1939).

POSTCRANIAL SKELETON

VERTEBRAL COLUMN AND RIBS: Lysorophoid vertebrae are noted for both neurocentral sutures and paired neural arches (e.g., figs. 1C, 7C, D, 29). The neurocentral suture was recognized by Cope (1877) in his description of the type material of *Lysorophus tricarinatus*. Case (1902a, 1902b) provided the first comment on an articulated series of vertebrae from *B. elongatus*, remarking that the red matrix holding the specimen accentuated the suture between the neural arch pairs.

The one piece centra are amphicoelous, notochordal, and biconid (hourglass shaped). They are generally 25 to 30 percent longer than wide and are trussed by five or possibly six carinae. Two of these occur lateral to the dorsal midline and support the neural arches. One appears on each lateral aspect of the centrum, and one, frequently broader than the others, occurs ventrally. The extra width of

the ventral carina may result from its being a paired structure composed of two slender carinae lying side by side. Sollas (1920) illustrated this condition with transverse sections (e.g., fig. 28T, this paper), which demonstrate an internal separation between the two ventral carinae. Externally, only a shallow indentation suggests the paired nature of this ventral ridge. The centra which Sollas illustrated are estimated to be approximately 3 mm long. Similar centra are available among the material used in this study and do show the shallow, longitudinal depression occurring between the crests of the paired ventral ridges. In larger centra the paired nature of the ventral carina is imperceptible.

In contrast to the biconid body of the centrum, which appears to be composed of compact bone only, the carinae are composed cancellous bone beneath a compact cortex. The gross histology of the carinae has functional significance as addressed in the discussion section.

Between the carinae in all lysorophoids are large fossae, whose depths emphasize the constriction of the biconid centrum. In relatively larger centra, any of these fossae, except those supporting the neural canals, may be spanned by accessory struts of bone. The fossa between the dorsolateral, neural arch-bearing carinae is roofed by the neural canal. The more ventral surfaces of the centra, including lateral and ventral carinae, may bear a punctate ornamentation and small pits.

The anterior and posterior rims of the centra are smooth, bearing no accessory intervertebral articulations. However, at its intersection with the lateral carinae, the posterior rim supports a pair of processes which bear shallow facets for articulation with rib capitula. Earlier workers (Williston, 1908a; Sollas, 1920) overlooked these facets in their search for a capitular articulation.

Nearly complete vertebral columns are known for *B. newberryi* (fig. 1C) and *B. elongatus* (Olson, 1971, UCLA-VP 2802). Presacral vertebral counts are estimated to be 69 in the former and 97 in the latter. One sacral vertebra is distinguishable in *B. elongatus*. Caudal vertebral counts are uncertain but at least 20 caudals are preserved in *B. elongatus*. These more complete vertebral columns show midtrunk centrum lengths to be relatively

uniform, but also that the centra in *B. elongatus* shorten abruptly proximal to the skull and sacrum.

As noted, the neural arches are paired structures, sutured at their dorsal midlines and to their centra. The spinal nerves passed intervertebrally as in most primitive tetrapods, but in contrast to the condition in aistopods and the nectridean *Crossotelos* in which they pierce the neural arches. The length of the arch pedicel is equal to roughly one-half to two-thirds the length of the centrum. In lateral view, the trace of the neurocentral suture may be upwardly concave or may take the form of an inverted chevron. Anterior to the apex of the chevron the neurocentral sutural surface is broad, either oval or rounded rectangular in shape (fig. 28F, K, P). Posterior to the apex the surface narrows abruptly.

Transverse processes rise solely from the neural arches and are directed slightly anteriorly. They may span a width which is 1.5 to 2.0 times greater than that of the centrum. The processes are oval in parasagittal section. The dorsal surfaces of the processes occasionally bear one or two pits which may have led to nutritive foramina.

Zygapophyses are borne on stout processes of the neural arches which do not project much beyond the width of the centrum. The zygapophyseal surfaces are oriented at low angles to the horizontal plane. There appears to be no important variation in their attitude along the column.

In small lysorophoid individuals the neural spines of all vertebrae behind the first are little more than very low ridges on the sloping neural arch roof. As absolute size increases, the neural spines develop into distinct processes (fig. 16A). There are no accessory intervertebral articulations on the neural arches.

The sloping posterior of the lysorophoid skull produces a gap between the occiput and the first neural arch. This gap is filled by a pair of broad, rather keystone-shaped plates labeled previously as proatlantes in analogy with similar elements in amniotes. They resemble neural arches in their general appearance. Their anterior edges appear to bear surfaces for articulation with the protruding rim of the foramen magnum (Sollas, 1920),

while the posterior margins rest against the anterior faces of the paired neural arches of the first vertebra. As Sollas (1920: 520) noted, the proatlantal pair may be asymmetrical, one member being larger than the other and their mutual suture set off the midline. There is no evidence of a centrum associated with these elements.

The centrum of the first vertebra (figs. 11C, 18A, B, D) is a broad, low element. It is expanded anteriorly into a tripartite occipital articulation. Medially, this articulation is a broad "odontoid" process which articulates with the posterior concavity of the basioccipital. On either side of the "odontoid" are flat facets which meet complementary facets on the posterior processes of the exoccipitals. It is recognized that cartilage, no longer present, may have tempered the morphologies of the occipital articulation. No ribs have been found with this vertebra.

The neural arch of the first vertebra, like other lysorophoid neural arches, is sutured to the centrum and is a paired structure. The neural arch pairs are tall, narrow elements supporting anterior and posterior zygapophyses.

The lysorophoid sacral vertebra shows little to distinguish it from adjacent vertebrae. Its position is estimated by the presence of hind limbs or elements of the pelvic girdle, either of which may be somewhat displaced. In one specimen of *B. elongatus*, vertebra 98 can be recognized as the sacrum by the absence of long, free ribs, such as on the vertebrae immediately anterior to it, and by the absence of both hemal arches and taller neural spines as found on the caudal vertebrae immediately posterior to it (figs. 17E, F, 20A).

Lysorophoid caudal vertebrae are preserved only in *Brachydectes* (figs. 1C, 17E, F, 18F). Their centra are not laterally compressed. Lateral carinae are indistinct; ventral carinae are paired. Caudal vertebrae may bear a foramen or two in the lateral aspect of the centrum.

Caudal neural arches are sutured to the centra and remain paired. In *B. newberryi* the neural arch appears to rest on a single centrum. In *B. elongatus* the anterior portion of the neural arch pedicel abuts against a facet on the posterior extreme of the preceding centrum (figs. 17F, 18F). In effect, the caudal

neural arch of *B. elongatus* spans the intervertebral articulation. Caudal neural spines are low in small individuals, but are quite distinct in large specimens and are angled posteriorly.

The presence of stout hemal arches clearly distinguishes the caudal vertebrae in both species of *Brachydectes*. Unfortunately the morphology of the arches in *B. newberryi* and their relationship to the caudal centra are uncertain, due to their indistinct preservation. In *B. elongatus* the arches appear to be relatively straight in lateral view when small, as in UCLA-VP 2802 (fig. 17E) and in the posterior portion of the series in USNM 23727 (fig. 18F), but are distinctly flexed when larger. In *B. elongatus*, the proximal rami of each pair articulate with the ventral carinae of individual centra. The hemal arches, therefore, appear not to be intercentral. The hemal arch pairs are fused distally, but bear no proximal crosspiece to enclose the hemal artery and vein.

Ribs are present on all presacral vertebrae except for the first and apparently the last one or two anterior to the sacrum. Ribs have not been found on the caudal vertebrae. Lysorophoid ribs are curved and bicipital. Although the ribs are robust and their bony cortex is thick, they are not strictly pachyostotic, since the marrow cavities, while narrow, are not obliterated. The tuberculum articulates with the transverse process, while the capitulum is supported by the facets on the posterior rim of the preceding centrum, as noted above. The rib bodies are oval or subcircular in cross section. Most noticeably in larger specimens, the gap between articular heads is spanned by a thin webbing of bone. Between the pectoral girdle and sacrum the rib cord is generally equal to the length of three or four adjacent centra, but is less in the ribs three or four vertebrae anterior to both the pectoral girdle and sacrum. The distal ends of the ribs are frequently concave, suggesting their completion in cartilage.

Each rib bears an alar process which originates at the tuberculum and runs along the posterodorsal aspect of the rib for two-thirds to three-quarters of its ossified length before tapering to the shaft. A rounded ridge rises on the anterior aspect of the rib between rib heads and becomes indistinct toward rib

midlength. There is no obvious regional variation in this rib morphology along the lysorophoid vertebral column. However, *P. clavatus* is distinct from other lysorophoids in the exaggerated alar processes of its ribs.

APPENDICULAR SKELETON: The pectoral girdle is found in the region of vertebrae 4–6. The endochondral portion of the girdle is represented by a pair of ossifications, presumably the scapulocoracoids, which generally take the form of rounded rectangular plates lacking foramina and distinct glenoids (figs. 11A, 19A, E). In larger specimens the posterior edges of these endochondral elements are frequently rounded and thickened.

The clavicles, cleithra, and interclavicle constitute the dermal girdles (figs. 7C, D, 11A, 16A, 19B, C, D, F, G, 26A, C). The clavicles are long, spindlelike elements with broadened or spatulate medial ends marking their contact with the interclavicle. Those in *Pleuroptyx* bear a distinct posteriorly directed process. Cleithra are short spindle- or splintlike bones in *B. newberryi* and *P. clavatus*, but have not been identified in *B. elongatus*.

The interclavicle differs in *Brachydectes* and *Pleuroptyx*. In the former, the element is a semicircular plate and is shallowly concave dorsally (figs. 16A, 19C, F, G). In *Pleuroptyx* the interclavicle is irregularly rhomboid and bears a faint, radiating sculpture (fig. 26C).

The limbs of lysorophoids are tiny. Humeri are preserved in *Brachydectes* and *Pleuroptyx*. In the smaller species, *B. newberryi* and *P. clavatus*, the humerus is a stout bone about the length of one adjacent centrum (figs. 7C, 10C, 11A, 26). It is constricted at midlength. Articular surfaces are indistinct and there is no indication of epicondylar foramina. Humeri in *B. elongatus* differ in being more gracile than those of the former two species (fig. 21). Articular surfaces of limbs are absent and presumably were fashioned in cartilage.

In lysorophoids, the radius and ulna are similar in size and proportion, and range from 0.5 to 0.7 the length of the humerus. Articular surfaces were completed in cartilage and the olecranon process of the ulna is indistinct. No carpal ossifications are displayed.

No manus is known in *B. elongatus*. That of *B. newberryi* possesses at least three digits with a phalangeal formula of 1-2-2 (fig. 10C),

but circumstances discussed in the description of that species (to follow) indicate that the count may have been four with a phalangeal formula of 3-23-3-2 (fig. 10D). *Pleuroptyx clavatus* has four metacarpals in its manus, but no phalanges have been preserved (fig. 26A).

Portions of the pelvic girdle are known in both species of *Brachydictes* (figs. 1C, 8C, 20C), but not in *Pleuroptyx*. The ilium, ischium, and pubis form a simple, triangular plate with a modest iliac blade at the apex, but do not co-ossify. There is no indication of the sacral rib attachment. The nature of the pelvic symphysis is unknown.

Hind limb elements are known in both species of *Brachydictes* (figs. 1C, 8C, 20B-D). Femora are stout, but constricted gently at midlength. They are roughly equal to the length of two adjacent centra and the articular surfaces are not ossified. The femora exhibit adductor crests, but no distinct processes.

The tibia and fibula in *Brachydictes* are stout, medially constricted bones, approximately half the length of the femur.

The tarsus and pes are known only in material referred to *B. newberryi* (figs. 8C, 12C, D). In the tarsus, three irregular discs are preserved. These have been identified as tibiale, intermedium, and fibulare. The pes possesses five digits with a phalangeal formula of 2-3-3-2.

DERMAL OSSIFICATIONS: In no lysorophoid are dorsal or ventral scales or gastralia known.

BRACHYDICTES COPE, 1868: 214

Brachydictes Cope, 1868: 214.

Cocytinus Cope, 1871: 177.

Lysorophus Cope, 1877: 187, partim.

Molgophis (Cope, 1868: 220) Romer, 1966: 363, partim.

TYPE SPECIES: *Brachydictes newberryi*.

REVISED DIAGNOSIS: *Brachydictes* is distinguished from similar *Pleuroptyx* by its narrower skull roof. Specifically, the width-to-length ratio of the parietal bone pair averages 1.32 (N = 13, range: 1.04–1.45) in *B. elongatus* and 1.03 (N = 5, range: 0.85–1.46) in *B. newberryi* versus a ratio of 1.60 in the sole specimen of *Pleuroptyx clavatus*. It also differs in having a rounded rectangular interclavicle, lacking the multiple processes found

in *Pleuroptyx*, and possesses spindlelike clavicles, lacking a posterior process at its base. The rib alae are much less conspicuous than those in *Pleuroptyx*.

Brachydictes newberryi Cope, 1868: 214

Brachydictes newberryi Cope, 1868: 214.

Cocytinus gyrenoides Cope, 1871: 177.

Molgophis wheatleyi (Cope, 1874: 263) Romer, 1930: 81.

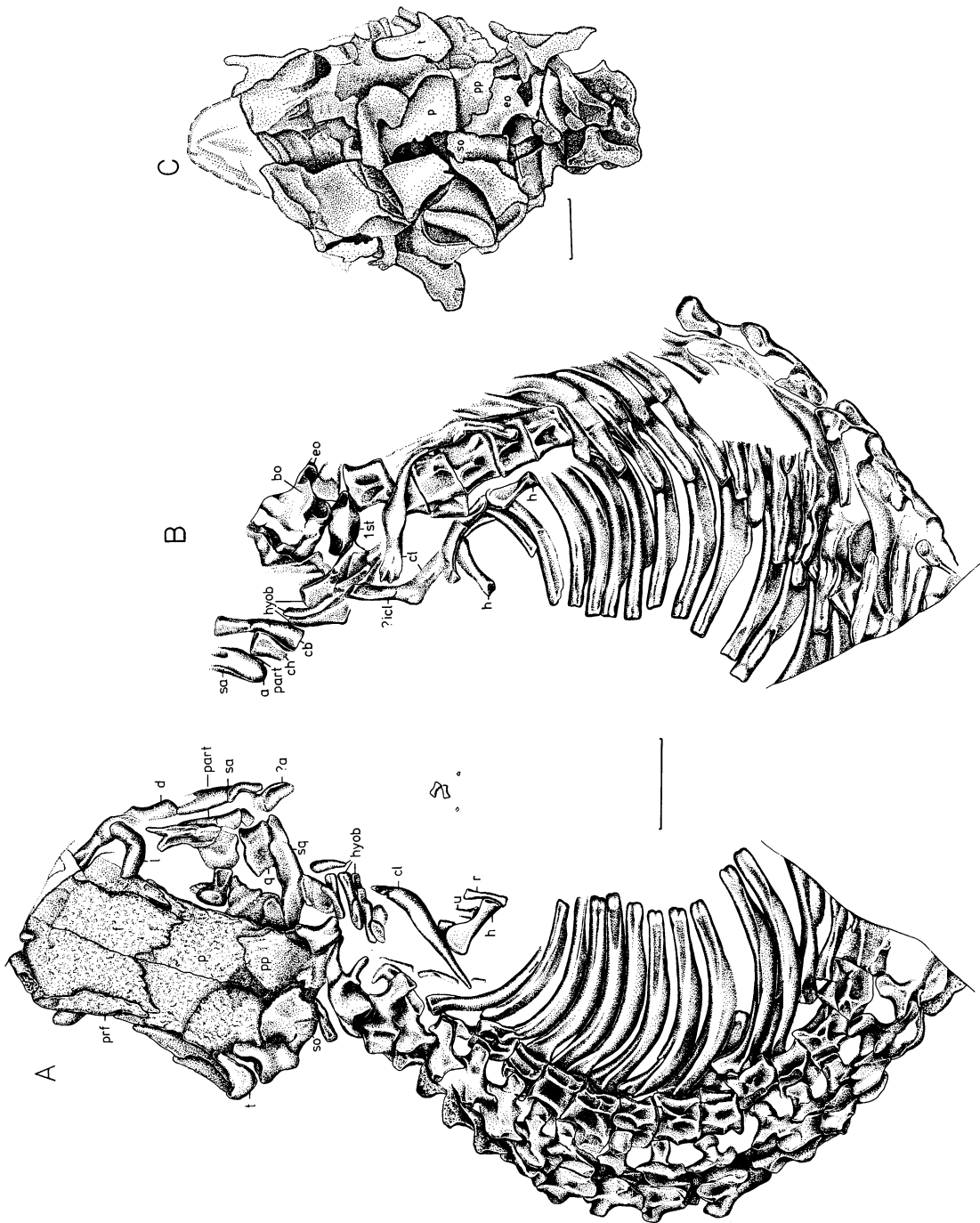
REVISED DIAGNOSIS BASED ON AMNH 6925, AMNH 6941, AND BM(NH) R.2544: *Brachydictes newberryi* is distinguished from *B. elongatus* of the Lower Permian by its greater skull length-to-width ratio (2.6:1 versus 1.8:1), its relatively low presacral vertebral count (69, estimated, versus 97), its distinctly elongate lateral mandibular fenestra, and the morphology of epibranchial 2, which is bifurcate distally.

HOLOTYPE: AMNH 6941, formerly 8604G, Newberry Collection. Nearly complete right mandible, left dentary, two premaxillae, and a right maxilla. As *Brachydictes newberryi*, Cope 1868: 214–215; 1869: 14–15; 1874: 268–269; 1875a: 375, 359, 388–389, pl. 27, fig. 2; Miller, 1889: 619, fig. 1180; Moodie, 1916: 175–176. As *Cocytinus gyrenoides*, Romer, 1930: 81–83. Figure 7A, B of this paper.

HORIZON: “Cannel coal below coal seam identified as the Upper Freeport Coal (Newberry, 1871, 1874), Allegheny Group, Middle Pennsylvanian; equivalent to late Westphalian D of Europe” (D. Baird, 1964; see also Hook, 1983: 7).

LOCALITY: Coal mine originally owned by the Ohio Diamond Coal Company (Murphy, 1980), Linton, Saline Township, Jefferson County, Ohio, approximately 2.5 km south of Wellsville, Ohio (Hook, 1983); NE ¼, sec 13, T9N R9W, Wellsville, Ohio, 7.5' quadrangle.

REFERRED MATERIAL, FIGURED (skulls with postcranial elements, all from Linton): **BM(NH) R.2544:** Purchased in 1895, possibly as part of Thomas Stock Collection. A nearly complete skeleton. As *Cocytinus gyrenoides*, Steen, 1931: 883, text fig. 21, pl. 6, figs. 2, 3, 4; Huene, 1948: 120, fig. 16; 1956: 29, fig. 27; Dechaseaux, 1955: fig. 27; Carroll and Gaskill, 1978: 188, fig. 132b; Carroll,



1988: 178, fig. 9-27b. Figures 1C, 8A-C of this paper. **AMNH 6861**: Formerly no. 7, Newberry Collection. As *Molgophis wheatleyi*, Moodie, 1916: 149-150. Figure 10A (detail) of this paper. **AMNH 6897**: Formerly 1101G, Newberry Collection. Holotype *Molgophis wheatleyi*, Cope, 1874: 263-264, 1875a: 369-370, pl. 45, fig. 1; Moodie, 1915: pl. 50, fig. 3; 1916: 149-150. As *Cocytinus gyrinoides*, Romer, 1930: 81-83. Figure 11A of this paper. **AMNH 6925**: Formerly 8613G, Newberry Collection. Holotype of *Cocytinus gyrinoides* in all earlier works, Cope, 1871: 177; 1874: 276-278; 1875a: 360-365, text fig. 5, pl. 39, fig. 4; Fritsch, 1883: 173, fig. 111; Miller, 1889: 620, fig. 1182; Moodie, 1916: 67-69, fig. 16; Romer, 1930: 81-83, fig. 1; Case, 1946: 409, fig. 172; Huene, 1948, fig. 17a; 1956: 30, fig. 29b. Figure 7C, D of this paper. **MCZ 2156**: C. M. Wheatley, collector. Figure 10B, C of this paper. **MCZ 2304**: Donald Baird party, collector, 1955. Figure 9C of this paper.

REFERRED MATERIAL, NOT FIGURED (skulls and postcranial elements, all from Linton except as noted): **BM(NH) R.2663**: J. W. Davis Collection. As *Cocytinus gyrinoides*, Steen, 1931: 882. **CM 25095**: R. Lund party, collector, 1970. **CM 25653**: R. Lund, collector, 1969. Monongahela "B" freshwater limestone, Monongahela Group, Upper Pennsylvanian (= Stephanian). "Elm Grove Channel," 1.2 km (¾ mi) east of Elm Grove, Ohio County, West Virginia, along highway I-70 (see Wheeling and Valley Grove, West Virginia, 7.5' quadrangles). As *Lysorophus dunkardensis*, Lund, 1972a, 1975: 176, 1976: 234, Lund, et al., 1979; Berman, 1979. **DSH 063.043**, **DSH 063.071**, **DSH 063.072**, **DSH 063.518**, **DSH 063.519**: David S. Hamilla, collector, 1983.

QUESTIONABLY REFERRED MATERIAL, FIGURED (except as noted, all material is from Linton and consists of vertebrae and ribs): **MCZ 2133**: Donald Baird collector, 1951. Figure 11B, C of this paper. **MCZ 2157**: Formerly 52a and b, C. M. Wheatley Collection. As "batrachian reptile," Wyman, 1857: 173; 1858: 163, fig. 2. As *Molgophis macrurus*,

Cope, 1875a: 368. Figure 6A, B of this paper. **PU 16533**: Donald Baird, collector, 1957. Series of caudal vertebrae and pedes. As *Molgophis* with reference to tail, D. Baird, 1965: 292. Figure 12C, D of this paper. **PU 20391**: G. R. Case, collector, 1968. Figure 9A, B of this paper. **USNM 4477**: Formerly #8, R. D. Lacoe Collection, Thomas Stock collector, 1888. Hyobranchial and postcranial elements, including pectoral girdle and forelimbs. As *Molgophis brevicostatus*, Moodie, 1909a: 27; as "*Pleuroptyx*," Romer, 1930: 107, fig. 12 (partim). Figure 10D of this paper. **USNM 4313**: Lacoe Collection. Francis Creek Shale, Carbondale Formation, Middle Pennsylvanian (= Westphalian D), from the bank of Mazon Creek, 10 km southeast of Morris, Grundy County, Illinois (Rayner, 1971). As aistopod *Phlegethontia mazonensis*, Gregory, 1950: 867. As *Cocytinus gyrinoides*, D. Baird, 1964: 14. As *Cocytinus*, A. R. Milner, 1982: 660. Figure 12A, B of this paper.

QUESTIONABLY REFERRED MATERIAL, NOT FIGURED (except as noted, all material is from Linton and consists of vertebrae and ribs): **AMNH 6901**: formerly 1100 G, Newberry Collection. *Molgophis brevicostatus*, Moodie, 1916: 148. **CM 21490**: R. Lund, collector, 1970. **CM 23570**: R. Lund, collector, 1972. **CM 26456a and b and CM 26460a and b**: R. Lund, collector, 1974. **CGH J94**. **DSH 063.013**, **DSH 063.090**, **DSH 063.091**, **DSH 063.092**: David S. Hamilla, collector, 1983. **MCZ 2145**: D. and L. Baird, collectors, 1950. **MCZ 2245**, **MCZ 2305 (partim)**, **MCZ 2306 (partim)**, **MCZ 2307**: Baird party, collectors, 1955. **MCZ 2486**: F. G. Thompson, collector, 1954. **PU 16541b and c and PU 23494**: D. and L. Baird, collectors, 1957. **UMMP 3574 and UMMP 3579**: R. N. Fearon, collector, 1883. **USNM 4479**: R. D. Lacoe Collection, Thomas Stock, collector, 1888. As *Pleuroptyx clavatus*, Moodie, 1916: 152-153.

SPECIMENS REMOVED FROM BRACHYDECTES: Specimen AMNH 2564, skull and short segment of vertebral column, referred to *Cocytinus* by Moodie (1916), has been transferred to the aistopod *Phlegethontia* by McGinnis

←
Fig. 9. *Brachydictes newberryi*. A, B, PU 20391. Part and counterpart (bar scale = 1 cm); C, MCZ 2304, skull detail (bar scale = 1 mm).

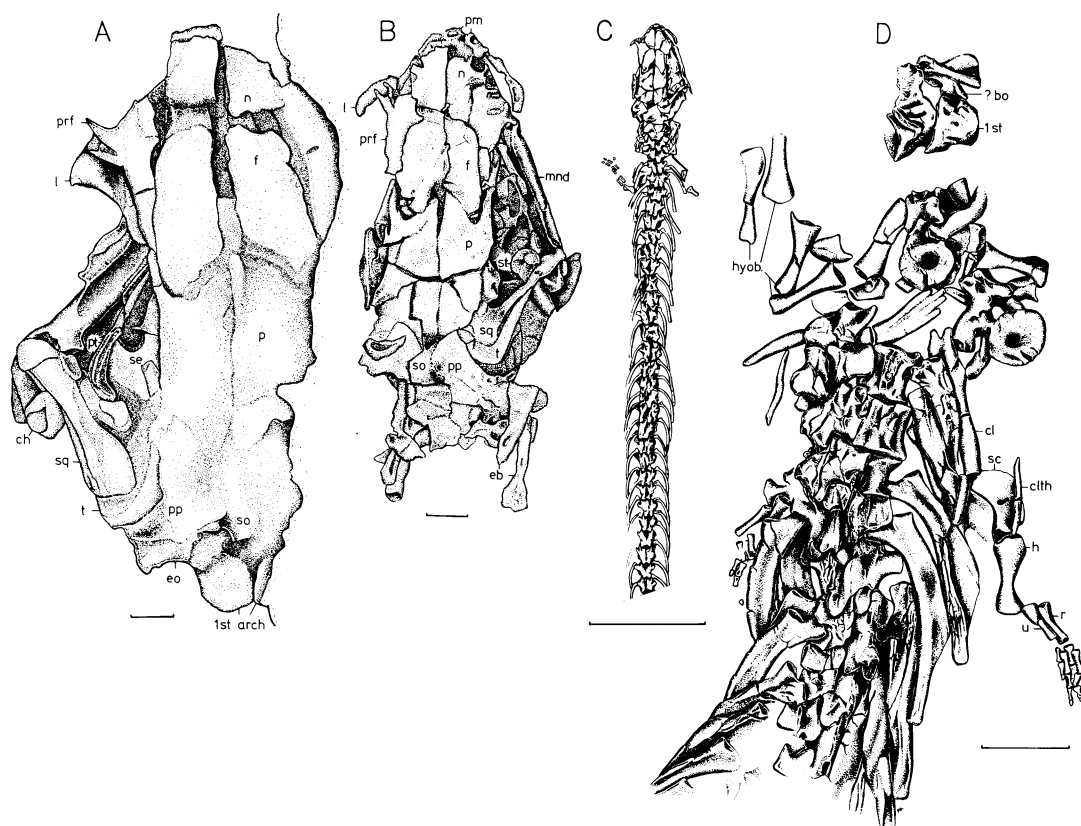


Fig. 10. *Brachydectes newberryi*. A, AMNH 6861. Detail of skull (bar scale = 1 mm); B, AMNH 2156. Detail of skull (bar scale = 1 mm); C, AMNH 2156. Specimen (bar scale = 1 cm); D, USNM 4477 (bar scale = 1 cm).

(1967: 3). Specimen AMNH 6898 (8699G, Newberry collection), referred by Moodie (1916) to *Molgophis wheatleyi* (= *Brachydectes newberryi*) on preparation proves to be the left mandible of a labyrinthodont, probably *Amphibamus* (Donald Baird and Robert Hook, personal commun.). Specimen BM(NH) R.2667, a mandible discussed by Steen (1931: 885) as representing a form closely related to *Cocytinus gyronoides* (= *B. newberryi*) has been shown to belong to a captorhinomorph reptile *Cephalerpeton* (Reisz and Baird, 1983).

DESCRIPTION

SKULL: While the skull of *B. newberryi* is quite similar to that of *B. elongatus* (fig. 13) in the elements present and in their disposition, it is proportionately narrower. The length-to-width ratio of the skull roof (as de-

fined in the methods section) in *B. newberryi* is approximately 2.6:1 (table 1) as compared with 1.8:1 in *B. elongatus*. The relationship between the skull roof dimensions is illustrated by regression lines in figure 23. Regression analysis has shown these lines to be statistically distinct above the $P = 0.95$ level.

Among the available specimens, the length of the skull roof ranges from approximately 5 mm in CM 25095 to 12.8 mm in AMNH 6925. The skull roof of a large, but questionably referred specimen, PU 20391, is incomplete anteriorly, but its original length can be estimated to be approximately 46 mm. Because of the incomplete nature of PU 20391 and severe disruption of the bones in CM 25095, these specimens were not included in the statistics discussed above.

Dermal ornamentation is rare among smaller individuals of *B. newberryi*. However, faint striae are present in BM(NH)

R.2544 (figs. 1C, 8A) and a rugose sculpture ornaments the skull roofs of relatively large specimens CM 25653 and PU 20391 (fig. 9A). The skull of the latter specimen is roughly six times the length of that of BM(NH) R.2544.

The dorsoventral flattening suffered by skulls of *B. newberryi* has obscured the relationships of the suspensoria and palate, although the quadrate is probably held between squamosal and pterygoid as in *B. elongatus*. This crushing has generally obscured the occiput also, although a few bones of the occiput of *B. newberryi* can be distinguished directly in MCZ 2304 (fig. 9C). Unfortunately, the view yields no information concerning the (?)posttemporal fenestrae. A ventral view of the occipital articulation may be seen in AMNH 6925 and PU 20391.

No complete maxilla is available, although dorsal and ventral surfaces of the anterior portion of a right maxilla may be seen in AMNH 6941 (fig. 7A, B). The medial process and the embayment for the maxillary process of the premaxilla are distinct. The ridge on the lateral margin of the maxilla posterior to the level of the medial process marks the rise of the modest facial process of the maxilla. However, the roughened surface posterior to this level suggests that most of this process and posterior portions of the maxilla have been broken away.

The anterior face of each premaxilla lacks the fossa noted in *B. elongatus* by Bolt and Wassersug (1975). Instead, they exhibit several (?)nutritive) foramina.

A major distinction between the mandibles of *B. newberryi* and *B. elongatus* is the size and shape of their lateral mandibular fenestrae. In *B. newberryi* the fenestra is elongate as seen in AMNH 6941 and AMNH 6897 (fig. 11A), but circular and much smaller in *B. elongatus*.

Except for the obscured retroarticular process, specimen AMNH 6941 yields a complete right mandible. This stout lower jaw is about 17 mm long and, because of its large size and displacement of the elements, exhibits features not observed in other lysorophoid mandibles. The coronoid process exhibits a series of ridges which may be scars representing the insertion of the mandibular adductor. Medially, the dentary exhibits a

prominent, medioventrally sloping shelf beneath the tooth row. This shelf is ornamented by a series of striae which lead to nutritive foramina. The Meckelian groove is a broad, attenuated feature, reaching the level of the third tooth anteriorly. The extreme anterior rim of the Meckelian groove exhibits two shallow embayments, best seen in the left dentary. These embayments, one slightly posteroventral to the other, accommodate the anterior ends of the prearticular and splenial bones. The symphysis is an elongate irregular surface extending anteriorly from the level of the first tooth.

The first of nine teeth in the left dentary appears to be only partially erupted. Posterior to tooth 4, the dentary exhibits a series of short ridges radiating from the base of each tooth. At the bases of teeth 6 and 8 in the right dentary are features which resemble resorption pits. A space represents the position of tooth 7 in the left dentary.

HYOBANCHIAL APPARATUS: In AMNH 6925 are preserved both hypohyal and ceratohyal pairs, ceratobranchials 1–2 and epibranchials 1–4. There is no evidence of ceratobranchials 3 and 4 in this specimen, although these elements can be identified in AMNH 6897 (fig. 11A). Epibranchial 1 in AMNH 6925 is the element noted by Cope (1874) as a possible “stylohyal.” Both left and right bifurcate second epibranchials are displayed in this specimen. It is uncertain whether or not the foramen in the second epibranchial pierces the bone.

VERTEBRAL COLUMN AND RIBS: The vertebral centra in *B. newberryi* exhibit typical lysorophoid characters and, although they are deeply amphicoelous, their notochordal nature can be confirmed only in fortuitous sections in referred specimen USNM 4313 (fig. 12A, B). Because the vertebrae are usually preserved in either dorsal or ventral, rather than lateral, views, the trace of the neurocentral suture is usually obscured in the plane of the matrix or by ribs. Fortunately, the trace is exposed in vertebrae 40–44 of USNM 2133 (fig. 11B), confirming that the neural arches were sutured, not fused, to the centra. Neurocentral sutural surfaces of the neural arches are obvious in AMNH 6925 (fig. 7D) and anteriorly in AMNH 6897 (fig. 11A), where they have been displaced and now lie along-

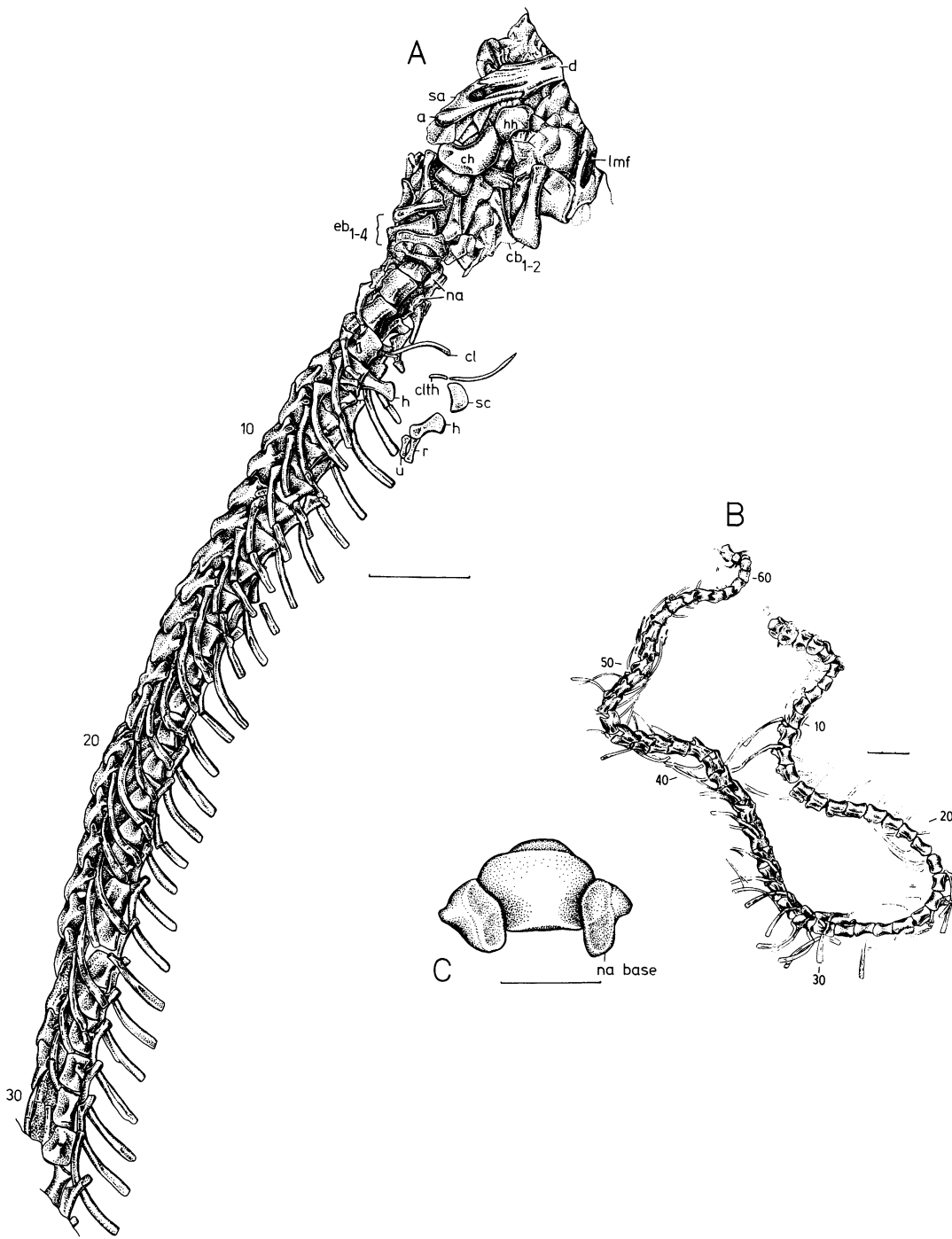


Fig. 11. *Brachydectes newberryi*. A, AMNH 6897, holotype of "*Molgophis wheatleyi*" (bar scale = 0.5 cm); B, MCZ 2133, specimen (bar scale = 3 mm); C, MCZ 2133, detail of first vertebra (bar scale = 1 mm).

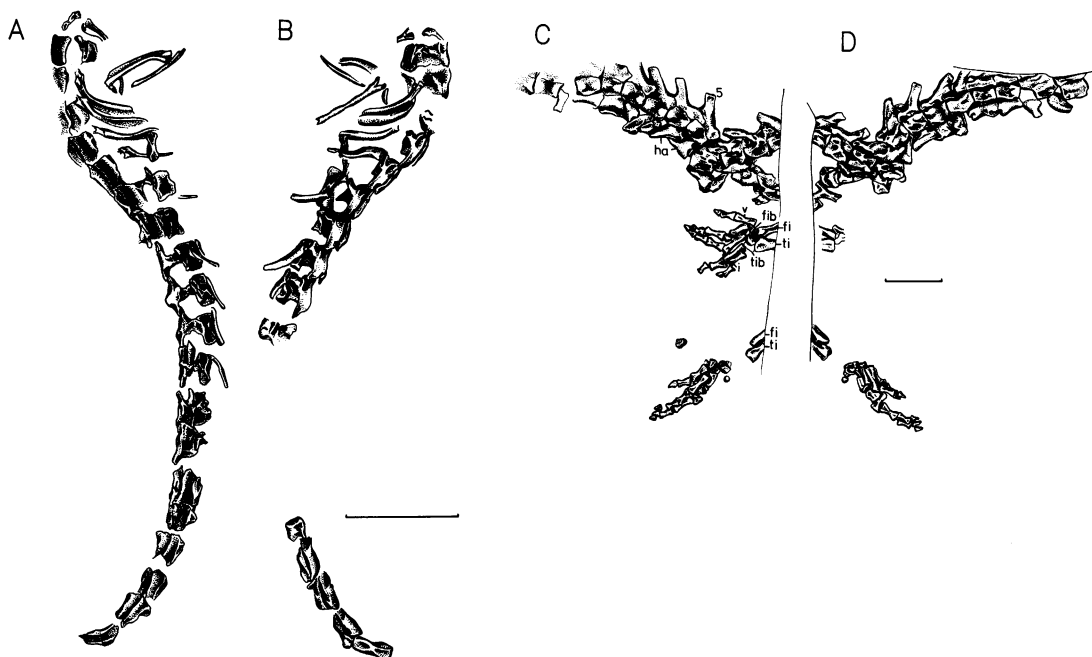


Fig. 12. *Brachydectes newberryi*. A, B, USNM 4313, part and counterpart (bar scale = 1 cm). C, D, PU 16533. Part and counterpart (bar scale = 1 cm).

side their centra. Dorsal views generally reveal the suture between neural arch halves as a linear trace of the sutural surface (figs. 7C, 1C).

The most complete specimen of *B. newberryi* is BM(NH) R.2544, which has an estimated length of 11 cm. It shows gradual, although slight, change in estimated centrum length along the column, increasing from 1.2 mm at the first vertebra to a maximum of 1.6 mm at centrum 47 (fig. 24). Posterior to this position the centra shorten. The last measurable centrum, caudal 9, is approximately 0.9 mm long.

The first centrum is exposed in few of the available specimens and then only in ventral or oblique views (figs. 7D, 9B, 11B, C).

The sacrum is in the vicinity of vertebra 70, a region of *B. newberryi* preserved only in BM(NH) R.2544. The vertebrae here are indistinctly preserved. No sacral differentiation is evident.

Ten caudal vertebrae are preserved in BM(NH) R.2544. Hemal arches associated with these vertebrae are indistinct, but appear to be roughly equal in length to the adjacent centra. Hemal arches in the question-

ably referred specimen PU 16533 (fig. 12C, D) are much like those in *B. elongatus* (cf. fig. 18F) and bear round facets for articulation with the ventral carinae of the caudal centra.

Comparison of the lengths of trunk centra among lysorophoid specimens yields a reasonable estimate of the relative sizes of individuals, even for incomplete specimens or for those otherwise not directly measurable (see Olson, 1956, 1970b; Olson and Bolles, 1975). This comparison is possible because of the nearly uniform lengths of lysorophoid trunk centra within the individual, as seen in figure 24. In *B. newberryi*, the smallest available specimen, PU 23494, is coiled upon itself, making measurement of the entire skeleton difficult. However, four of its trunk centra average 0.46 mm in length. The largest specimen of *B. newberryi* is PU 20391. It is incomplete, but five of its trunk centra average 4.8 mm in length. This indicates that there is a minimum tenfold size range in available specimens of *B. newberryi*. Multiplication of these average centrum lengths by the 69 presacral vertebrae in *B. newberryi* yields estimated presacral vertebral column lengths of

approximately 32 mm for PU 23494 and 33 cm for PU 20391.

The ribs are of typical lysorophoid morphology. Throughout most of the column, the length of the chord of a rib is approximately equal to the length of three local centra. Posterior to vertebra 63, they abruptly shorten. However, if specimen PU 20391 (fig. 9A, B) is correctly assigned to *B. newberryi*, it demonstrates that the ribs grow differentially longer during ontogeny, for in this large specimen the rib chord is equal in length to four or five vertebrae.

Similarly, the well-developed alar processes of the ribs in this specimen and questionably referred specimen USNM 4477 seem to indicate that this feature also grows disproportionately during ontogeny in *B. newberryi*. This allometric increase in alar development in *B. newberryi* creates an uncertainty with regard to *Pleuroptyx*, originally distinguished on the basis of exaggerated rib alae. This uncertainty, as well as criteria for recognizing *Pleuroptyx*, is addressed in the description and discussion of that genus.

APPENDICULAR SKELETON: Clavicles and cleithra can be identified in referred material of *B. newberryi* (figs. 7C, D, 9A, B, 10C, D, 11A). They are generally simple splintlike elements. Clavicles in the larger specimen USNM 4477 (fig. 10D) are fimbriated at their medial ends. Its cleithra are relatively more robust than those in the smaller examples, but little more complicated in their morphology.

Identification of an interclavicle or a scapulocoracoid is more difficult, because elements potentially representing either bone are present only in AMNH 6897 (fig. 11A) and USNM 4477 (fig. 10D) and only as single bones. Their unpaired nature suggests that they might be interclavicles. However, they are not bilaterally symmetrical as one might expect in a median element and are interpreted as elements of the endochondral girdle, probably scapulocoracoids. In both AMNH 6897 and USNM 4477, the bones are irregularly rounded rectangles and have maximum dimensions roughly equivalent to the length of one adjacent vertebral centrum. The scapulocoracoid in AMNH 6897 is a simple plate. That in USNM 4477 has a

thickened posterior edge and a distinct concavity in its posteroventral corner, which may represent the glenoid. Upon close examination, its surface is roughened, suggesting that it may have been finished in cartilage.

The humerus of *B. newberryi* is roughly equivalent to only 1 percent of the body length as estimated from BM(NH) R.2544. Its proximal end is broader than the distal, perhaps due to differential ossification. Otherwise, the humerus is comparatively featureless. Its exposed surface is flattened in most specimens, probably by postburial compression.

Like the humerus, the ulna and radius are small bones, constricted at midlength. The radius is the stouter of the two and is more broadly expanded distally. The ulna is slim distally and the olecranon is only modestly developed. Both radius and ulna also appear to be flattened by compression. As preserved, the radius is approximately 0.6 the length of the humerus and is slightly longer than the ulna, which is approximately 0.5 the length of the humerus.

Carpal bones are not preserved in any specimen of *B. newberryi*, suggesting their cartilaginous nature. Three digits are preserved in the left manus of AMNH 2156 (fig. 10C). Metacarpals I–III are approximately 0.4, 0.5, and 0.5 mm long, respectively. They are well-ossified elongate bones, constricted at the midlength. The count of preserved phalanges is 1-2-2. The proximal phalanges are roughly twice as long as they are broad. All are distinctly waisted.

The right manus in questionably referred USNM 4477 (fig. 10D) clearly displays four metacarpals and has a phalangeal count of 3-?3-3-2. Metacarpals I–III are 2.2, 2.0, and 2.5 mm long, respectively. The proximal end of metacarpal IV has been broken away. Its length is estimated at 1.8 mm.

The discrepancy in digit number between AMNH 2156 and USNM 4477 could be due to loss or poor ossification in the smaller specimen, since the possibly missing metacarpal would be only about 0.2 mm long. This digit might also lie slightly deeper in the matrix, displaced from the plane of the other digits, and have escaped notice during preparation. If the taxonomic assignment of USNM 4477 is correct and the difference in

digit number between it and AMNH 2156 is due to some variance in ossification, it is problematic whether the disparity is caused by individual or ontogenetic variation, since rates of ossification and digit growth in *Brachydectes* are unknown.

The pelvis and hind limbs in *B. newberryi* are preserved only in specimen BM(NH) R.2544 (figs. 1C, 8C) among the confidently assigned material. The elements of the pelvis are dissociated. The ilia are elongate bones, expanded ventrally in a spatulate manner. As seen in the right ilium, the expanded end bears a triangular depression which is interpreted as a portion of the acetabulum. The semicircular depression on the medial aspect of the left ilium is perhaps a consequence of the acetabular depression of the lateral side.

The ischia are posteriorly attenuated bones. While they appear triangular, their shapes cannot be assessed accurately, as their anterior extremities are obscured by the right ilium.

The femora in BM(NH) R.2544 are approximately 2.8 mm long, which is 2.5 percent of body length. They bear no distinctive processes. As the bones are crushed at their extremities, and because of poor ossification, the articular surfaces cannot be described.

While the tibia is more robust than the fibula, both are roughly half the length of the femur and are similarly crushed, obliterating any evidence of articulating surfaces.

Four metatarsals are preserved in the foot, yet their crushed condition yields little information. The most clearly exposed metapodial, probably I, is about one-third the length of the femur. The most clearly exposed phalanx is a short bone, constricted medially.

Questionably referred specimen PU 16533 (fig. 12C, D) exhibits portions of both left and right tarsi and pedes. Three thickened, irregular discs, here identified as tibiale, intermedium, and fibulare, are evident in the tarsus. Five digits are preserved in the right foot with a phalangeal count of 2-3-3-3-2. Metatarsals and proximal phalanges are stout-waisted bones. The terminal phalanges are pointed.

DERMAL OSSIFICATIONS: When present in the skeletons of other amphibian species at Linton, dorsal and ventral scales are superbly

preserved. Their absence in all specimens of lysorophoids can be taken as evidence that these elements were not present in their skeletons.

Brachydectes elongatus, new species

Lysorophus tricarinatus Cope, 1877: 187 (partim).

DIAGNOSIS: A species of *Brachydectes* distinguished from *B. newberryi* by its relatively broad skull roof (length : width ratio = 1.8:1 versus 2.6:1), its greater presacral vertebral count (97 estimated, versus 69), its smaller, markedly less elongate lateral mandibular fenestra, and its nonbifurcate epibranchial 2.

HOLOTYPE: UCLA-VP 2802 (Olson, 1971: figs. 1-3), a nearly complete skeleton, roughly 50 cm long. Figures 17A-F, 18E, 19E, 20A and B, 21M, 24B, and table 3 of this paper.

HORIZON: Fairmont Shale, Hennessey Group, Lower Permian (Leonardian) (Olson, 1971; Olson and Bolles, 1975; Simpson, 1979).

LOCALITY: SW $\frac{1}{4}$, NW $\frac{1}{4}$, sec 13, T8N, R2W, Cleveland County, Oklahoma (Olson, 1971), roughly 5 mi southeast of the center of the University of Oklahoma main campus (Olson, personal commun.).

REFERRED MATERIAL: All specimens listed below would generally have been referred to *Lysorophus* cf. *tricarinatus* in earlier works. All but four of them are from Permian rocks of north-central Texas. Exceptions are specimens from the Permian of Kansas: KU 28345, KU 28346, KU 28348, and KU 28350. The locality data come primarily from museum catalog cards. In the case of the Texas specimens this information is often scanty, since the specimens were collected before pertinent topographic sheets were generally available and before local stratigraphy had been established (see Cummins, 1908; Romer, 1928, 1935, 1974).

Several of the Texas specimens are specifically recorded as coming from sites within the Clear Fork Group of the Lower Permian. Other Texas specimens listed below can reasonably be assumed to have come from the Clear Fork Group, too, in recognition of similarities of matrix, who collected the specimens, and when they were collected. In some cases, the Arroyo, Vale, and Choza forma-

TABLE 3
Measurements (mm) of UCLA-VP 2802,
Holotype of *Brachydictes elongatus* (from Olson,
1971, table 1)

TOTAL LENGTH OF SKELETON	510-530
Skull length (maximum)	17.2
First five "cervicals" (maximum)	10.0
5th-98th vertebrae (maximum)	440.0
99th vertebrae to tip of tail (maximum)	67.0
	534.2
SKULL MEASUREMENTS:	
Dorsal length (occiput to tip of snout)	17.2
Parietal length (midline)	6.1
Frontal length (midline)	4.6
Nasal length (midline)	4.5
Interorbital width (minimum)	6.4
Posterior width (maximum)	11.7
VERTEBRAL MEASUREMENTS (MAXIMUM LENGTH OF VENTRAL, MEDIAN MARGIN OF CENTRUM):	
Precaudal	
12th ^a	4.3
39th	4.8
40th	4.6
41st	4.9
52nd	4.9
95th	4.6
97th	3.8
Caudal	
101st ^a	3.1
102nd	2.9
103rd	2.8
104th	2.7
107th	2.1
109th	2.1
111th	2.1
116th	1.2
LIMB ELEMENTS:	
Femur	
Length (maximum)	7.4
Proximal width (maximum)	3.3
Distal width (maximum)	2.5
Shaft width (minimum)	1.9
Humerus	
Length (maximum)	4.3
Proximal width (maximum)	1.7
Distal width (maximum)	0.8
Shaft width (minimum)	0.4

^a Ordinal numbers indicate position in series posterior to skull.

tions of the Clear Fork Group are specified as the sources of these specimens. This information is included below to reflect original specimen data. However, one should be aware that a recent revision of Texas Permian stratigraphy does not recognize these formations, but retains the Clear Fork Group as undivided (Brown and Goodson, 1972; Hentz and Brown, 1987).

SKULLS, FIGURED: AMNH 4699: E. C. Case, collector, 1906. Figures 16D, E of this paper. **AMNH 4762a:** C. H. Sternberg, collector, 1902. Baylor County, Texas. Figure 14F of this paper. **AMNH 6172:** C. H. Sternberg, collector, 1918. Craddock bonebed, Baylor County, Texas. Carroll and Gaskill, 1978: 188, fig. 132b; Carroll, 1988: 180, fig. 9-31. Figure 13A-D of this paper.

SKULLS, NOT FIGURED: AMNH 4698 and 4700: E. C. Case, collector, 1906. **AMNH 4884:** E. C. Case, collector, 1908. **AMNH 21920:** C. H. Sternberg, collector, 1902. Baylor County, Texas. **UMMP V9769:** E. C. Case, collector. Clear Fork Group; north side of Big Wichita River, Wilbarger County, Texas.

PARTIAL BRAINCASE, FIGURED: AMNH 7558: C. H. Sternberg, collector, 1902. Arroyo Formation, Clear Fork Group; West Coffee Creek, Baylor County, Texas. Figure 15A-E of this paper.

SKULLS WITH POSTCRANIAL ELEMENTS, FIGURED: AMNH 4696: E. C. Case, collector, 1906. As *Lysorophus*, Huene, 1913a: 322-326, fig. 10B. Figure 14A, B of this paper. **AMNH 4701:** E. C. Case, collector, 1906. Figure 13E, F of this paper. **AMNH 4761:** C. H. Sternberg, collector, 1902. Baylor County, Texas. As *Lysorophus*, Huene, 1913a: 322-326, figs. 7, 8A; 1913b: 390, 392. Broom, 1918: 237-238. **FMNH PR 1456:** Formerly part of FMNH UR 344. E. C. Case, collector. Figures 16A-C, 18A-C, 19A-D, 21A-D, I, J of this paper. **UMMP V3036:** E. C. Case, collector. Clear Fork Group, Wilbarger County, Texas. Figure 20C, D of this paper.

SKULLS WITH POSTCRANIAL ELEMENTS, NOT FIGURED: MCZ 2254: T. E. White and L. I. Price, collectors, 1935. Arroyo Formation, Clear Fork Group; 1.6 km (1 mi) northwest of Sternberg Hill, Sect. 85, Blk. 2, H. and TC. Railroad Survey, Baylor County, Texas. **KU 28345:** R. W. Coldiron and W. D. Coldiron, Jr., collectors, 1974. Blue Rapids Shale, just below the Funston Limestone; SE¼, sec 4,

T7S, R9E, south of State Lake, Westmoreland, Pottawatomie County, Kansas (H.-P. Schultze, personal commun.); see also Westmoreland NW, Kansas, 7.5' quadrangle, 1964. **UMMP V21485**: E. C. Case, collector. Clear Fork Group, Wilbarger County, Texas. **USNM 8891 and 8893 (partim)**: Formerly "number 18." C. H. and L. Sternberg, collectors. 1917. Clear Fork Group, Baylor County, Texas.

POSTCRANIAL SPECIMENS, FIGURED: FMNH UR 344: formerly part of UC 635. E. C. Case, collector. Three nodules bearing series of vertebrae and associated ribs. As *Lysorophus*, Case, 1902a: 45–46, pl. 9, figs. 1 and 2; 1902b: 256–257, pl. 1, figs. 1 and 2. This specimen formerly included material now in FMNH PR 1456, listed above. However, two individuals clearly seemed to be represented. Therefore, the latter material has been given its own number. **RM 14-728**: Richard Seltin, collector. Vertebrae, associated ribs, pectoral girdle, and limb elements. Vale Formation; Seltin Locality 4-40 (B4) (R. Seltin, personal commun.); N $\frac{1}{2}$, NW $\frac{1}{4}$, Soap Creek, Baylor County, Texas, 7.5' quadrangle. Figures 19F, G, 21E–H, K, L of this paper. **USNM 23727**: Formerly "number 18." C. H. and L. Sternberg, collectors, 1917. Series of vertebrae, including caudals, associated ribs, pectoral girdle and forelimb elements. Arroyo Formation; Coffee Creek, Baylor County, Texas. As *Lysorophus*, Carroll, 1968: 1189, fig. 9. Figure 18F of this paper.

POSTCRANIAL SPECIMENS, NOT FIGURED: AMNH 4757: C. H. Sternberg, collector, 1902. With (?fore)limb material. Big Wichita River, west of Hog Creek, Baylor County, Texas. **FMNH UR 440**: Arroyo Formation; Clear Fork Group, Middle Coffee Creek, Baylor County, Texas. **KU 28346**: R. W. Coldiron, collector, 1974; **KU 28348** and **KU 28350**, R. W. Coldiron and W. D. Coldiron, Jr., collectors, 1974. Blue Rapids Shale, just below the Funston Limestone; SE $\frac{1}{4}$, sec 4, T7S, R9E, south of State Lake, Westmoreland, Pottawatomie County, Kansas (H.-P. Schultze, personal commun.). See also Westmoreland NW, Kansas, 7.5' quadrangle, 1964. **MCZ 2202**: E. C. Case, collector. Clear Fork Group; north of Seymour (?Pony Creek), Wilbarger County, Texas. **MCZ 2253**: T. E. White, collector, 1935. With forelimb elements. *Lysorophus* Quarry, Arroyo For-

mation, Clear Fork Group; Coffee Creek, Sect. 78, Blk. 2, H. and TC. Railroad Survey, Baylor County, Texas. **MCZ 2255 (partim)**: L. I. Price, collector, 1934. Arroyo Formation, Clear Fork Group; head of Pony Creek, Sect. 139, T. and NO. Railroad Survey, Abstract 331, Baylor County, Texas. **MCZ 2256**: A. S. Romer party, collector, 1952. *Lysorophus* Quarry, Arroyo Formation, Clear Fork Group; Coffee Creek, Sect. 78, Blk. 2, H. and TC. Railroad Survey, Baylor County, Texas. **MCZ 2808**: A. S. Romer party, collector, 1952. Arroyo Formation, Clear Fork Group; Coffee Creek, Sect. 79, Blk. 2, H. and TC. Railroad Survey, Baylor County, Texas. **UW 6874**: Two nodules, one cut to show centra in frontal section.

This list includes only a small fraction of the *B. elongatus* material collected from the Permian of the midcontinent. Hundreds of other prepared, unprepared, and even uncataloged bulk sample specimens lie in storage in the major collections referred to above. Williston (1908a) and Broom (1918) documented this abundance from the Arroyo Formation of Texas. Olson (1970b) recorded hundreds of specimens from the Hennessey of Oklahoma, he (Olson, 1958) and Seltin (personal commun.) have reported *B. elongatus* from several sites in the Vale and Choza Formations of Texas.

It is appropriate at this point to comment on two other specimens important to our knowledge of *B. elongatus*. These are "Specimen 1" and "Specimen 2" serially sectioned by Sollas (1920) for his description of the skull of *B. elongatus*. Bolt and Wassersug (1975: 323) reported that Sollas' collection of glass-plate photographic negatives of serial sections from Specimen 1 is housed in the Field Museum under number FMNH PR 706. The location of similar negatives from Specimen 2 is unknown. This circumstance is lamentable, since Sollas based his conclusions regarding *B. elongatus* primarily on the sections of Specimen 2 (Sollas, 1920: 487).

ETYMOLOGY: The specific epithet refers to the relatively great length of the vertebral column in the species.

DESCRIPTION

SKULL: The skull of this species has been treated by several earlier workers including

TABLE 4
Skull Roof as Proportion of Skull Length in
Brachydictes elongatus

Specimen	(A) Length of skull roof (mm)	(B) Length of skull (mm)	A/B
AMNH 6172	14.3	18.0	0.80
AMNH 4762a	10.4	14.5	0.72
AMNH 4700	13.6	15.5	0.88
AMNH 4884	9.4	11.0	0.85
UMMP 3036	13.5	17.0	0.79
		$\bar{x} =$	0.80

Case (1908), Williston (1908a), Broili (1904a, 1908a), Huene (1913a, 1913b), Broom (1918), and Sollas (1918). To date, the most comprehensive descriptions have been those of Sollas (1920) and Bolt and Wassersug (1975). The skull is distinguished from that of *B. newberryi* principally through its stouter proportions, indicated by the 1.8:1 length-to-width ratio of the skull roof (fig. 23, table 1). Additionally, the median suture shared by the parietals is frequently interdigitated, as viewed dorsally, unlike the straight or gently sinuous suture seen in *B. newberryi* or *P. clavatus*.

Because the skull of *B. elongatus* formed the basis of the description of the lysorophoid skull in the general anatomy section above, a separate description of it will not be repeated here. However, some comment on size is appropriate. Skulls of *B. elongatus* sufficiently complete for consideration range in length from 11 mm, measured directly in AMNH 4884, to 19.2 mm, estimated in AMNH 4761 from the length of the skull roof, which in *B. elongatus* averages 0.80 of the snout-occipital length (table 4).

In a much larger individual, FMNH PR 1456, the skull is incomplete anterior to the level of the quadrates. However, from the width of the skull roof (15 mm), both the length of the skull roof (26 mm) and the snout-occiput length (33 mm) can be estimated, considering the relationship between length and width of the skull roof plotted in figure 23 and the proportion calculated in table 4. Olson (1939) also reported a skull of *B. elongatus* with a total length of 33 mm. These relatively large skulls are twice the length of

the skull in the holotype and appear to be the largest skulls reported for the species.

MANDIBLE: The mandible of *B. elongatus* is closely similar to that of *B. newberryi* in number and form of elements, but is distinguished by its smaller, circular lateral mandibular fenestra. The ventral surface of the dentary anterior to the mental foramen is produced broadly toward the midline (fig. 13C). Sollas (1920: 512) referred to this ventral flange of the dentary as a "thickening." The intermandibular suture is limited to the more anterior third of the ventral expansion. A similar expansion of the dentary, medial to the tooth row and described by Sollas as a "horizontal edge," cannot be confirmed, because the mandibles are held more or less against the skull in the available material.

More posteriorly, a series of two or three foramina may occur along or near the suture between the angular and prearticular. These probably accommodated branches of fifth and seventh nerves. Elements of the skull and matrix obscure mandibular tooth rows in the available material. However, Sollas (1920) found from 10 to 11 teeth in the dentary, while Williston (1908a) counted 12.

HYOBRANCHIAL APPARATUS: The hyobranchial apparatus of *B. elongatus* presents a few variations from the pattern described in the section on general anatomy. For example, wedged between the first ceratobranchial and epibranchial are elements unique to *B. elongatus*, which Sollas termed "accidental bones." The elements have been found in only two of the available specimens (ac, fig. 16A, C, E). Their homology is uncertain.

The conical shape of epibranchial 1 in a small skull of *B. elongatus* (fig. 16D) appears to be due to poor ossification or may be an artifact of preparation, because the same bone in FMNH PR 1456 is a medially constricted cylinder like other epibranchials in the species.

Unlike epibranchial 2 in Carboniferous lysorophoids, epibranchial 2 in this species is undifferentiated from the other epibranchials.

No foramina were found in any of the hyobranchial elements (contra Broili, 1904a).

VERTEBRAE AND RIBS: In the referred specimens, the lengths of midtrunk centra range from approximately 1.2 mm in KU 28345 to

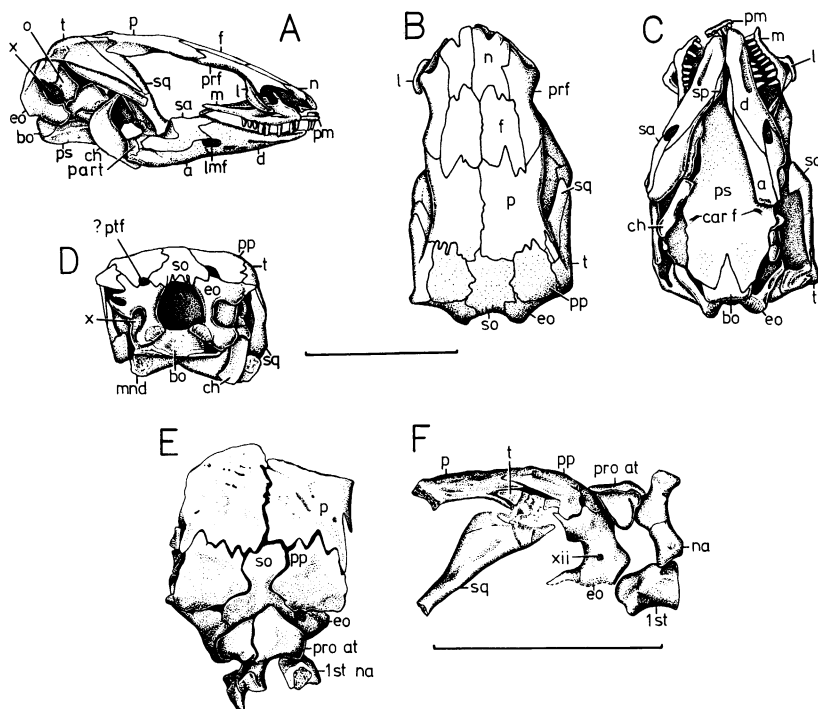


Fig. 13. *Brachyectes elongatus*. A-D, AMNH 6172, right lateral, dorsal, ventral, and posterior views, respectively, of skull and mandibles. After Carroll and Gaskill, 1978, and Carroll, 1988. Bar scale = 1 cm. E, F, AMNH 4701, dorsal and left lateral views, respectively (bar scale = 1 cm).

9.5 mm in FMNH UR 440 and RM 14-728. Olson and Bolles (1975) reported a greater range, noting individuals with midtrunk centra as long as 13.5 mm. Estimated snout-to-sacrum lengths for individuals represented by the size extremes would be 11 cm and 150 cm, respectively, which suggests that *B. elongatus* experienced a lifetime size increase somewhat greater than the tenfold size increase found in *B. newberryi*.

The punctate ornamentation of the centra common in other lysorophoids is present in *B. elongatus* and is exhibited in individuals with trunk centra as small as 2 mm in length. This ornamentation appears in larger individuals as well, but proliferation of auxillary struts and ridges as seen in other lysorophoids is rare, appearing only feebly in individual centra of AMNH 4701 and RM 14-728 among the study material.

The neural arches of presacral vertebrae in *B. elongatus* are very similar to those of *B. newberryi*, but are sufficiently well preserved three-dimensionally to reveal some regional differentiation. For example, Sollas (1920)

distinguished the anterior four vertebrae in *B. elongatus* as cervicals, not only because of their position anterior to the pectoral girdle, but also because the height of their neural arches exceeded that of their centra. In the trunk vertebrae, the heights of the centrum and neural arch are more nearly equal.

Sollas (1920) and Olson (1971) both indicated that the neural arches of the first four or five vertebrae are proportionately shorter anteroposteriorly than those that follow. This seems to be the case in UCLA-VP 2802 (fig. 17). The extreme is seen in the very short, but tall, neural arch of the first vertebra in FMNH PR 1456 (figs. 16A, 18B). In this specimen, which represents an individual roughly twice the size of those illustrated by Sollas and Olson, the neural spines are prominent.

Sollas (1920) made three further claims regarding variation in the vertebral column, but which cannot be confirmed. These are (1) that the diameters of the spinal cord lumina in the first four vertebrae are larger than the diameters of the centra in these vertebrae,

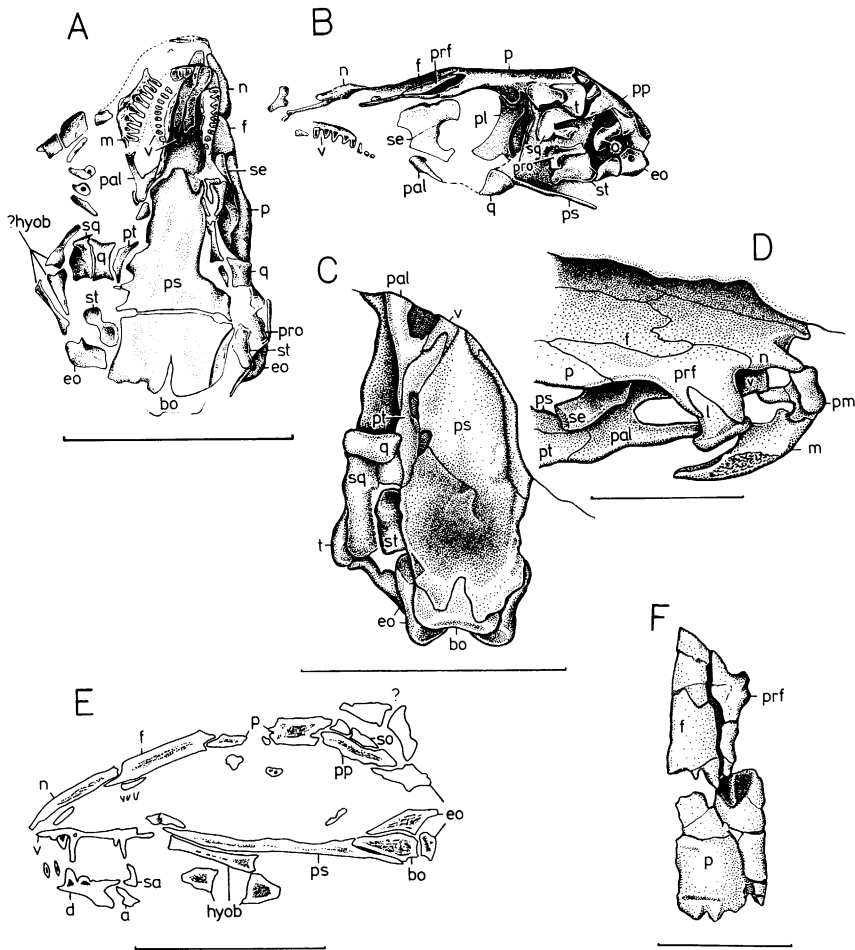


Fig. 14. *Brachyectes elongatus*. A, B, AMNH 4696, ventral and left lateral views of skull, respectively (bar scale = 1 cm); C, D, UMMP V3036, ventral and oblique-dorsal views of skull (bar scale = 0.5 cm); E, UCLA-VP 3684, parasagittal section of skull, anterior to left (bar scale = 1 cm); F, AMNH 4762a, detail of skull (bar scale = 0.5 cm).

whereas the reverse is true more posteriorly (cf. Gregory, 1948: 649), (2) that the trunk vertebrae undergo (unspecified) slight changes in form as they approach the cervical region, and (3) that the attitude of the transverse processes changes from anterolateral to posterolateral in the transition from trunk to cervical vertebrae.

The first centrum of *B. elongatus* is displayed in specimens FMNH PR 1456 (figs. 16A, 18A, B) and AMNH 4701 (fig. 18D). In contrast to the condition seen in more posterior vertebrae, the transverse processes rise from the centrum, just below the neurocentral suture. The length of the first centrum in

FMNH PR 1456 is 2.5 times that in AMNH 4701. Its carinae, fossae, and transverse processes are more strongly developed and the length of the centrum has obviously increased relative to its width. In lateral view the first centrum of FMNH PR 1456 is seen to possess a protruding ventral expansion of its posterior rim which is absent in the smaller specimen. Unless this expansion was completed dorsally in cartilage, it produces an irregular posterior surface for articulation with the ordinary, circular anterior rim of the following centrum. This ventral expansion might represent an intercentrum. However, there is no obvious facet on the anterior rim of the

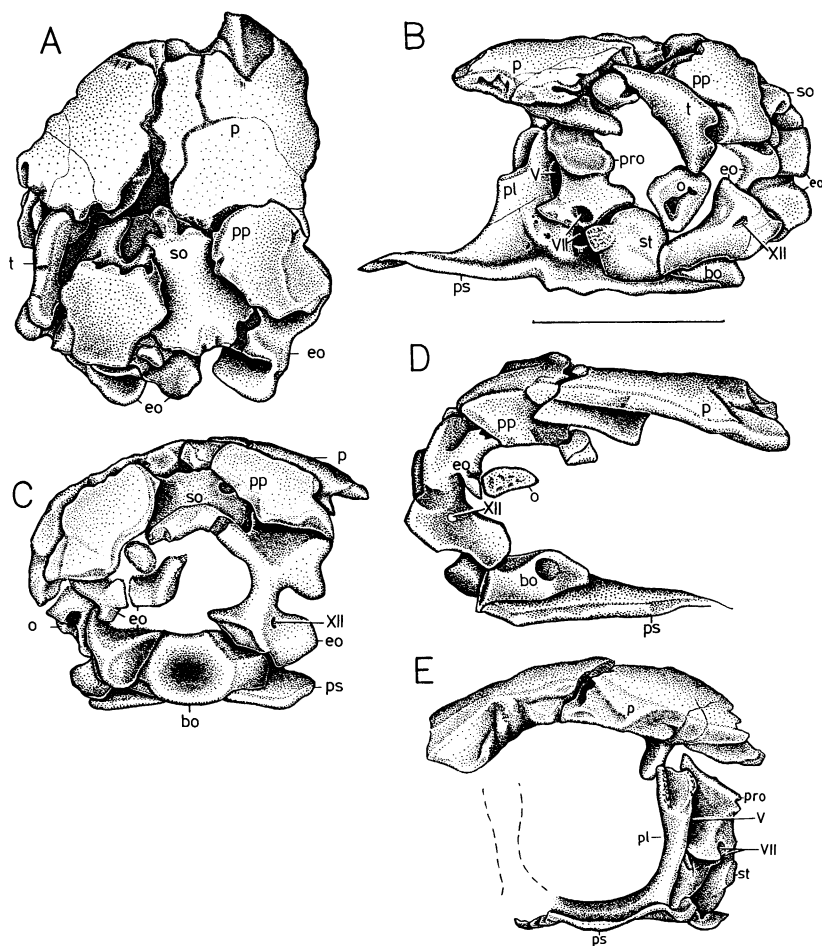


Fig. 15. *Brachydictes elongatus*. A-E, AMNH 7558. Dorsal, left lateral, posterior, right lateral, and anterior views, respectively, of braincase and associated dermal bones (bar scale = 0.5 cm).

succeeding vertebra to accommodate an intercentrum. Minus this ventral expansion, the centrum has approximately the same length-to-width proportions as the smaller first centrum in AMNH 4701, suggesting that the expansion may have been present in the smaller centrum, but entirely cartilaginous. Unfortunately, the smaller centrum cannot be conveniently prepared to reveal possible unfinished bone on its posterior surface.

The sacrum has been interpreted only in UCLA-VP 2802 (figs. 17F, 20A). Posterior to this vertebra, counted as number 98, the vertebrae clearly seem to be caudals. Anterior to it, the vertebrae bear free ribs. The sacral vertebra is poorly exposed, being nearly surrounded by other elements and obscured by matrix. Its neural arch is clearly paired and

not noticeably differentiated from neural arches preceding it.

Approximately 20 caudal vertebrae are preserved in UCLA-VP 2802. Williston (1908a) and Finney (1912) reported similar counts. Most are indistinct due to their small size or poor ossification and are obscured by matrix. The anterior five caudals from the series are illustrated in figure 17E, F. A series of 15 caudal vertebrae is preserved in USNM 23727 (fig. 18F). These belong to an individual estimated to be some 50 percent larger than UCLA-VP 2802. The centra are full-bodied, not laterally compressed. In both UCLA-VP 2802 and USNM 23727 the lateral carinae are weakly developed. However, the fossae are much deeper in USNM 23727, perhaps as a result of the larger size of the

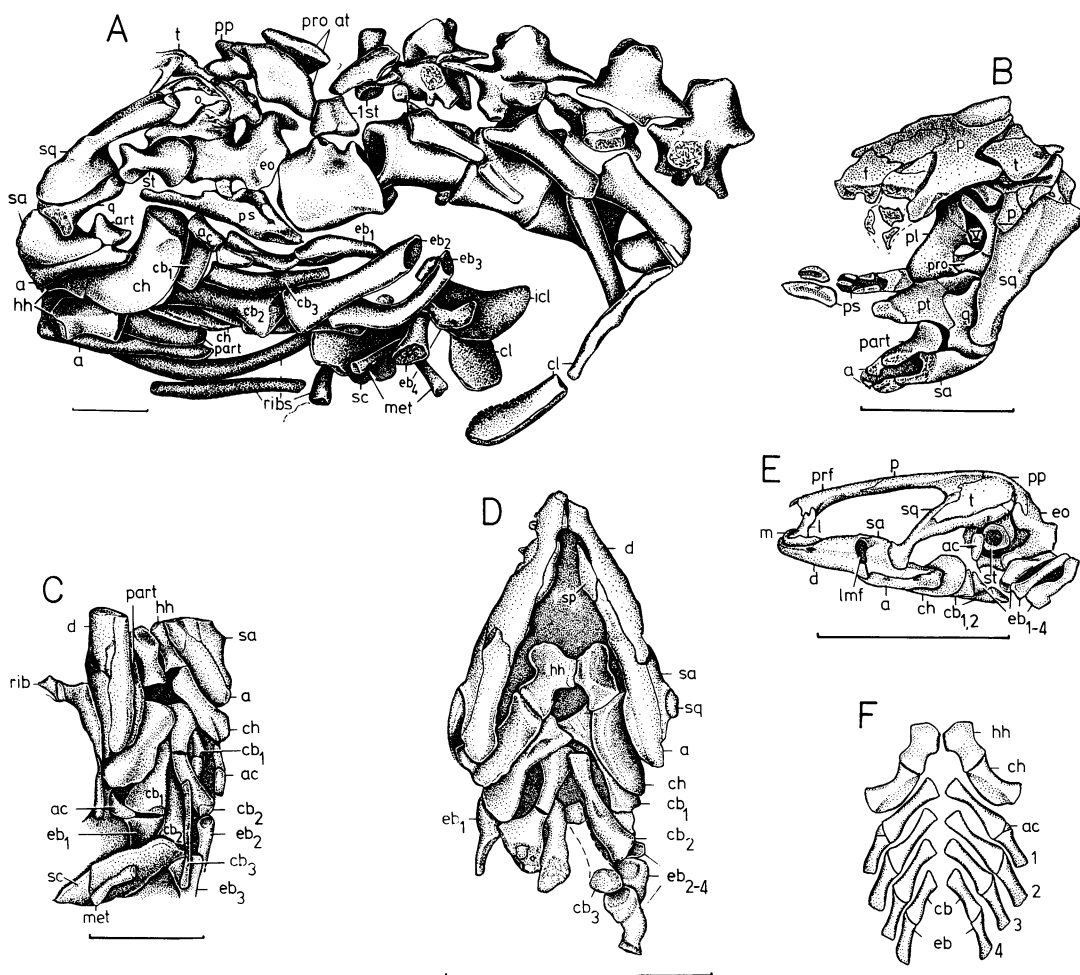


Fig. 16. *Brachydictes elongatus*. A, FMNH PR 1456, detail of posterior region of skull, hyobranchial skeleton, anterior vertebrae and ribs (bar scale = 0.5 cm); B, FMNH PR 1456, oblique dorsal view of skull (bar scale = 1 cm); C, FMNH PR 1456, oblique ventral view of mandible and hyobranchial skeleton (bar scale = 1 cm); D, E, AMNH 4699, ventral and left lateral views of skull (bar scale = 1 cm); F, reconstruction of hyobranchial apparatus, ventral view (bar scale = 0.5 cm).

centra. Several of the illustrated centra bear foramina at midheight.

Each caudal neural arch spans the intervertebral articulation and contracts the posterior rim of the preceding centrum. The caudal centra thus bear two pair of neurocentral sutural surfaces, one anteriorly and one posteriorly. Ipsilateral neural arch sutural surfaces are connected by respective dorsolateral carinae. Neural spines are tall and angled posteriorly.

The hemal arches articulate with the ventral carinae of the caudal centra, rather than

being intercentral in position. Seen in lateral view, they are relatively straight when small, such as in UCLA-VP 2802 (fig. 17E) and in posterior portions of USNM 23727 (fig. 18F). They are distinctly flexed when larger as in the anterior portion of USNM 23727. The hemal arch pairs are fused distally, but bear no crosspiece proximally to enclose the hemal artery and vein.

Ribs in *B. elongatus* are similar to those of *B. newberryi* described above. Olson (1971) reports that ribs are found on all presacral vertebrae in *B. elongatus*. However, the pres-

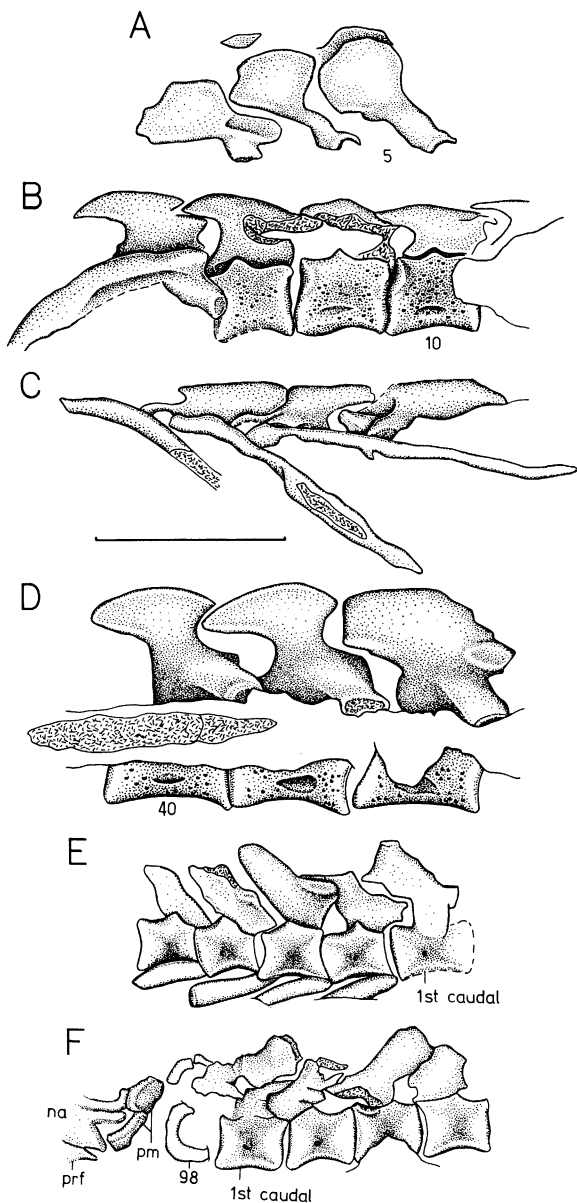


Fig. 17. *Brachydictes elongatus*. A-F, Holo-type, UCLA-VP 2802, lateral views of segments of vertebral column, showing regional variation in neural spine morphology. E and F show right and left lateral views of caudal vertebrae. Vertebra 98 is the presumed sacral vertebra. As seen in 17F, the skeleton coils upon itself, causing skull to be adjacent to sacral region. Bar scale = 1 cm.

ence of ribs on the first vertebra cannot be confirmed in the available material. The left rib of the second vertebra is associated with its centrum and is well exposed in FMNH

PR 1456 (fig. 16A); however, its distal portion has been broken away.

APPENDICULAR SKELETON: Williston (1908a) made the first report of limb elements in *B. elongatus*. Finney (1912) confirmed this report, discovering limb elements in 15 of 200 specimens of *B. elongatus* she examined. She briefly described a presumed femur, tibia, fibula, two metatarsals, and the only two phalanges ever noted in *B. elongatus*. Finney found no indication of the tarsus and concluded that it was not ossified. Unfortunately, Williston and Finney reported no catalog numbers for their specimens nor did they illustrate the elements described. Recent attempts to relocate these specimens have been unsuccessful (J. R. Bolt, personal commun.).

Huene (1913b) reported on limb elements discovered in unnumbered specimens of *B. elongatus* in the university collection at Tübingen (GPIT specimen, unnumbered). He figured a bone interpreted here as a humerus and two lower limb elements, which seem to be a stout tibia and a more slender fibula (Huene, 1913b: figs. 4, 5). Huene mentioned, but did not illustrate, two other elements which he thought might be girdle elements. Sollas (1920) described the first certain forelimb and pectoral girdle elements. These are discussed below.

Among material available to the study, a presumed scapulocoracoid is preserved in UCLA-VP 2802 (fig. 19E) and a pair of scapulocoracoids are exhibited in FMNH PR 1456 (fig. 19A). The scapulocoracoids of these two specimens are 4 mm and 13 mm, respectively, in greatest dimension. In both cases, this length roughly equals the length of two local centra. In UCLA-VP 2802 the scapulocoracoid is triangular, although, as Olson (1971) commented, it may have been completed in cartilage. Sollas (1920) also reported that the endochondral pectoral girdle element which he identified was triangular. This bone was only 2.6 mm long. In contrast, the larger scapulocoracoids in FMNH PR 1456 are rounded rectangles.

From its position relative to the vertebral column, Olson (1971) reasonably interpreted the one scapulocoracoid exposed in UCLA-VP 2802 as the left one. However, even in the better ossified specimens, such as FMNH

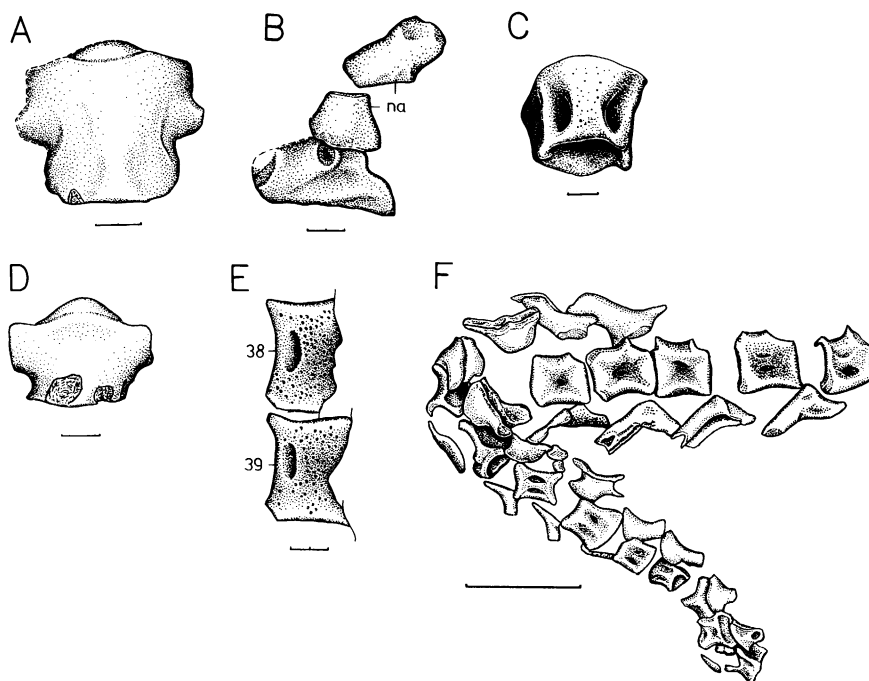


Fig. 18. *Brachydectes elongatus*. A, B, FMNH PR 1456, detail, ventral and left lateral views of first vertebra (bar scale = 2 mm); C, FMNH PR 1456, detail, ventral view of trunk centrum (bar scale = 2 mm); D, AMNH 4701, detail, ventral view of first centrum (bar scale = 1 mm); E, holotype, UCLA-VP 2802, detail, trunk centra 38 and 39 (bar scale = 2 mm); F, USNM 23727, detail, caudal series (bar scale = 1 cm).

PR 1456, the element presents no feature surely distinguishing medial from lateral aspect and, thus, left from right.

One endochondral element in FMNH PR 1456 bears a deep notch along one edge, possibly due to breakage. The corresponding edge in its mate can be seen to bear a groove which leads to a rounded concavity. Possibly this grooved edge was finished in cartilage with the concavity marking the position of the glenoid. No other evidence of the glenoid is found in the available material, although Sollas (1920: 522) suggested the presence of a distinct glenoid in his specimens. The presumed posterior edge of the scapulocoracoid is rounded and apparently thicker than the anterior, as seen in ventral view.

The interclavicle has been identified in FMNH PR 1456 (fig. 19C), possibly also in RM 14-728 (fig. 19F, G) and MCZ 2255 (not figured), and is a semicircular plate of bone, the length of which is roughly equal to half that of an adjacent centrum. Both surfaces

have been prepared in RM 14-728, but no distinct dermal ornamentation or traces of clavicular contact are present. However, a narrow ledge is present along the presumed anterior and lateral edges of the bone. Although the ledge is not obvious in the other interclavicle, it may mark the contact of other pectoral elements such as the clavicles. One element questionably identified as a clavicle by Sollas (1920: 522, fig. 2) may be the interclavicle, judging from relative size, position, and stout form.

Clavicles in FMNH PR 1456 (fig. 19B) are approximately 19 mm long, roughly equal to the length of three local centra. They are rod-like bones, oval in cross section, with flattened and broadened medial ends. The clavicle in the specimens Sollas (1920) illustrated is similar in proportion, but is perhaps incomplete, for it is only as long as $1\frac{1}{2}$ centra, or 4 mm in this case. No distinct surfaces of contact with the interclavicle are seen on the flattened ends of the clavicles.

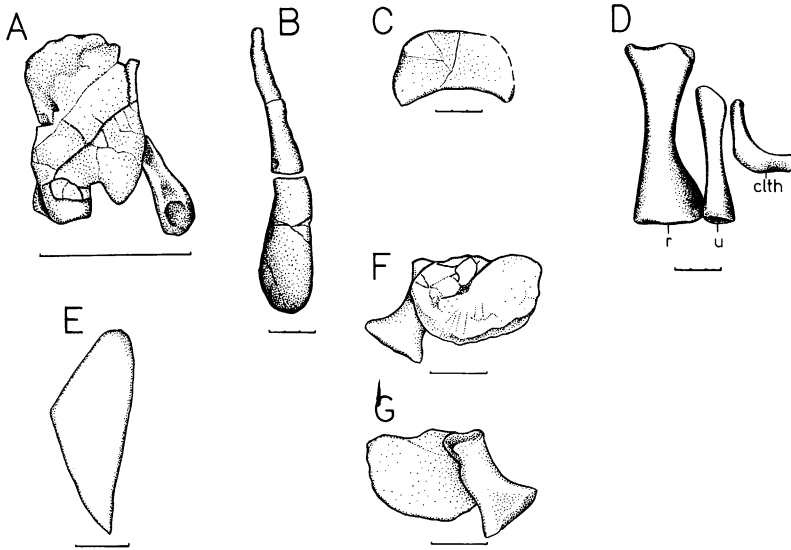


Fig. 19. *Brachydictes elongatus*. A, FMNH PR 1456, detail, lateral (?medial) and ventral views of scapulocoracoid pair (bar scale = 1 cm); B, FMNH PR 1456, detail, clavicle (bar scale = 3 mm); C, FMNH PR 1456, detail, interclavicle, visceral view (bar scale = 3 mm); D, FMNH PR 1456, detail, radius, ulna, cleithrum (bar scale = 3 mm); E, holotype, UCLA-VP 2802, detail, scapulocoracoid (bar scale = 1 mm); F, G, RM 14-728, detail, views of interclavicle and radius (bar scale = 0.5 cm).

A curved element in FMNH PR 1456 associated with the radius and ulna is tentatively interpreted as a cleithrum (fig. 19D). No other cleithra have been identified in the available material of *B. elongatus*, although Sollas (1920) suggested that one element in his specimen was a cleithrum. From its robust nature, it seems more likely that this element is a clavicle.

Single humeri are known in MCZ 2253, UCLA-VP 2802, USNM 23727, FMNH PR 1456, and possibly AMNH 4757. Both left and right humeri are present in RM 14-728 (measurements in table 5). The humerus is a simple, slender bone (fig. 21), expanded at proximal and distal ends. In cross section the proximal end is roughly pear-shaped, while the distal extremity resembles a rounded triangle. Humeri in the smaller specimens such as MCZ 2253, UCLA-VP 2802, and USNM 23727 are equal in length to one local centrum. In UCLA-VP 2802, this length is 0.8 percent of the presacral body length. In larger specimens such as RM 14-728 and FMNH PR 1456 the humeri are equal in length to two and three centra, respectively. The greater relative length of the humerus in these latter two specimens may be due to positive

allometry or, perhaps more likely, to a greater degree of ossification. The humeri in FMNH PR 1456 and RM 14-728 have been removed from their matrix and respectively exhibit 25 and 40° of torsion between proximal and distal extremities (fig. 21I-L). The difference in degree of torsion in the humeri of these two specimens seems great. While it may be due to distortion or either individual or ontogenetic variation, one should note that the humerus in FMNH PR 1456 has been broken in several places during or since preparation. The contrast in torsion between this humerus and those in RM 14-728 could be due to imperfect repair of the element in FMNH PR 1456.

There is no entepicondylar foramen in the humerus. Its most distinctive feature is the deltopectoral crest, which is easily distinguished even in the small humerus of the holotype (fig. 21M). The concavities marking the proximal end of the humerus may mark muscle attachments.

The radius in FMNH PR 1456 is a comparatively stout bone (fig. 19D), approximately 12.3 mm long, or about 0.7 the length of the humerus. It is expanded and somewhat flattened at both extremities. The distal ex-

TABLE 5
Lengths of Humeri in *Brachydectes elongatus*

Specimen	Length of humerus (mm)	Length of adjacent centrum (mm)
MCZ 2253	1.8	1.8 (est.)
UCLA-VP 2802	4.3	4.3
USNM 23727	8.0	7.0 (est.)
FMNH PR 1456	18.0	6.0
RM 14-728	21.0	9.5

tremity is one-third broader than is the proximal. The shaft is constricted at midlength. The ossified portion of the ulna in FMNH PR 1456 is about 10.5 mm long or 0.6 the length of the humerus. The olecranon is not ossified. The width of the distal extremity is only two-thirds that of the apparently incomplete proximal. Sollas (1920) has described similar bones in his specimens. In addition to these illustrated examples, radii and ulnae are present in smaller specimens MCZ 2253 and USNM 23727. In these specimens also, the radii and ulnae are approximately 0.7 the length of the humerus.

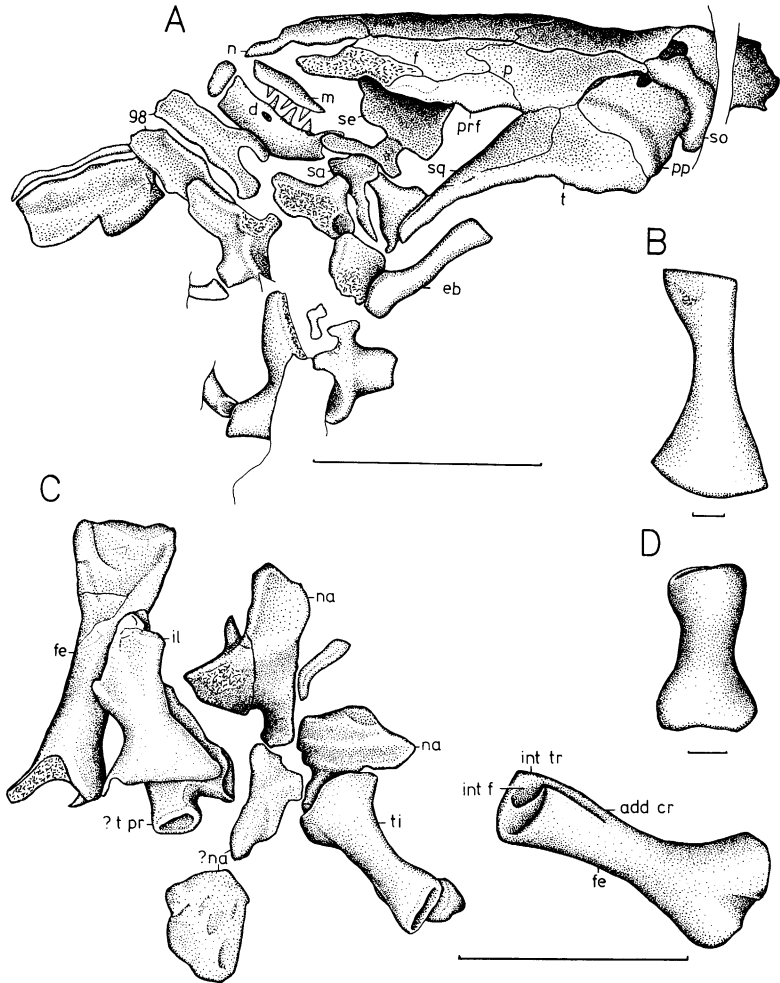


Fig. 20. *Brachydectes elongatus*. A, Holotype, UCLA-VP 2802, detail, skull and sacral region (bar scale = 1 cm); B, holotype, UCLA-VP 2802, detail, femur (bar scale = 1 mm); C, UMMP 3036, detail, pelvic girdle and hind limb elements (bar scale = 2 mm); D, UMMP 3036, detail, tibia (bar scale = 1 mm).

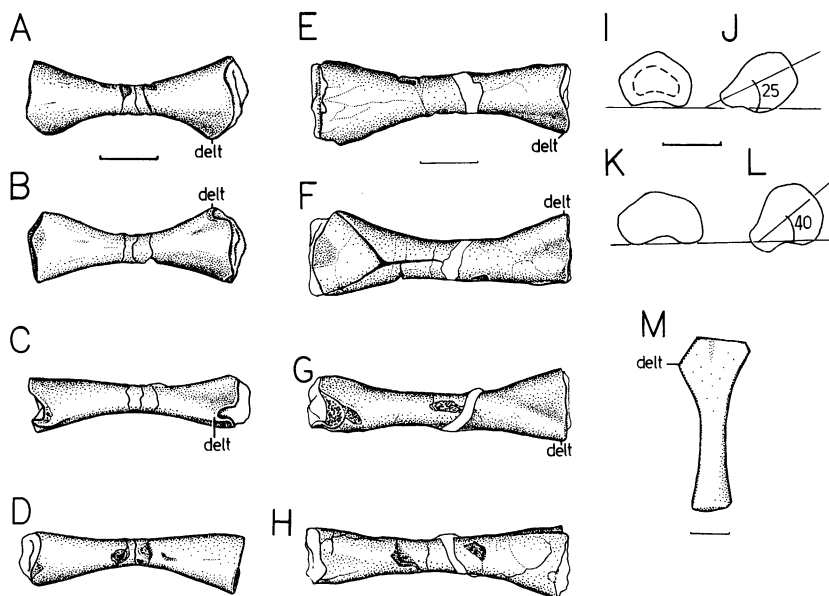


Fig. 21. *Brachydectes elongatus*. A-D, FMNH PR 1456, detail, dorsal, ventral, anterior, and posterior views, respectively, of right humerus (bar scale = 0.5 cm); E-H, RM 14-728, detail, dorsal, ventral, anterior, and posterior views, respectively, of right humerus (bar scale = 0.5 cm); I, J, FMNH PR 1456, detail, distal and proximal silhouettes of right humerus (bar scale = 0.5 cm); K, L, RM 14-728, detail, distal and proximal silhouettes of right humerus (bar scale = 0.5 cm); M, holotype, UCLA-VP 2802, detail, humerus (bar scale = 1 mm).

What may be a radius accompanies the humerus in AMNH 4757. An incomplete ulna is described in UCLA-VP 2802 (Olson, 1971: fig. 2B) and an incomplete radius is known in RM 14-728 (fig. 19F, G).

A left ilium is preserved in UMMP V3036, which is the only specimen of *B. elongatus* to exhibit an element identifiable as part of the pelvic girdle (fig. 20C). The base of the ilium is triangular. Its blade is broad, rather rectangular, and angled anteriorly, supporting a modest posterior process. The acetabulum cannot be described, unfortunately, because only the medial surface of the ilium is exposed. The apparent notch near the posterior limit of the base of the ilium is due to breakage.

One femur is known from UCLA-VP 2802 (fig. 20B) and a pair have been found in UMMP V3036 (fig. 20C). In these small specimens, the bones are 7.4 and 8 mm long, respectively, which is roughly the length of two adjacent centra and, in UCLA-VP 2802, represents about 1.4 percent of the body length. In UCLA-VP 2802, in which both humerus and femur are known, the femur

proves to be the more robust of the two (Olson, 1971: 446) and is some 70 percent longer than the humerus. The right femur in UMMP V3036 is uncrushed and the intertrochanteric and intercondylar fossae, as well as the adductor crest, are distinct. The femur is unusual in that the intertrochanteric and intercondylar fossae are not strictly on ventral and dorsal surfaces of the bone, respectively. The intertrochanteric fossa seems to have been rotated perhaps more than 90° to face anteriorly. However, as ossified articular surfaces are lacking, this perception may be exaggerated.

The sole posterior zeugopodial element available is a tibia in UMMP V3036 (fig. 20C, D). It is half as long as the associated femora and is a broad element, constricted medially. The proximal end is roughly 25 percent broader than the distal end.

Brachydectes sp. (Romer, 1952: 75)

SPECIMEN CM 8564: Holotype of *Lysorophus minutus* Romer, 1952: 75-76, pl. 1, fig. 7. Part and counterpart of skull and vertebral

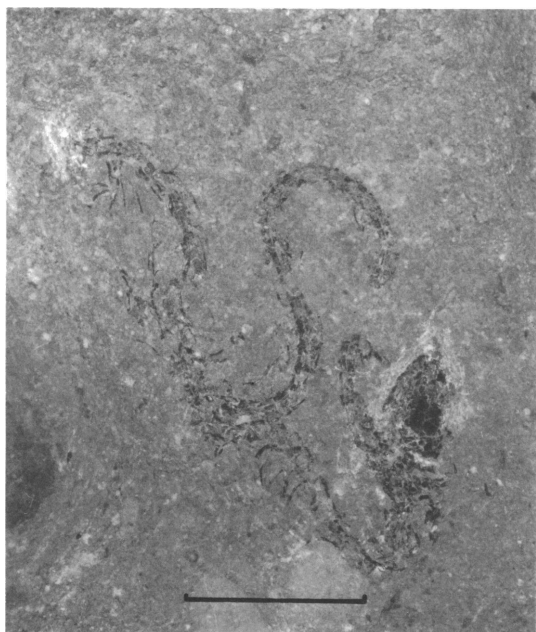


Fig. 22. *Brachydictes* sp., CM 8564, holotype of "*Lysorophus minutus*" (bar scale = 0.5 cm).

column. Burke and Moran party, collectors, 1933.

HORIZON: Greene Formation, Dunkard Group, possibly the Upper Rockport Limestone (Moran, 1952: 37; Beerbower, 1963: 37), Wolfcampian, Lower Permian (= Sakmarian).

LOCALITY: CM Locality 30. Franklin District, Marshall County, West Virginia (Moran, 1952: 37).

DESCRIPTION

The specimen is preserved in limestone blocks apparently containing numerous ostracods. The skeleton is very small, perhaps 9 cm in total length (fig. 22). It loops across itself and is exposed along a fracture plane which passes irregularly through the specimen.

The skull is badly crushed, although a region of relatively intact bone is interpretable as the parietal pair. The proportion and rectangular shape of these bones are characteristic for lysorophoid parietals and give the impression that the skull roof had appropriately subparallel lateral edges. In relationship to the median suture, the skull is preserved

asymmetrically, with a greater portion to the left of the midline than to the right. At the extreme left of the skull, a bone surface slants away from the major portion of the skull as it passes posteriorly. This surface is identifiable as the left mandible. It is considerably shorter than the skull roof and roughly twice the length of the presumed parietals, as in other lysorophoids. At its posterior end it bears a concavity similar to the articular notch in *Brachydictes* and *Pleuroptyx* and a short retroarticular process.

As many as 60 vertebrae appear to be represented in the preserved column, but because no elements identifiable as limbs or girdles are exposed, it is impossible to discriminate the presacral portion of this vertebral column. In neither part nor counterpart are the vertebral centra well exposed. Ribs are generally exposed as short broken segments. Where occasionally extended portions of ribs are preserved, their chord is roughly the length of three centra. The neural arches are paired, as is demonstrated by median sutures between neural arch halves in a segment of the vertebral column immediately to the left of the skull, as well as in a curved segment anterior and to the left of the skull.

Insufficient evidence exists to diagnose this specimen as a distinct species of lysorophoid or to assign it to any other species. *Lysorophus minutus* thus is a nomen dubium. Noted details of the skull roof, mandible, and neural arches, however, suggest that the specimen is assignable to *Brachydictes*.

Pleuroptyx Cope, 1875a: 370

Molgophis (Cope, 1868: 220). Schwarz 1908: 73 (partim). Abel, 1919: 259 (partim). Romer, 1966: 363 (partim).

Colosteus of Romer, 1930: 101 (partim).

TYPE SPECIES: *Pleuroptyx clavatus* Cope.

REVISED DIAGNOSIS BASED ON REFERRED SPECIMENS MCZ 2303 (Fig. 26A, B) AND USNM 4509 (Fig. 26C): *Pleuroptyx* is distinguished from *Brachydictes* by its broad posterior skull roof (width-to-length ratio of parietal pair = 1.60; table 2), transverse ridge spanning the skull roof, an irregularly rhomboid interclavicle, clavicles each with a pointed posterior process, and ribs bearing hypertrophied alae.

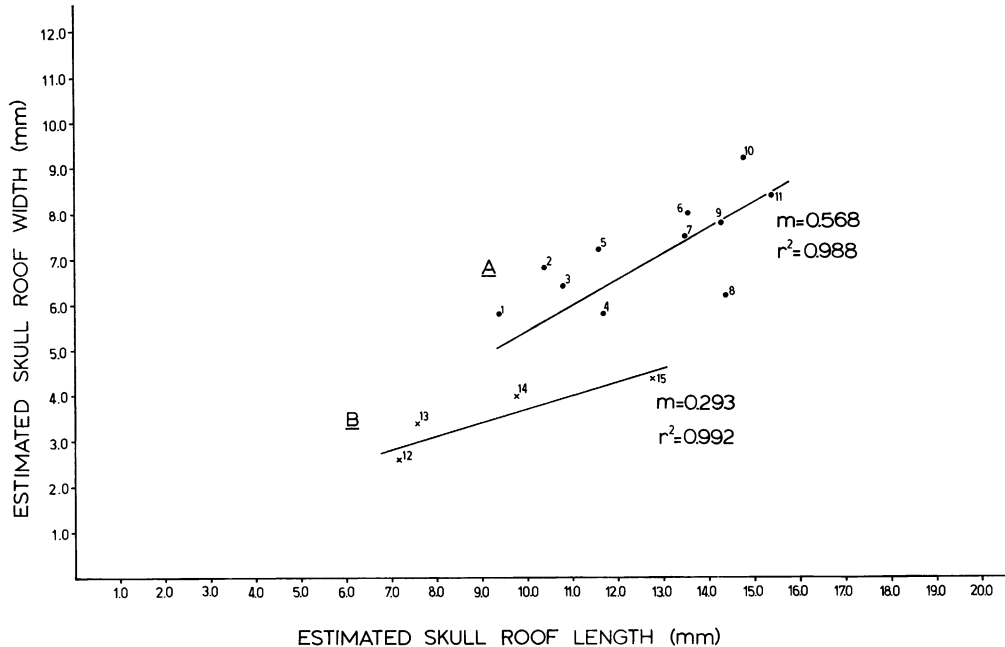


Fig. 23. Graph of skull roof proportions. **A**, *Brachydictes elongatus*. 1. AMNH 4884. 2. AMNH 4762a. 3. USNM 8892. 4. AMNH 21910. 5. AMNH 4699. 6. UMMP V3036. 7. AMNH 4700. 8. Sollas' Specimen 2 (Sollas, 1920). 9. AMNH 6172. 10. AMNH 4698. 11. AMNH 4761. **B**, *Brachydictes newberryi*. 12. AMNH 2156. 13. BM(NH) R.2544. 14. AMNH 6861. 15. AMNH 6925.

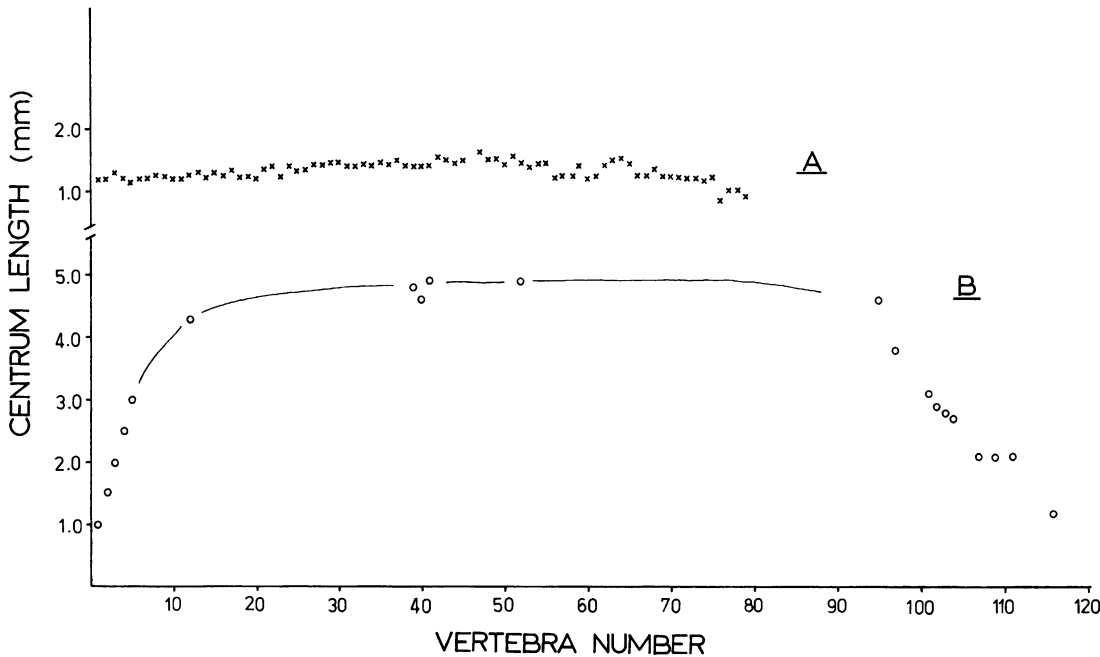


Fig. 24. Graphs of regional variation in centrum lengths. **A**, *Brachydictes newberryi*, BM(NH) R.2544; **B**, *Brachydictes elongatus*. Most data points for *B. elongatus* are from Olson (1971). See table 3 of this paper. Data points representing vertebrae 1-5 are estimated from Olson's data. The line drawn through points is interpretive.

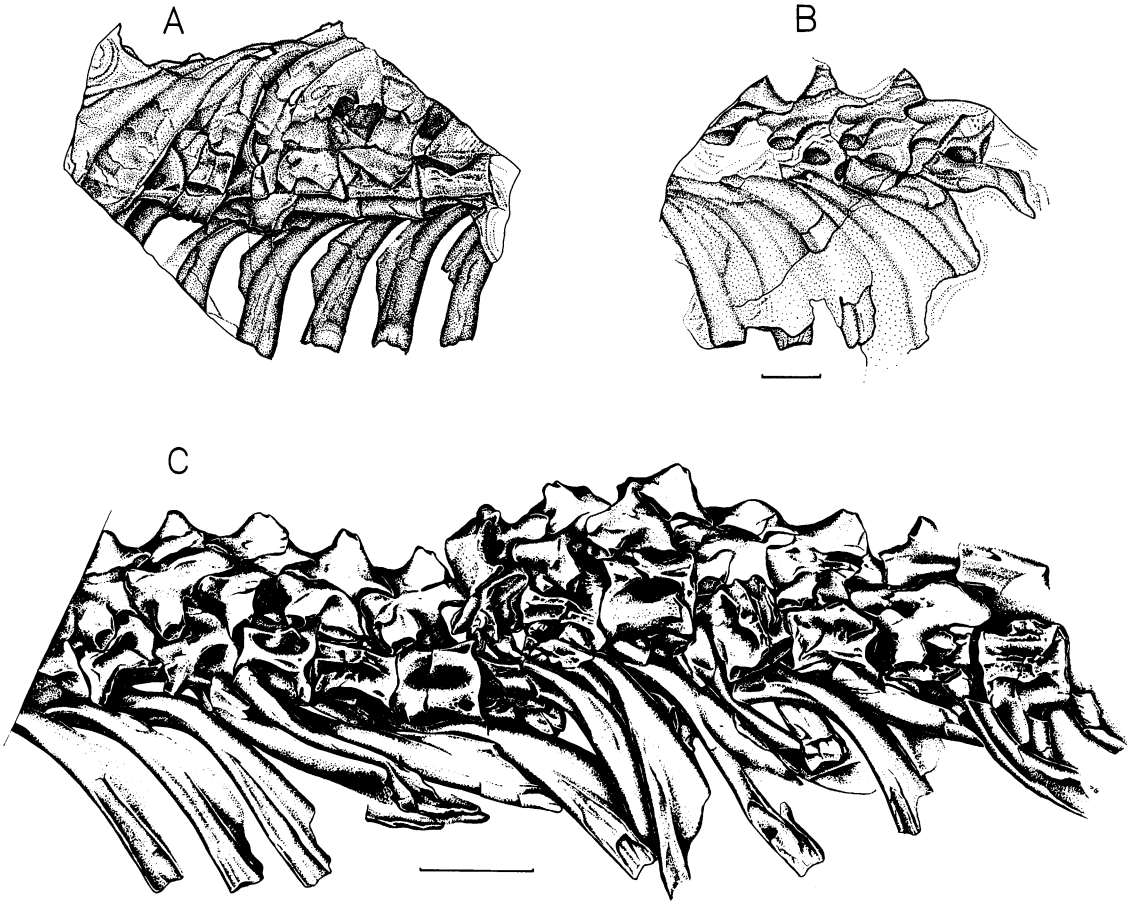


Fig. 25. *Pleuroptyx clavatus*. A, B, Holotype, AMNH 6838, part and counterpart (bar scale = 1 cm); C, AMNH 6863 (bar scale = 1 cm).

Cope (1875a: 370) established the genus on the basis of "five-probably six-specimens," which offered him various views of segments of the vertebral column. At the time, the genus was distinguished, in part, through the broad alae of its ribs. While Cope did not identify his specimens by field or serial numbers, he did differentiate the following four: two (presumably relatively large) "types," a "smaller specimen," and a limb specimen. Cope supplied illustrations of three specimens from this series (Cope, 1875a: pl. 42, fig. 1 and pl. 44, figs. 2 and 2a) but provided no specific correlation between his text and figures. However, the figures are identifiable through inspection as Linton specimens AMNH 6863, AMNH 6838, and AMNH 6839, respectively.

Judging from their relative sizes AMNH 6838, with centra 14 mm long, is probably one of the two "type" specimens, while

AMNH 6863 with centra 8 mm long, is probably the "smaller specimen." This conclusion is supported by the single set of measurements supplied by Cope, presumably from the type material, which correspond to elements of AMNH 6838 and are too large to represent AMNH 6863.

Because Cope differentiated between his type specimens and a "smaller specimen," but not between the two types themselves, one could infer that the two types were probably quite similar. One presumed Cope-type, AMNH 6838, has been prepared recently by Donald Baird and is known from both part and counterpart. Cope conceivably may have interpreted the obscured morphology of the unprepared counterparts of AMNH 6838 as two distinct specimens.

Whether AMNH 6838 represents one or both of Cope's types, Moodie (1916) was clearly confused in taking the smaller speci-

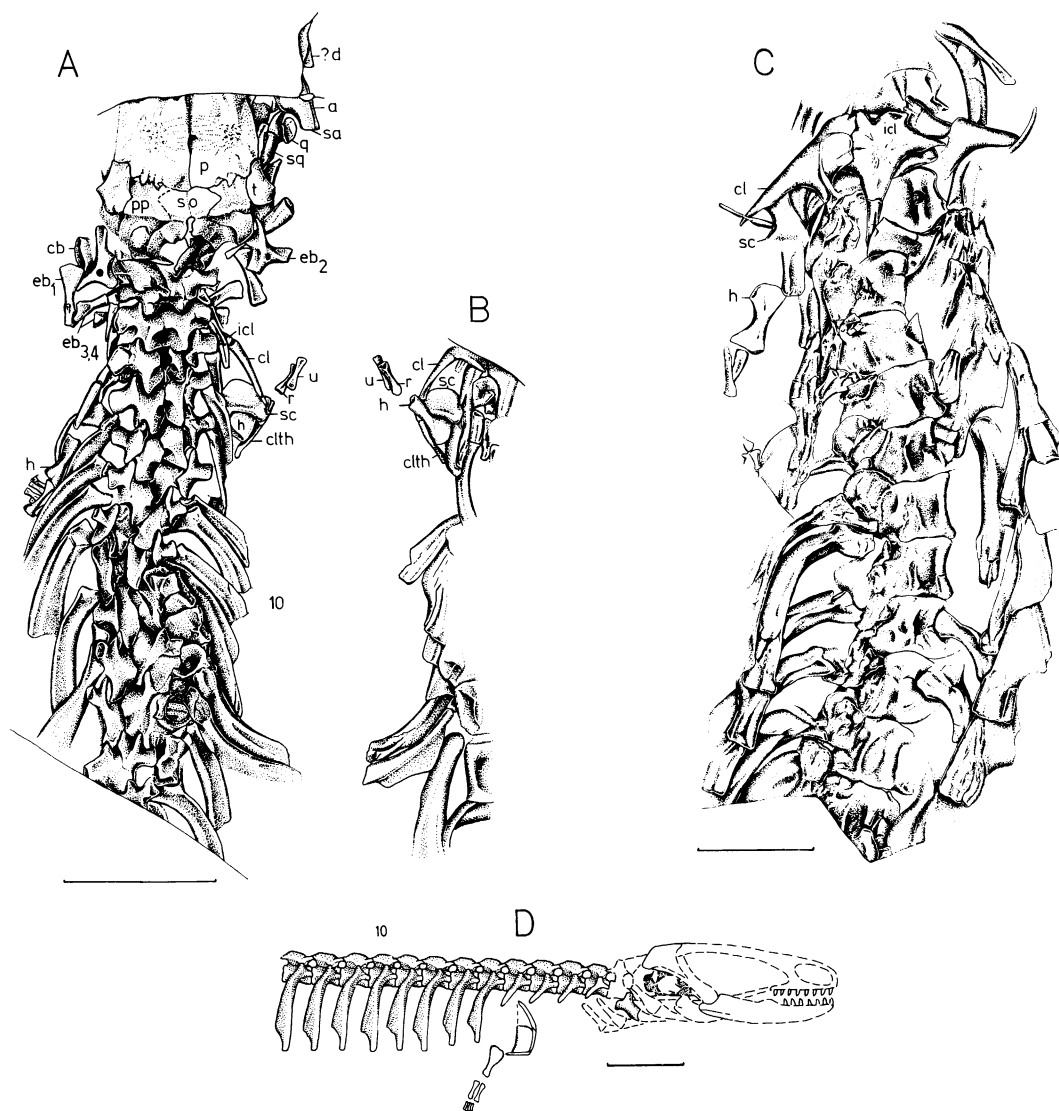


Fig. 26. *Pleuroptyx clavatus*. A, B, MCZ 2303, part and counterpart; C, USNM 4509; D, reconstruction based on MCZ 2303. Bar scale = 1 cm.

men, AMNH 6863, to be the type, while using Cope's original measurements of AMNH 6838 in his description.

Specimen AMNH 6839 is certainly the isolated limb which Cope referred to *Pleuroptyx*. However, Hook (1983) has commented on its similarity to the hind limb of the colosteoid temnospondyl *Greererpeton*. There is no basis for retaining the specimen in *Pleuroptyx*.

The remaining one or two specimens of Cope's type series of *Pleuroptyx* have not been accounted for.

Specimen USNM 4484, assigned to the genus by Moodie (1916), has been correctly re-

ferred to the aïstopod *Phlegethontia* by McGinnis (1967: 3).

Pleuroptyx clavatus Cope, 1875a: 370

Molgophis cf. *brevicostatus* (Cope, 1875a: 369).
Schwarz, 1908: 73 (partim).

REVISED DIAGNOSIS: As for genus.

HOLOTYPE: AMNH 6838, formerly 8616G, Newberry Collection. A series of five vertebrae and associated ribs. As *Pleuroptyx clavatus*, Cope, 1875a: 370–371, pl. 44, fig. 2; Moodie, 1909a: 27; 1916: 151–153; Steen, 1931: 886. As temnospondyl *Colosteus scu-*

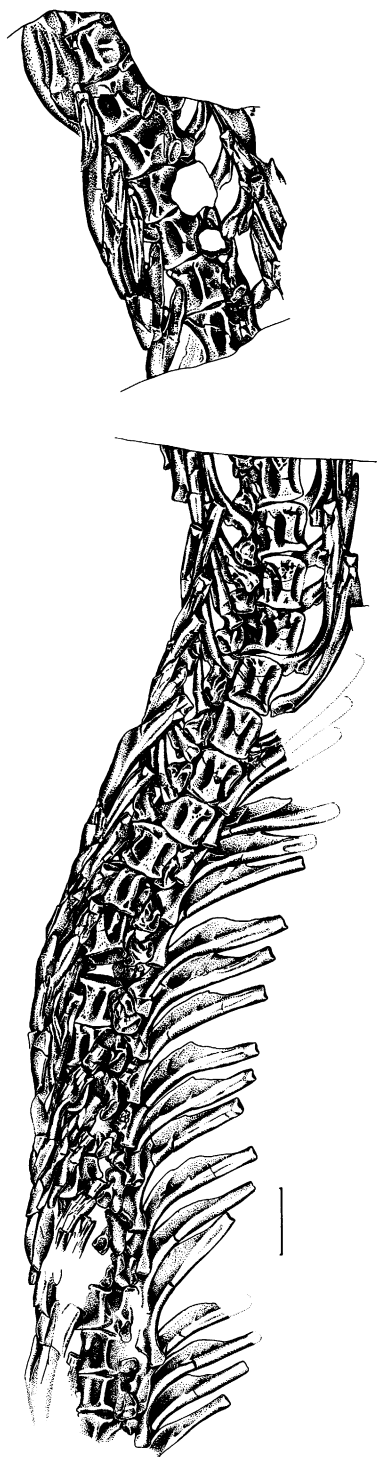


Fig. 27. *Pleuroptyx clavatus*, MB. Am 47 (bar scale = 1 cm).

tellatus, Romer, 1930: 101. Figure 25A, B of this paper.

HORIZON: Cannel coal below coal seam identified as the Upper Freeport Coal (Newberry, 1871, 1874), Allegheny Group, Middle Pennsylvanian; equivalent to late Westphalian D of Europe (D. Baird, 1964; see also Hook, 1983: 7).

LOCALITY: Coal mine originally owned by the Ohio Diamond Coal Company (Murphy, 1980), Linton, Saline Township, Jefferson County, Ohio, approximately 2.5 km south of Wellsville, Ohio (Hook, 1983); NE $\frac{1}{2}$, sec 13, T9N R2W, Wellsville, Ohio, 7.5' quadrangle.

REFERRED MATERIAL, FIGURED (all material from Linton): **AMNH 6863:** Formerly 8617G, Newberry Collection. All or portions of 12 vertebrae and associated ribs. As *Pleuroptyx clavatus*, Cope, 1875a: 370–371, pl. 42, fig. 1; Moodie, 1916: 151, erroneously as holotype. As temnospondyl *Colosteus scutellatus*, Romer, 1930: 101. Figure 25C of this paper. **BM(NH) R.2676:** J. W. Davis Collection. All or portions of 12 vertebrae and associated ribs. As *Pleuroptyx clavatus*, Steen, 1931: 885–886, pl. 6, fig. 5. **MB. Am 47:** A series of 30–34 vertebrae and associated ribs. As *Molgophis* cf. *brevicostatus*, Schwarz, 1908: 73, fig. 11; as *Mologophis*, Abel, 1919: 259, fig. 198. Figure 27 of this paper. **MCZ 2303:** Donald Baird party, collector, 1955. Posterior portion of skull roof, pectoral girdle, and forelimb elements and portions of 13 vertebrae with associated ribs. Figures 26A, B of this paper. **USNM 4509:** 13–14 vertebrae, associated ribs, pectoral girdle, and forelimb elements. *Pleuroptyx clavatus*, Moodie, 1909a: 27; 1916: 153. Figure 26C of this paper.

DESCRIPTION

SKULL: Elements of the skull are known only from referred specimen MCZ 2303 (fig. 26A). In this specimen only the more dorsal portions posterior to the frontoparietal suture are preserved, but from what can be seen, the skull is quite similar to that of *Brachydectes* in suture pattern and bone configuration.

The parietals bear a faint, radiating ornamentation and share a relatively straight medial suture. The dorsal portion of the tabular

in *Pleuroptyx* is more angular and broader than in *Brachydictes*, but it retains the characteristic attenuated anteroventral process.

The transition from skull roof to occiput appears to be more angular in this specimen than in *Brachydictes* and is marked by a ridge spanning the width of the skull across the tabulars, postparietals, and supraoccipital. This ridge and the relatively broad, flat dorsal expression of the tabulars possibly indicate an attachment of epaxial musculature distinct from that in *Brachydictes*. The supraoccipital is the only occipital element exposed. It is considerably broader than that in *Brachydictes*.

Between the right edge of the skull roof and the broken squamosal is an indeterminate portion of the palate. To the right of the squamosal is an element which may be the quadrate.

Posterior portions of the surangular and angular are the only portions of the mandible which can be identified positively. Nevertheless, this portion of the mandible clearly exhibits the retroarticular process and articular notch characteristic of lysorophoids.

Near the right and left posterolateral corners of the skull roof are assemblages of hyobranchial elements. Distinctive among these is a pair of triradiate bones, each bearing a conspicuous foramen and which are identified as second epibranchials in analogy with similar elements in *Brachydictes newberryi*. The morphology of epibranchial 2 in *Pleuroptyx* is more distinct than in *B. newberryi* in that, rather than having merely rounded surfaces, the three arms of each bear ridges. Medial semicircular embayments are obvious in each element. Left epibranchial 1 bears a small process at midlength, perhaps marking the attachment of a hyobranchial muscle.

VERTEBRAE AND RIBS: The vertebrae and ribs in specimens assigned to *Pleuroptyx* are similar to those of other lysorophoids. Exaggerated rib alae, characteristic of the genus, are clearly displayed in the holotype, but neurocentral sutures are obscured. Neurocentral sutural surfaces are seen upon close examination in referred specimens AMNH 6863, USNM 4509, and MB. Am 47 and lineations indicating the sutures between neural arch halves are evident in MCZ 2303. In this latter specimen are also displayed the neural arches

of the first vertebra, but proatlantes have not been identified.

While no complete specimens of *Pleuroptyx* are known, a composite of two specimens suggests that regional variation in its presacral vertebral column is modest. Specimen MCZ 2303 (fig. 26A, B) displays the first 13 vertebrae of an individual which has its pectoral girdle in the region of centra 4–6. A second specimen, MB. Am 47 (fig. 27), is a series of at least 32 trunk vertebrae (estimating two centra for the covered region) and associated ribs of a size similar to those in MCZ 2303. No regional variation is apparent in this series. Since there is no indication of pectoral girdle in MB. Am 47, this series must begin at least as far behind the skull as vertebra number 7 or 8, and, therefore, continues to vertebra number 39 or 40. Together, MCZ 2303 and MB. Am 47 demonstrate a series of at least 40 presacral vertebrae of *Pleuroptyx* over which there is no obvious variation in vertebral or rib morphology, particularly none in the expression of rib alae. This example also demonstrates that the hypertrophied rib alae are not merely phenomena of the anterior column as Romer (1930, 1952) suggested, but continue well posteriorly.

Romer's object in suggesting that hypertrophied alae were phenomena of the anterior ribs in lysorophoids was to invoke regional variation of trunk rib morphology in support of his synonymy of *Pleuroptyx* and *Molgophis*, which is discussed in a later section. However, no such extreme regional variation in rib morphology is found in the composite series described above in *Pleuroptyx*, nor in either of the complete presacral series available in *Brachydictes newberryi* and *B. elongatus*.

APPENDICULAR SKELETON: The interclavicle (fig. 26C) exhibits four short, pointed processes, two directed anteriorly and one each laterally, as well as a moderately long, posteriorly directed stem. The left anterior process is broken and appears bifurcate. The right lateral process is covered by the right clavicle. The external surface of the interclavicle bears faint radiating striae.

The clavicles are attenuated wedges, broadest where they overlap the interclavicle. The medial portion of the clavicular blade

bears a short posteriorly directed process. Further from the midline, the clavicle bears a beveled surface (fig. 26B) which probably marks its contact with the endochondral girdle and cleithrum. The cleithrum is essentially a tapered continuation of the clavicle. Upon closer examination, it is also seen to bear elongate, flat surfaces of contact with the clavicle and endochondral element.

Portions of the endochondral girdle are exhibited in both MCZ 2303 and USNM 4509, but the lateral surface is exposed only in the left element of MCZ 2303. Unfortunately, other bones conceal the region possibly bearing the glenoid. The left humerus (fig. 26A), as seen in dorsal view in MCZ 2303, is about 3.5 mm long. Its deltopectoral crest, and ent- and ectepicondyles are distinct, although modest in their development. The proximal and distal expansions of the humerus are set at low angles to each other. The right humerus, seen in ventral view in USNM 4509 (fig. 26C), is 6.2 mm long and displays a distinct pectoral crest perhaps as a result of its greater size.

The radius and ulna are not well differentiated, although each is roughly 0.6 the length of the humerus. Four left metacarpals are partially exposed in MCZ 2303. They appear to be typical constricted cylinders, somewhat flattened through distortion. A few stout phalanges of the right manus are displayed in USNM 4509.

LYSOROPHIA, INCERTAE SEDIS

Lysorophus Cope, 1877: 187

Cope established this genus on the basis of two holospondylous centra and "portion of a third" from Pennsylvanian rocks near Danville, Illinois. Initially, he did not assign the genus to class. However, the fact that the neural arches were obviously sutured, rather than fused, to the vertebral centra made these centra similar to those he had assigned to *Theropleura* (Cope, 1878 = *Ophiacodon*, Romer and Price, 1940) and seems to have convinced him that the centra represented a clepsydroid pelycosaur (Cope, 1878, 1881). *Lysorophus* remained among the pelycosaurs until the early 1900s (Hay, 1902), when Case et al. described similar vertebrae and asso-

ciated material from the Texas Permian redbeds as *Lysorophus*.

Subsequent debate satisfactorily demonstrated the amphibian nature of *Lysorophus* (see synopsis of earlier work, above). However, generalized similarities between original *Lysorophus* material from Danville, and vertebrae of the redbed species offer no compelling evidence of their conspecificity. Therefore, lysorophoid material from the Permian redbeds of the U.S. Great Plains and Southwest, commonly referred to as "*Lysorophus*," has been described separately as *Brachydectes elongatus* (see above). Cope's original material is treated below.

Lysorophus tricarinatus Cope, 1877: 187

LECTOTYPE: FMNH UC 6526 (Case, 1900: 715), collected by William E. Gurley. A left anterior quarter of a holospondylous vertebral centrum. Noted as "type" by Case (1900, 1901, 1911) and as "holotype" by Olson (1946) and in the catalog of the Field Museum of Natural History (J. Clay Bruner, personal commun.). However no holotype was designated in the original description by Cope (1877). Case (1900) made the first published designation of this specimen as the type of *L. tricarinatus* and it would seem to be more appropriately considered a lectotype. Figure 28A–D of this paper.

HORIZON: Modesto Formation, McLeansboro Group (Geologic Map of Illinois as cited by DeMar, 1970), mid-Missourian Stage (M. E. Hopkins, as cited in DeMar, 1970), ?=mid Conemaugh Series (= Stephanian of Europe).

LOCALITY: North bank of Salt Fork at the tip of Horseshoe Bend, 2 mi south of Oakwood, Vermilion County, Illinois (Moodie, 1909b, 1916); SE $\frac{1}{4}$, SE $\frac{1}{4}$, sec 23, T19N, R13W, Vermilion County, Illinois (Olson, 1946; Oakwood, 7.5' quadrangle, 1968, see also DeMar, 1970).

REFERRED MATERIAL (all collected by W. E. Gurley from same locality and horizon as FMNH UC 6526, above): FMNH UC 6527a, b: Two vertebral centra. As *Lysorophus tricarinatus* by Cope, 1877: 187; Case, 1900: 714–715, pl. 22, fig. 12A–C (FMNH UC 6527a), 1901: 19–20, pl. 2, fig. 12A–C

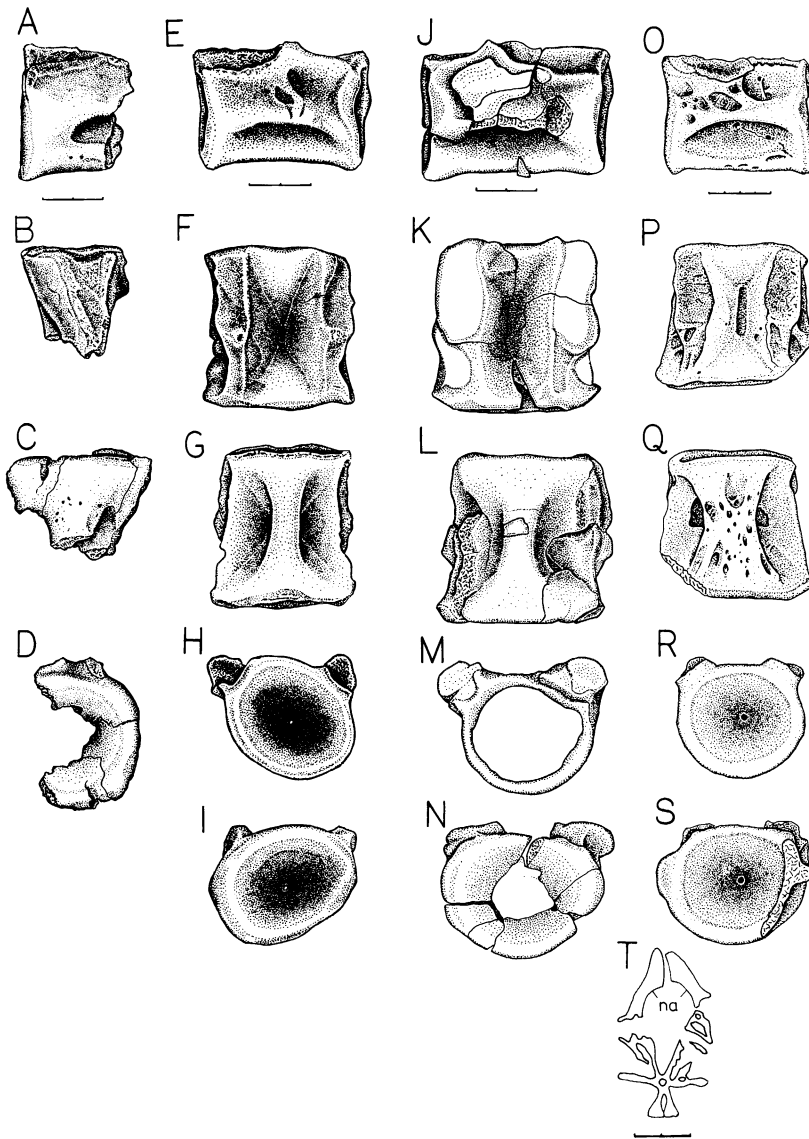


Fig. 28. *Lysorophus*. A-D, *Lysorophus tricarinatus*, holotype, FMNH UC 6526, left lateral, dorsal, ventral, and anterior views (bar scale = 2 mm); E-I, *Lysorophus tricarinatus*, FMNH UC 6527a, left lateral, dorsal, ventral, anterior, and posterior views (bar scale = 2 mm); J-N, *Lysorophus tricarinatus*, FMNH UC 6527b, right lateral, dorsal, ventral, anterior, and posterior views (bar scale = 2 mm); O-S, *Lysorophus dunkardensis*, holotype, CM 8581, left lateral, dorsal, ventral, anterior, and posterior views (bar scale = 4 mm); T, *Brachydectes elongatus*, section of trunk vertebra (from Sollas, 1920) (bar scale = 2 mm).

(FMNH UC 6527a), 1911: 68; and Olson, 1946: 289. Figures 28E-I (FMNH UC 6527a) and 28J-N (FMNH UC 6527b) of this paper. **FMNH UC 6528:** 17 whole or partial vertebral centra. As *L. tricarinatus* by Case, 1900:

714-715, 1901: 19-20, 1911: 68; Olson, 1946: 289. Two of these centra are illustrated in figure 29 of this paper.

COMMENTS: In reviewing the fossil vertebrates from the Danville locality, Case (1900,

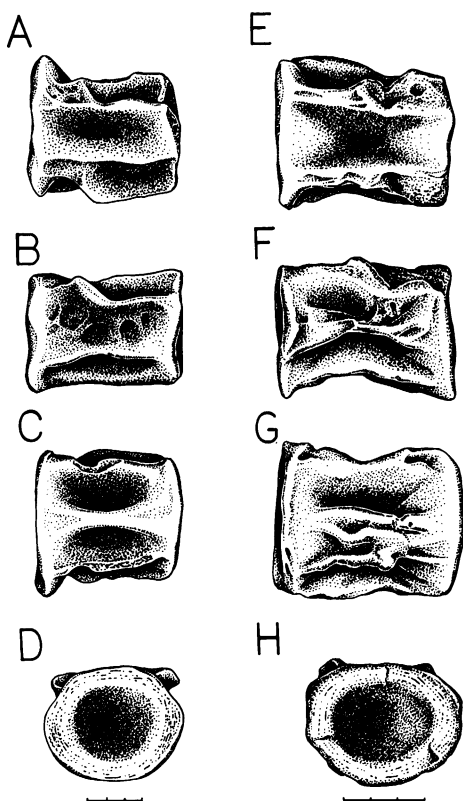


Fig. 29. *Lysorophus tricarinatus*, FMNH UC 6528, dorsal (A, E), right lateral (B, F), ventral (C, G), and posterior (D, H) views of two centra (bar scale = 3 mm).

see also 1901) quoted Cope's original description of the type *Lysorophus* material and referred to three specimens under the Walker Museum numbers "6526, 6527 and 6528." These specimens, among others, were later transferred to the Field Museum and now bear its prefix (e.g., FMNH UC 6526). Case (1900, 1901) referred to what is now FMNH UC 6526 (fig. 28A–D) as the "type specimen," noting that it was badly broken. It is assumed here that Case's type specimen is the partial centrum to which Cope referred.

Claiming to have figured Cope's original specimens, Case supplied figures of two centra which he identified as *Lysorophus tricarinatus* and *Lysorophus* sp., respectively (Case, 1900: pl. 2, figs. 12, 13). Case's figure 12 most closely resembles FMNH UC 6527a, illustrated here in figure 28E–I. Case's figure 12

also resembles illustrations of *Lysorophus* in work by Cope and Matthew (1915: pl. III, fig. 19). Illustrations in Cope and Matthew (1915: pl. III, figs. 19, 20) are the only figures of *L. tricarinatus* prepared under Cope's direction (Donald Baird, personal commun.).

Case's figure 13 may have been meant to illustrate FMNH UC 6527b, but depicts a centrum of the pelycosaur *Clepsydraps*, as Romer and Price (1940: 215) have already noted.

In the lectotype, which Case failed to illustrate, remnants of the ventral and left lateral carinae are present, as well as definite indications of the intervening fossa. The left neurocentral suture is distinct, as is the anterior concavity of the probably amphicoelous centrum. A few pits ornament the remnant of the ventral carina.

The referred material in FMNH UC 6527, especially 6527a (fig. 23E–I), exhibits the neurocentral suture, posterior facets for rib articulation, and the tricarinate, amphicoelous, and notochordal nature of these centra. Matrix which, if removed, might seriously weaken the fossil, obscures the notochordal nature and neurocentral sutural surfaces of fracture-laced FMNH UC 6527b (fig. 28J–N).

Most of the centra in lot FMNH UC 6528 (e.g., fig. 29A–D) conform to the morphology of FMNH UC 6527 and what can be seen in the holotype. However, six centra and the fragment of a seventh differ in morphology of the carinae, which are complicated by anastomosing secondary ridges (fig. 29E–H). Because all the centra are of comparable size, the complication of the carinae seen in these latter seven specimens is probably not the size-related effect seen in other lysorophoids, nor is there indication in more completely preserved lysorophoids that this sort of carina morphology is the result of regional variation. There remain the possibilities that these more complicated centra represent a pathological condition or a species distinct from *L. tricarinatus*.

The material representing *Lysorophus tricarinatus* conforms to the general pattern of lysorophoid centra, but exhibits no feature allowing its diagnosis as a distinct species or its assignment to any of the better established lysorophoid species. *Lysorophus tricarinatus* must be considered a nomen dubium.

Lysorophus dunkardensis Romer, 1952: 74

HOLOTYPE: CM 8581, Burke party, collector, 1937. Isolated holospondylous vertebral centrum. Figure 28O–S of this paper.

HORIZON: A four-inch thick brown, limey clay of uncertain stratigraphic position within the Greene Formation, Dunkard Group (Moran, 1952: 40; Beerbower, 1963: 37), Wolfcampian, Lower Permian (= Sakmarian).

LOCALITY: CM locality 37, approximately 1.1 km (0.7 mi) west of Silver Hill, Proctor District, Wetzel County, West Virginia, on the east side of the road to Macedonia School (Moran, 1952: 40).

REFERRED MATERIAL: CM 8584 (not examined): Burke party, collector, 1934–1935. Fragments of vertebrae (Romer, 1952: 74). Much of the specimen may be lost. **Horizon:** Freshwater limestone bed approximately 15 m (about 50 ft) below Windy Gap Coal, Greene Formation, Dunkard Group (Moran, 1952: 38), Wolfcampian, Lower Permian (= Sakmarian). **Locality:** CM locality 34, north side of Newdale-West P.O. Road, Proctor District, Wetzel County, West Virginia, about 0.33 km (0.2 mi) northeast of Newdale, West Virginia (Moran, 1952: 38).

CM 8585 (not examined): Burke party, collector, 1934–1937. Three disarticulated centra (Romer, 1952: 74). **Horizon:** A 60 cm (2 ft) thick sandy shale apparently underlying the Windy Gap Coal horizon by approximately 12 m (about 40 ft), Greene Formation, Dunkard Group (Moran, 1952: 39; Beerbower, 1963: 37), Wolfcampian, Lower Permian (= Sakmarian). **Locality:** CM locality 35, south side of West P.O.-Silver Hill Road, about 1 km (0.6 mi) east of West P.O., Proctor District, Wetzel County, West Virginia (Moran, 1952: 39).

CM 8586: Burke party, collector, 1936. Limestone slab bearing disordered vertebral elements and ribs (Romer, 1952: 74). **Horizon:** Freshwater limestone bed within the Pittsburgh Limestone, lying 12 m (40 ft) below the base of the Pittsburgh Coal, Cone-maugh Group (Moran, 1952: 10–11), Upper Pennsylvanian (= Stephanian). **Locality:** CM locality 1, a quarry on east side of Soho Street, approximately 0.25 km (0.2 to 0.3 mi) north of Fifth Avenue, Pittsburgh, Allegheny County, Pennsylvania. The site is now cov-

ered by a housing development (Moran, 1952: 10; Beerbower, 1963: 35).

CM 8587 (partim): Burke party, collector, 1937. Limestone slab bearing disordered vertebral elements and ribs (Romer, 1952: 75; Lund et al., 1979: 106, 107). **Horizon:** Union-town Limestone, Monongahela Group (Moran, 1952: 12–13), Upper Pennsylvanian (= Stephanian). **Locality:** CM locality 3, an outcrop just north of Owl Run, approximately 2.0 km (1.0 to 1.5 mi) northeast of Sistersville, Lincoln District, Tyler County, West Virginia, on the west side of West Virginia Route 2 to Paden City, West Virginia.

CM 8590: Burke party, collector, 1937. A limestone slab bearing disordered vertebral elements and ribs (Romer, 1952: 75). **Horizon:** Interbedded limestone and shale at a horizon equivalent to the Mount Morris Limestone of West Virginia and Pennsylvania, approximately 2.3 m (7–10 ft) beneath the Waynesburg “A” Coal, Washington Formation, Dunkard Group (Moran, 1952: 19; Beerbower, 1963: 36), Wolfcampian, Lower Permian (= Sakmarian). **Locality:** CM locality 6, an outcrop in SW¼, sec 18, T3N, R2W, Adams Township, Monroe County, Ohio (Moran, 1952: 18; see also Olson, 1970a).

COMMENTS: Romer distinguished the species by its “large” size. The holotype (CM 8581, fig. 28O–S) is a presacral vertebral centrum and, among the material examined, is by far the largest centrum assigned to the species. However, its length, 9 mm, is well within the range of centrum lengths for both Permian and Carboniferous lysorophoids known currently, as well as when the species was diagnosed. Alae on ribs in the referred material show some differential development in the manner of *Pleuroptyx*, but its significance is uncertain.

With the failure of the criterion of large size, *L. dunkardensis* can only be said to exhibit characteristic lysorophoid morphology. The type specimen of *L. dunkardensis* and its referred material share no derived characters suggesting their conspecificity, nor is there any basis for confidently distinguishing them from, or assigning them to, any of the better known lysorophoid species. *Lysorophus dunkardensis* must be considered a nomen dubium. However, CM 8584 and CM 8585 appear to be the latest-known lysorophoids in eastern North America.

Lysorophus sp.

Noted below are several published accounts of fossil remains suggested as representing *Lysorophus* or described as "lysorophid."

A. FMNH PR 992: R. DeMar, collector. Dorsal half of lysorophoid vertebral centrum, fractured along a frontal plane. As *Lysorophus* sp., DeMar, 1980: 240. **Horizon:** Mattoon Formation, Upper Pennsylvanian (= Stephanian). **Locality:** Jasper County (Falmouth) locality. SW $\frac{1}{4}$, sec 15, T7N, R10E, Jasper County, Illinois (Greenup, Illinois, 15' quadrangle). Not figured in this paper.

B. G91.15: Articulated series of all or portions of 21 presacral vertebrae and associated ribs. A "lysorophid" (Boyd, 1980: 925-929, fig. 1a-d). **Horizon:** Black shale overlying Northumberland Low Main Seam, Westphalian B. **Locality:** Hannah Pit at Newsham, Northumberland, England (Boyd, 1984).

C. G152.04: Single presacral vertebra. A possible "lysorophid" (Boyd, 1980: 925-929, fig. 1h, i). **Horizon and locality:** Possibly Black Bed Coal, Westphalian A of Toftshaw; available data indicate only "Coal Measures of Low Moor, near Bradford in west Yorkshire" (Boyd, 1980: 926).

D. UNNUMBERED SPECIMEN: Whipple, Case and Hussey, collectors, 1930. Vertebrae similar to those of "*Lysorophus*" (Whipple and Case, 1930: 371). Romer (1952) could not locate this specimen. One specimen from Limestone Hill, West Virginia, held in the teaching collection of the Geology Department of Marietta College, Marietta, Ohio, may be the specimen which Whipple and Case noted (D. Baird, personal commun.). It consists of portions of three or four vertebrae of lysorophoid morphology. Centra in this specimen are 15 mm long. **Horizon:** Upper Rockport Limestone or Nineveh Limestone, Greene Formation, Dunkard Group, Wolfcampian, Lower Permian (= Sakmarian). **Locality:** Limestone Hill, boundary between Wood and Wirt Counties, West Virginia, 30 mi south of Marietta, Ohio, on road to Ravenswood, West Virginia (Whipple and Case, 1930: 371; also, NW $\frac{1}{4}$, SE $\frac{1}{4}$, Rockport, West Virginia, 7.5' quadrangle, 1960).

E. UNNUMBERED SPECIMEN (not examined): Unspecified elements. "*Lysorophus*" (Lund,

1972b: 57). Not figured in this paper. The whereabouts of this specimen are unknown. **Horizon:** Upper Washington Limestone, Washington Formation, Dunkard Group, Wolfcampian, Lower Permian (= Sakmarian). **Locality:** Washington Stone Company quarry, Vance, Pennsylvania (Lund, 1972b: 56), just north of intersection of interstate highways 70 and 79, east of Washington, Washington County, Pennsylvania (Washington East, Pennsylvania, 7.5' quadrangle, 1953).

COMMENTS: Specimens noted under A and B above are probably lysorophoids. The ribs in B, G91.15, lack exaggerated alae and, therefore, do not represent *Pleuroptyx*, but no more specific assignment can be made. Specimen G152.04, C above, is unusual for a lysorophoid in that the neural arch is fused to the centrum. (See further discussion of the significance of neural arch sutures in the section on paedomorphosis.) If indeed a lysorophoid, the apparent Westphalian A age of the specimen marks it as the oldest known lysorophoid.

If the specimen noted in D (above) is actually the specimen mentioned by Whipple and Case (1930), it may represent a large lysorophoid. However, the specimen and a longer series of roughly two dozen vertebrae including caudals discovered at Limestone Hill by Whipple in 1932 are also quite similar to vertebrae of *Megamolgophis*, discussed below as distinct from lysorophoids.

The specimen listed under E may represent a lysorophoid. However, its identification cannot be verified, because its location is unknown.

Molgophis Cope, 1868: 220

TYPE SPECIES: *Molgophis macrurus*.

Cope (1868) established the genus on the basis of three series of vertebrae, in two of which he discerned ribs and which, by his count, included 16 and 14 vertebrae each. The third specimen appeared to lack ribs and was interpreted as a series of 22 caudal vertebrae. Although none of these specimens are illustrated in the original descriptions, one may reason from comparisons of vertebral counts that the so-called 16-vertebrae series is AMNH 6913 (fig. 30B, C) and that the 14-

vertebrae series is AMNH 6968 (fig. 30A). Preparation demonstrates that AMNH 6913 and AMNH 6968 actually exhibit all or portions of 17 and 15 vertebrae, respectively.

The alleged caudal series is nowhere to be found among the available *Molgophis* material. However, circumstances suggest that Cope (1871) later established this specimen as the holotype of the aïstopod *Phlegethontia serpens* (AMNH 6899, = *P. linearis* Romer, 1930; see also McGinnis, 1967) without formally removing it from *Molgophis* (D. Baird, personal commun.). Like the missing caudal series, AMNH 6899 is a series of 21 or 22 vertebrae described by Cope (1871, 1875a) in terms very similar to those in his description of the alleged *Molgophis* caudals. Whatever the case, McGinnis (1967) has noted, that AMNH 6899 is actually a series of precaudal vertebrae bearing very slender ribs, which Cope (1868: 220) appears to have mistaken for impressions of tendons.

Cope named two other species of *Molgophis*: *M. wheatleyi* (Cope, 1874: 263, now a synonym of *Brachydetes newberryi*) and *M. brevicostatus* (Cope, 1875a: 369). Cope based *M. brevicostatus* on an indeterminate number of specimens, mentioning only two series of vertebrae, bearing 13 and 9 pairs of ribs, respectively. Of these, the former specimen, AMNH 6840, was figured by Cope (1875a: pl. 44, fig. 1) and was specifically designated the holotype of the species by Moodie (1916: 148). The specimen bearing nine pairs of ribs cannot be accounted for.

Moodie (1916) made reference to the following six additional specimens of *Molgophis*: AMNH 6901 (Newberry 1100G), AMNH 6902 (Newberry 8466G), two AMNH specimens bearing no serial numbers, another bearing only Newberry number 158, and lastly specimen USNM 4477. Communication with Robert Hook, as well as firsthand examination of AMNH 6901, #158, and USNM 4477, demonstrate that AMNH 6901 and USNM 4477 may be questionably referred to *B. newberryi*. Specimen #158 is unusual in that the most readily identifiable elements are claspers of a xenacanth shark (Hook and Hansen, 1985). Specimen AMNH 6902 represents *Erpetosaurus radiatus*. The two specimens lacking catalog numbers have not been accounted for.

Although Cope established *Molgophis* and its species in a technically correct manner, the morphologies of the specimens present no basis for diagnosing *Molgophis* as distinct from other lysorophoid genera nor for confidently synonymizing it with any of them. *Molgophis*, therefore, is a nomen dubium. Specimens retained in the genus almost certainly belong in the Lysorophia, but their position within the order is uncertain. They are described briefly below for purposes of comparison with other members of the order.

Molgophis macrurus Cope, 1868: 220

Molgophis macrurus Cope, 1868: 220.

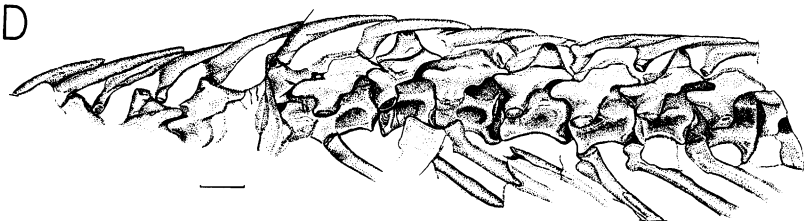
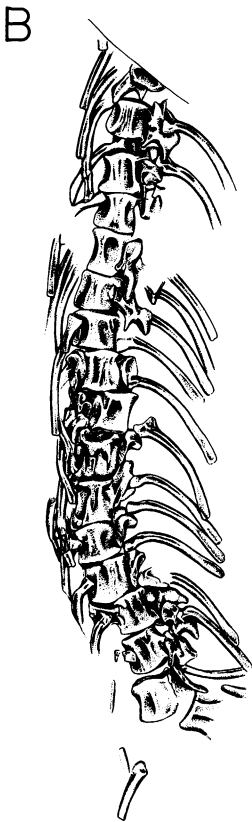
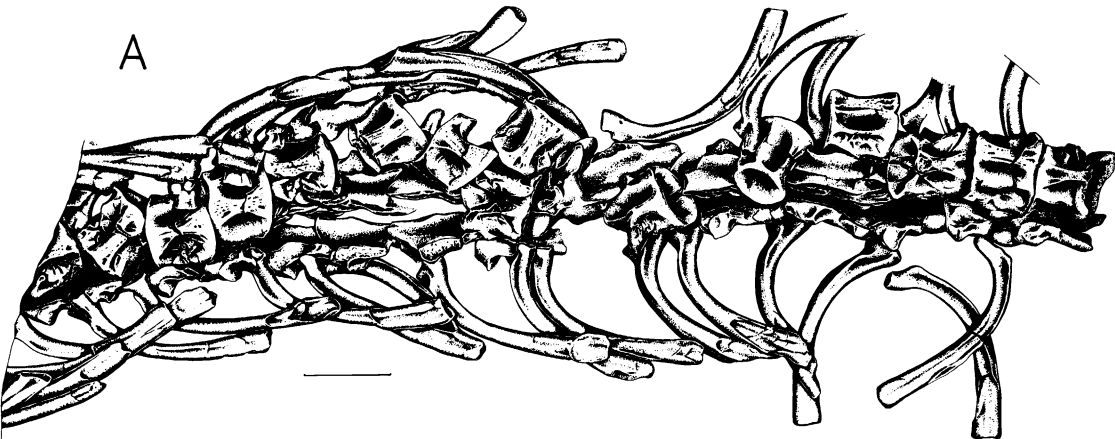
Molgophis brevicostatus Cope, 1875a: 369.

LECTOTYPE: AMNH 6968, a series of all or part of 15 vertebrae and associated ribs chosen here as lectotype because it is the first specimen illustrated as *Molgophis macrurus* by Cope. As *Molgophis macrurus*, Cope, 1868: 220–221; 1869: 20–21; 1874: 263; 1875a: 368, pl. 43, fig. 3; Moodie, 1916: 147–148. (Moodie erred in listing AMNH 6863 as holotype of *M. macrurus*. This specimen is one of the type series of *Pleuroptyx clavatus*, above.) As *Colosteus scutellatus*, Romer, 1930: 101. Figure 30A of this paper.

HORIZON: Cannel coal below coal seam identified as the Upper Freeport Coal (Newberry, 1871, 1874), Allegheny Group, Middle Pennsylvanian; equivalent to late Westphalian D of Europe (D. Baird, 1964; see also Hook, 1983: 7).

LOCALITY: Coal mine originally owned by the Ohio Diamond Coal Company (Murphy, 1980), Linton, Saline Township, Jefferson County, Ohio, approximately 2.5 km south of Wellsville, Ohio (Hook, 1983); NE½, sec 13, T9N R2W, Wellsville, Ohio, 7.5' quadrangle.

REFERRED MATERIAL, FIGURED (all from Linton): AMNH 6913: formerly 1103G, Newberry Collection. Part and counterpart of all or portions of 17 vertebrae and associated ribs. As *Molgophis macrurus*, Cope, 1868: 220–221; 1869: 20–21; 1874: 263; 1875a: 368; Moodie, 1916: 147–148. Figure 30B, C of this paper. AMNH 6840: formerly 8341G, Newberry Collection. Part and counterpart of a series of all or portions of 11



vertebrae and associated ribs. As *Molgophis brevicostatus*, Cope, 1875a: 369, pl. 44, fig. 1; Miller, 1889: 623, fig. 1188; Fritsch, 1883: 107, fig. 55; Moodie, 1909a: 27, as holotype; 1916: 148–149, fig. 32. As *Colosteus scutellatus*, Romer, 1930: 101. Figure 30D of this paper.

REFERRED MATERIAL, NOT FIGURED: AMNH 6963: formerly 8007G, Newberry Collection. Part and counterpart of a series of all or portions of perhaps five vertebrae and associated ribs. Possibly part of original material of "*M. brevicostatus*" (Donald Baird, personal commun.). From Linton. Referred specimens MCZ 2289, 2290, 2291, 2294, and 2812, discussed below, were collected by D. and L. Baird in 1955. All are from the Cone-maugh Group, Upper Pennsylvanian (West-phalian D) of Ohio. All but MCZ 2812 are from the freshwater Ewing Limestone. MCZ 2289: *Molgophis* scrap. Condit's Jewett bonebed (Condit, 1912: 39, 190, 283); first cut on north side of railroad tracks, west of grade crossing of Ohio Route 151, about 1.3 km (0.8 mi) west of town limits of Jewett, Ohio (Donald Baird, personal commun.). SE¼, NW¼, sec 7, T7N, R9W, Rumley Township, Harrison County, Ohio (Jewett, Ohio—Harrison County, 7.5' quadrangle, 1961). MCZ 2290: *Molgophis* vertebra. Locality P-c-4b, cut on east side of U.S. Route 21, just north of junction with Noble County Route 37 (Donald Baird, personal commun.). SE¼, NW¼, sec 7, T7N, R9W, Noble Township, Noble County, Ohio (Caldwell North, Ohio, 7.5' quadrangle, 1961). MCZ 2291: *Molgophis* vertebra. Locality P-c-5, under Jefferson County Route 36 viaduct on a long, abandoned railroad cut about 1.6 km (1 mi) west of Skelly Station (also called Broadacre or Fairplay), Wayne Township, Jefferson County, Ohio (Donald Baird, personal commun.); also SW¼, SE¼, SE¼, sec 24, Wayne Township, Ohio (Romer, 1963: 417–418). MCZ 2294: *Molgophis* vertebra. Locality P-c-4a, a "cut off nose" just west of West Fork of Duck Creek, railroad tracks and U.S. Route 21 (Donald Baird, personal commun.). Central

section 30, T8N, R9W, Noble Township, Noble County, Ohio (Caldwell North, Ohio, 7.5' quadrangle, 1961). MCZ 2812: *Molgophis* scrap. Everly "bonebed," freshwater Summerfield Limestone; C. H. Everly's pasture, south side of Ohio Route 78, just west of its junction with Ohio Route 147 (Donald Baird, personal commun.). Central section 30, T7N, R8W, Center Township, Noble County, Ohio (Sarahsville, Ohio, 7.5' quadrangle, 1961).

DESCRIPTION

Molgophis vertebrae exhibit typical lysorophoid characteristics as described in the section on general anatomy, including ornamentation consistent with their relatively large size. Centra in the lectotype are roughly 7 mm long. Centra in referred specimens AMNH 6913, AMNH 6840, and AMNH 6963 are about 9.0 mm, 13.5 mm, and 13.5 mm long, respectively. There is no indication of where along the presacral vertebral column these segments may have lain.

In the lectotype and in AMNH 6913, views of the neurocentral sutural surface may be seen on either the centrum or neural arch pedicel on close examination. The sutural surfaces between arch pairs are gently sinuous. Comparison between AMNH 6913 and the lectotype show the post- and prezygapophyseal surfaces to be respectively somewhat convex and concave rather than planar.

Neural spines are better developed in the larger *Molgophis* specimens than they are in AMNH 6968. However, regional variation in neural spine morphology seen in *B. elongatus*, although modest, has shown that one cannot be certain that such variation is ontogenetic and not regional or taxonomic.

The impression of alternation of neural spine morphology between the fourth and eleventh spines in specimen AMNH 6840 (Fig. 30D) is belied by the fact that the alternation is not continued forward through the first three vertebrae and by the probability that the low stature of some neural spines

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Fig. 30. *Molgophis macrurus*. A, Lectotype, AMNH 6968; B, C, AMNH 6913, part and counterpart; D, AMNH 6840, holotype of "*Molgophis brevicostatus*." Bar scale = 1 cm.

is due to breakage, as suggested by cracks in the neural spines of the sixth, eighth, and tenth vertebrae.

Molgophis specimens appear to represent relatively large individuals among Linton lysorophoids, but are comparable in size to those of *Pleuroptyx*. The absence of well-developed alar processes from ribs in *Molgophis* tends to confirm that exaggerated alae, as found in *Pleuroptyx*, are not merely the result of large size.

BM(NH) R.8468

Horizon: Impure, anthracite-rank coal (Hook and Hower, 1988) in the lower portion of Jarrow Coal, Middle Westphalian A (Lower Pennsylvanian) (Hook, personal commun.; Rayner, 1971; Panchen, 1977). **Locality:** Jarrow Colliery, Leinster Coalfield, 3 km northeast of Castlecomer, County Kilkenny, Ireland (Hook, personal commun.).

COMMENTS: BM(NH) R.8468 is a poorly preserved specimen consisting of a skull and left mandible, elements of the pectoral girdle, left lower limb and manus, and a series of 20 to 30 vertebrae and associated ribs. There is no indication of the pelvic girdle or hind limbs.

The skull roof appears to be composed principally of three pairs of rectangular bones,

presumably the parietals, frontals, and nasals. The left naris seems to be quite large and there is no distinct orbit.

Postcranially, the neural arches are sutured at the midline, but it is impossible to tell whether or not they were also sutured to the vertebral centra. The left manus possesses at least three digits. Ribs possess proportions appropriate to lysorophoids, but lack the exaggerated alar processes characteristic of *Pleuroptyx*.

These observations suggest that BM(NH) R.8468 may represent a lysorophoid. However, the left craniomandibular articulation appears to be close to the posterior limit of the skull and the mandible appears to be nearly as long as the skull, in contrast to the condition in known lysorophoids. Also, the forelimb seems more gracile and the manus proportionately larger and better ossified than in other lysorophoids.

The presence of lysorophoids at Jarrow would not be unexpected, since Boyd (1980) has presented evidence for their presence in England at Newsham (specimen G91.15, above, Westphalian B) and, apparently, at Toftshaw (specimen G152.04, above, Westphalian A) which lies at a horizon stratigraphically equivalent to Jarrow (fig. 4). Unfortunately, the poor condition of BM(NH) R.8468 makes the specimen undiagnosable.

DISCUSSION

ANATOMY AND HABITUS

Lysorophoids were aquatic amphibians, judging from their extensive hyobranchial apparatus, their elongate, tiny-limbed bodies (suggestive of undulatory locomotion), and the occurrence of their remains primarily in sediments of freshwater ponds and lakes. Moreover, all lysorophoids share with aquatic urodeles several features of the skull, mandible, and hyobranchial skeleton, which suggest that they were carnivores and utilized aquatic inertial feeding.

All Carboniferous lysorophoids appear to have been free-swimming throughout their lives. However, the first skeletons of the Permian species, *Brachydectes elongatus*, were found loosely coiled in nodules (Case, 1902a,

1902b), which suggested both to Case and to Williston (1908a, 1908b) that it burrowed, possibly to avoid drought. Olson and Bolles (1975) were certain that this is the case (but see Schultze, 1985, discussed below under Burrowing in Lysorophoids). Broili (1908a), Zangerl (1944), and Bolt and Wassersug (1975) elaborated on similarities between *B. elongatus*, on one hand, and burrowing amphibians and reptiles, particularly amphisbaenids, on the other. Specific similarities which they cited are large nostrils, large orbitotemporal fenestrae, a broad flat palate, relatively thick bones of the skull roof, a close association of the stapes with the craniomandibular joint, anteriorly placed quadrates, and mandibular adaptations for a wider gape.

Superficially, these comparisons are accu-

rate, but they may go too far in implying that *B. elongatus* was adapted to a largely subterranean life, since it also shares most of these similarities with Carboniferous lysorophoids, for which there is no taphonomic evidence of burrowing (see also comment by Olson and Vaughn, 1970: 131), and with aquatic urodeles, most of which do not burrow. Furthermore, there is no evidence that *B. elongatus* burrowed beyond the extent of its nodules and, as argued below, it appears that *B. elongatus* entered the substrate only intermittently. The closely similar skulls of *B. elongatus* and the Carboniferous lysorophoids suggest that factors other than fossorial habitus are responsible for the morphology of the lysorophoid skull.

ADAPTATION OF SKULL TO STRESS

One of the major factors affecting lysorophoid skull morphology may have been small size, judging from modifications often necessary to accommodate the accompanying relative increase in brain size (Hanken, 1983, and references therein). An apparent minimum functional size of the brain, eye, and otic capsule results in these organs becoming relatively larger as skulls become smaller. In the process, the braincase, particularly the otic capsules, may impinge on the adductor fossae, decreasing available sites for adductor origin, giving impetus to the development of fenestrated cheeks and the movement of the adductors onto the edges of the fenestrae or the external surfaces of the skull. Among extant vertebrates, this result is seen in anurans and urodeles (Carroll and Holmes, 1980) among amphibians, and in amphisbaenids (Zangerl, 1944; Gans, 1960, 1974), and other nonanapsid reptiles (Frazetta, 1968; Rieppel, 1981; Rieppel and Gronowski, 1981). In lysorophoids, accommodation of a relatively larger braincase may have been resolved through the orbitotemporal fenestration seen in both aquatic and periodically burrowing species.

As a result of its relatively large size and the consequent loss of bones roofing the adductor fossae, the braincase, including its dermal coverings, becomes the major structural element in the skull. In lysorophoids, apodans, urodeles, amphisbaenids, and aisto-

pods, this development has resulted in a co-ossification of elements of the braincase and/or a closer integration with dermal covering bones, tending to make the braincase akinetic.

In lysorophoids, the braincase and dermal bones are integrated in the occipital region through the complicated interrelationships of parietals, postparietals, and supraoccipital, and more anteriorly through fusion of the pleurosphenoids to the parasphenoid and through their peg-in-socket articulation with the parietals. Multiple overlappings of sutures between suspensorium and skull roof and the immobile nature of the pterygoquadrate suture (Bolt and Wassersug, 1975) suggest that the rodlike suspensorium may also have offered support for the braincase and would have limited movement at the basiptyergoid joint. Bolt and Wassersug (1975) further suggested that the presence of the pterygoquadrate suture at the level of the basiptyergoid joint may have provided support for the suspensorium, and thereby for the braincase, by bracing it against medial displacement.

The parasphenoid, as the ventral dermal sheath of the braincase, becomes the largest bone in the lysorophoid skull, emphasizing the increase in relative size and structural importance of the braincase. Nevertheless, there is no extreme fusion of braincase elements as seen in apodans, aistopods (*Phlegethontia*), and amphisbaenids, perhaps because of the generally greater absolute size of the skull in lysorophoids.

The stout prootics seem also to have supported the braincase, as well as the stapes, through their contacts with the parietals and basal portions of the pleurosphenoids.

The median dermal roofing series forms the dorsal sheath of the braincase and exhibits a number of adaptations against mechanical stress. As is common in other tetrapods, most of the sutures between these bones, particularly the transverse sutures, are beveled (squamous). Beveling reduces stress at the sutures, while allowing growth between bones (Herring, 1972; Bolt, 1974; Gans, 1974) and may also stabilize skull elements against tension by increasing the area of contact beyond that of simple butt joints (Herring, 1972). These sutures are also interdigitated, sug-

gesting an adaptation against levels of stress greater than those endured by merely beveled sutures (Moss, 1957), possibly presented by shearing forces (Herring, 1972). Compressional forces were presumably resisted by the increased surface area of the complicated sutures and by the thick bones of the skull roof. The elongate prefrontal may have further strengthened the skull roof by spanning the sutures between parietal, frontal, and nasal bones. In return, it may have received support from them for resisting stresses imparted from the palate through the lacrimal.

In contrast, the palatal bones, particularly those of the marginal arcade, seem frail, especially if one considers the lacrimal link between maxilla and prefrontal, or the abbreviated contacts between premaxillae and nasals. The slender condition of these elements contributes partly to the impression of comparatively large nares imparted by the lysorophoid skull (cf. Hanken, 1984).

Sutures between palatal elements are beveled, but lack the interdigitation found in the skull roof. This circumstance suggests that the sutures were capable of some adjustive displacement to reduce stress (Herring, 1972; Bolt and Wassersug, 1975) and indicates that stress was primarily compressional. The loss of the ectopterygoid in lysorophoids is paralleled in apodans, amphisbaenids, and urodeles. It effects a simplification of the palate and might have strengthened it through elimination of sutures.

STAPES

The close relationship between stapes and mandible, or lower portion of the suspensorium, is very similar to that in aquatic urodeles and may be a retention of the condition found in rhipidistian fishes and in very early tetrapods in which the hyomandibular serves to brace the braincase against the cheek (Carroll, 1980; Smithson, 1982; Smithson and Thomson, 1982). The importance of this brace in lysorophoids would seem to be minor considering the support the stout suspensorium receives at the skull roof and pterygoid and is questionable in view of the extensive cartilage or ligament necessary to link the stapes with the mandible or suspensorium.

Kingsbury and Reed (1909) and Monath (1965) suggested that in modern urodeles a close association of stapes and craniomandibular articulation functions to transmit sound from a dense medium such as water or substrate to the ear via the lower jaw. Unfortunately, there is no physiological support for this presumed function of the stapes (e.g., Wever, 1978).

CRANIAL KINESIS

The open nature of the lysorophoid skull and delicate appearance of the palatal margin has led to speculation concerning the kinetic nature of the skull. Bolt and Wassersug (1975) concluded that kinesis was unlikely in the skull roof, braincase, or at the basiptyergoid joint in *B. elongatus* and was improbable in the palate, because of the relatively large combined area of sutural overlap and interdigitation.

As they suggested, it is possible that pressure from a solid object, such as the substrate, may have caused the premaxillae to rotate passively about their limited contacts with the nasals, tending to push the maxillae posteriorly along overlapping sutures with the palatines and lacrimals. Such a response seems reasonable considering Herring's comments on the slippage between bones at beveled sutures (Herring, 1972). However, rotation of the premaxillae would have been resisted in the midline by the vomers.

FEEDING ADAPTATIONS

Bolt and Wassersug (1975) have suggested that the bite of *B. elongatus* may have been relatively weak compared to that in species with similarly sized, solidly roofed skulls, because of the loss of sites for jaw adductor origin through orbitotemporal fenestration. Similarities of skull morphology, including the frail appearance of the palatal and upper dentigerous bones, attests to this possibility in all lysorophoids. The loss of bones roofing the adductor chamber was probably not compensated by expansion of the adductors onto the top of the skull as occurs in anurans and urodeles (Carroll and Holmes, 1980), amphisbaenids (Gans, 1960), and mammals (e.g., Romer and Parsons, 1986), since the sharp angle between the dorsal and lateral aspects

of the skull would have placed the muscle at a mechanical disadvantage (Bolt and Wassersug, 1975).

However, whereas the general absence of muscle scars hampers identification of muscle attachments, some space for muscle origins would seem to have been available on the underside of the skull roof (fig. 14C), particularly if the adductors expanded anteriorly toward the orbit as Bolt and Wassersug have suggested. Portions of the adductor appear also to have expanded onto the suspensorium, occupying distinct facets in the lateral surfaces of the squamosal and tabular, somewhat as did the adductor externus lateralis in dicynodonts (Crompton and Hotton, 1967; Kemp, 1982). Such a distribution of origin sites from orbit to suspensorium may have allowed the adductors to maintain, or perhaps to increase, their mass while broadening the range of maximum effectiveness, since that portion near the orbit would contribute its greatest force when the jaw was open, while more posterior portions would reach their greatest effectiveness when the jaw was nearly closed. However, the total adductor force brought to bear at any time may not have been great, as Bolt and Wassersug have suggested.

In any event, the jaws may have needed to do no more than briefly restrain prey, since lysorophoids seem primarily adapted for aquatic inertial feeding (discussed in recent forms by Regal, 1966; Ozeti and Wake, 1969; Gans, 1969; Severtsov, 1966, 1969; Larsen and Guthrie, 1975; Shaffer and Lauder, 1985), as demonstrated by their possession of an anteriorly placed craniomandibular joint, consequently short mandibles, extensive hyobranchial apparatus, and an array of vomerine teeth positioned anteriorly in the mouth and roughly concentric to the marginal dentition. These features are also found in aquatic larvae and neotenic adults of urodeles such as *Necturus*, *Siren*, *Amphiuma*, *Typhlomolge*, and *Ambystoma* (axolotl). They function in a system which involves the sudden abduction of the mandible and hyobranchial skeleton which creates a flow of water and food items into the mouth and pharynx. Incoming water is expelled through gill slits, presumably present in lysorophoids.

This method of feeding is important when

the prey item is quicker than the predator (e.g., Alexander, 1974). Such may often have been the case for lysorophoids, since Aleev (1963) has noted that lateral undulation, presumably practiced by lysorophoids (see below), is one of the least effective methods of aquatic locomotion, especially if, like lysorophoids, the organism is not laterally compressed. Lysorophoids may have waited in ambush, using suction to capture prey that ventured too near.

The antieriad position of the craniomandibular joint places the corners of the mouth anterior to skull midlength, limiting the size of the mouth, somewhat as do fleshy labial lobes in certain aquatic urodeles (Ozeti and Wake, 1969). A smaller mouth improves the accuracy and efficiency of the incurrent stream by increasing its velocity and by causing it to come more directly from in front of the skull (Alexander, 1974; DeJongh, 1968; Ozeti and Wake, 1969). Bolt and Wassersug (1975) have suggested that another advantage of short jaws could have been the resulting reduction of intermandibular surface area, which may have facilitated opening the mouth in restricted spaces, such as in a burrow, as these authors may have had in mind, or among the debris of a pond bottom. Moreover, the short mandibles could have served to maximize the biting force of available adductor musculature (Radinsky, 1987).

The forward shift of the jaw joint would seem to have necessitated the development of a depressor mandibulae relatively longer than in less derived skulls, assuming the muscle continued to have its origin in the occipital or anterior cervical region. In conjunction with the relatively short retroarticular process of the mandible, the advantages derived would have included a wider gape and more rapid opening of the jaw for a given degree of depressor contraction (Gans, 1966; Gans and Bock, 1965: 122; Radinsky, 1987). The position of the mandibular glenoid slightly below tooth row would have supplemented this effect by yielding a greater gape for a given angular displacement of the jaws (Gans, 1960). Increasing the speed with which a given gape was achieved would have created greater negative pressure in the oral cavity, enhancing the velocity of the food-bearing incurrent stream.

The lysorophoid hyobranchial skeleton would have been critical to the function of the aquatic inertial feeding system. Abduction of the hyobranchial skeleton would have lowered the floor of the oral cavity and expanded the pharynx, helping to create the food-bearing incurrent stream. The extent of this skeleton and the stout nature of its elements are reflected in Broili's comment that the hypohyals and ceratohyals nearly fill the intermandibular area (Broili, 1904a) and suggest how effective abduction of these elements may have been in expanding the buccopharyngeal cavity.

The stout condition of the hyobranchial elements also suggests that if a distinct tongue was present, it must have been relatively immobile and, therefore, incapable of manipulating food items or of macerating them against the palatal dentition prior to swallowing. This circumstance is reflected in the limited array of palatal teeth, which, by analogy with modern urodeles (Regal, 1966), might have been expected to extend beyond the vomers onto more posterior bones, if they had functioned with the tongue in processing food prior to swallowing. In lysorophoids, the tongue and the palatal teeth probably played a more limited role by restraining captured prey for subsequent swallowing sequences. The prey may then have been released into the incoming current to be swallowed directly, or, if awkward in shape, held stationary while the kinetic force of the passing stream tore it into a more easily swallowed form (Regal, 1966).

RESPIRATION

Judging from analogs among modern urodeles, the presence of epibranchials and the utilization of aquatic inertial feeding demand the presence of gill slits in lysorophoids to allow the exit of waters taken in during feeding sequences. However, the well-developed hyobranchial skeleton does not guarantee the presence of either external or internal gills, since among extant urodeles, the aquatic forms *Amphiuma* and *Cryptobranchus* possess extensive hyobranchial skeletons and gill slits, yet lack gills as adults.

There is no *direct* evidence for gills in lysorophoids, as noted in the section on general

anatomy. If these organs were indeed absent, it follows that respiration in lysorophoids was presumably pulmonary, cutaneous, or some combination of the two. Olson (1971) suggested that, as adults, lysorophoids used lungs for respiration. The attitude of the rib heads, oblique to the transverse plane, suggests that lysorophoids may have used costal ventilation of the lungs, if this feature is not merely a retention from a more terrestrial ancestor.

POSTCRANIAL SKELETON

The high presacral vertebral counts in lysorophoids indicate considerable flexibility in the vertebral column, presumably adapted for lateral undulation. The gross similarity of lysorophoid vertebral centra to those of teleost fish offers some support for this assumption. Broili (1904a) and Sollas (1920) commented on this resemblance, while Laerm's characterization of teleost centra (Laerm, 1976: 238) could easily pass for a brief description of lysorophoid centra. His histological study shows that the biconid, or hourglass, portion of the teleost centrum is composed of compact bone, as it is in lysorophoids, and that the struts, or carinae, are similarly made of spongiosa. Laerm (1976) suggested that for teleosts both the carinae and their cancellous internal structure are adaptations against the stresses of lateral undulation. A similar interpretation seems reasonable for lysorophoid vertebral centra.

No purpose is known for the punctate ornamentation frequently seen on the ventral carinae of the vertebral centra. The vascular function which Sollas (1920) attributed to it cannot be confirmed.

Uniformity of vertebral morphology, such as that seen in lysorophoids and which includes trunk centrum length, is expected in forms with reduced limbs and elongate vertebral columns (Hoffstetter and Gasc, 1969). Modern examples are semifossorial to fossorial reptiles such as the lizards *Chalcides* and *Ophisaurus* and the snake *Casarea* (Hoffstetter and Gasc, 1969: figs. 39, 68), but also aquatic urodeles such as *Amphiuma* and *Necturus*. The amphicoelous nature of lysorophoid vertebrae and their lack of auxiliary intervertebral articulations, such as are present in snakes and lizards (Romer, 1956; Auf-

fenberg, 1963), as well as their diminutive limbs, suggest an inability to move easily on land.

The modest expression of neural spines in lysorophoids suggests a relatively simple epaxial musculature. This impression is reinforced by the absence of exaggerated vertebral processes or laminae such as are found in specialized aquatic urodeles like *Amphiuma* and *Siren* (Auffenberg, 1959), indicating by analogy, that lysorophoids may have lacked a great facility for vertical bending of the vertebral column, but like *Necturus*, may have been limited principally to lateral flexure.

Somewhat better developed neural spines seen in the presacral columns of larger lysorophoid individuals suggest that a stronger, but not necessarily more specialized, musculature was needed to support an ontogenetically larger skeleton. Caudally, more distinct neural spines, the presence of hemal spines, and the intercentral position of neural arches (in *B. elongatus*) may have served to stiffen the tail as a locomotory organ.

A greater number of precaudal vertebrae, and proportionately greater length, distinguish *B. elongatus* with a relatively slimmer body than that of *B. newberryi*. Gans (1960, 1974) argued with respect to burrowers that such body proportions allow an animal to move more easily through close surroundings. Particularly in the case of *B. elongatus*, these surroundings may have included the burrows of intended prey. However, Gans' comments seem applicable to species which might move among submerged debris or through thick aquatic vegetation, as well. Judging from analogs such as *Amphiuma* and *Siren*, slimmer body proportions may also have offered such an advantage to *B. elongatus*.

The decrease in trunk centrum length as head and tail are approached is also characteristic of elongate, reduced-limbed forms (Hoffstetter and Gasc, 1969). The reduced mass of the shorter anterior vertebrae and comparatively smaller skull in *B. elongatus* may have supplemented the increased flexibility and greater length of the vertebral column in yielding a smoother propulsion and reduced lateral wobbling of the skull as has been suggested for other tetrapods utilizing

lateral undulation for locomotion (Gans, 1974). The proatlantes may have served to further stiffen the craniovertebral joint against such wobbling. Posteriorly, the rapid decrease in vertebral size suggests a tapered, but relatively short tail, useful in swimming, but perhaps also in the limited subterranean excursions of *B. elongatus*.

The presence of ridges and alae on lysorophoid ribs indicates an increase in the size, although not necessarily in the differentiation, of the epaxial musculature and an increase in the importance of the musculature in facilitating not only lateral undulation, but also the formation of lateral arcs of short radius so evident in aestivating individuals of *B. elongatus*.

The alae do not overlap as do those of *Ichthyostega* or *Thrinaxodon* (Kemp, 1980, 1982) and, therefore, likely did not provide similar skeletal support for the internal organs or vertebral column. Nor was their function the support of the pectoral girdle, as is that of uncinat processes in birds, certain reptiles (e.g., *Sphenodon*) and temnospondyls (e.g., *Eryops*), since, on one hand, the alae are distributed on all ribs far posterior to the lysorophoid pectoral girdle, and, on the other, the support implied by this suggestion seems pointless in an animal with such diminutive limbs.

EVIDENCE OF GROWTH

Regression lines calculated for plots of skull measurements in *B. elongatus* and *B. newberryi* (fig. 23) suggest that, for the size range available, the skulls of lysorophoids grew isometrically. Unfortunately, the fragmentary nature of most lysorophoid specimens makes it difficult to assemble an ontogenetic series for any lysorophoid species in order to study growth processes or even to document size ranges. However, indirect methods examined in the descriptive section suggest at least a tenfold size range for both species of *Brachydectes*. Such a range is broad, but is comparable to that in *Andrias japonicus*, for example, which hatches at a length of 3 cm, metamorphoses at 20 to 25 cm, and has a known maximum length of 180 cm (Grzimek, 1974).

In the descriptive section some differential

development of vertebrae, ribs, and humeri has been noted. Unfortunately, effects of allometry are obscured by the small sample available, incomplete ossification of skeletal elements, and by ignorance of ossification rates in lysorophoids.

An example of the confusion introduced by such ignorance is provided by the humerus in the two species of *Brachydectes*. In Pennsylvanian *B. newberryi* the ossified portion of the humerus approximates the length of a local centrum in specimens of a variety of sizes. Judging from BM(NH) R.2544 (fig. 1C), the humerus is 1 percent of the body length. In specimen UCLA-VP 2802 of the Permian species, *B. elongatus*, the ossified portion of the humerus is also equal to one centrum in length, but is roughly only 0.8 percent of body length. As an index of limb length, the humerus seems relatively shorter in the longer-bodied species, as one might expect from work by Gans (1975) and Lande (1978) on limb reduction in elongate tetrapods. However, in another specimen of *B. elongatus*, FMNH PR 1456, which is estimated to be some 50 percent larger than UCLA-VP 2802, the humerus is the length of three local centra and is 2.5 percent of the estimated body length. It seems, therefore, to have grown disproportionately relative to the body and contradicts the indication of a relatively shorter humerus in *B. elongatus* over that in *B. newberryi*.

Positive allometry may have been responsible for a portion of the relatively greater length of the humerus in FMNH PR 1456. However, the proximal and distal extremities of all lysorophoid limb bones are unossified and the relatively greater length of the humerus in FMNH PR 1456 may be due to more complete ossification. Currie and Carroll (1984), for example, demonstrated that this factor can make a substantial difference in the preserved morphology of limb elements in fossil tetrapods.

BURROWING

The familiar Permian lysorophoid, *B. elongatus*, is characteristically found coiled within nodules. This circumstance has been explained as an aestivating behavior. However, Schultze (1985) has suggested that Low-

er Permian lysorophoids inhabited near-shore marine environments and that burrowing provided them a refuge during tidal changes.

Only one very small specimen from Linton, PU 23494, referred to the Carboniferous species *B. newberryi*, has been found coiled upon itself, although not enclosed in a nodule. Since *B. newberryi* would seem to have been in little danger of desiccation in a sodden deltaic environment, the coiled attitude of PU 23494 may be merely a coincidental postmortem pose, but might possibly be an attitude assumed by lysorophoids when resting or as a general response to any environmental stress.

In contrast to the apparently rare occurrence of coiling in Carboniferous lysorophoids, as well as in those from the Dunkard Permian, nodules containing coiled *B. elongatus* commonly occur in local concentrations of a few square meters at a density of roughly 5/m² (Olson, 1970b). Each concentration holds individuals of approximately the same size. Each nodule generally holds one individual, but may hold as many as three (Olson, 1956, 1958, 1970b, 1971; Olson and Bolles, 1975). The nodules vary in shape, governed roughly by body size. Ovoid nodules hold specimens with a mean midtrunk centrum length of 10 mm or less, while larger individuals occur in elongate burrows (Olson and Bolles, 1975). The coiled attitude of encapsulated *B. elongatus* and the occasional clustering of several in the same nodule may have been a behavioral adaptation against desiccation (Olson and Bolles, 1975), as also reported in salamanders (Ray, 1958; Heatwole, 1960; Spight, 1968; Gehlbach et al., 1969).

From among the clusters of aestivating individuals, Olson and Bolles have distinguished five size classes which they feel may represent regular, perhaps annual, growth stages. They have suggested that aggregation of similarly sized individuals may result from similar abilities to deal with substrate conditions (e.g., moistness and ease of penetration). They have eliminated schooling behavior as an interesting alternative explanation, because strata holding uncoiled, apparently free-swimming individuals of *B. elongatus* (see Olson, 1955, 1956, 1958, 1970a, 1970b, 1971; with Bolles, 1975) yield

a variety of sizes, suggesting that as swimmers they mixed freely, exhibiting none of the segregation seen in nodule clusters.

Occasionally, mixtures of both coiled and uncoiled individuals occur, as in the Vale and Choza formations of Texas and in the Fairmont Shale of Oklahoma (Olson, 1971; with Bolles, 1975). In one case, large individuals (midtrunk centra over 10 mm long) are found in nodules, while smaller individuals are found uncoiled and apparently were free-swimming at death (Olson and Bolles, 1975). Possibly these smaller individuals were temporarily better able to cope with the restricted areal extent and shallowness of drying ponds than were larger ones. In another instance, the mixture of coiled and uncoiled individuals is attributed to redeposition of nodules into basins preserving endemic free-swimming individuals (Olson, 1971).

How *B. elongatus* entered the substrate is uncertain. Assuming it burrowed, it may have used its relatively flat head as a digging tool, somewhat as amphisbaenids do (Gans, 1960). The broader proportions of its skull, compared with that of *B. newberryi*, may have better resisted the stresses of digging. The relatively greater width of the occiput and posterior skull roof may have provided relatively greater area of insertion for epaxial muscles used in digging.

However, that *B. elongatus* actually did burrow is not assured. Absence of burrow networks identifiable as lysorophoid excavations suggests that the subterranean activities of this species were limited to the formation of its coil.

If it entered the substrate to avoid desiccation, it presumably did so before the last of a pond had evaporated. Rather than excavate a discrete hole, it may merely have wriggled into the soft pond bottom, enveloping itself in water-saturated sediment. The coiled state in which its remains are commonly found indicates that the substrate was sufficiently plastic to allow such freedom of movement.

The nature of the nodules themselves is in agreement with this assessment. Olson and Bolles (1975) have reported that there is no distinct boundary between the nodules in which *B. elongatus* occurs and the surrounding matrix. The subterranean activities of *B.*

elongatus seem not to have compacted the sides of its "burrow" as did those of the contemporary lungfish, *Gnathorhiza* (Carlson, 1968), nor did any excavation remain open long enough to receive any distinguishing clastic sediments. The nodules weather cleanly from the matrix, suggesting differential cementation of the sediments in the nodule, as confirmed by the presence of greater amounts of dolomite in the nodules than in the matrix. The presence of the dolomite is apparently correlated with the presence of a large amount of organic material (Olson and Bolles, 1975), perhaps the lysorophoid itself. In this manner, the coiled skeleton of *B. elongatus* is not so much enclosed in a burrow of its own making, but in a differentially cemented lump, resulting from the interaction of its decaying body and interstitial fluids.

PAEDOMORPHOSIS

The author's initial inclination was to argue that lysorophoids exhibited paedomorphosis through their possession of such features as (1) a well-developed, ossified hyobranchial skeleton, apparently useful in expanding the pharynx as a feeding adaptation, (2) a palatal dental array anteriorly situated and concentric to the marginal dentition, (3) an anteriorly displaced craniomandibular joint, and (4) the failure of the neural arch halves to fuse to each other and to their centra, producing the neural arch sutures characteristic of the order.

By analogy with modern amphibians, particularly urodeles, the lysorophoid hyobranchial skeleton, the distribution of the palatal dentition, and the position of the craniomandibular joint suggest a larval or juvenile condition. Extension of the analogy suggests metamorphosis in lysorophoids and, therefore, at least in some lepospondyls. However, unlike labyrinthodonts for which externally gilled, apparently larval forms are known (e.g., Romer, 1939; Watson, 1963; Boy, 1974; Milner, 1982), there is no independent evidence for metamorphosis among lepospondyls (D. Baird, 1964). The juveniles seem merely to be smaller versions of the adults.

Having no assurance that juvenile lepospondyl morphology was greatly different from that of the adult other than in size, and,

as yet, no analysis of what the common ancestor of the Lysorophia and its sister group (apparently the microsaur) may have been like, it is not without risk that one assumes the paedomorphic nature of the particular lysorophoid characters noted above. The hyobranchial apparatus could represent a retention of a primitive condition (e.g., Rosen et al., 1981), lost or reduced among the various microsaur, while the palatal dental array and jaw joint position could be neomorphs, homoplastic with similar conditions in urodeles.

In mature amniotes, persistence of sutural attachments between neural arch halves and centra would indicate paedomorphosis, since in amniotes these sutural features appear during development, but are later obliterated (Williams, 1959). However, in lysorophoids and microsaur, the sutural features could equally well represent the primitive condition, as seen in labyrinthodonts and sarcopterygian fishes (Jarvik, 1980; Lauder, 1980). Ultimate resolution of the primitive or paedomorphic status of neural arch sutures in lysorophoids would seem to depend on whether the common ancestor of microsaur and lysorophoids possessed the sutures, in which case these features would be primitive, or whether vertebral development in the ancestor included an amniotelike fusion of elements, as seen in some microsaur, in which case the sutures would indeed be paedomorphic.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

NORTH AMERICA

Lysorophoids are known primarily from the United States, where they first appear in Upper Pennsylvanian rocks (Westphalian C and D) of the eastern interior and continue through much of the Lower Permian there and in the redbeds of the American southwest (figs. 4, 5). Their geographic distribution parallels that described for North American Permian-Carboniferous amphibians in general (Olson and Vaughn, 1970; Panchen, 1973, 1977; Milner, 1987), approximating the equator and spreading westward with time. This westward drift of lysorophoids may derive merely from the facts that they lived in

bodies of water on coastal plains along the Paleozoic epeiric sea covering the interior of North America and that the coast moved westward with time as the sea regressed. As a result, the oldest known North American lysorophoid comes from a Pennsylvanian deltaic complex in Illinois and, not surprisingly, the last known comes from a Permian deltaic complex in Texas.

MAZON CREEK: The geologically earliest known North American lysorophoid (D. Baird, 1964: 14) is part of the "Braidwood" fauna of Mazon Creek (see G. C. Baird et al., 1985; Nitecki, 1979) in Will and Grundy counties, Illinois (mid-Pennsylvanian = Westphalian D). Vertebrates there, as well as invertebrates and plants, are preserved in sideritic concretions in the Francis Creek Shale of the Carbondale Formation, which overlies the No. 2 (Colchester) coal of Illinois (Richardson, 1956; Johnson and Richardson, 1966; Rayner, 1971). While the Francis Creek has been considered a roofing shale (Moodie, 1916; Gregory, 1948; Panchen, 1970), unlike other roofing shales discussed below, it did not accumulate solely in a pond or lake, but appears to have been part of a deltaic complex (Richardson, 1956; Johnson and Richardson, 1966; Rayner, 1971; Shabica, 1979), the northeastern (inland) portion of which accumulated in a delta plain (Richardson, 1956) while its southwestern portion represents a shallow marine embayment (e.g., G. C. Baird et al., 1985; Wanless, 1929). A. R. Milner (1987) presented a discussion of ecological and geographical factors possibly affecting the vertebrate assemblages at Mazon Creek, as well as at other Westphalian sites, three of which are concerned in this report: Jarrow, Newsham, and Linton.

The sole lysorophoid specimen from Mazon Creek is USNM 4313, questionably assigned to *Brachydectes newberryi*.

LINTON: The locality yielding the single greatest variety of lysorophoid specimens is the Linton site (mid-Pennsylvanian = Westphalian D) in the Pennsylvanian coal fields of eastern Ohio. The site represents an abandoned stream channel, gradually in-filled by plant debris and fine-grained inorganic sediments. Hook and Ferm (1985, 1988) and Hook and Hower (1988) provided the most extensive analyses of the sedimentary envi-

ronment which produced the locality. Hook and Baird (1986, 1988) have presented the most recent reviews of the history and vertebrate fauna of the Linton site.

These works emphasize that the diverse vertebrate fauna at Linton is autochthonous and comes from a cannel coal immediately overlain by the Upper Freeport, a humic coal at the top of the Allegheny Formation. The cannel accumulated in abandoned portions of a fluviodeltaic channel estimated to have been 15 m in depth. This considerable depth and the general absence of inorganic in-fill allowed a prolonged accumulation of both vertebrate remains and cannel-producing spores and macerated plant debris. Conditions produced in this anaerobic environment discouraged scavengers which otherwise might have destroyed the vertebrate skeletons.

Lysorophoids at Linton are represented by type and referred material of *Brachydictes newberryi*, *Pleuroptyx clavatus*, and "*Molgophis macrurus*."

DANVILLE, ILLINOIS: *Lysorophus* was established on the basis of disarticulated vertebral material from the Danville ("Oakwood" or "Vermilion County") locality (Upper Pennsylvanian = Stephanian) of east-central Illinois, summarized by DeMar (1980). As he notes, the exact location of the site is uncertain for no one has found it since 1907 (Moodie, 1916). The consensus appears to be that the vertebrates at Danville came from a red and gray shale, although there has been some discussion of the point (Olson, 1946). Olson (1946) visited the vicinity of the site and suggested that the shales are, at least in part, non-marine, judging from the absence of marine invertebrates.

Disarticulated vertebral centra from this site (FMNH UC 6526, 6527a & b, 6528) formed the basis for the species *Lysorophus tricarinatus*.

FALMOUTH, ILLINOIS: The Falmouth site (Upper Pennsylvanian = Stephanian) in southeastern Illinois, is, after Mazon Creek and Danville, the third site in that state to yield lysorophoid remains (DeMar, 1980; also Olson, 1946), although the Falmouth lysorophoid material consists only of a fragment of a single centrum (FMNH PR 992). According to Olson, the site is a channel about

4.5 m (15 ft) long and about 0.6 m (2 ft) thick, exposed in a road cut. The channel is filled with sandstone, shale, and clay pebbles and is bounded below by a marine limestone and above by an unfossiliferous gray shale. The precise stratigraphic location of the site is not known, but it lies not far above the Reisner Limestone (DeMar, 1970).

DIVERSE SITES IN THE UPPER PENNSYLVANIAN OF OHIO, PENNSYLVANIA, AND WEST VIRGINIA: An epeiric sea fluctuated east- and westward across the eastern interior through the late Pennsylvanian and at least once in the Permian (Cross, 1975). This fluctuation is amply reflected in the scatter of tetrapod-bearing coastal or deltaic sediments found across the interior lowland from Illinois to Pennsylvania and West Virginia. The Appalachian Plateau remained a low-lying coastal plain in whose ponds and lakes developed several freshwater limestones which yield lysorophoid remains. As noted in the systematic section, isolated lysorophoid vertebrae are known from a number of such limestones of the Conemaugh Group. These include the Summerfield Limestone of Noble County, Ohio, and the Ewing Limestone of Harrison, Jefferson, and Noble counties, Ohio, both of which have produced vertebral remains referred to "*Molgophis*." At Pittsburgh, Pennsylvania, the Duquesne Limestone has yielded a single battered lysorophoid centrum (CM 19124) which has not figured in earlier systematic considerations. Also at Pittsburgh, the Pittsburgh Limestone has produced a series of ribs and vertebral elements referred to "*Lysorophus dunkardensis*."

In the Monongahela Group (Upper Pennsylvanian = Stephanian), the freshwater Monongahela "B" Limestone of Ohio County, West Virginia, has produced an articulated partial skeleton of *Brachydictes* with skull (Lund, 1972a), while the freshwater Uniontown Limestone of Tyler County, West Virginia, has yielded a series of lysorophoid vertebrae and ribs (CM 8587, "*Lysorophus dunkardensis*," Romer, 1952).

DUNKARD GROUP: The Dunkard Group (Lower Permian, see Barlow, 1975; Lund, 1976; Olson and Vaughn, 1970) of Ohio, West Virginia, and Pennsylvania also yields lysorophoid specimens from freshwater lime-

stones and associated sediments. These include a mass of postcrania from the Mt. Morris Limestone of Monroe County, Ohio, assigned to "*L. dunkardensis*," and an isolated vertebra (PU 19305, D. Baird, personal commun.) from a channel deposit (Belpre Bonebed) near the top of the Washington Formation (Lower Permian = Sakmarian) near Belpre, Ohio (see also Hlavin, 1972; Hlavin et al., 1968; Olson, 1970a). Lund (1972b) also reported lysorophoid material from the Upper Washington Limestone at the top of the Washington Formation in Washington County, Pennsylvania.

In the overlying Greene Formation, the Upper Rockport Limestone of Wirt and Wood counties, West Virginia, has yielded lysorophoid vertebrae (Whipple and Case, 1930), while a displaced freshwater limestone block, thought to come from the Upper Rockport of Marshall County, West Virginia, has yielded a very small skeleton referable to *Brachydectes* (CM 8564, = *Lysorophus minutus* Romer, 1952). In the upper third of the formation in Wetzel County, West Virginia, three sites have produced a number of lysorophoid vertebrae and rib fragments referred to *L. dunkardensis* (Romer, 1952). These latter three sites may be equivalent in stratigraphic position, lying some 12–15 m below the Windy Gap Coal (Moran, 1952), but the varied lithologies at this horizon apparently hamper regional correlation.

Lysorophoids are known from younger rocks elsewhere in North America as discussed below. However, in the eastern interior lowland, any lysorophoid-preserving strata above the Dunkard Group have been eroded away and with it, perhaps, most clues to the cause of the extinction of lysorophoids in this region.

PERMIAN OF THE NORTH AMERICAN WEST AND CONTINENTAL INTERIOR: The epeiric sea regressed to midcontinent during the early Permian. As in the Pennsylvanian, sequences of deltaic and channel clastics were deposited along its margins. The regional climate becomes more arid as indicated by the absence of coal and presence of evaporites in the Clear Fork Group of Texas and its equivalents in Oklahoma (e.g., Olson and Vaughn, 1970). Vertebrate-bearing clastics of particular in-

terest in the following discussion are those in Nebraska, Kansas, Oklahoma, Texas, Utah, and New Mexico, which include portions of the classic Permian redbeds of North America.

Articulated specimens assigned to *Brachydectes elongatus* are known from fine-grained sediments such as the Blue Rapids Shale of Pottawatomie County, Kansas, the Clear Fork Group of Baylor, Wilbarger, Knox and Foard counties, Texas, and the Norman-sec 13 site in the Fairmont Shale (Hennessey Group) of Oklahoma. Olson (1967) reported *B. elongatus* also from the Orlando site in the Wellington Formation of Oklahoma. All these sites are Wolfcampian in age. The majority of these lysorophoid specimens occur in colonies or clusters of individuals coiled in nodules suggestive of aestivation. Olson (1958 and 1977) noted specifically that the enveloping sediments are primarily pond deposits. Occasionally, articulated specimens enclosed in nodules are found in fluvial clastics. However, these appear to be allochthonous specimens, washed in from their aestivation sites (Olson, 1956: 316; 1971: 445; personal commun.).

Sediments representing environments of higher energy tend to yield disarticulated specimens. For example, lysorophoid vertebrae have been reported from Wolfcampian channel deposits at single sites in the Indian Cave Sandstone of Nebraska (CM 23518), Halgaito Shale of Lisbon Valley, Utah (Olson and Vaughn, 1970; UCLA-VP 2883, Vaughn, personal commun.), and Sangre de Cristo Formation of Miguel County, New Mexico (Vaughn, 1964, 1969a; Brill, 1952; CM 26587). Similar remains have come from red shales at the South Grandfield site in the Garber Formation (Leonardian) of Oklahoma (Daly, 1973) and from two sites representing a near-shore marine environment in the Leuders Formation (Leonardian) of Baylor County, Texas (Berman, 1970). These latter specimens are considered allochthonous, with stream transport to the shore or subsequent wave action responsible for disarticulation of the original carcasses.

Except for these reports from the Leuders Formation, no lysorophoid remains are known from the Wichita Group of north-cen-

tral Texas, in contrast to their abundance in the overlying Clear Fork Group. Differences between the faunas of Wichita and Clear Fork groups have been noted by others (e.g., Olson and Vaughn, 1970), and in the case of lysorophoids might be explained by the greater marine influence on sediments of the Wichita Group than on those of the classic Clear Fork tetrapod sites (Romer, 1958, 1974; Hentz and Brown, 1987). Within the Clear Fork, as well, lysorophoids disappear from tetrapod faunas when marine rocks become more common, some 200 km to the south of the well-known collecting areas (Olson and Mead, 1982). Marine influence could have been critical had lysorophoids been intolerant of brackish or marine conditions, as would seem reasonable for amphibians (cf. Schultze, 1985; Cunningham, 1989).

Lysorophoids have not been found in sediments above the Clear Fork. Olson and Beerbower (1953) suggested that extreme aridity extinguished the fauna characteristic of the Clear Fork Group in Texas, including the lysorophoids. One might presume that similar conditions eliminated them in neighboring Oklahoma.

In southeastern Utah, changes in the fauna and flora between the Halgaito and Organ Rock shales (fig. 4) indicate an earlier onset of more arid conditions in the Four-Corners area of Colorado, Utah, New Mexico, and Arizona than in Texas and Oklahoma (Vaughn, 1969b). Vaughn suggested that a rain shadow cast by the Ancestral Rockies may have contributed to this aridity. In any case, the paucity of lysorophoid remains suggests that any rocks preserving concentrations of them, comparable to those in Texas and Oklahoma, have yet to be discovered or have been lost to erosion.

In summary, relatively complete specimens of lysorophoids tend to come from Permian-Carboniferous fine-grained sediments, which in most cases, are indicative of lakes and ponds. Contemporary coarser, fluvial clastics have yielded fragmentary specimens and isolated vertebral centra. Occasionally, more complete specimens are discovered in these coarser sediments, but such materials are allochthonous. Marine influence seems to have limited lysorophoid distribution. In-

creasing aridity has been cited as a possible cause of lysorophoid extinction in the Permian of the American mid-continent and southwest.

GREAT BRITAIN AND THE REPUBLIC OF IRELAND

Lysorophoids are known with some uncertainty from England and the Republic of Ireland. Referred material occurs in association with coals which are Westphalian A and B in age and which, therefore, are considerably older than North American representatives.

JARROW: Specimen BM(NH) R.8468, referred tentatively to *B. newberryi*, comes from Jarrow Colliery (Westphalian A), Leinster, Ireland. The site is similar to Linton in that it is thought to represent the in-filling of an abandoned stream channel (Hook and Ferm, 1985; see also Milner, 1987). The coal at Jarrow is an anthracite, suggesting that the serious loss of detail frequently suffered by fossils from the site is the result of metamorphism (see *Discussion* in Hook and Howler, 1988).

NEWSHAM AND TOFTSHAW: Black roofing shales at Newsham (Westphalian B) and, possibly Toftshaw (Westphalian A), have yielded lysorophoid vertebrae and ribs (Boyd, 1980). The Toftshaw specimen is questionable because, in addition to morphological irregularities, its provenance is uncertain. The fossiliferous roofing shales overlie the Black Bed coal at Toftshaw and the Northumberland Low Main coal at Newsham. Rayner (1971) and Boyd (1984) described the shale at Newsham as well-bedded and pyritous. The Newsham fauna and its geological circumstances suggest that it represents a large body of water, possibly an abandoned channel or oxbow lake (Panchen, 1970; A. R. Milner, 1980, 1987; Boyd, 1984). One should also refer to work by Hook and Ferm (1985) for comments regarding the sedimentary environments at both Newsham and Toftshaw.

No lysorophoids have been found outside North America and the British Isles. They may have been kept from Europe by the Appalachian-Caledonide and Hercynian mountain complexes. Their "niche" at a site such

as Nýřany was possibly filled by long-bodied microbrachid microsaur (Milner and Panchen, 1973; Panchen, 1977). Southwestern portions of the Appalachian system may have kept them from spreading to the Gondwanan continents, bordering what are now the east and gulf coasts of North America. Oceanic and latitudinally induced climatic barriers (e.g., Ziegler et al., 1977; Panchen, 1973) may have kept lysorophoids from other continents. Otherwise, the absence of any record of these amphibians from these continents may be due to any of a variety of sedimentological, ecological, or preservational biases or human oversights.

DOUBTFUL OCCURRENCES

A very poorly preserved specimen, NMI. G. 50:1959 of the National Museum of Ireland, is an elongate form about 60 cm in total length with a skull 2.3 cm long. Its provenance is unknown but it almost certainly came from the Jarrow Colliery (K. Bossy, personal commun.), Westphalian A (Lower Pennsylvanian), County Kilkenny, Ireland (Rayner, 1971; Panchen, 1977). Donald Baird (personal commun.) suggested that it is a lysorophoid. However, the specimen exhibits no limbs or girdles, its ribs appear to be straight, it displays a small, indistinct patch of elongate, ventral dermal ossicles anteriorly, and possesses a mandible equal in length to the skull. The specimen is more reasonably considered an aïstopod (see D. Baird, 1964, 1965).

Donald Baird (1964) has suggested that a specimen from Autunian rocks at La Machine, Nièvre, France, originally described as an aïstopod by Thévinin (1910), may be a lysorophoid. However, Carroll (personal commun.) commented that the condition of the specimen is too poor to allow its discrimination as either aïstopod or lysorophoid.

Lysorophoids have not been found in strata younger than the upper portion of the Clear Fork Group (Choza Formation) of the Lower Permian of Texas. An alleged Upper Triassic "lysorophoid" is *Lysorocephalus gwyneddensis* Huene and Bock, 1954, the sole specimen of which comes from the vicinity of Gwynedd, Pennsylvania. D. Baird (1964) reported

that the specimen appears to be the damaged skull roof of a palaeoniscoid fish.

PHYLOGENETIC RELATIONSHIPS

RELATIONSHIPS WITHIN THE LYSOROPHIA

Lysorophoid species are very similar to one another, although their morphology is unique among vertebrates. This distinction suggests not only that the lysorophoids are closely related to one another as a group, but that the order is monophyletic.

Deciding on the relationships between lysorophoids and other amphibians is more difficult. In the absence of generally accepted evidence to the contrary, it is assumed that the tetrapods are a monophyletic group. Therefore, the lysorophoids must share phylogenetic relationships with other tetrapods and some groups must be more closely related than others. Since lysorophoids are Paleozoic amphibians, such relationships are more reasonably sought among other amphibians, especially labyrinthodonts and other lepospondyls, rather than among reptiles, birds, or mammals. Lysorophoids appear to be too specialized to have given rise to any of the modern amphibians, although at some taxonomic level they must share a common ancestor. Lysorophoids do not resemble any known labyrinthodont or other lepospondyl in general body form. One must therefore rely on specific skeletal characteristics to indicate relationships. In this situation, a few shared derived characters become extremely important in discussing phylogeny.

Romer (1950, 1966) has suggested that lysorophoids might possibly be microsaur, although atypical for that order. Carroll and Gaskill (1978) drew a distinction between lysorophoids and microsaur, but suggested that something like a microsauroid could have given rise to the lysorophoids. Despite the skeletal specializations which lysorophoids exhibit, it is reassuring to find that lysorophoids appear to share with the microsaur a characteristic craniovertebral articulation which distinguishes them from other tetrapods. The similarity of the articulation is especially evident in the odontoid of the holospondylous first centrum, accommodated by the concave surface of the basioccipital. As discussed in the

sacral vertebrae held by *B. newberryi*, unless there has been a reduction in presacral vertebral number within the order. The 97 presacral vertebrae in *B. elongatus* (character 8) represents continued elongation of the vertebral column in *Brachydectes* over that in *B. newberryi* and is interpreted as a derived state. Such a broad range in vertebral count within a genus is unusual among less elongate vertebrates but not unheard of among apodans (e.g., *Chthonerpeton*, *Caecilia*, or *Osaecilia*, Taylor, 1968).

9. The exaggerated development of rib alae in *Pleuroptyx* probably represents a derived character within the Lysorophia, since, with the exception of *Megamolgophis*, adelogyrinids and the cervicals of the microsauro *Microbrachis*, they do not occur among other lepospondyls. Somewhat similar structures, uncinat processes, occur only irregularly among distantly related species of labyrinthodonts, reptiles, and birds.

Length-to-width proportions of the skull roof in *B. newberryi* and *B. elongatus* (table 1) and the width-to-length proportions of the parietal pair in *B. newberryi*, *B. elongatus*, and *Pleuroptyx clavatus* (table 2) indicate that *B. elongatus* and *P. clavatus* both possess relatively broader skulls than does *B. newberryi*. This fact might be used to link *B. elongatus* more closely with *P. clavatus* than with *B. newberryi*. However, a significant difference between the width-to-length ratios of the parietal pairs in *B. elongatus* and *P. clavatus* suggests independent achievement of greater skull width in the two species. This leaves open the possibility that the skull in *B. elongatus* increased in width after its split from the lineage of *B. newberryi* and would conform to the hypothesis that *B. elongatus* and *B. newberryi* are more closely related to each other than to *P. clavatus*. Without better indication of the primitive state of skull proportions in common ancestor A, the character is difficult to use in assessing the phylogenetic relationships among lysorophoids.

A similar situation exists for the bifurcated second epibranchial found in *B. newberryi* and *P. clavatus*. If the bifurcated epibranchial were present in ancestor A, its absence in *B. elongatus* could be explained as a loss. However, differences in detail of the element between *B. newberryi* and *P. clavatus* suggest

that it was independently developed in these two species. Without knowledge of the condition of epibranchial 2 in ancestor A, it is difficult to assess the phylogenetic significance of this character.

LYSOROPHOID RELATIONSHIPS TO MICROSAURS

As already noted, similar craniovertebral joints suggest a close relationship between microsaurs and lysorophoids. A possible exception could be the microbrachiomorph *Odonterpeton* (Carroll and Gaskill, 1978) in which the articulation is comparatively narrow and no distinct odontoid is present. Nevertheless, the anterior surface of the first centrum in *Odonterpeton* does appear to bear two facets for the exoccipitals. These meet at the midline producing a modest process which may have articulated with the basioccipital as in other microsaurs. Comparison with other microsaurs suggests the possibility that the condition of the craniovertebral articulation in *Odonterpeton* may be derived relative to them.

The microsaurian craniovertebral joint is like that in labyrinthodonts in that the cranial portion is composed of parts of both exoccipitals and the basioccipital. However, the broad microsaurian articulation is distinct from the shallowly concave, subcircular joint present in primitive labyrinthodonts and from the bicondylar joints of more derived ones. The strap-shaped articulation in the large terrestrial labyrinthodont *Eryops* is somewhat similar to that in microsaurs and lysorophoids, but the multipartite atlas-axis complex present in all labyrinthodonts is distinct from the holospondylous first cervical vertebra present in microsaurs and lysorophoids.

Carroll and Gaskill (1978) noted that the microsaurian craniovertebral joint is distinct from those known in aistopods and in most urocordylid and all keraterpetontid nectrideans. The urocordylid nectridean *Ptyonius marshi* appears to possess a "microsaurian" cranial portion of the craniovertebral articulation, but this condition must be independently derived, since the primitive state for urocordylids is a simple condyle (Bossy, 1976).

On the basis of skull morphology, the tudi-

tanomorph microsaur demonstrate a greater potential for having given rise to the lysorophoids than do microbrachomorph microsaur. Table 6 lists a series of derived features characteristic of lysorophoids and a listing of tuditanomorph microsaur which possess similar morphologies.

In addition to these characters, the supraoccipitals in *Pantylus*; *Rhynchonkos* (= *Goniorhynchus* Olson, 1970; Schultze and Foreman, 1981) and the ostodolepids *Micraroter* and *Pelodosotis* are relatively large and form the roof of the posterior portion of the braincase, somewhat as in lysorophoids. The supraoccipitals in *Pantylus* and *Pelodosotis* are also clearly overlapped by the postparietals (Carroll and Gaskill, 1978). The supraoccipital of lysorophoids may be a more derived instance of this arrangement, having been integrated into the dermal skull roof, separating the postparietals and contacting the parietals.

Ostodolepids, especially *Pelodosotis*, exhibit all the lysorophoid characters listed in table 6 except the anteriorly sloping suspensorium. Interestingly, *Pelodosotis* also exhibits the highest presacral vertebral count (45) among microsaur. Unfortunately, the overhanging snouts of ostodolepids, and goniorhynchids as well, distinguish these families as too specialized to have given rise directly to lysorophoids. Furthermore, the time gap of some 30 million years between the first well-known lysorophoid (Westphalian D) and these Permian tuditanomorph microsaur emphasizes the possibility that these similarities have been developed independently.

Among microbrachomorph microsaur, only *Odonterpeton* exhibits an obvious specialization which might link it with lysorophoids. This one character is a somewhat anteriorly placed craniomandibular articulation, which, as noted above, has been developed also in certain tuditanomorphs.

Like the microbrachomorph *Brachystelechus*, *Odonterpeton* also lacks distinct tabular bones. Both *Brachystelechus* and *Odonterpeton* exhibit other specializations of the skull roof, such as fusion or loss of postparietals or the presence of interfrontal bones, not found in lysorophoids.

In *Hyoplesion*, the squamosal rises to contact the parietal as in lysorophoids, but, as a result, the tabular is a small and very super-

TABLE 6
Derived Characters Shared by Lysorophoids and Certain Microsaur

Character	Taxon
1) Orbitotemporal region fenestrated without lower bar	Hapsidopareiontidae, ^a Ostodolepidae
2) Rodlike suspensorium (squamosal and tabular)	Hapsidopareiontidae, ^a Ostodolepidae
3) Arched/sloping occiput	Ostodolepidae, <i>Rhynchonkos</i>
4) Exoccipital is posterior extremity of skull	Ostodolepidae, Gymnarthridae
5) Anteriorly placed jaw articulation	<i>Rhynchonkos</i> , several gymnarthrids
6) Extensive basisphenoid/pleurophenoid ossification	<i>Pantylus</i> , <i>Pelodosotis</i>
7) Lacrimal with distinct prefrontal process	Ostodolepidae, <i>Crinodon</i>

^a No skull is known for the hapsidopareiontid *Ricnodon* from Jogjins and Nýřany. The skull of hapsidopareiontid *Saxonerpeton* from Niederhasslich exhibits none of these characters. All other taxa are from the Lower Permian redbeds of Texas and Oklahoma.

ficial bone, not an integral part of the skull roof and suspensorium as it appears to be in lysorophoids.

In general, the skulls of all microbrachomorph microsaur, especially that of *Microbrachis*, appear to be too low and broad for microbrachomorphs to have given rise to lysorophoids.

In addition to cranial similarities shared with tuditanomorph microsaur, lysorophoids share the following postcranial characters with some or all microsaur: (1) lightly constructed interclavicle with reduced stem and gracile clavicles, all lacking ornamentation, (2) holospondylous centra in the presacral column, (3) presence of neurocentral sutures, (4) presence of transverse processes which rise from the neural arches, rather than from the centra, and (5) presence of capitular facets on the posterior rims of the centra. In a general manner, these characters serve to distinguish lysorophoids from two other major lepospondyl orders, the Aistopoda and Nectridea, but their distribution among the various microsaure genera is not understood well enough for special taxonomic significance to be attached to them, especially since

combinations of the vertebral characters also appear in adelogyrinids and in *Megamolgothis*.

The lysorophoid and microsaur lines had possibly diverged by Westphalian A times, since possible lysorophoids are known from Jarrow [BM(NH) R.8648] and Toftshaw (Boyd, 1980). Similarly, possible microsaur appear at Jarrow (Carroll and Gaskill, 1978) and definite ones are known from Joggins (Westphalian B, Carroll and Gaskill, 1978).

LYSOROPHOID RELATIONSHIPS TO OTHER LEPOSONDYLS

The adelogyrinids are a group of four genera from the Lower Carboniferous of Scotland discussed most recently by Carroll and Gaskill (1978; also Carroll, 1967; Brough and Brough, 1967). They were once allied with the lysorophoids in the order Adelospondyli (Watson, 1929), but Romer (1930) later recognized that the two groups were distinct. Adelogyrinid skulls are solidly roofed and exhibit no feature suggesting a direct relationship with the lysorophoids. However, like the lysorophoids, the adelogyrinids retain only one bone from the primitive temporal series and one bone from the primitive cheek of early tetrapods. These bones have been identified, respectively, as tabular (squamosal or supratemporal) and quadratojugal in adelogyrinids (Carroll, 1967; Carroll and Gaskill, 1978) and as tabular and squamosal in lysorophoids (this paper; Carroll and Gaskill, 1978). The homologies involved here are uncertain.

Adelogyrinid vertebrae are very similar to those of lysorophoids, as Watson (1929) noted. The centra are holospondylous and biconid. They possess neurocentral sutures, lateral and ventral carinae, and capitular facets on their posterior rims. In contrast, however, the neural arches are not paired (Watson, 1929; Brough and Brough, 1967; S. Mahala Andrews, personal commun.) and, while the ribs possess alar processes, they appear to lack the anterior ridge noted in lysorophoids.

The reduction of the complement of bones in the cheek and temporal series, as well as their unusual arrangement and sizes make the adelogyrinids too specialized to have given rise to the microsaur. One cannot so easily

dismiss a possible sister-group relationship between adelogyrinids and lysorophoids, considering the early occurrence of the adelogyrinids and the great restructuring the lysorophoid skull must have experienced, whatever its origin. This implies that lysorophoids and adelogyrinids share a more recent common ancestor among themselves than either does with the microsaur. However, the adelogyrinids are poorly known and suggestions regarding their phylogenetic relationships are speculative at this point. Moreover, the loss or fusion of dermal bones in the temporal series is not an infrequent occurrence among lepospondyls. The reduction of the dermal complements in adelogyrinid and lysorophoid skulls may have been achieved independently.

Megamolgothis agostini has been associated with lysorophoids since its description by Romer (1952). Type and referred material come from the Conemaugh (Upper Pennsylvanian) and Dunkard (Lower Permian) groups of West Virginia and Pennsylvania. Postcranial elements in this material are grossly similar to those of lysorophoids, microsaur, and adelogyrinids. However, skull material assigned to the species (CM 8614) is quite different from that of the lysorophoids, based on personal observation and Romer's description. The skull roof is proportionately much narrower than that of lysorophoids and the mandible seems to be nearly as long as the skull roof, indicating that the craniomandibular joint was near the level of the occiput, a position primitive to that seen in lysorophoids. The postparietals meet at the midline and there is no evidence of the supraoccipital in the skull roof. What are apparently tabular bones give rise to posteriorly directed processes or horns. The skull roof has an abrupt posterior edge which suggests that the occipital surface met the roof at a steep angle. This edge bears a pronounced scar which continues onto the medial surfaces of the tabular horns and probably marks the insertion of epaxial muscle.

In the occiput, the exoccipitals appear to be directed toward the tabular bones and not toward the postparietals. A broad space above the foramen magnum and between the postparietals and exoccipitals was probably filled by an unossified portion of the braincase such

as the supraoccipital or opisthotics. The craniovertebral articulation is similar to that of lysorophoids and microsaur in that the first vertebra bears an odontoid, but differs in that the facets lateral to the odontoid are very small.

On the basis of skull material, *M. agostini* is clearly not a lysorophoid, but through possession of tabular horns, exhibits an intriguing, yet puzzling, resemblance to certain labyrinthodonts. Considering the generally lepospondylous nature of its postcranial skeleton, Romer (1952) admitted that the association of skull and postcranial material in CM 8614 may have been accidental. If so, the postcranial material may represent a lysorophoid, a microsauro, or possibly an adelogyrinid. Resolution of this problem awaits redescription of *M. agostini* (Wellstead, in prep.).

Among other amphibians traditionally regarded as lepospondyls are the orders Aistopoda and Nectridea. Like lysorophoids, aistopods are elongate animals, but were already limbless by the mid-Viséan (Wellstead, 1982). Their skulls are fenestrated but retain circumorbital bones and indications of a lower temporal bar, while lacking nasal bones. The craniomandibular articulation is primitive in position. The braincase is co-ossified in the derived genus *Phlegethontia* and the cranial portion of the craniovertebral articulation is a cotylar pit (McGinnis, 1967).

Nectrideans exhibit no great tendency for presacral elongation and possess small but well-developed limbs. The distinctive shape of urocordylid and keraterpetontid skulls marks them as too specialized to have given rise to lysorophoids. Most nectrideans have lost the intertemporal and supratemporal bones from the skull roof, but the scincosaurids have also lost the postparietals (Bossy, 1976; A. C. Milner, 1980).

In contrast to lysorophoids and microsaur, the vertebrae of nectrideans and aistopods exhibit no neurocentral sutures and their neural arches are not known to be paired. Their vertebrae, unlike those of microsaur, are holospondylous throughout the column. They have no carinae on their centra or capitular facets on their posterior rims. Recently placed in their own superorder (Bossy (1976), aistopods and nectrideans are well-

circumscribed groups distinct from lysorophoids (and microsaur, Thomson and Bossy, 1970; Bossy, 1976; A. C. Milner, 1980).

A final family sometimes considered among the lepospondyls is the Acherontiscidae, represented by the sole species *Acherontiscus caledoniae*. It is distinct from any lysorophoid in possessing a fully roofed skull, full complement of circumorbital and cheek bones, a craniomandibular joint placed primitively at the level of the occiput, well-developed dermal pectoral girdle, and a vertebral centrum arrangement resembling that of embolomeres. Carroll (1969) initially suggested that, as a lepospondyl, its affinities might lie with microsaur and "lysorophoids," rather than with aistopods or nectrideans, because of its intercentral vertebral elements. More recently, Carroll and Gaskill (1978) rejected a close relationship between it and microsaur. Hook (1983) commented on the similarities between the skull of *A. caledoniae* and those of colosteoid labyrinthodonts. There appears to be no basis for associating it with the lysorophoids.

LYSOROPHOID RELATIONSHIPS TO LABYRINTHODONTS

The amphibian subclass Lepospondyli has been distinguished, in part, by possession of one-piece (holospondylous) vertebral centra, in contrast to the multipartite vertebral centra characteristic of the Labyrinthodontia. However, the presence of intercentral vertebral ossifications in microsaur demonstrates that completely holospondylous vertebrae are not possessed by all groups traditionally considered to be lepospondyls. In terms of the work of Williams (1959), these intercentral elements suggest that the main central element is a pleurocentrum. In nectrideans, which are truly holospondylous, the fusion of hemal arches directly to the caudal centra suggests that the centrum in these lepospondyls may be an intercentrum. Because neural arches are usually associated with the pleurocentra, the intercentral position of caudal neural arches in the lysorophoid *Brachydectes elongatus* further complicates interpretations of vertebral homologies.

Inconsistencies in such interpretations, not only within the lepospondyls, but among

them, labyrinthodonts and rhipidistian fishes, have been addressed by Panchen (1967), Thomson and Bossy (1970), Wake (1970), and Bossy (1976), among others. Their general conclusion is that the various vertebral elements are present to meet mechanical requirements and that strict homologies cannot be drawn across the amphibian subclasses.

Other criteria supposedly distinguishing lepospondyls from labyrinthodonts, such as the absence of both labyrinthine infolding of tooth enamel and large palatal fangs, are difficult to use in establishing relationships, because they may be functions of small size or may merely represent the loss of primitive characters.

Because traditional distinctions between labyrinthodonts and lepospondyls are of questionable significance, attempts have been made recently to link various lepospondyl groups with individual labyrinthodont orders. Thomson and Bossy (1970) and Bossy (1976) have suggested that aïstopods and, especially, nectrideans exhibit a number of similarities to "anthracosaurs," indicating that they share a closer phylogenetic relationship among themselves than any does with other lepospondyls or labyrinthodonts.

Similarly, Smithson (1982; also, Panchen and Smithson, 1988) has noted that temnospondyls and microsaurs share a suite of characters which sets them apart from the anthracosaur-nectridean-aïstopod group. These include common possession of (1) no more than four digits in the manus, (2) a contact between the exoccipital and postparietal bones, and (3) an akinetic skull roof and basiptyergoid articulation. These characters are also shared by the lysorophoids, as discussed below, and present an opportunity to establish a hypothesis of phylogenetic relationship between lysorophoids, microsaurs, and temnospondyls.

1. MAXIMUM OF FOUR DIGITS IN MANUS: As in temnospondyls and microsaurs, no more than four digits are known in any lysorophoid. Because this character presumably represents digit reduction from a primitive tetrapod count of five (six? see Lebedev, 1984), it could have been achieved independently by lysorophoids as a function of limb reduction (e.g., Lande, 1978).

2. EXOCCIPITAL-POSTPARIETAL CONTACT: This contact is a convenient character uniting temnospondyls, microsaurs, and lysorophoids as a group distinct from anthracosaurs, nectrideans, and aïstopods. Smithson (1982) noted that possible exceptions may be the anthracosaurs *Kotlassia* and *Eoherpeton*, which have been thought to possess a temnospondyl-like condition. Smithson added, however, that new material of *Eoherpeton* demonstrates that there is no exoccipital-postparietal contact in this genus and that it therefore conforms to the expected anthracosaur occipital morphology. *Kotlassia*, on the other hand, will require redescription in order to resolve the arrangement of the bones in its occiput.

Hook (1983) found other possible exceptions in the keraterpetontid nectridean *Diploceraspis* and in the adelogyrinid *Adelospondylus*. The significance of the exoccipital-postparietal contact in *Diploceraspis* (also probably *Diplocaulus*; Beerbower, 1963; Douthitt, 1917) is difficult to assess since the great specialization of the skull has clearly affected the morphology and relationships of the exoccipital (Beerbower, 1963; Case, 1911). In the more primitive urocordylid nectrideans the occiput is poorly known and much of it may have been unossified. Nevertheless, ossified exoccipitals are present as part of the craniovertebral articulation and some evidence of their contact with the postparietals might be expected if it existed. Indeed, such contact may be blocked by the presence of a supraoccipital, as noted in *Sauroplorea pectinata* (Bossy, 1976). If so, the exoccipital-postparietal contact in *Diploceraspis* and *Diplocaulus* would be convergent upon the temnospondyl condition.

The exoccipital-postparietal contact in adelogyrinids does not necessarily provide an exception to Smithson's scheme. A review of the adelogyrinids is badly needed, but for the moment, their akinetic skulls and vertebral similarities to lysorophoids and microsaurs, as well as the noted exoccipital-postparietal contact, hint that their broad affinities may lie with the temnospondyl-microsaur-lysorophoid group also.

3. AKINETIC SKULL ROOF AND BASAL ARTICULATION: Temnospondyls and microsaurs

have solidly integrated the skull table and cheek, obliterating the primitive kinetic margin seen in rhipidistian fish, anthracosaurs (but see Clack, 1987), and urocordylid nectrideans. The skull roof and what remains of the dermal cheek are also integrated in lysorophoids.

By itself, the lysorophoid skull does not reveal whether the cheek was attached solidly to the skull roof prior to development of the orbitotemporal fenestration or whether the squamosal and skull roof became more closely integrated in order to compensate for the loss of support from the other cheek bones as fenestration progressed. However, because the lysorophoids are most closely related to microsaurs, they presumably inherited an akinetic skull roof from their common ancestor and developed the orbitotemporal fenestration after the split from the microsaurs line.

According to Smithson (1982), the development of an akinetic skull roof implies loss of mobility at the basiptyergoid joint, because such mobility can no longer be accommodated at the lateral margin of the skull table (see also Panchen, 1964, 1970; Bossy, 1976). The mobility of the basiptyergoid joint is reflected in its morphology. Appropriately, the mobile basiptyergoid joint in anthracosaurs is marked by well-developed articular facets on both the basicranium and pterygoid and/or epiptyergoid. This is apparently also the case in urocordylid nectrideans (*Sauroplesura scalaris* and *Ptyonius marshi*; Bossy, 1976).

In temnospondyls, the primitive colosteid *Greererpeton* lacks facets at the basiptyergoid joint, but possesses an immobile, peg-in-socket relationship between the basicranium and pterygoid, as one might expect considering its akinetic skull roof (Smithson, 1982). Advanced temnospondyls, like *Eryops* (Sawin, 1941) later fuse the basiptyergoid joint. In lysorophoids the basiptyergoid articulation was possibly kept immobile through a combination of bony struts and overlapping, interdigitated sutures between the skull roof and suspensorium, as discussed earlier.

A temnospondyl such as *Edops* (Romer and Witter, 1942) provides an exception to this argument, for even though its skull roof is akinetic, it possesses distinct facets at the ba-

siptyergoid articulation. Similarly in microsaurs (Carroll and Gaskill, 1978), one finds potentially mobile basiptyergoid joints in species with akinetic skull roofs. Were these basiptyergoid articulations mobile, indication of how the skull roofs accommodated movement would be welcome. Possibly, the basicranial articulations in such species were finished in cartilage only to cushion the braincase against shock and were functionally immobile because of the integrated skull table and cheek.

In his assessment of phylogenetic relationships between microsaurs and temnospondyls outlined above, Smithson did not discuss the presence of a tabular-parietal contact in the skull roof of microsaurs (or lysorophoids). This contact is absent from temnospondyls, but is characteristic of anthracosaurs and is also present in nectrideans and at least one aïstopod. Its presence in anthracosaurs, nectrideans, and aïstopods was used by Thomson and Bossy (1970) and Bossy (1976) to unite these three groups and to differentiate them from temnospondyls. The presence of a tabular-parietal contact also in microsaurs and lysorophoids would appear to muddle this distinction. However, it is possible that microsaurs and lysorophoids acquired their tabular-parietal contact independently from that in anthracosaurs, nectrideans, and aïstopods through the loss of the discrete supratemporal.

The variable occurrence of the tabular-parietal contact presents a problem for the unity of Bossy's nectridean-aïstopod grouping and for their proposed relationship to the anthracosaurs, because, of the four better-known aïstopod genera, only *Ophiderpeton* can confidently be said to possess the feature. The situation in *Coloraderpeton* is not known. *Phlegethontia* is highly specialized in that the posterior portion of its skull is co-ossified; the presence of a tabular is uncertain and there is no discrete parietal. Tabulars and parietals appear to be present in *Lethiscus*, but their contact is prevented by a squamosal-postparietal contact (Wellstead, 1982).

However, the vagaries of the tabular-parietal contact do not seriously affect Smithson's concept of temnospondyl-microsaur relationships. The exoccipital-postparietal

contact and akinetic skull roof shared by temnospondyls and microsaurs, as well as by lysorophoids, provide reasonable indications that these groups are more closely related to each other than they are to anthracosaurs, nectrideans, or aïstopods.

Should the Bossy and Smithson hypotheses of lepospondyl and labyrinthodont interrelationship find further support, the sharp size distinction between lepospondyls and labyrinthodonts would be removed. Currently, among the recognized labyrinthodonts and lepospondyls (approximately 40 and 20 families, respectively; Carroll and Winer, 1977), there are extremely few adult labyrinthodonts as small as urocordylid nectrideans or most microsaurs and few lepospondyls of even moderate size. This size distinction may be significant, if support for the classic dichotomy of lepospondyls and labyrinthodonts can be found, but the limited range in sizes exhibited within these two subclasses is unusual and appears artificial when compared with the great variety of sizes present within existing class-level groups, such as the urodeles, lizards, mammals, and birds. In view of the morphological arguments advanced by Bossy and Smithson, it seems at least possible that aïstopods and nectrideans, on one hand, and microsaurs and lysorophoids (possibly also adelogyrinids and *Megamolgophis*), on the other, represent the "missing" small anthracosaurs and temnospondyls, respectively.

As an alternative to current perceptions, one can envision early temnospondyls and anthracosaurs diversifying not only into "niches" appropriate for the large terrestrial and aquatic forms familiar to paleontologists, but also into those appropriate for small forms. The tendencies toward holospondyly seen in lepospondyl groups can then be interpreted as an exploitation of a potential present in labyrinthodonts, as seen in *Dole-serpeton* (Bolt, 1969) and stereospondyls [e.g., Thomson and Bossy (1970)] and which represent, in part, a functional response to small size (Bossy and Thomson, 1970; Bossy, 1976; Bolt, 1979).

Wake (1970: 50) concluded that the derivation of holospondylous vertebrae from diplospondylous vertebrae would require no great developmental change. One suggested

mechanism for this development is paedomorphosis (Wake, 1970: 50; Bolt, 1979). Similarly, Carroll (1986) has suggested that precocial ossification of diplospondylous vertebrae may have produced the holospondylous tendencies seen in lepospondyls.

Note however, that among the lepospondyls, aïstopods and nectrideans lack the neural arch sutures common among microsaurs, lysorophoids, adelogyrinids, and *Megamolgophis*, but, in turn, possess completely holospondylous vertebrae and intravertebral spinal nerve foramina, which lysorophoids, microsaurs, adelogyrinids, and *Megamolgophis* lack. These differences suggest a dichotomy in vertebral development between these two groups of lepospondyls which conforms to the work of Bossy and Smithson. Their hypotheses appear to be constructive responses to the shortcomings of the classical distinctions between labyrinthodonts and lepospondyls.

LYSOROPHOID RELATIONSHIPS TO MODERN AMPHIBIA

The amphibian status of the lysorophoids was established in the first two decades of this century (see Sollas, 1920 and references therein). Although relationships to apodans and urodeles were suggested, lysorophoids have been considered too derived to have given rise to either of these modern groups. This is particularly the case for urodeles in consideration of the elongate vertebral column and reduced limbs of lysorophoids. Additionally, the presence in urodeles of transverse processes on the centra rather than on the neural arches, as well as the absence of neurocentral sutures from any stage of development (Wake, 1970) offers a distinct contrast to lysorophoid vertebral morphology. Furthermore, the extensive bone loss and fusion, as well as extensive reorganization of the suspensorium and posterior braincase necessary to derive a urodele from a lysorophoid would be sufficient to derive a urodele from any small Paleozoic amphibian. Carroll and Holmes (1980) offer evidence that urodeles more likely rose from among microsaurs.

Recently, Nussbaum (1983), like Moodie (1909b, 1911), Romer (1950), and Gregory

et al. (1956) before him, has suggested a close phylogenetic relationship between apodans and "lysorophids" or "*Lysorophus*"-like microsaur. The similarities he noted are the orbitotemporal fenestrae, elongate vertebral column, small limbs, short tail, elongate and curved ribs, fossorial habits, and a similar skull topography.

However, the details of orbitotemporal fenestration are quite distinct between apodans and lysorophoids. The other features can be interpreted as functional adaptations for either fossorial or aquatic locomotion developed convergently by many amphibians and reptiles, both extant and extinct. As discussed above, only the lysorophoid *B. elongatus* was fossorial, and then only intermittently. The presence of elongate ribs is surely primitive. The skull of the microsaure *Rhynchonkos* exhibits more specific similarities to that of apodans (Carroll and Currie, 1975) than does that of any lysorophoid, while considerable modification of the lysorophoid skull would be necessary to derive an apodan skull. The most obvious of these alterations would be (1) the loss of bones of the posterior skull roof and occiput, (2) the fusion of brain-

case elements, (3) expansion of the pleuro-sphenoid, (4) alteration of relationships between exoccipital bones and jugular and hypoglossal foramina, and (5) a great broadening of the skull resulting from redevelopment of the cheek through secondary stegokrotaphy (Nussbaum, 1983) and through substantial reorganization of the suspensorium. Unlikely, however, would be the redevelopment of (1) a second circumorbital bone to accompany the prefrontal, (2) a second mandibular tooth row, and (3) the interpterygoid vacuities.

While any of these alterations may be possible, there is no autapomorphy linking apodans and lysorophoids. Furthermore, with reference to secondary stegokrotaphy, one would also have to explain why apodans secondarily close orbitotemporal fenestrae in response to burrowing, while amphisbaenids (which have comparably small skulls) and lysorophoids have been argued to have opened theirs in response to the same behavior. Until the phylogenetic relationships of apodans have been analyzed, any relationships between lysorophoids and apodans based on skull morphology are speculative.

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