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NEW RECORD OF *CTENODUS* (OSTEICHTHYES: DIPNOI) FROM THE CARBONIFEROUS OF MONTANA

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ABSTRACT

A partial tooth plate of *Ctenodus* cf. *C. interruptus* from the uppermost Heath Formation (Chesterian, equivalent to Namurian E 2b), Montana, is described. This record extends the occurrence of *Ctenodus* to the western part of North America. *Ctenodus* species are common in Europe and have also been recorded from the eastern side of North America and from Australia.

KEY WORDS: fossil lungfish, *Ctenodus*, Carboniferous, Montana

INTRODUCTION

Few Paleozoic dipnoans are more widespread in occurrence than the Carboniferous genus *Ctenodus* (Agassiz, 1838). Once considered to be characteristic of European deposits (Woodward, 1891; Romer and Smith, 1934), recent records of *Ctenodus* and related genera have suggested that in fact the genus has a worldwide, if sporadic, distribution (Thomson, 1965; Baird, 1978; Long and Campbell, 1985).

A number of species of *Ctenodus* from Europe were described late in the 19th century (Agassiz, 1838; Barkas, 1869; Fritsch, 1885–1889). Although Woodward (1891) applied some judicious synonymies to this plethora of species, recent descriptions or redescriptions of *Ctenodus* and related taxa (Thomson, 1965; Baird, 1978; Long and Campbell, 1985) have increased the number of valid taxa referrable to the group. Revision of the genus is, however, beyond the scope of this report of the incidence of a tooth plate of *Ctenodus* from Carboniferous deposits in Montana. This specimen is conspecific with the tooth plate described by Baird (1978) as *Ctenodus interruptus*, from Carboniferous deposits at Grand Etang, Nova Scotia. Neither specimen conforms completely to the characters of *Ctenodus interruptus* (Barkas, 1869) because both are broader than European specimens of the species, but reassignment of the material is deferred pending a complete review of the family Ctenodontidae.

Abbreviations are as follows: CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; YPM (PU), Princeton University Collection at Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

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Subclass Dipnoi Müller 1845
Family Ctenodontidae Woodward 1891
Genus *Ctenodus* cf. *C. interruptus* Barkas 1869
(Fig. 1)

Schultze (1992) gives a complete synonymy list.

Geological Setting.—Surenuff Sand Channel, uppermost Heath Formation (Chesterian, equivalent to Namurian E 2b), Big Snowy Group of Forest Grove, Fergus County, Montana. There is some doubt regarding the precise biostratigraphic determination of the horizon from which the specimen was obtained, although a Chesterian age is the most plausible. The Surenuff beds lie above and at the western edge of the Bear Gulch Limestone beds, within the Heath Formation, according to Horner (1985). The Heath Formation is entirely contained within the Namurian E 2b, and is bounded above by an unconformity believed to mark the Mississippian–Pennsylvanian boundary in this area. The channel at this locality could also be Morrowan (Lower Pennsylvanian) or Lower Jurassic. The latter age is impossible because a cochliodont tooth plate is found in the same deposit, and the former is also unlikely because the lower Morrowan deposits at this locality are terrestrial. With the *Ctenodus* specimen are found a cochliodont tooth plate that does not occur in the Bear Gulch Limestone and has not been found elsewhere in the Heath Formation, as well as linguloid brachiopods, unidentified large ganoid scales, and other fish bones. It is found in a strongly crossbedded coarse oolitic sand channel deposit. This lentil is traceable southward over approximately 2 km distance along the outcrop into laminar Surenuff silty limestone beds (Horner, 1985). These beds have a sparse but typical Chesterian articulate brachiopod fauna and contain scales of the crossopterygian *Strepsodus* sp. and skeletal elements of *Acanthodes* that typify the fish fauna of the western edge of the Bear Gulch beds. The sedimentology and atypical faunal association suggest that the *Ctenodus* specimen was found in a delta or estuarine deposit on the edge of a bay or an estuary. The *Ctenodus* specimen, therefore, could have come from either a fresh-water fish or from an animal that lived in brackish water.

Description.—The specimen, CMNH 62780A + B, part and counterpart, consists of the posterior three-quarters of a broad upper tooth plate (Fig. 1). Ridges bearing short conical cusps radiate slightly from the curved mediolingual junction. The labial extremities of the ridges are missing. All cusps present are heavily abraded, although still distinct. The inter-ridge furrows carry grooves formed by occlusion with the cusps of the matching lower tooth plate. This indicates that the jaw movements involved subterminal rotational grinding, as found in more derived dipnoans (Kemp, 1991).

Ten ridges are present in CMNH 62780A. The first ridge and most of the second are missing but the remaining eight are complete except for the labial margin. Cusps in the second ridge show traces of doubling, and the eighth ridge is bifid (Fig. 1). Ridges seven and nine are consequently displaced. This anomaly, bifid instead of single ridges, is common in *Ctenodus interruptus*, and also found in other species of *Ctenodus*. Apart from the displaced portions, the ridges are subparallel.

A similar specimen, YPM (PU) 21741, described by Baird in 1978, comes from the Pomquet Formation, Mabou Group, latest Mississippian (Namurian A) at Grand Etang, Inverness County, Cape Breton Island, Nova Scotia. This is a complete upper left tooth plate, almost as broad as it is long, with 11 ridges and a curved mediolingual margin. The specimen has undivided ridges, each with a single row of cusps. The ridges radiate from a point situated mediolingually, and have no trace of the parallel arrangement found in other specimens of this genus.

Both CMNH 62780A and YPM (PU) 21741 have an unusual double curvature of the occlusal surface. Most of the occlusal surface is concave, but the concavity rises to an irregular crest close to the mediolingual aspect of the tooth plate and then shelves downwards towards the mediolingual junction.

Fig. 1.—Tooth plate of *Ctenodus* cf. *C. interruptus*, CMNH 62780A, from the uppermost Heath Formation (Chesterian, equivalent to Namurian E 2b), Montana. Scale bar = 2 cm.

Remarks.—The appearance of the tooth plate from the Surenuff Sand Channel is consistent with that of an early species of *Ctenodus*, similar to *Ctenodus interruptus*. It differs from this species in the greater breadth of the tooth plate. The Grand Etang specimen is also unusually broad, but otherwise similar to *Ctenodus interruptus*. Unfortunately, most of the preserved characters of these specimens are heavily influenced by growth and wear of the structure in life, and have no taxonomic validity (Kemp, 1993, 1997*a*, 1997*b*).

Species of *Ctenodus* are not confined to the Northern Hemisphere. In addition to the extensive records of the genus from northern England and Scotland (Schultze, 1992), the genus, or genera within the same family, are represented in eastern Europe (Fritsch, 1885–1889) as well as both sides of the North American continent, and in Australia (Woodward, 1906; Long and Campbell 1985). Although the description by Long and Campbell (1985) includes a skull roof, originally described by Woodward (1906), that is consistent with other specimens of the genus *Ctenodus* (Watson and Gill, 1923), the presence of dipnoan tooth plates in the same locality that are not classically ctenodontid in form led Long and Campbell (1985) to redescribe the material in a related genus, *Delatitia*. The recent find of a perfect upper tooth plate with typical *Ctenodus* characteristics from the mid-Viséan Ducabrook Formation at Middle Paddock, Drummond Basin, east-central Queensland, indicates that this genus is truly a part of the Australian Carboniferous fauna. This deposit is fresh-water, and includes early tetrapods (Thulborn et al., 1996).

Most records of *Ctenodus* belong in the Lower Carboniferous, but they are widely distributed geographically, and seem to occur in fresh-water as well as in brackish or marine deposits.

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Dr. D. Baird, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, provided access to a cast of YPM (PU) 21741 and assisted with discussions on the occurrence of dipnoans in the eastern United States. Comparative material was borrowed from Dr. S. Turner, Queensland Museum, Brisbane, Australia; the Hancock Museum in Newcastle, England; and the National Museum of Scotland, Edinburgh, Scotland. Assistance from all sources is acknowledged with many thanks.

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SNAKE FAUNA ASSOCIATED WITH THE "EARLIEST RECENT" MAMMALIAN FAUNA IN NORTHEASTERN NORTH AMERICA

J. Alan Holman[1]

Abstract

The Hosterman's Pit Local Fauna, Centre County, Pennsylvania, produced what was considered to be the earliest known date for a "Recent" mammalian fauna in northeastern North America (Guilday, 1967). The few snake bones from the site represent five species (*Diadophis punctatus, Coluber constrictor, Elaphe obsoleta, Thamnophis sirtalis*, and *Crotalus horridus*), all of which presently occur in Centre County. The snakes could have lived in a woodland situation with rocky outcrops and ledges.

The Hosterman's Pit Local Fauna

This local fauna accumulated in a limestone cave in Centre County, Pennsylvania, latitude 40°53′34″ N, longitude 77°26′22″ W at an elevation of 378 m. Approximately 150 m southwest of the 22.5-m-deep pit opening, a deposit of mixed talus, vertebrate bones, and charcoal was found beneath dome pits that were sealed and no longer open to the surface. The bones are presumed to be the remains of animals that fell down these former sinkhole openings (Guilday, 1967).

Charcoal fragments, presumably derived from forest fires near the cave, were radiocarbon dated at 7290 BC ± 1000. The modern nature of the Hosterman's Pit mammalian local fauna is reflected by the presence of temperate mammals such as the southern flying squirrel (*Glaucomys volans*), southern bog lemming (*Synaptomys cooperi*), pine mouse (*Microtus pinetorum*), cottontail rabbit (*Sylvilagus floridanus*), and white-tailed deer (*Odocoileus virginianus*) and the lack of any boreal species such as the northern flying squirrel (*Glaucomys sabrinus*), northern bog lemming (*Synaptomys borealis*), collared lemming (*Dicrostonyx hudsonius*), yellow-cheeked vole (*Microtus xanthognathus*), and caribou (*Rangifer tarandus*) that occurred in the area in early post-Wisconsinan times (Guilday, 1967). A mammalian fauna with boreal species was found in the New Paris 4 cave deposit 105 km southwest of Hosterman's Pit. The New Paris site had a radiocarbon date of 9300 BC ± 1000 and Guilday (1967) suggested that the change to a "Recent" mammalian fauna in the area took place between about 9300 to 7290 BC, a time span of about 2,000 years.

The snake remains were collected from the Hosterman's Pit local fauna by Allen D. McCrady, Research Associate, Carnegie Museum of Natural History, on 18 September 1961, and subsequently donated to the Section of Paleontology and Geology of the State Museum of Pennsylvania, Harrisburg. Following is an annotated taxonomic list of those snake remains. Numbers are those of the Vertebrate Paleontological Collections of the State Museum of Pennsylvania (SMP VP-).

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Submitted 17 December 1997.

ANNOTATED LIST

Family Colubridae
Subfamily Xenodontinae
Diadophis punctatus (Linnaeus, 1766)
Ring-necked Snake

Material.—A single trunk vertebra SMP VP-1047.

Remarks.—The trunk vertebrae of the xenodontine genera *Diadophis* and *Carphophis* (worm snakes) are very similar although these taxa are strikingly different in their external appearance and other aspects of their morphology. The trunk vertebrae of both genera have the platyspondylous (very depressed neural arch) condition, with very low neural spines and wide, indistinct hemal keels.

Differences between *Diadophis punctatus* and *Carphophis amoenus* are very subtle and hinge on the fact that *Diadophis punctatus* has a somewhat longer vertebral form and more laterally truncated postzygapophyseal buttresses than in *Carphophis amoenus*. The Hosterman's Pit vertebra was identified as *Diadophis punctatus* on the basis of its relatively elongate vertebral form, laterally truncated postzygapophyseal buttresses, and relatively large size. The fossil specimen was larger than a trunk vertebra (see Holman, 1995:94–98) from the middle of the postcervical- precaudal region of a *Diadophis punctatus* specimen with a total length of 31 cm. The longest *Carphophis amoenus* recorded is 33.7 cm (Conant and Collins, 1991) and most specimens are much smaller.

Presently, the Northern Ringneck Snake, *Diadophis punctatus edwardsii*, occurs in Centre County, Pennsylvania (McCoy, 1982:map 64). This taxon is a secretive woodland species that presently requires logs, stumps, fallen bark, rocks, or human debris under which to hide. Earthworms, salamanders, and small insects are the most frequent food in eastern *Diadophis punctatus* (Ernst and Barbour, 1989).

Subfamily Colubrinae
Coluber constrictor Linnaeus, 1758
Racer

Material.—Two trunk vertebrae SMP VP-1048.

Remarks.—Auffenberg (1963) discussed the identification of fossil *Coluber constrictor* on the basis of individual trunk vertebrae. The two above specimens represent small racers. Presently the Northern Black Racer, *Coluber constrictor constrictor*, occurs in Centre County, Pennsylvania (McCoy, 1982:map 66).

Eastern *Coluber constrictor* prefers woodlands and woodland edges where water is available and sometimes hibernates with *Crotalus horridus* (Ernst and Barbour, 1989). The racer has been found hibernating in a cave (Sexton and Hunt, 1980). In eastern North America this species eats a very wide variety of food including insects, salamanders, frogs, lizards, snakes, small mammals, and bird nestlings and eggs (Ernst and Barbour, 1989).

Elaphe obsoleta (Say, 1823)
Rat Snake

Material.—Four trunk vertebrae SMP VP-1049.

Remarks.—Auffenberg (1963) discussed the identification of fossil *Elaphe obsoleta* on the basis of individual trunk vertebrae. Presently the Black Rat Snake, *Elaphe obsoleta obsoleta*, occurs in Centre County, Pennsylvania (McCoy, 1982:

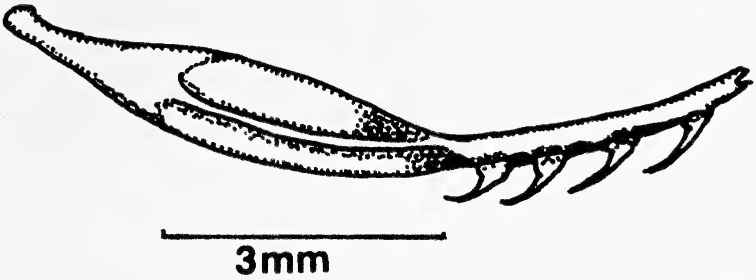

Fig. 1.—Right pterygoid in lateral view of *Crotalus horridus* (SMP VP-1052) from Hosterman's Pit Local Fauna, Centre County, Pennsylvania.

map 69). The natural habitat of Black Rat Snakes consists of a variety of woodland situations. They often hibernate with *Coluber constrictor* and *Crotalus horridus* (Ernst and Barbour, 1989). *Elaphe obsoleta* that overwinter in caves are active and may change their position several times in the winter (Sexton and Hunt, 1980). Adults eat a wide variety of small endothermic vertebrates as well as frogs.

Subfamily Natricinae
Thamnophis sirtalis Linnaeus, 1758
Common Garter Snake

Material.— Four trunk vertebrae SMP VP-1050.

Remarks.—Holman (1984) discussed the identification of fossil *Thamnophis sirtalis* on the basis of individual trunk vertebrae. Presently the Eastern Garter Snake, *Thamnophis sirtalis sirtalis*, occurs in Centre County, Pennsylvania (McCoy, 1982:map 61). Eastern Garter Snakes occupy many kinds of habitats and are generalistic feeders, eating earthworms, small fishes, small snakes, salamanders, frogs, toads, small fishes, mice, and even nestling birds. They sometimes hibernate with *Diadophis punctatus* (Ernst and Barbour, 1989).

Indeterminate Colubidae

Material.—One broken vertebra SMP VP-1051.

Remarks.—One rather elongate vertebra belongs to a colubrid, but it is not complete enough to assign to subfamily or genus.

Family Viperidae
Subfamily Crotalinae
Crotalus horridus Linnaeus, 1758
Timber Rattlesnake

Material.—One right pterygoid (Fig. 1) and eight trunk vertebrae SMP VP-1052.

Remarks.—Holman (1967) discussed the identification of *Crotalus horridus* on the basis of individual vertebrae. The pterygoid of *Crotalus horridus* (Fig. 1) is rather similar to that of *Agkistrodon contortrix*, but differs in that a prominent, dorsally projecting, notched, ectopterygoidal process is absent in *Crotalus horridus* and present in *Agkistrodon contortrix*. This process is absent in the fossil (Fig. 1). Presently *Crotalus horridus* occurs in Centre County, Pennsylvania (Mc-

Coy, 1982:map 73). Timber rattlesnakes are commonly found in wooded areas with rocky outcrops and ledges. Congregations of *Crotalus horridus* near rock outcrops and hibernating dens in spring and autumn were historically common in upland, wooded regions in Pennsylvania and Hartwig (1966) saw as many as 17 at one time near a 6 m rock. Adult timber rattlesnakes feed mainly on small, endothermic vertebrates (Ernst and Barbour, 1989).

Indeterminate Viperidae

Material.— Seventeen vertebrae SMP VP-1053.

Remarks.—These vertebrae are either fragmentary or come from an undiagnostic portion of the vertebral column and I am unable to identify them to the generic level.

Indeterminate Snake

Material.—Eleven vertebrae SMP VP-1054.

Remarks.—These are fragmentary vertebrae and caudal vertebrae that I am unable to identify to the familial level.

COMMENTS

All of the Hosterman's Pit snake species are extant and presently occur in Centre County, Pennsylvania. Like the mammalian fauna of the site which was reported as the earliest "Recent" mammalian fauna in the northeastern United States (Guilday, 1967), the snake fauna has a completely modern aspect.

Usually, Appalachian Quaternary cave faunas (Holman, 1995) yield hundreds of snake vertebrae representing relatively few species. Thus, one of the most interesting aspects of the Hosterman's Pit snake fauna is the relatively large number of species represented by a very small number of snake bones. Only 48 vertebrae and one pterygoid represent five species in two families and three subfamilies.

The snakes represent an assemblage that could have occurred in woodland or woodland-edge situations with rocky outcrops and ledges. Presently, the three large snakes (*Coluber constrictor*, *Elaphe obsoleta*, and *Crotalus horridus*) often occur in the same hibernaculum and the same is true of the two small snakes *Diadophis punctatus* and *Thamnophis sirtalis* (Ernst and Barbour, 1989). Both *Coluber constrictor* and *Elaphe obsoleta* have been recorded hibernating in caves (Sexton and Hunt, 1980). Thus, it could be suggested that at least some of the Hosterman's Pit fossil snakes were hibernating in or near the cave. With the exception of *Elaphe obsoleta*, which can climb in an out of sinkhole caves (personal observations), it is possible that, over the years, other species were trapped by falling into the cave.

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NEW ATOKAN PRODUCTOID BRACHIOPODS FROM THE UPPER CARBONIFEROUS LADRONES LIMESTONE OF SOUTHEASTERN ALASKA, WITH A PRELIMINARY NOTE ON THE PHYLOGENY AND CLASSIFICATION OF THE TRIBE RETARIINI

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ABSTRACT

One new genus and two new species of productoid brachiopods of the Subfamily Productininae are described from the Carboniferous Ladrones Limestone (Atokan, late Bashkirian or early Moscovian) of Prince of Wales Island, southeastern Alaska. The new genus *Caruthia*, type species *Caruthia borealis* n. sp., is assigned to the Tribe Productinini. A new species of the genus *Rugivestis* Muir-Wood and Cooper, 1960, of the Tribe Paramarginiferini, *R. girtyi*, is similar and probably closely related to *Rugivestis pristina* Carter and Poletaev, 1998, of approximately the same age, from Ellesmere Island, Canadian Arctic Archipelago.

Discovery of a shagreen texture within the ventral beak region of the genera *Keokukia* Carter, 1991, *Tesuquea* Sutherland and Harlow, 1973, and at least two species of *Spinocarinifera* Roberts, 1971, necessitates a new interpretation of the phylogenetic relationships and derivation of the Tribe Retariini (Subfamily Productinae). We suggest that Eurasian *Antiquatonia* Miloradovich, 1945, and North American *Tesuquea* Sutherland and Harlow, 1973, were sister genera, both derived from *Keokukia* Carter, 1991, common to both continents, and probably derived from the Tournaisian *Spinocarinifera nigra–arcuata* group.

KEY WORDS: brachiopods, productoids, Carboniferous, Atokan, Alaska, Ladrones Limestone, *Caruthia*

INTRODUCTION

The diverse brachiopod fauna of the Ladrones Limestone of southeastern Alaska is undescribed. G. H. Girty, of the U. S. Geological Survey, made sizable collections from this formation in 1918 and initiated identification of the fauna but did not publish on it although he apparently recognized its unusual nature; several of Girty's sorted taxa are labeled as new species. Several nonbrachiopod faunal elements of the Ladrones Limestone fauna have been described. Savage and Barkeley (1985) described the conodonts, Hahn and Hahn (1991, 1992) the trilobites, and Douglas (1971) the fusulinids.

The Ladrones Limestone was named by Eberlein and Churkin (1970:59) for about 300 m of thick or indistinctly bedded gray sublithographic limestone exposed on the Ladrones Islands in Trocadero Bay near Prince of Wales Island, southeastern Alaska. The fossils described here are from two very small islands composed entirely of Ladrones Limestone with no good indication of relative stratigraphic position.

The precise age of these collections is not certain. The age of the Ladrones

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Submitted 31 July 1998.

Limestone fusulinids is Middle Pennsylvanian according to Douglas (1971). According to Savage and Barkeley (1985) the Ladrones Limestone is Lower to Middle Pennsylvanian as based on several conodont samples. The brachiopods suggest an Atokan age. The generic composition of the brachiopod fauna is closely similar to that of the Hare Fiord Formation of Ellesmere Island which is known to be of Atokan age (Nassichuk, 1975).

This paper contains descriptions of two new productoid species in the Ladrones Limestone fauna and represents the first description of Alaskan Carboniferous brachiopods.

All of the specimens upon which these new species are based were collected by G. H. Girty of the U. S. Geological Survey in 1918 from small unnamed islands of the Ladrones group in Trocadero Bay, about six and one-half miles south-southeast of Craig (Craig Quadrangle), Prince of Wales Island, Alaska. In May 1997, the junior author collected more specimens from these localities, although none of the specimens described here was collected at that time. The three collections used here—USGS 3708-PC, 3762-PC, and 3763-PC—are from the south coast of a small island in the middle of the Ladrones Islands, near the mouth of Trocadero Bay, Prince of Wales Island, Alaska. Girty gave the coordinates of locality 3708-PC as latitude 55°23′00″ N, longitude 133°04′52″ W as based on an old coastal chart. Coordinates of latitude 55°23.095′ N, longitude 133°05.136′ W were obtained using a GPS device in 1997 for a locality probably slightly to the west of Girty's 3708-PC locality. USGS 3762-PC includes specimens from various localities on the south coast of this island. USGS 3763-PC is located just east of locality 3708-PC.

SYSTEMATIC PALEONTOLOGY

A revised classification of the Order Productida was recently published by Brunton et al. (1995). In general, that classification is followed here.

All primary types are deposited in the National Museum of Natural History, Washington, D.C. (acronym USNM). The specimens in Figure 3 are in the collections of the Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania.

Suborder Productidina Waagen, 1883
Superfamily Productoidea Gray, 1840
Family Productellidae Schuchert, 1929
Subfamily Productininae Schuchert, 1929
Tribe Productinini Muir-Wood and Cooper, 1960
[= Chonetellini Likharev, 1960]
Caruthia, **new genus**

Type Species.—*Caruthia borealis*, n. sp.

Derivation of Name.—This genus is named in honor of Ruth C. Carter and is derived from her surname and first name.

Diagnosis.—Small, outline subtriangular but not nasute; disc concavoconvex with shallow corpus; lateral profile nearly semicircular or moderately asymmetrical but without clear geniculation; venter near midlength weakly convex, flattened or with weak sulcus, dorsum occasionally with low fold; ornament consisting of fine weak ribs on both valves, excluding posterior part of visceral disc, and weak rugae on dorsal valve; rare thick spines only on ventral valve, including row of spines at base of flanks; interiors of both valves with strong lateral ridges bordering ears and extending anteriorly as weak marginal ridges; muscle scars weakly impressed in both valves.

Comments.—The discovery of this genus permits us to suggest a new phylogeny and systematic composition for the Subfamily Productininae, as submitted for the forthcoming revised edition of the Treatise on Invertebrate Paleontology (see also the revised classification proposed by Brunton et al., 1995). The latter was based on the assumption that the Tribe Chonetellini appeared in the Permian, being derived from the Paramarginiferini by the loss of ribbing. Now we have evidence to suggest two parallel lineages during the Carboniferous and Permian. One of them, the Productinini [= Chonetellini] was more conservative, that is, without pronounced ribbing, always with a shallow corpus cavity, lacking a cincture, and with a row of spines on the flanks. The second lineage consisted of the Tribe Paramarginiferini, forms with a shallow or moderately deep corpus cavity, stronger ribbing, sometimes with a cincture, and lacking a row of spines on the flanks. Both lineages are comprised in the Subfamily Productininae, characterized by a subtrigonal outline (sometimes nasute anteriorly), a few coarse spines on the ventral valve only, the development of marginal structures inside both valves, and the peculiar orientation of the brachial ridges (with the anterior lobe axes directed anteromediad).

Comparisons.—*Caruthia* differs from all other members of the Tribe Productinini in its weak, obscure ribbing and strong lateral ridges inside each valve. In addition, it differs from *Productina* Sutton, 1938, in its costate nonlamellose dorsal valve. *Argentiproductus* Cooper and Muir-Wood, 1951, is much more transverse and less convex and has a lamellose dorsal exterior. Similarly, *Dorsirugatia* Lazarev, 1992, from the Late Devonian of Mongolia, is more transverse in outline and has a lamellose, more weakly costate dorsal exterior. *Productellina* Reed, 1943, from the very early Carboniferous of England, is similar in outline to *Caruthia* but differs in having a strongly lamellose, noncostate dorsal exterior, in addition to the general differences noted above.

Age and Distribution.—Atokan (late Bashkirian or early Moscovian) of southeastern Alaska.

Species Assigned.—Type species only.

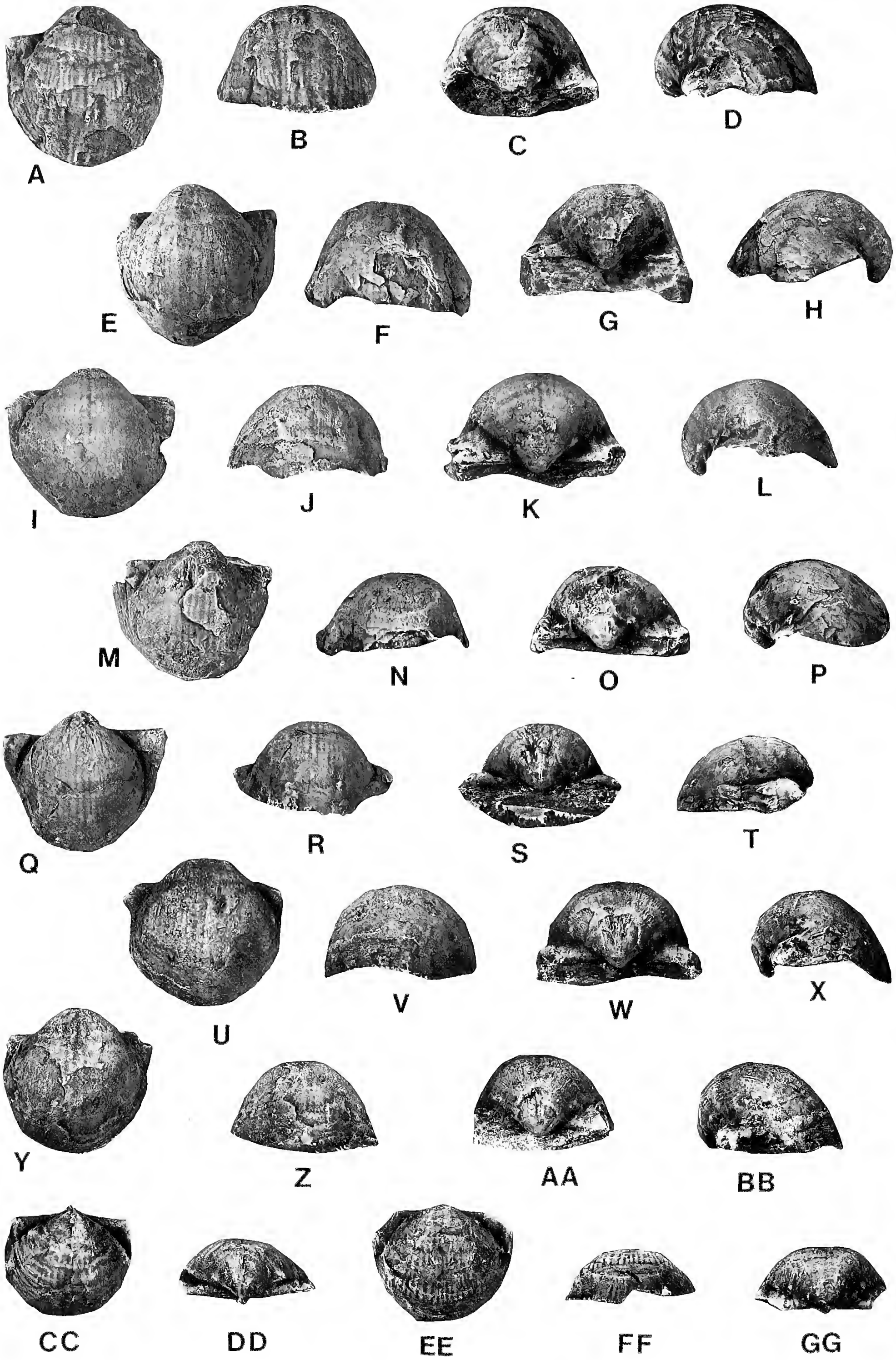
Caruthia borealis, **new species**
(Fig. 1A–GG)

Holotype.—A ventral valve, USNM 498809 (Fig. 1A–D), from USGS locality 3708-PC.

Paratypes.—Four ventral valves, USNM 498810– 498813 (Fig. 1E–T), from USGS locality 3708-PC; a natural mold of the dorsal exterior, USNM 498817 (Fig. 1EE–GG), from USGS locality 3708-PC; two ventral valves, USNM 498814 and 498815 (Fig. 1U–BB), from USGS locality 3763-PC; a dorsal interior, USNM 498816 (Fig. 1CC, DD), from USGS locality 3763-PC.

Description.—Shell small (length of hinge up to 16 mm), length of visceral disc 6–8 mm; outline subtriangular with acute cardinal extremities forming cardinal angle of about 45°; corpus cavity shallow (about 2 mm deep); shell material moderately thick; trails present in both valves but not well separated, being approximately the same length or a little longer than visceral disc.

Ventral valve strongly inflated, hemispherical in transverse profile; venter generally without sulcus but occasionally flattened; beak overhanging hingeline, wide; umbonal angle a little less than 90°; ears subtriangular, flattened, sharply delimited from umbonal region by concave flexures; weak costellae present on anterior part of visceral disc and trail; irregular fluting present on trail of some specimens;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rare thick spines (diameter 0.6–0.8 mm, sometimes up to 1 mm) scattered on trail; hinge spines absent; rare spines scattered on venter and trail; curving row of up to four spines wraps around ears and down flanks.

Dorsal valve moderately concave; dorsum commonly arched as low fold; ornament consisting of weak concentric rugae, weak ribs, and rounded pits complementary to ventral spines.

Ventral interior with strong, but not crenulated, lateral ridges becoming weaker anteriorly; muscle scars generally not seen, or more rarely, short adductor scars situated medially near posterior ends of larger diductor impressions.

Dorsal interior with lateral and marginal ridges bordering corpus and peripheral cavities as in ventral valve, with ridges following closely those of ventral valve but being placed slightly outside those of opposite valve; cardinal process wide, quadrilobed internally; dorsal muscle scars almost indistinguishable; brachial ridges not impressed; surface finely tuberculate excepting posteromedianly in both valves.

Measurements.—See Table 1.

Distribution.—USGS Locality 3708-PC (more than 60 specimens) and USGS locality 3763-PC (about 30 specimens).

Tribe Paramarginiferini Lazarev, 1986
Genus *Rugivestis* Muir-Wood and Cooper, 1960
Rugivestis girtyi, **new species**
(Fig. 2A–R)

Holotype.—A ventral valve, USNM 498817 (Fig. 2E–H), from USGS locality 3708-PC.

Paratypes.—Three partial ventral valves missing the ventral visceral disks, USNM 498818, 498821, and 498822 (Fig. 2A–D, M–R); a ventral valve, USNM 498820 (Fig. 2I–L); all from USGS locality 3708-PC.

Diagnosis.—This species is characterized by relatively weak concentric rugae on the visceral disc and coarse costae on the trail.

Description.—Shell small (width up to 2 cm), length of visceral disc about 7–9 mm; outline transversely subtrigonal, variably nasute anteriorly but commonly with well- defined, incomplete siphon; both valves geniculate, angle between visceral disc and trail 90°; corpus cavity shallow (about 2 mm).

Ventral visceral disc weakly convex, without sulcus but medially flattened or with very weak depression; beak small, obtuse, slightly overhanging hingeline; ears subtriangular, flattened, well delineated from flanks and trail; cardinal angle about 60°; trail approximately twice as long as visceral disc, almost straight in longitudinal profile but with small concave flexure posterior to nasute extension; posterior part of trail flat in transverse profile or with weak sinus; lateral portions of trail sloping steeply to commissures near ears; outline of nasute extension variable in ventral view but sharply delimited from remainder of trail; radial ribs covering most of surface, excluding beak and ears; weak rugae present on visceral disc, where ribs are better developed than rugae, 6–9 ribs per 5 mm (commonly 7–9) near point of geniculation; width of ribs increases anteriorly but becoming more variable (3–7 per 5 mm); nasute region generally with weaker ribbing; rugae variably developed but commonly with less relief than ribs, or when well developed they can cover the point of geniculation; spines rare and of moderate diameter (0.3–0.4 mm), often difficult to detect; interior with strong lateral ridges

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Fig. 1.—*Caruthia borealis*, n. gen. n. sp. A–D. Ventral, anterior, posterior, and lateral views of the holotype from USGS locality 3708-PC, USNM 498809. E–T. Ventral, anterior, posterior, and lateral views of four ventral valve paratypes from USGS locality 3708-PC, USNM 498810–498813. U–BB. Ventral, anterior, posterior, and lateral views of two ventral valve paratypes from USGS locality 3763-PC, USNM 498821, 498822. CC, DD. Dorsal and posterior views of a dorsal valve interior paratype with cardinal process from USGS locality 3763-PC, USNM 498816. EE–GG. Dorsal, anterior, and posterior views of a natural mold of a dorsal valve exterior paratype from USGS locality 3708-PC, USNM 498817. All × 2.

Table 1.—*Measurements in mm of the type specimens of* Caruthia borealis, *n. gen. n. sp. DV = dorsal valve.*

USNM #	Locality	Length	Width	Height	Surface measure
498809	3708-PC	11.7	+11.8	7.2	21.0
498810	3708-PC	11.7	12.2	7.1	19.5
498811	3708-PC	11.2	12.6	6.9	20.2
498812	3708-PC	10.0	11.4	7.8	17.1
498813	3708-PC	10.1	12.1	6.0	14.8
498817 (DV)	3708-PC	8.6	+10.2	4.3	11.3
498814	3763-PC	11.2	+11.5	7.2	19.1
498815	3763-PC	10.1	+11.0	6.7	18.0
498816 (DV)	3763-PC	7.9	9.7	3.3	10.5

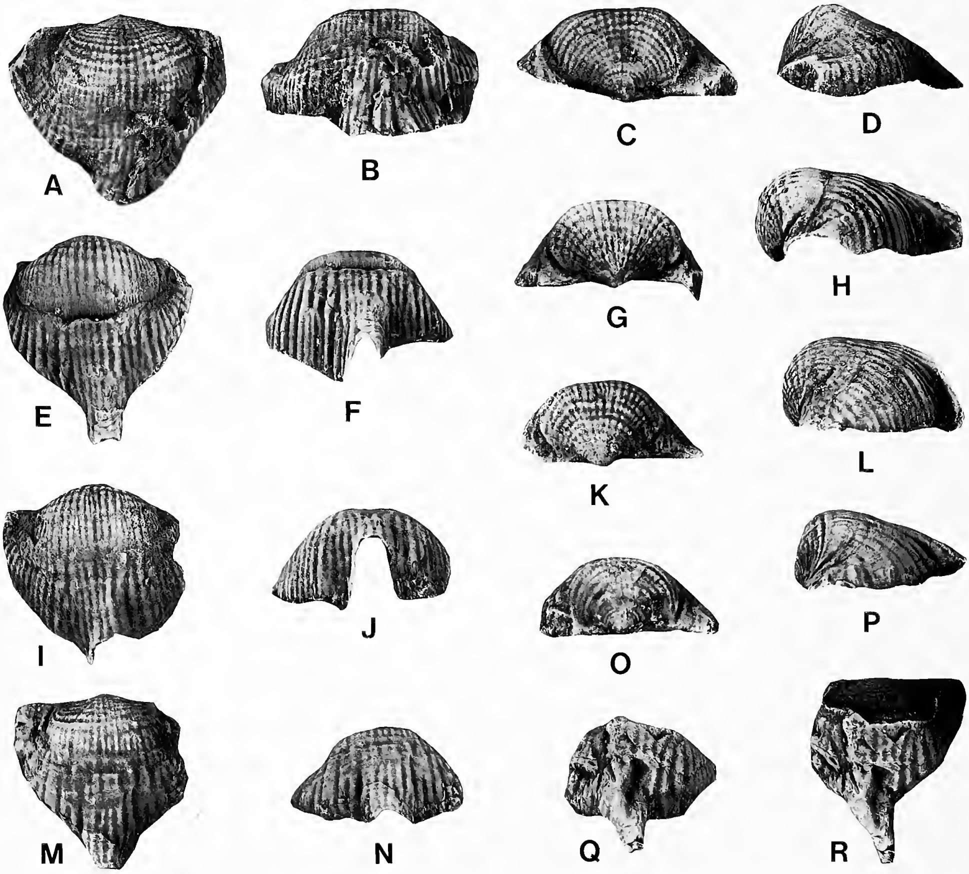

Fig. 2.—*Rugivestis girtyi*, n. sp. A–D. Ventral, anterior, posterior, and lateral views of a large paratype with the visceral disc removed leaving the ventral trail and mold of the dorsal exterior, USNM 498818. E–H. Ventral, anterior, posterior, and lateral views of the nearly complete ventral valve holotype, USNM 498819. I–L. Ventral, anterior, posterior, and lateral views of a ventral valve paratype, USNM 498820. M–P. Ventral, anterior, posterior, and lateral views of a paratype with the visceral disc removed leaving the ventral trail and mold of the dorsal exterior, USNM 498821. Q, R. Anterior and ventral views of a partial specimen with the corpus missing of an unusually elongated nasute paratype, USNM 498822. All × 1.5; all from USGS locality 3708-PC.

Table 2.—*Measurements in mm of the type specimens of* Rugivestis girtyi, *n. sp. from USGS locality 3708-PC.*

USNM #	Length	Width	Height	Surface measure
498818	17.0	+19.7	6.8	23.4
498819	18.5	16.7	8.3	26.7
498820	16.1	+17.2	8.6	27.0
498821	15.8	+15.9	6.7	21.2
498822	16.4	+14.0	6.1	—

which merge into thick marginal ridge anteriorly; cincture sometimes formed externally, marking internal thickened marginal ridge and producing weakly concave resupination in longitudinal profile; muscle scars not impressed.

Visceral disk of dorsal valve flatter and more sharply geniculate than opposite valve; ears delimited from flanks by narrow ridges; trail slightly longer than visceral disc but anterior portion of trail not forming nasute extension; ribs weaker than those of ventral valve; concentric rugae dominate over ribs in visceral disk, unlike ventral valve; spines and pits lacking; internally with vague, short, lateral ridges which delimit ears in juvenile stages; cardinal process short and wide; adductor muscle scars forming obscure triangular thickening.

Measurements.—See Table 2.

Comparisons.—This new species differs from *R. pristina* Carter and Poletaev, 1998, from similar-aged strata of Ellesmere Island in having broader ribs, much weaker rugae and a narrower, better defined anterior nasute extension. The weak ornamentation of the visceral disc also differentiates *R. girtyi* from other species of the genus *Rugivestis*.

Comments.—A well-preserved dorsal interior of this distinctive genus is still not known.

Distribution.—USGS Locality 3708-PC (more than 60 specimens); USGS locality 3763-PC (about 25 specimens); USGS locality 3762-PC (3 specimens).

A PRELIMINARY NOTE ON THE PHYLOGENY AND CLASSIFICATION OF THE TRIBE RETARIINI

During the past several years, ideas about the phylogeny and systematics of the group of productoids with a deep corpus cavity, commonly referred to the productoid Family Dictyoclostidae of Muir-Wood and Cooper (1960), have changed fundamentally. This is due to reevaluation of the systematic importance of the internal characters of productidines as a whole. This reevaluation is based on the sequence of the appearance of these morphological characters during ontogeny (Brunton et al., 1995). In particular, the appearance of the deep corpus cavity (formerly termed the body cavity) and the marginal or peripheral cavities separated from this deep corpus, which functioned as a defense against penetration of the mantle cavity by undesirable particulate matter, are of great evolutionary significance (Lazarev, 1985). This note is a preliminary report on the ongoing investigation of the nature of the ventral portion of the corpus cavity.

Here we emphasize the systematic importance of a relatively recently appreciated morphological character, the presence of a shagreen (rough or pitted) texture on the inner umbonal surface of the ventral valve beak. Lazarev (1985, 1990) discussed the nature of the coelomic cavity of productoids at some length.

The ventral beak region posterior to the muscle scars within most productoids is smooth, indicating that a normal visceral or coelomic cavity was present. However, some productoids have fine pits or irregular grooves posterior to the muscle scars that may indicate gonadal attachment. Small tubercles (or endospines) that are the sites of papillae may be present. This rough shagreen texture indicates the extension of mantle cavity posterior to the ventral muscle field. In other words we infer that the mantle cavity, with concomitant gonads and papillae, has occupied the ventral beak region. Thus, the visceral or coelomic cavity hung suspended freely between the dorsal valve cardinal process and the adductor field, except for the distal portion of the ventral beak. The position and size of the suspended portion of the visceral cavity was associated with migration of the dorsal adductor field anteriorly from the hingeline during ontogeny. For example, in the early Viséan genus *Keokukia* Carter, 1991, the distance between the cardinal process and the adductor scars is relatively great (Carter, 1991:fig. 6.1, 6.2). This anterior position of the adductor scars is additional, indirect evidence of a penetration by the mantle cavity of the middle portion of the ventral valve beak region.

The Tribe Retariini of the Subfamily Productinae, as perceived in this paper, consists of genera now known to bear a shagreen texture in the ventral beak. It would include most of the genera assigned by Lazarev (1990) to his Subfamily Retariinae, namely *Retaria* Muir-Wood and Cooper, 1960, *Kutorginella* Ivanova, 1951, *Antiquatonia* Miloradovich, 1945, *Tesuquea* Sutherland and Harlow, 1973, *Thamnosia* Cooper and Grant, 1969, *Thuleproductus* Sarycheva and Waterhouse, 1972, and *Tubaria* Muir-Wood and Cooper, 1960. A shagreen texture has been observed in the ventral umbo in all of the preceeding genera by the senior author. Until recently we have not known of true retariins older than the Upper Viséan, but it is now clear that the Lower Viséan genus *Keokukia* belongs in the Tribe Retariini because the inner beak of its ventral valve has the shagreen texture (see Fig. 3A of *Keokukia rotunda* Carter) discussed above. This suggests that *Keokukia* might be the ancestor of the Upper Viséan retariin genus *Antiquatonia* and the later retariins. In *Keokukia sulcata* Carter there is a short row of spines on the flanks anterior to the point of geniculation, a feature that is also suggestive of the genus *Antiquatonia.*

The ancestor of the earliest retariin *Keokukia* probably most closely resembled some species of the genus *Spinocarinifera* Roberts, 1971. We have detected the shagreen texture inside the ventral beak, characteristic of the retariins, in *Spinocarinifera nigra* (Gosselet, 1888) from northeastern France (Fig. 3D) and *S. arcuata* (Hall, 1858) from northeastern Missouri (Fig. 3B). These *Spinocarinifera* species differ from typical *Keokukia* in their smaller size, more posteriorly positioned dorsal adductor scars, and the usual absence of a row of spines on the flanks in front of the ears.

Therefore, we regard the *Spinocarinifera nigra–arcuata* group to be the probable ancestor for all of the deep corpus productoids with the shagreen-textured inner surface of the ventral beak. These include the genus *Dictyoclostus* Muir-Wood, 1930 (in the strict sense) which belongs in the Subfamily Dictyoclostinae (the senior author has observed a shagreen texture in the ventral beak of this entire subfamily). It seems likely that the genus *Keokukia*, which occurs in both North America and Eurasia, was the ancestor of the Eurasian genus *Antiquatonia* Miloradovich, 1945, because of its morphology and stratigraphic age.

No authentic species of the genus *Antiquatonia* (species with shagreen texture in the ventral beak) is known from North America. We have examined the inner surfaces of the ventral umbones of several North American species formerly assigned to *Antiquatonia* such as "*A.*". *hermosana* (Girty, 1903), "*A.*" *colora-*

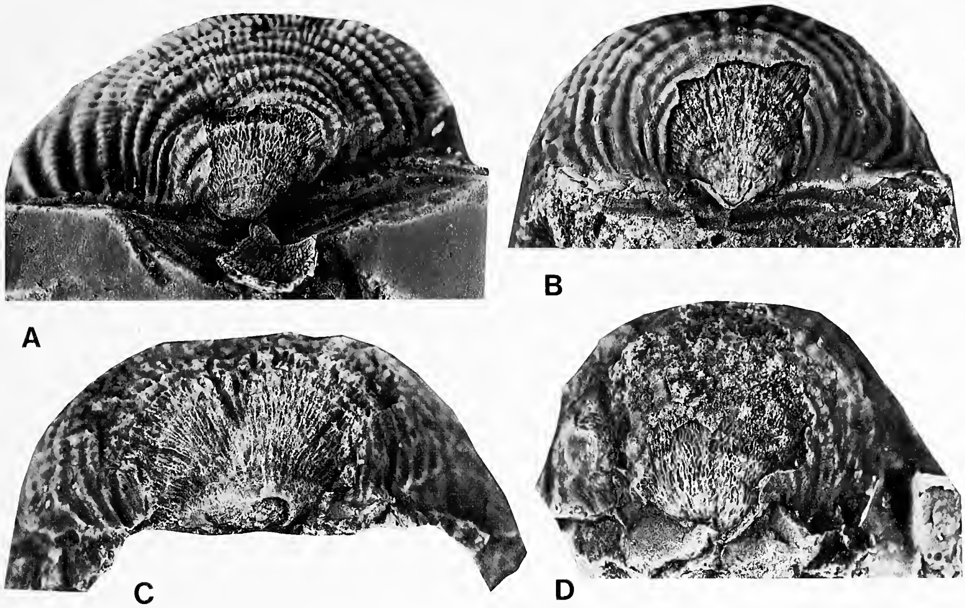

Fig. 3.—Posterior views of four taxa showing the shagreen texture within the ventral beak. A. *Keokukia rotunda* Carter, 1991, from the Keokuk Limestone of eastern Missouri (SL468), CM 45656. B. *Spinocarinifera arcuata* (Hall, 1858) from the Chouteau Limestone of northeastern Missouri (SL610), CM 45657. C. *Tesuquea formosa* Sutherland and Harlow, 1973, from the lower Gobbler Formation of southwestern New Mexico (SL4758), CM 45658. D. *Spinocarinifera nigra* (Gosselet, 1888) from the Calcaire d'Avesnelles Formation (lower Hastarian?) of northeastern France (M. Legrand-Blain Collection, SL 1244), CM 45659. All × 3.

doensis (Girty, 1915), "*A.*" *crassicostata* (Dunbar and Condra, 1932), and "*A.*" *portlockiana* (Norwood and Pratten, 1855). None of these species has the shagreen texture inside the ventral umbones, nor do any of the Permian species assigned to the genus *Antiquatonia* by Cooper and Grant (1975). The North American species assigned to *Antiquatonia* may represent an undescribed homeomorph of considerably later origin than true Eurasian *Antiquatonia* of Viséan and Serpukhovian age. This unnamed North American genus is closely related to the genus *Reticulatia* Muir-Wood and Cooper, 1960, of Upper Carboniferous and Lower Permian age, which lacks the shagreen texture characteristic of the retariins. In fact, *Reticulatia* has a row of spines delimiting the ears and essentially differs externally from the so-called North American *Antiquatonia* only in lacking the ear ridge bearing the row of spines.

Following the Lower Viséan *Keokukia*, there are no other retariins in North America until the appearance of the Morrowan genus *Tesuquea* Sutherland and Harlow, 1973, which also bears a shagreen texture in the ventral beak (Fig. 3C). Sutherland and Harlow (1973) suggested close affinity of their new genus with *Antiquatonia* and noted the lack of an external ridge delimiting the ears and supporting the row of spines. However, a dorsal internal ridge delimiting the ears is absent in *Antiquatonia* but appears in the retariin genus *Kutorginella* Ivanova, 1951. Thus, similar morphologies and stratigraphic distributions suggest to us that *Tesuquea* and *Kutorginella* are sister genera, not *Tesuquea* and *Antiquatonia* as suggested by Sutherland and Harlow (1973). In North America, *Kutorginella* appears in the late Desmoinesian as *K. lasallensis* (Worthen, 1873) and ranges through the Missourian and Virgilian of the midcontinent; in Eurasia, the genus appears much earlier. The shagreen texture within the ventral umbo of *K. lasallensis* attests to its assignment to the genus *Kutorginella.*

The genera of the lineage *Keokukia–Antiquatonia–Kutorginella* are widely distributed in Eurasia. In North America, only *Keokukia* and *Kutorginella* are present, but the endemic genus *Tesuquea* replaces *Antiquatonia.* If this line of reasoning is correct, it permits us to draw the following conclusions:

1) The genus *Keokukia* probably appeared first in Eurasia in the late Tournaisian and migrated to North America by the late Osagean or early Viséan. In Eurasia, *Keokukia* gave rise to true *Antiquatonia,* whereas in North America, much later, it gave rise to *Tesuquea.*

2) The marine connection between North America and Eurasia during the Moscovian may have been temporary and short- lived. *Kutorginella* appeared in North America only near the end of the Desmoinesian (Moscovian). The North American sister genus of Eurasian *Antiquatonia, Tesuquea,* also was derived from *Keokukia* and appeared earlier than *Kutorginella,* sometime in the Morrowan (Bashkirian). It was endemic to North America and appeared allopatrically, becoming extinct later in the Morrowan.

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EOCENE DECAPOD CRUSTACEANS FROM PULALI POINT, WASHINGTON

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ABSTRACT

A robust decapod fauna, including ten species in nine genera, has been recovered from the Eocene ?Aldwell Formation near Pulali Point, Washington. New taxa include *Portunites macrospinus* n. sp., *Carpilius occidentalis* n. sp., *Pulalius dunhamorum* n. gen. and sp. *Pulalius vulgaris* (Rathbun, 1926) new combination has been removed from *Zanthopsis* McCoy. *Palaeopinnixa rathbunae* new name is offered as a replacement name for *Pinnixa eocenica* Rathbun which is herein referred to *Palaeopinnixa* Via. *Palaeopinnixa* is placed within the Hexapodidae. This is the first notice of *Carpilius* Leach *in* Desmarest in the eastern Pacific region. The decapod fauna is typical of those previously reported from deep-water, continental slope settings of the Pacific Northwest with the exception of the occurrence of *Carpilius*, which has a mainly tropical distribution, and *Palaeopinnixa* which has previously been reported primarily from lower-latitude settings.

KEY WORDS: Decapoda, Brachyura, Eocene, Olympic Peninsula, Washington

INTRODUCTION

A previously undescribed decapod fauna from Eocene rocks at Pulali Point, Washington, has yielded ten species in nine genera, including one new genus and four new species. The decapod fauna was mentioned by Squires et al. (1992) and illustrated by Tucker et al. (1994); however, neither report provided a detailed systematic treatment of the fauna. The fauna is composed of several decapod taxa common in continental slope deposits of the Pacific Northwest including *Macroacaena* Tucker, *Laeviranina* Lörenthey and Beurlen, *Raninoides* H. Milne Edwards, *Portunites* Bell, *Branchioplax* Rathbun, *Pulalius* n. gen., and *Neopilumnoplax* Serène *in* Guinot. This report marks the first notice of the genus *Carpilius* Leach *in* Desmarest in the fossil record, based upon material other than a manus, and on the west coast of North America. This decapod fauna is significant biogeographically because it represents a mix of taxa typical of the west coast of North America (Rathbun, 1926; Tucker and Feldmann, 1990; Feldmann et al., 1991; Schweitzer and Feldmann, 1999) and taxa not previously reported from the eastern Pacific region.

Institutional abbreviations used throughout this paper are: CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; GHUNLPam, Geology Col-

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lection, National University of La Pampa, Santa Rosa, Argentina; In., The Natural History Museum, London, United Kingdom; SM, Sedgwick Museum, Cambridge University, Cambridge, United Kingdom; USNM, United States National Museum of Natural History, Washington, D.C.; and JSHC, private collection of J. S. H. Collins, Forest Hill, London, England.

GEOLOGIC SETTING

Decapod fossils were collected from the northeast coast of Pulali Point which extends into the Hood Canal of Puget Sound, south of Quilcene, Washington, in the N1/2, Sec. 18, T26N, R1W, of the Seabeck 7.5 minute quadrangle (Fig. 1). The section at Pulali Point (Fig. 2) includes two major units, the Crescent Formation and an overlying sedimentary sequence that has been questionably assigned to the Eocene Aldwell Formation based upon lithology, paleontology, age, and geographic location (Squires et al., 1992). Squires et al. (1992) determined that the unit should be referred either to the Aldwell or the Humptulips Formation, because the two units are similar in both age and lithology. They assigned the sedimentary rocks at Pulali Point to the ?Aldwell Formation because that unit crops out within 15 km to the north of the site. The Humptulips Formation crops out about 80 km to the southwest of Pulali Point (Squires et al., 1992). Because our study is concerned primarily with decapod systematics, we have no basis for offering new information concerning the identity of the rocks and concur with their decision to assign the rocks to the ?Aldwell Formation.

The Crescent Formation, which at Pulali Point occurs as basalts alternating with basaltic sandstone, basalt pebble conglomerate, and siltstone, lies unconformably beneath the sedimentary sequence referred to as the ?Aldwell Formation (Squires et al., 1992). They reported one decapod fossil, a specimen of *Glyphithyreus weaveri* (Rathbun) from the Crescent Formation, but no decapods in this report were recovered from that unit. The Crescent Formation was reported to be of Penutian to Ulatisian age based upon calcareous nannofossils, benthic foraminifera, and macrofossils (Squires et al., 1992). Babcock et al., (1994:145) reported that the Crescent Formation in the vicinity of Pulali Point had an age of 50.5–1.6 ma based upon ^{40}Ar-^{39}Ar geochronometry.

The sedimentary sequence at the Pulali Point locality, which is assigned to the ?Aldwell Formation, unconformably overlies the Crescent Formation. It consists of boulder conglomerate, sandy siltstone, and siltstone with gradational contacts between each (Squires et al., 1992). The boulder conglomerate, located at the base of the section, contains crab fossils in siltstone concretions occurring with a predominance of basalt boulders (Squires et al., 1992). The concretions were considered by Squires et al. (1992) to have been reworked. Decapods were also recovered from the silty sandstone facies and were contained within reworked, well-indurated siltstone concretions (Squires et al., 1992). Squires et al. (1992) reported a middle Eocene (early Narizian) age for the formation based upon benthic foraminifera and macrofossils. Babcock et al. (1994) reported that the ?Ald-

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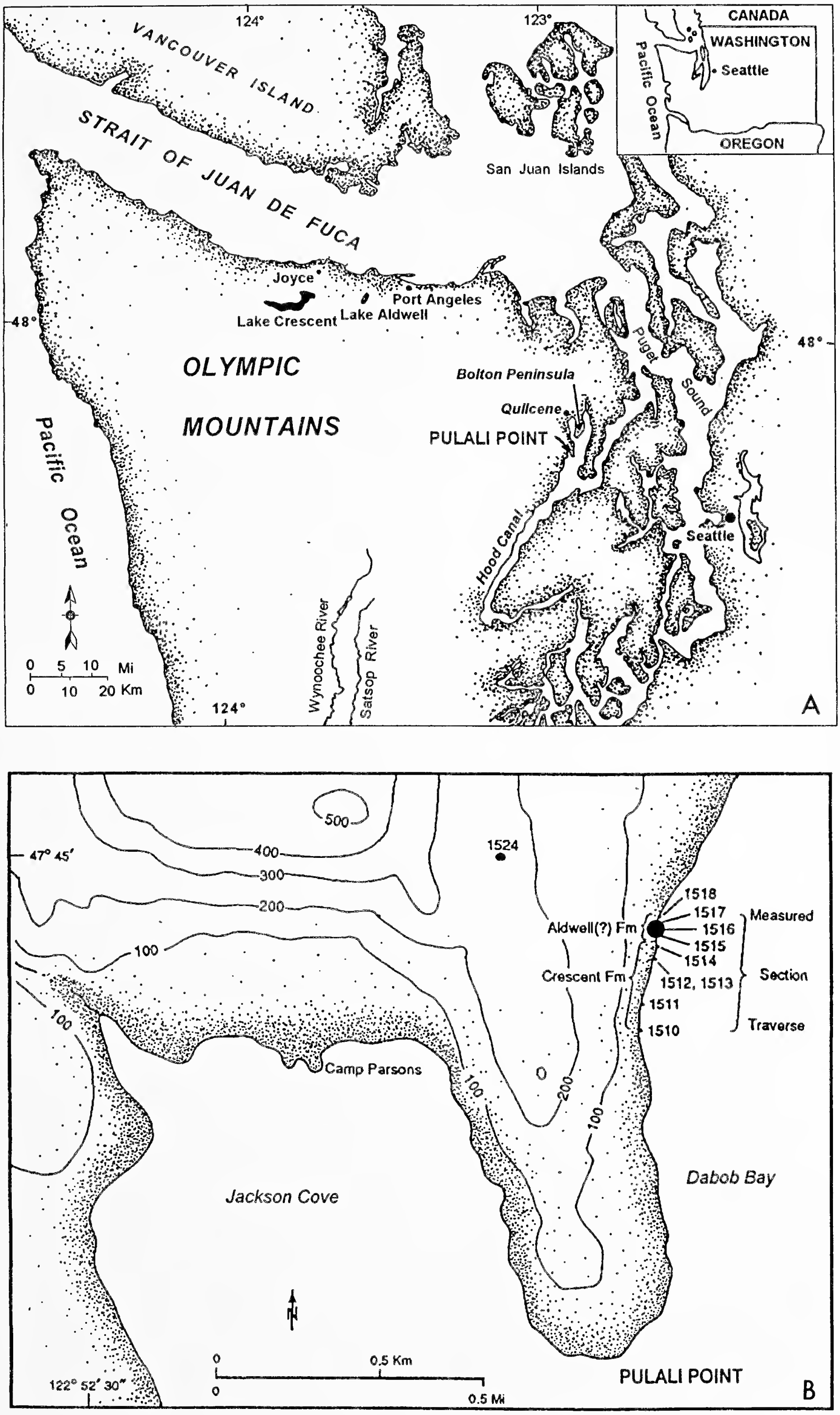
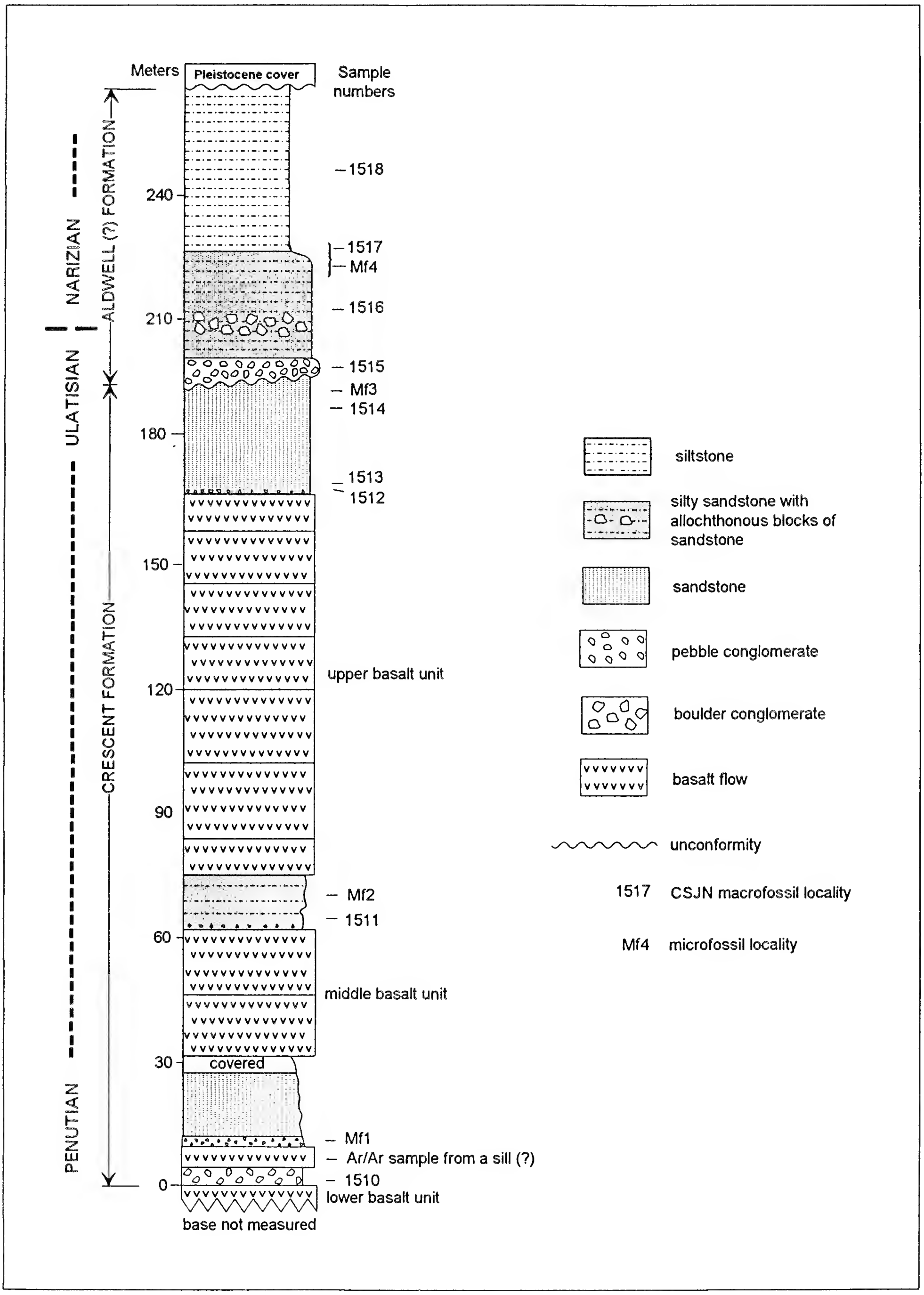
Fig. 1.—A. Locality map of the Olympic Peninsula, Washington, showing the Pulali Point collecting locality (modified from Squires et al., 1992). B. Map of the Pulali Point area, indicating California State University, Northridge (CSUN) collecting localities, and the location at which the stratigraphic section in Figure 2 was measured (modified from Squires et al., 1992).


124°
123°
CANADA
WASHINGTON
Seattle
Pacific Ocean
OREGON
VANCOUVER ISLAND
STRAIT OF JUAN DE FUCA
San Juan Islands
Joyce
Port Angeles
Lake Crescent
Lake Aldwell
48°
48°
OLYMPIC
MOUNTAINS
Bolton Peninsula
Quilcene
PULALI POINT
Puget Sound
Seattle
Hood Canal
Pacific Ocean
Wynoochee River
Satsop River
0 5 10 Mi
0 10 20 Km
124°
A
47° 45′
500
400
300
200
100
100
1524
1518
1517
1516
1515
1514
1512, 1513
1511
1510
Measured
Section
Traverse
Aldwell(?) Fm
Crescent Fm
Camp Parsons
100
0
200
100
Dabob Bay
Jackson Cove
N
0 0.5 Km
0 0.5 Mi
122° 52′ 30″
PULALI POINT
B



Modified from Squires et al., 1992

Fig. 2.—Stratigraphic section of the rocks exposed at Pulali Point. Decapods were reported by Squires et al. (1992) from CSUN macrofossil localities 1515 and 1516 (modified from Squires et al., 1992).

well rocks at Pulali Point interfinger with the Crescent basalts, suggesting that they were syndepositional and placing the age of the ?Aldwell Formation at Pulali Point as Penutian–Narizian age, the age of the Crescent Formation near Pulali Point. Squires et al. (1992) had not noted interfingering of these two units and instead described an angular unconformity between the two units. Decapod occurrences support an Eocene age for this unit.

Babcock et al. (1994) summarized the depositional environment of the Aldwell Formation sensu stricto as being cold, deep, and predominated by submarine landslides. The depositional environment of the ?Aldwell Formation at Pulali Point is reported to have been part of a deep-water, submarine fan complex (Squires et al., 1992). The basalt boulder conglomerates were considered to have been proximal turbidite deposits, and the silty sandstones were interpreted to have been derived from multiple provenances, based upon the occurrence of reworked concretions in that facies (Squires et al., 1992). Both the boulder conglomerate and the silty sandstone contain decapods, and these fossils were interpreted to have been derived from both deep- and shallow- water environments (Squires et al., 1992), also supporting the theory of multiple provenances for the sediments. Some of the decapods reported here have modern congeners that are typical of deep-water environments, including *Raninoides* (Tucker, 1995) and *Neopilumnoplax* (Feldmann et al., 1991). The fossil genus *Branchioplax* was reported from the Eocene Orca Group, suggested to have been deposited at bathyal depths (Feldmann et al., 1991). The two fossil genera *Portunites* and *Pulalius* have been reported from rocks on the west coast of North America that are interpreted to have been deep-water, continental-slope deposits. Conversely, the modern species of *Carpilius* have been reported from relatively shallow, sublittoral depths of approximately 5–35 m (Sakai, 1976). The mixed depth preferences of these decapods supports the interpretation that these rocks were deposited in a deep-water, continental-slope setting with some downslope mixing of the fauna, possibly explaining the reworked concretions.

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1803
Infraorder Brachyura Latreille, 1803
Section Podotremata Guinot, 1977
Family Raninidae de Haan, 1841
Subfamily Lyreidinae Guinot, 1993
Genus *Macroacaena* Tucker, 1998

Type Species.— *Lyreidus succedanus* Collins and Rasmussen, 1992.

Remarks.—*Macroacaena* Tucker is characterized by possession of a tridentate front, two orbital fissures, an anterolateral margin with a hypertrophied spine at the anterolateral corner and usually a small protuberence just posterior to the midlength of the anterolateral margin, and a moderately distinct median ridge (Tucker, 1998). The fronto-orbital width of members of this genus is typically greater than the posterior margin (Tucker, 1998). Specimens from the Pulali Point locality are referred to the genus based upon possession of a moderately distinct ridge, an extremely reduced anterolateral spine, and a hypertrophied spine at the anterolateral corner. This combination of characters is unique to *Macroacaena* (Table 1). Characteristics of the rostrum or orbits are not available because the front is broken. The posterior width exceeds the fronto-orbital width, occupying

Table 1.—*Distinguishing characters of the dorsal carapace useful in differentiating among the genera* Lyreidus, Lysirude, *and* Macroaceana. *FOW = Fronto-orbital width, PW = posterior width.*

Character	*Lyreidus*	*Lysirude*	*Macracaena*
Carapace shape	Fusiform, much longer than wide	Carapace moderately wide	Carapace widest of the three genera
Orbital fissures	One	One	Two
Orbital teeth	One	One	Two
Dorsal ridge	Absent or indistinct	Absent or indistinct	Present
FOW vs. PW	FOW always narrower	FOW equal to or wider	FOW wider
Rostrum	Typically less produced	Typically more produced	Typically more produced
Front	Tridentate	Tridentate	Tridentate
Anterolateral spines	Short or absent	One hypertrophied; one much reduced	One hypertrophied; one much reduced
Anterolateral spines	One	Two or less often, one	Two

approximately 0.45 and 0.41 the maximum carapace width respectively. This falls outside the range typically ascribed to the genus by Tucker (1998), who described *Macroacaena* as having a fronto-orbital margin that is usually wider than the posterior margin (p. 325).

Distinguishing members of the genus *Macracoaena* from members of the two closely related genera *Lyreidus* de Haan and *Lysirude* Goeke can be difficult, as has been addressed by Tucker (1998) and Feldmann (1989, 1992). The three genera possess many overlapping characteristics that indicate that a morphological gradation exists with *Lyreidus* and *Macroacaena* as end members and *Lysirude* occupying an intermediate morphologic position (Table 1). However, the combination of characters of the dorsal carapace for each genus is unique, and distinguishing members of each genus is relatively straightforward if specimens are well preserved. The relative width of the front and the posterior margin should be used with care. For example, the two genera *Macroacaena* and *Lysirude* were characterized by Tucker (1998) as possessing a posterior width that is often less than the fronto-orbital width. *Lyreidus* was described as possessing a fronto-orbital width that is usually less than the posterior width and is always much less than one-half the maximum carapace width (p. 324). The specimen from Pulali Point, which has a combination of other characters that clearly place it in *Macroacaena*, has a posterior margin that is slightly wider than the fronto-orbital width, such as is often seen in *Lyreidus*. Additionally, Goeke (*in* Tucker, 1998) noted that the relative fronto-orbital width with respect to the total width in some species of *Lysirude* changes during growth, so that younger individuals typically possess relatively wider fronto-orbital margins. Therefore, it is possible that this character may not be useful in disinguishing among *Lyreidus*, *Lysirude*, and *Macroacaena*.

Macroacaena alseanus (Rathbun, 1932)
(Fig. 3B)

Lyreidus alseanus Rathbun, 1932:239, 240, 242, fig. 3, 4. Glaessner, 1960:17; Bennett, 1964:24; Feldmann, 1989:63–69, fig. 1.1, 1.2, 3.1–3.8, text fig. 4.1–4.3.
Lyreidus (*Lysirude*) *alseanus* Rathbun. Feldmann, 1992: 951, fig. 4.10, 4.11.

Material Examined.—CM 45822, 45823, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—Only one of the two specimens from Pulali Point is well preserved,

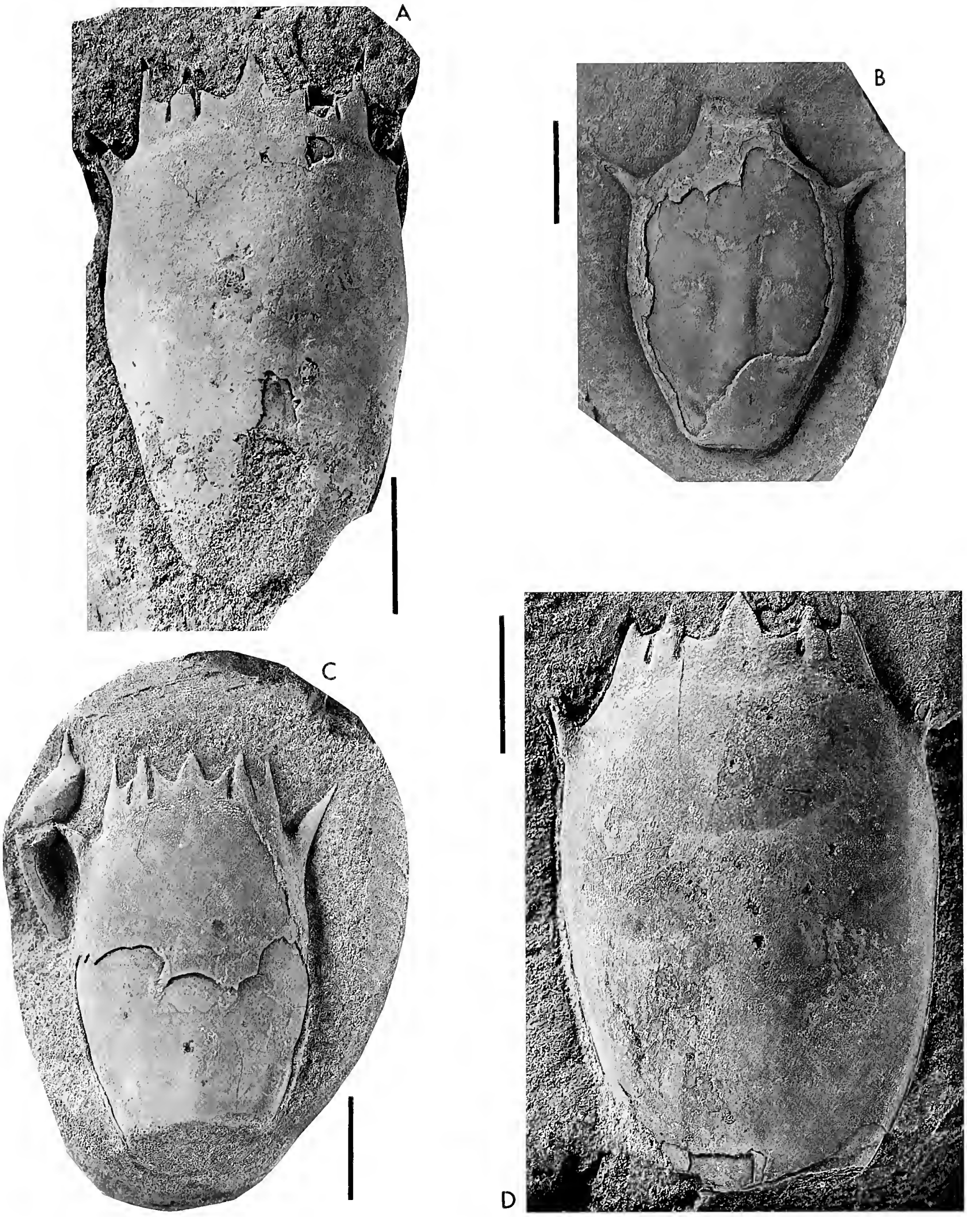


Fig. 3.—A. *Laeviranina vaderensis* (Rathbun), CM 45829. B. *Macroacaena alseanus* (Rathbun), CM 45822. C. *Raninoides fulgidus* Rathbun, CM 45824. D. *Laeviranina goedertorum* Tucker, CM 45827. Scale bars = 1 cm.

and unfortunately, the entire rostrum and orbital region are missing. Nevertheless, the specimens can be confidently referred to this species based on several characters. The length/width ratio is less than 0.65, the front is narrow and occupies about 0.41 the maximum carapace width, the anterolateral margin has an extremely reduced spine and a hypertrophied spine at the anterolateral angle, the lateral

Table 2.—*Number of species in the genera* Laeviranina *and* Raninoides *with wide orbital fissures, narrow orbital fissures, or grooves.*

Character of orbit	*Laeviranina*	*Raninoides*
Well-developed grooves	1	8
Narrow grooves	10	4
Fissures	1	1

margins are nearly straight, the posterolateral margins are slightly concave and converge posteriorly, and there is a moderately well-developed axial ridge on the dorsal carapace. All of these characteristics conform to the description of the species provided by Feldmann (1989).

Because the front is missing on this specimen, making it impossible to observe characteristics of the rostrum and orbits, it is possible to confuse it with members of another genus known from the Pacific Coast of North America, *Carinaranina* Tucker. Members of *Carinaranina* and *Macroacaena* look superficially similar if characters of the front are discounted. Species of *Carinaranina* typically possess a hypertrophied spine at the anterolateral corner but do not possess the reduced spine on the anterolateral margin (Tucker, 1998). This appears to be the best method of distinguishing *Macroacaena alseanus* (Rathbun) from members of *Carinaranina*, especially *C. naselensis* (Rathbun), which has a very narrow front as seen in species of *Macroacaena*. Other characteristics that distinguish members of *Carinaranina* from members of *Macroacaena* are the more well-developed axial ridge of *Carinaranina* that extends the entire length of the dorsal carapace onto the rostrum, the coarsely punctate ornamentation of *Carinaranina*, and the wider orbital grooves and better-developed orbital teeth of *Carinaranina*. Distinguishing members of the two genera is relatively straightforward if the orbits and rostrum are preserved since those areas are distinctly different in each genus.

Subfamily Raninoidinae de Haan, 1841

Remarks.—The problem of differentiating *Laeviranina* Lörenthey and Beurlen from *Raninoides* H. Milne Edwards has been addressed on numerous occasions. Tucker (1998) summarized previous work on this problem, noting that several criteria have been proposed to differentiate the two genera including the nature of the orbital fissures, the placement of the anterolateral spine with respect to the total length of the carapace, the presence or absence of a postfrontal ridge, and several characteristics of the sternum.

Laeviranina has been considered to possess orbital fissures, while *Raninoides* has been considered to possess orbital grooves; however, Tucker (1998) indicated that both character states occur in each genus. Data from 25 species analyzed in this study indicates that this character does indeed occur in both species (Table 2), but that there is a general tendency for members of the genus *Laeviranina* to possess narrow orbital grooves or fissures and for members of the genus *Raninoides* to possess relatively more open orbital grooves. Feldmann (1991) listed several features of the sternum that he believed could be used to differentiate the two genera, including the shape of sternal element four and the nature of the cleft in sternal element five. Tucker (1998) indicated that these sternal characteristics are mixed between the two genera as well. According to the key to the genera of the Raninoidinae provided by Tucker (1998), in species of *Raninoides*, the ster-

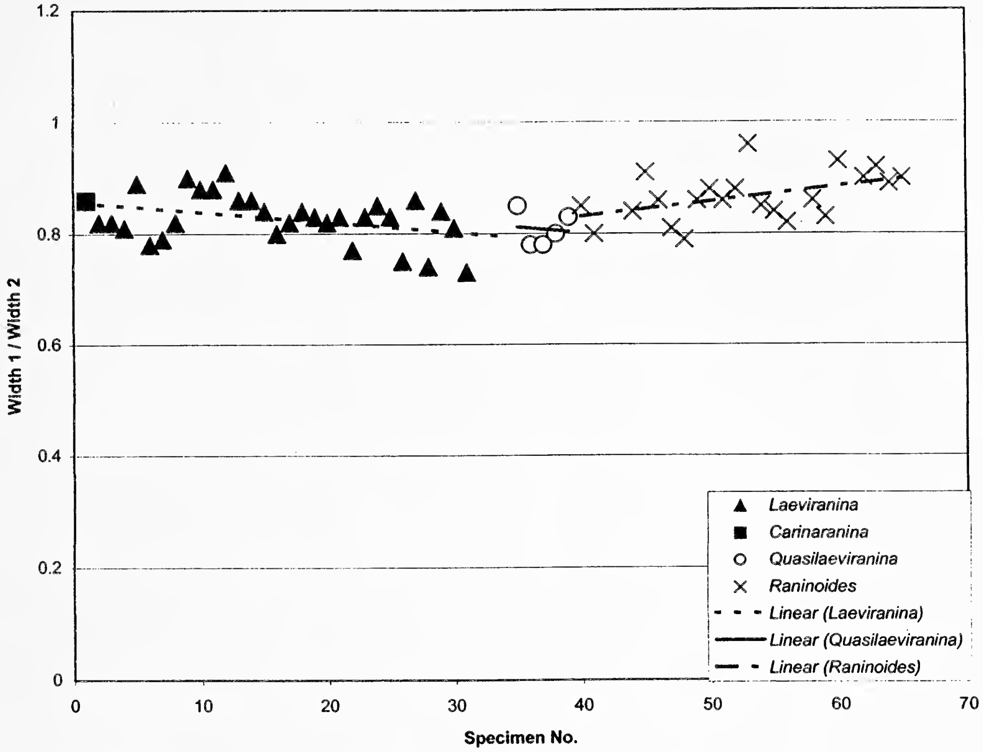


Fig. 4.—Specimens of *Laeviranina*, *Raninoides*, *Quasilaeviranina*, and *Carinaranina* plotted by the ratio of the width between the bases of the anterolateral spines (W2) to the maximum carapace width (W1). Linear regression lines show trends in ratios within taxa.

num between the third pereiopods is "usually quite wide" (p. 347), where it is known, and this same area, where known, is "moderately narrow" (p. 347) in species of *Laeviranina*. However, she did not list this as a useful character in differentiating the two genera (Tucker, 1998). It is necessary to bear in mind that the generic characteristics of the sternum of *Laeviranina* are not well known due to poor or lack of preservation (Tucker, 1998), so this character needs further investigation as more material becomes available. Tucker (1998) also noted that the ischium of the first pereiopod of species of *Raninoides* bears a spine; however, this element of the pereiopods of *Laeviranina* is unknown. This character could prove useful if more and better fossil material is discovered.

Members of the two genera have also been differentiated based on the relative width of the carapace with respect to the total length, the position of the anterolateral spines with respect to the total length, and the width of the fronto-orbital margin with respect to the maximum width. To test this, specimens and illustrations of specimens referred to nearly all species of both genera, as assigned by Tucker (1998), were measured, and relevant ratios were calculated. Scatter diagrams of the results of this work indicate that there is absolutely no difference between the two genera with respect to the ratios calculated (Fig. 4–6). Therefore, the relative width of the carapace, the position of the anterolateral spine, and the position of maximum width with respect to the total length of the carapace cannot

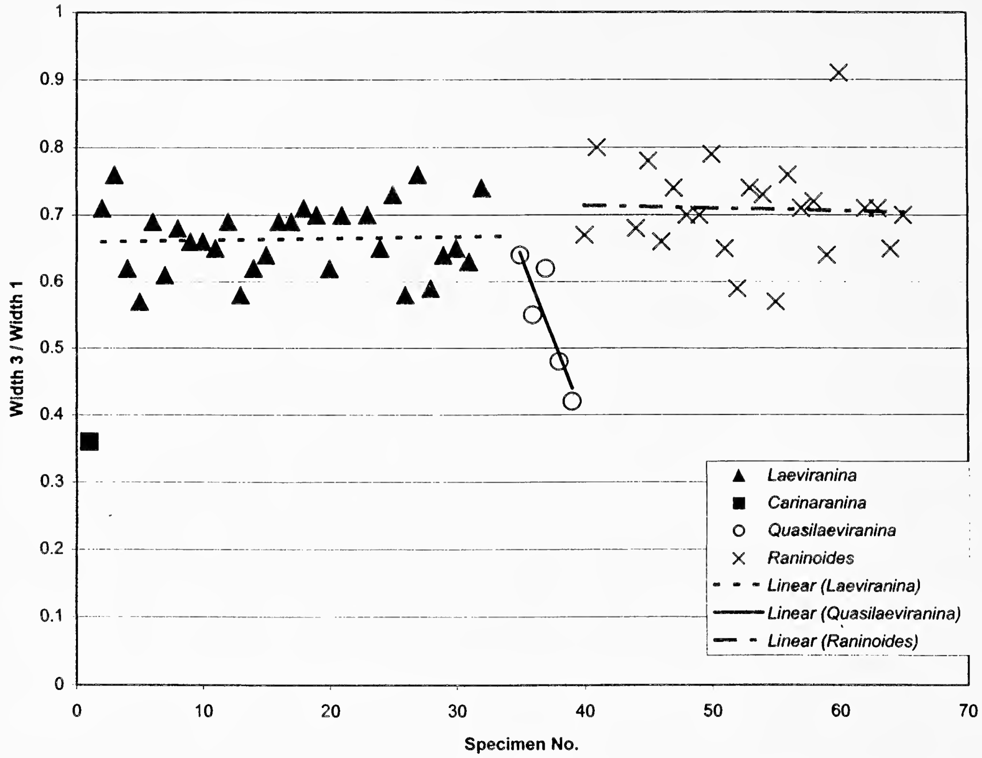


Fig. 5.—Specimens of *Laeviranina*, *Raninoides*, *Quasilaeviranina*, and *Carinaranina* plotted by the ratio of the fronto-orbital width (W3) to maximum carapace width (W1). Linear regression lines show trends in ratios within taxa.

be used reliably to differentiate between the two genera. Ratios for members of another closely related genus, *Quasilaeviranina* Tucker and the sole specimen of *Carinaranina* from Pulali Point, were included on the scatter diagrams for comparative purposes.

Tucker (1998) indicated that one characteristic that can reliably be used to differentiate between the two genera, especially in fossil taxa, is the presence or absence of a postfrontal ridge. Members of species currently assigned to *Laeviranina* possess such a ridge while members of most species of *Raninoides* do not. However, there are several problems that arise when using this single character to assign specimens to either *Laeviranina* or *Raninoides*. Use of the ridge to differentiate between the two genera may be hampered by differential preservation of the ridge, because in some specimens, the ridge is very poorly preserved. More importantly, members of several extant species of *Raninoides* possess weakly developed postfrontal ridges in some specimens. For example, specimens of *Raninoides louisianensis* Rathbun (USNM 12002; each of the USNM specimens contains a lot of several specimens, ranging from one to approximately 50 individuals) have a weakly developed postfrontal ridge marginally but the ridge is not developed axially. Members of *Raninoides bouvieri* Capart (USNM 121423) possess a very weak postfrontal ridge. Finally, members of the species *R. personatus* Henderson (USNM 216741) and *R. lamarcki* Milne Edwards and Bouvier

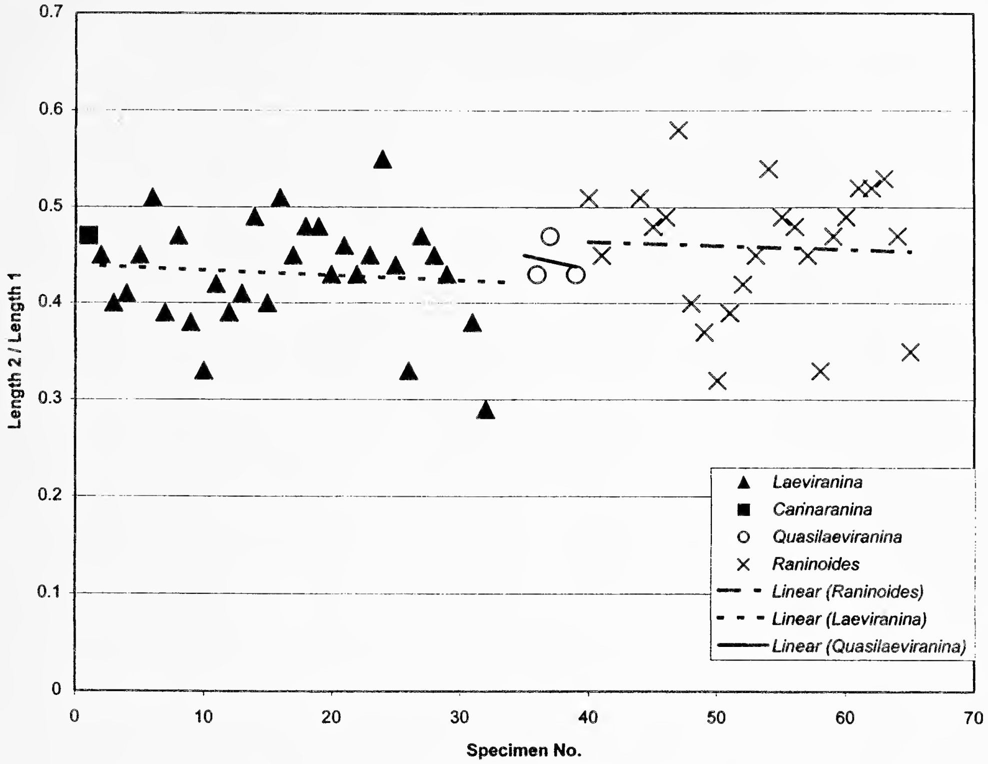


Fig. 6—Specimens of *Laeviranina*, *Raninoides*, *Quasilaeviranina*, and *Carinaranina* plotted by the ratio of the length to the position of maximum carapace width (L2) to the total length of the carapace (L1). Linear regression lines show trends in ratios within taxa.

(USNM 121660) possess weak postfrontal ridges which are best developed on larger specimens. Additionally, the degree of development of the ridges appears to vary within each species, sometimes, but apparently not always, associated with overall carapace size. Specimens of the extant species *R. benedicti* Rathbun (USNM 268507) and *R. loevis* (Latreille) (USNM 273193) exhibit the smooth, ridgeless, postfrontal regions that have traditionally been ascribed to members of that genus.

Generic assignment of taxa to *Raninoides* or *Laeviranina*, therefore, is difficult at best, especially since there are no unequivocal characters with which to accomplish this. While generic assignment of specimens with well- developed postfrontal ridges or smooth postfrontal regions is relatively straightforward, some taxa possess ridges that are poorly or variably developed. Development of a postfrontal ridge on several extant species of *Raninoides* casts further doubt upon the use of the postfrontal ridge as the only reliable means by which to distinguish between the two genera *Laeviranina* and *Raninoides*. It appears, therefore, that all of the characters that have been suggested as being useful for differentiating between the two genera are problematic, unreliable, and mixed between members of the two genera. While it is premature to assert that these two genera are synonymous, it is suggested that this possibility be further investigated, especially with regard to features of the sternum as first noted by Feldmann (1991).

Genus *Laeviranina* Lörenthey and Beurlen, 1929

Type Species.—*Ranina budapestinensis* [sic] Lörenthey, 1897:23.

Remarks.—Tucker (1998) provided a summary of all species that have been assigned to the genus *Laeviranina*, including several species from the Pacific Coast of North America that were originally assigned to the genus *Raninoides*. North American species originally assigned to *Raninoides* include *L. lewisanus* (Rathbun) and *L. vaderensis* (Rathbun); Tucker (1998) assigned them to *Laeviranina* based upon their possession of a postfrontal ridge. Upon examination of these two species, it is apparent that they are synonymous. Rathbun (1926) originally differentiated between the two species by observing that *L. lewisana* had a wider fronto-orbital width, a more anteriorly placed anterolateral spine, a less convex lateral margin, a straighter posterolateral margin, and a more convex dorsal surface. However, examination of illustrations of both *L. lewisana* and *L. vaderensis* in Rathbun's work (1926) shows that the fronto-orbital width to total width ratio is 0.70 and 0.68 respectively, not a significant difference. Further, examination of illustrations of specimens subsequently referred to each species by Tucker and Feldmann (1990) and Tucker (1998) shows that the two species do not differ substantially in the range of fronto-orbital width to total width ratios, averaging 0.70 in *L. lewisana* and 0.67 in *L. vaderensis*. Rathbun (1926) indicated that the anterolateral spine was placed more anteriorly in *L. lewisana*, and examination of her plates confirms this (plate 22, fig. 4, 5). However, examination of figures of specimens referred to each species by Tucker and Feldmann (1990) and Tucker (1998) indicates that the two species overlap in range in this ratio also. The length to the base of the anterolateral spine occupies an average of 0.20 of the total length in *L. lewisana* and 0.21 in *L. vaderensis*. Tucker (1995) reported that the orbital spines were slightly shorter than the rostrum in *L. lewisana* but she did not quantify the length of the orbital spines with respect to the rostrum for *L. vaderensis*. Rathbun's (1926) illustrations indicate that the orbital spines do not extend as far as the rostrum in *L. vaderensis*, but she did not comment on the length of the spines in her descriptions of either *L. vaderensis* or *L. lewisana*. Examination of figures of specimens referred to each species by Tucker and Feldmann (1990) and Tucker (1998) indicates that there is a range in orbital spine length with respect to the rostrum in both species, ultimately not providing a means of differentiating the two species. The orbital spines in specimens assigned to *L. lewisana* are typically longer than those of specimens of *L. vaderensis*, but there is a range in the length of the spines within each species.

Tucker (1998) provided several means by which the two species could be differentiated, including the greater width of the fronto-orbital margin in *L. lewisana* which has already been shown to be virtually the same in each species. She also suggested that the more egg-shaped, ovate carapace of *L. lewisana* might be used to distinguish the two genera. However, there appears to be a range of variation with regard to this character in both species, and in fact, Rathbun (1926) reported that the lateral margins of *L. lewisana* were "not so strongly outcurved behind the [anterolateral] spine" and that the posterolateral margin was straighter than that of *L. vaderensis* (p. 94), seemingly contradicting Tucker (1998). Tucker (1998) suggested that the posterior width of *L. lewisana* was slightly wider than that of *L. vaderensis*, but there is a large degree of overlap in the ratio of the posterior width to the maximum width in the two species in this character. Based upon measurements in Tucker (1995), the posterior width to maximum width ratio averages 0.46 in *L. vaderensis* with a range of 0.44–0.46 and that ratio averages 0.41 in *L. lewisana* with a range of 0.37–0.45. She also suggested that the anterolateral spines form a V-shaped angle with the anterolateral margin in *L. lewisana*, while in *L. vaderensis*, they form a U- shaped angle. Examination of plates of specimens referred to these two taxa by Rathbun (1926), Tucker and Feldmann (1990), and Tucker (1998) indicates that there is a range of variation in the shape of the angle in both species and that both U-shaped and V-shaped angles occur in each species. *Laeviranina vaderensis* was distinguished from *L. lewisana* by Tucker (1998) based on its less distinct postfrontal ridge that is steeply and tightly arched. However, it has been demonstrated above that use of the postfrontal ridge may not be useful in differentiating between *Raninoides* and *Laeviranina*, because the ridge can be variable in degree and nature of development within genera and even within species. Therefore, it seems unlikely that this particular character will be useful for differentiating taxa at the species level, especially when used as the sole distinguishing characteristic. Based upon this evidence, therefore, the two taxa are herein synonymized, with *L. lewisana* being the junior synonym.

Laeviranina vaderensis has previously been reported from the middle Eocene of Alaska and Oregon and the upper Eocene of Washington, and *L. lewisana* was previously reported from the Eocene of Washington. The range of *L. vaderensis* is therefore not extended either geographically or chronologically by the synonymy.

Laeviranina vaderensis (Rathbun, 1926)
(Fig. 3A)

Raninoides vaderensis Rathbun, 1926:93, pl. 22, fig. 5. Glaessner, 1929:372; Tucker and Feldmann, 1990:412, fig. 3.1, 3.2; Karasawa, 1992:1252.

Laeviranina vaderensis (Rathbun): Tucker, 1998:353, pl. 17, 18.

Raninoides lewisana Rathbun, 1926:94, pl. 22, fig. 4. Glaessner, 1929:372; Förster and Mundlos, 1982: 158.

Laeviranina lewisana (Rathbun): Glaessner and Withers, 1931:490, 491; Via, 1965:263; Via, 1969: 125; Tucker, 1998:351, fig. 15, 16.

Material Examined.—CM 45829–45832, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—The specimens here referred to *L. vaderensis* possess several characters diagnostic of the species and are therefore confidently referred to this species. They possess an oblong carapace that ranges from being oblong-ovate to ovate. The fronto-orbital width occupies about 0.70 the maximum carapace width, and the orbital spines range from extending about half the length of the rostrum to extending to about the same length as the rostrum. The postfrontal ridge is subtle, arcuate, and slightly sinuous. The anterolateral spines extend more forward than laterally and form a U-shaped or V-shaped angle with the anterolateral margins. The posterolateral margins taper markedly to their intersection with the posterior margin. Some of the specimens here referred to *Laeviranina vaderensis* possess long orbital spines that extend to the same length as the rostrum, which is at the long end of the range of variation for the species. However, some specimens possess orbital spines that extend only about half the distance of the rostrum, clearly illustrating the range of variation in the species.

Laeviranina vaderensis has previously been reported from the middle Eocene Orca Group of Alaska, the middle Eocene of Oregon, and the upper Eocene Tejon Formation and Hoko River Formation of Washington (Tucker, 1998). This occurrence extends the geographic range of the species to the eastern Olympic Peninsula, Washington.

Laeviranina goedertorum Tucker, 1998
(Fig. 3D)

Laeviranina goedertorum Tucker, 1998:348, fig. 13, 14.

Material Examined.—CM 45827, 45828 deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—The Pulali Point specimens referred to *Laeviranina goedertorum* Tucker possess a suite of characters that place them in this species as described by Tucker (1998). The specimens possess an elongate carapace that achieves its maximum width at about the midpoint and converges slightly posteriorly, as seen in *L. goedertorum*. The front on the Pulali specimens and *L. goedertorum* converges anteriorly, producing a relatively narrow fronto-orbital width of around 0.60 the maximum carapace width. The postfrontal ridge on *L. goedertorum* and the Pulali specimens is sinuous and moderately well developed. The orbital teeth are shorter than the rostrum in both the new specimens and *L. goedertorum*. The specimens are therefore confidently referred to this species.

The maximum carapace width of *Laeviranina goedertorum* has been described as being located about one-third the distance posteriorly on the carapace. Dimensions of the new specimens indicate that there is a range from about one-third the distance to just under half the distance posteriorly on the carapace. The posterolateral margins of the carapace do not converge as acutely in this species as they do in other species of the genus. *Laeviranina goedertorum* is therefore wider along its entire length than other species of the genus and possesses a relatively wide posterior margin that is markedly wider than that seen in *L. vaderensis*. The two species may also be distinguished based upon several other criteria as well. The front of *Laeviranina goedertorum* converges anteriorly, resulting in an overall narrower fronto-orbital width to maximum width ratio in *L. goedertorum* as compared to *L. vaderensis*. The postfrontal ridge of *L. goedertorum* is better developed and more sinuous than that of *L. vaderensis*.

Laeviranina goedertorum has previously been reported from the Eocene Hoko River Formation (Tucker, 1998). This occurrence in the Eocene Aldwell Formation extends the geographic range to the eastern Olympic Peninsula, Washington.

Genus *Raninoides* H. Milne Edwards, 1837

Type Species.—*Ranina laevis* Latreille, 1825.

Remarks.—The specimens here referred to *Raninoides* H. Milne Edwards lack a postfrontal ridge, the main characteristic that can be reliably used to differentiate between the two genera *Laeviranina* and *Raninoides*. These specimens can therefore be unequivocally assigned to *Raninoides* because they possess a completely smooth postfrontal region.

Raninoides fulgidus Rathbun, 1926
(Fig. 3C)

Raninoides fulgidus Rathbun, 1926:96–97.

Material Examined.—CM 45824–45826 deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—Two specimens from the Pulali Point locality exhibit a combination of characteristics that place them in the species *Raninoides fulgidus* Rathbun. The specimens possess relatively long orbital and anterolateral spines and wide orbital fissures, characteristic of the species *R. fulgidus*. The rostrum does not extend as far as the orbital spines as described for this species by Tucker (1998); however, she described the inner orbital fissure as being deeper than the outer. In the Pulali Point specimens, the fissures are the same length.

Section Heterotremata Guinot, 1977
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Subfamily Polybiinae Ortmann, 1893
Genus *Portunites* Bell, 1858

Type Species.—*Portunites incerta* Bell, 1858.

Remarks.—The diagnosis for the genus *Portunites* Bell given by Glaessner (1969) describes the genus as having a hexagonal carapace that is not much wider than long, a four-toothed front, an anterolateral margin with four or five teeth with the last being the longest, an arcuate ridge extending from the lateral tooth to the medial area, a straight or concave posterolateral margin, well-defined gastrocardiac regions, and fifth pereiopods with dactyli that are not flattened (p. R513). Tucker and Feldmann (1990) emended the generic diagnosis to include a paddlelike dactylus on the fifth pereiopod based on its presence in *Portunites alaskensis* Rathbun.

Glaessner (1969) did not mention the width of the orbits in this genus, each of which occupies a little over one-third the fronto-orbital width in most members of the genus and about one-fifth to one-quarter the maximum carapace width. The fronto-orbital width of most members of the genus occupies greater than two-thirds the maximum carapace width. Bell (1858:21) described the orbits in the type species, *P. incerta* Bell, as extending to the middle of the hepatic region, and measurements of individuals of this species indicate that the fronto-orbital width occupies approximately two-thirds the maximum width of the carapace. A cast of a previously unillustrated specimen of *P. incerta* (JSHC 1732d) (Fig. 7B) documents the great width of the orbits in the type species of the genus. The front is not clearly evident in previously published plates. The subsequently named British species including *P. stintoni* Quayle and *P. sylviae* Quayle and Collins have orbits that are similar in relative size to those of the type species. The orbits of *P. alaskensis* Rathbun are extremely large; the fronto-orbital width in this species occupies more than 0.70 the maximum width of the carapace. The fronto-orbital width of the new species to be described below, *Portunites macrospinus*, occupies 0.67 the maximum carapace width.

Two species of *Portunites* possess relatively narrow fronto-orbital width-to-width ratios but can be assigned to the genus based upon a combination of other important characters. The orbits of *Portunites insculpta* Rathbun occupy approximately 0.50 the maximum carapace width, but this taxon can be assigned to *Portunites* based upon its possession of a well-developed epibranchial ridge, carapace shape and regions typical of the genus, and four anterolateral spines excluding the outer orbital spines. *Portunites kattachiensis* Karasawa possesses a fronto-orbital width which occupies about 0.53 the maximum carapace width. However, *Portunites kattachiensis* has several other generic characters that clearly

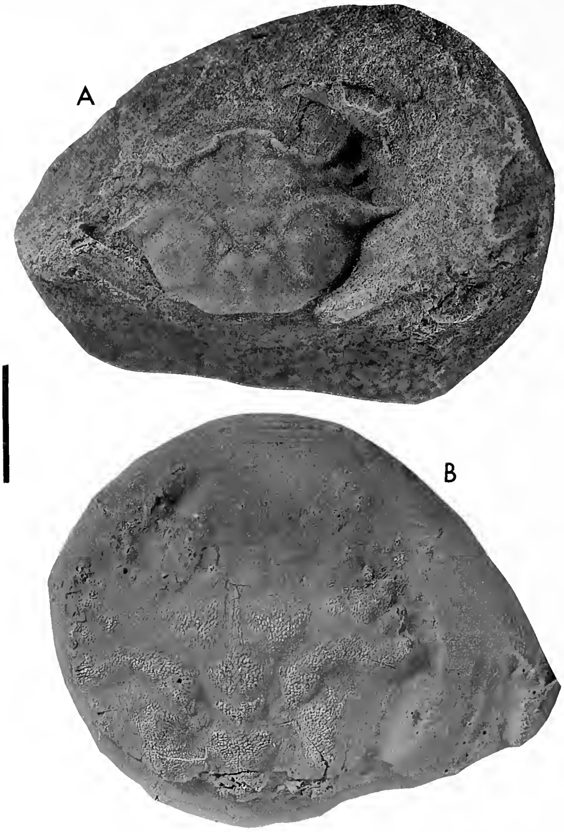


Fig. 7.—A. *Portunites macrospinus*, new species, holotype, CM 45833. B. Cast of *Portunites incerta* Bell, JSHC 1732d. Scale bar = 1 cm.

place it in *Portunites*, including a well-developed epibranchial spine, a relatively straight front with very small teeth, four anterolateral spines excluding the outer orbital spine, two orbital fissures, an ovate-hexagonal carapace, and carapace regions typical of species of *Portunites*. It is therefore suggested that the diagnosis of the genus be expanded to include a statement pertaining to the relatively great width of the orbits in members of this genus, occupying more than one-half and generally two-thirds or greater the maximum carapace width. The size of the orbits cannot be determined for *P. eocenica* Lörenthey and Beurlen, for which the type specimen has been lost (Quayle and Collins, 1981).

Portunites triangulum Rathbun differs from members of the genus *Portunites* in several important aspects. *Portunites triangulum* possesses rather small orbits; they occupy approximately 0.52 of the maximum width of the carapace, which does fall within the range for the genus. Schweitzer and Feldmann (1999) listed several differences between *Portunites triangulum* and other members of the genus, including overall carapace dimensions, the relative length of the anterolateral spines, definition of the carapace regions, and carapace shape. At that time those differences were considered to be specific; however, additional observations indicate that there are further differences between *Portunites triangulum* and other members of the genus. *Portunites triangulum* possesses four sharp spines on the front in addition to small inner-orbital spines; species of *Portunites* have only four spines or bosses including the inner-orbital spine. The epibranchial ridge on *Portunites triangulum* is not as well developed as on the other species of *Portunites* and it lacks the transverse ridges on the hepatic and protogastric regions typical of *Portunites*. Because of these important differences between this species and other species of *Portunites*, reevaluation of its generic assignment is necessary. Reassignment at this time is premature, but the problem currently is being addressed by two of the authors (Feldmann and Schweitzer) and other workers (Karasawa, personal communication, 1998). Because of the strong probability that *Portunites triangulum* will be removed from the genus, interpretations about the genus presented in this paper therefore will exclude this taxon.

It is also suggested herein that the diagnosis of the genus be emended to describe the frontal margin as ranging from relatively straight to possessing four blunt knobs or small spines. *Portunites incerta*, *P. stintoni*, *P. sylviae*, and *P. kattachiensis* all possess four very small, blunt knobs or spines on the frontal margin. The species *P. alaskensis* possesses four small but distinct and sharp spines, and *P. insculpta* Rathbun appears to possess four small spines. The new species *P. macrospinus* possesses two very small, blunt spines axially and blunt swellings on the inner-orbital margin which are not developed as spines. Because of this, it is necessary to state that the front in members of this genus may possess very small spines or blunt knobs, since the current diagnosis (Glaessner, 1969) indicates that the front must possess four spines. *Portunites triangulum* possesses rather large, well-developed spines on the frontal margin, again suggesting that it may be referrable to a different genus.

Portunites macrospinus, **new species**
(Fig. 7A, 8)

Diagnosis.—Carapace rounded-hexagonal in outline; postorbital spine extremely long, sharp, and attenuated; anterolateral spines sharp, last anterolateral spine extremely long, attenuated and sharp; orbits very broad and deeply excavated; carapace moderately vaulted; frontal spines very weakly developed.

Description.—Carapace rounded-hexagonal in outline; carapace length 64% maximum width; widest at position of last anterolateral spine; position of maximum width situated approximately one-third the total distance posteriorly; carapace moderately vaulted both transversely and longitudinally.

Front about 0.21 maximum carapace width; relatively straight; extending only slightly beyond orbits; with blunt bilobed projection axially; axially sulcate; very poorly developed blunt projections on inner orbital margin. Orbits large; fronto-orbital width about 0.67 maximum carapace width; each orbit about 0.35 fronto-orbital width; orbits sinuous, curving posteriorly, then slightly anteriorly, and finally posteriorly before intersecting anterolateral margin; directed anterolaterally; rimmed; two closed fissures; deeply excavated laterally and shallowly excavated axially.

Anterolateral margins short, bearing four or five spines including extra-orbital spine; extra-orbital spine extremely long, projecting anteriorly and well beyond the rostrum; acute and attenuated, sometimes with small triangular spine at base; next two anterolateral spines smaller, triangular, acute, projecting anterolaterally; last anterolateral spine longest, attenuated, acute, projecting laterally.

Posterolateral margins weakly concave, sinuous, with pronounced, rimmed reentrant at posterolateral corner. Posterior margin weakly concave; rimmed; about 0.31 maximum carapace width.

Carapace regions moderately well defined by grooves. Frontal region with two weakly inflated areas on either side of the axis; protogastric regions weakly ovate, moderately inflated, with very weak transverse ridge; hepatic regions with transverse ridge extending from second anterolateral spine across region; mesogastric region extremely narrow anteriorly and widening posteriorly, straight-sided anteriorly, convex posteriorly, posterior margin nearly straight; meso- and metagastric regions not differentiated; urogastric region weakly differentiated, narrow, depressed, with concave lateral margins; cardiac region rounded-triangular in shape, apex directed posteriorly, with two large swollen bosses

Table 3.—*Measurements (in mm) taken on the dorsal carapace of specimens of* Portunites macrospinus. *Orientation of measurements is illustrated in Figure 8. L1 = maximum length of carapace, W1 = maximum width of carapace, W2 = fronto-orbital width, W3 = frontal width, W4 = posterior width, W5 = orbital width.*

Specimen number	L1	W1	W2	W3	W5	W4
CM 45834	20.5	30.0	19.3	9.4	15.3	6.4
CM 45836	16.8	24.6	17.6	—	—	6.0
CM 45833	15.2	26.2	16.9	7.0	7.4	6.0
CM 45835	15.9	26.0	18.4	—	9.0	6.7

anteriorly placed on either side of the axis, very weakly developed boss at apex of triangle; intestinal region flattened.

Branchial regions not well differentiated; well-developed epibranchial ridge, extending from last anterolateral spine, curving first anteriorly, then posteriorly, terminating at lateral margin of mesogastric region; branchial region inflated axially, sloping to posterolateral margin, flattening along posterior margin.

Chelipeds poorly known, manus appearing to be rather short; venter unknown.

Measurements.—Measurements, in millimeters, taken on specimens of *Portunites macrospinus* are found in Table 3. The orientation of measurements taken is indicated in Figure 8.

Etymology.—The trivial name is a combination of "macro," meaning long, with the word "spine," to indicate the extremely long postorbital and anterolateral spines which are diagnostic for the species.

Types.—The holotype, CM 45833, and paratypes, CM 45834–45836, are deposted in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—Four specimens from the Pulali Point locality can be referred to this species. All four specimens exhibit most of the dorsal carapace, two of which are quite well preserved. Portions of the cheliped and fragments of pereiopods are present in all four specimens; however, none of these elements is well-enough preserved to permit description. No aspects of the venter were preserved.

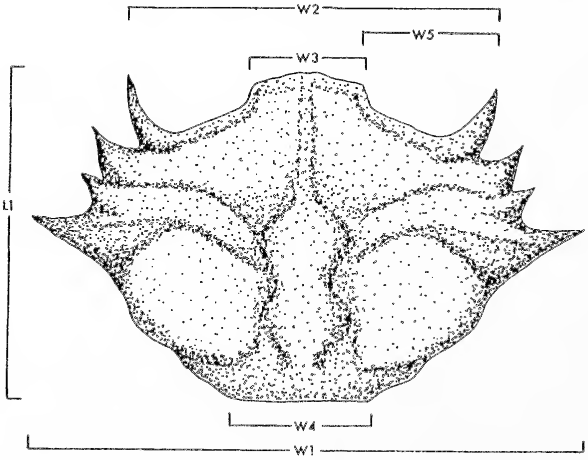


Fig. 8.—Line drawing of *Portunites macrospinus* showing position and orientation of measurements taken.

The new species can be distinguished immediately from all other members of the genus because of its extremely long, attenuated postorbital spine; sinuous, deeply excavated orbits; and sharp, attenuated anterolateral spines. The new species is most like the three species *Portunites alaskensis*, *P. kattachiensis*, and *P. hexagonalis* Nagao, but differs from those species in several ways. *Portunites alaskensis* has a well-developed ridge on the hepatic region that extends onto the protogastric region; this ridge is weakly developed in *P. macrospinus*. The carapace of *Portunites macrospinus* is more ovate and less hexagonal than that of *P. alaskensis*, and the frontal teeth, especially the axial pair, of *P. alaskensis* are much better developed than in *P. macrospinus*. *Portunites alaskensis* possesses three well-developed bosses on the cardiac region, while only two well-developed bosses are present on that region in *P. macrospinus*. Furthermore, the carapace in *P. alaskensis* is more flattened than that of *P. macrospinus*, which has a moderately vaulted carapace. The spines on *P. hexagonalis* are shorter and more triangular than those of *P. macrospinus*. The last anterolateral spine is directed slightly posterolaterally in *P. hexagonalis*, while that of *P. macrospinus* is directed laterally. The frontal spines of *P. hexagonalis* are much better developed than in *P. macrospinus*.

Portunites macrospinus can be differentiated from *P. kattachiensis* because *P. macrospinus* has wider, more widely spaced orbits, longer and more attenuated anterolateral spines, and a less tightly arched epibranchial ridge than *P. kattachiensis*. Furthermore, the epibranchial ridge in *P. kattachiensis* terminates in a tubercle, and there is a tubercle on the protogastric region and two tubercles on the branchial region in *P. kattachiensis*; all of these are missing in *P. macrospinus*. Additionally, *P. kattachiensis* has a much better developed urogastric region than does *P. macrospinus*.

The description of this new species brings the number of species to nine that are referrable to the genus *Portunites*. This occurrence brings the number of species of *Portunites* in North America to three and the number of North Pacific species to five. The five species from the North Pacific region (*P. alaskensis*, *P. hexagonalis*, *P. insculpta*, *P. kattachiensis*, and *P. macrospinus*) are more similar morphologically and therefore are probably more closely related to each other than to the other species of the genus, which are known from the Eocene of Europe. Species from the North Pacific range in age from Eocene to Oligocene. *Portunites macrospinus* is currently known only from the Eocene Aldwell Formation and the Pulali Point localities, not extending the geologic range of the genus.

Superfamily Xanthoidea Dana, 1851
Family Xanthidae Dana, 1851
Genus *Pulalius*, **new genus**

Type Species.—*Zanthopsis vulgaris* Rathbun, 1926.

Diagnosis.—Carapace ovate or hexagonal, highly vaulted longitudinally; carapace regions inflated; front four-lobed; orbits oval, with one orbital fissure; epibranchial region forming linear transverse ridge across dorsal carapace; anterolateral margin with three small, blunt spines, last spine longest, last spine at end of transverse epibranchial ridge; branchial region large and inflated; posterolateral margins convex; abdominal somites free.

Etymology.—The genus takes its name from Pulali Point, a prominent geographic feature near the collecting locality for the new species, *Pulalius dunhamorum*, to be described below.

Remarks.—The collection of previously undescribed fossils from the Aldwell Formation contains a group of specimens that are clearly congeneric with specimens assigned to *Zanthopsis vulgaris* Rathbun and which have been assigned to the new species described below. The new species and *Z. vulgaris* share many significant features. The two species possess a four-lobed front which occupies about 0.25 the maximum carapace width; oval orbits with one orbital fissure; an anterolateral margin with three blunt spines with the last being the longest; broad, inflated protogastric regions with well-defined lateral margins and poorly defined axial margins; inflated carapace regions; a carapace that is highly vaulted longitudinally; an inflated epigastric region that forms a transverse ridge; large, inflated metabranchial regions; flattened intestinal regions; convex anterolateral and posterolateral margins; a similar arrangement and shape of the mesogastric, urogastric, and cardiac regions; an abdomen with somites 3–5 free; sternites of similar size and shape; and major chelae with similar shape and ornamentation. Based on these numerous similarities, it is apparent that the two species must be congeneric.

Inspection of all known species of the genus *Zanthopsis* McCoy indicates that *Z. vulgaris* and the new species differ significantly from the type species, *Z. leachi* Desmarest, and cannot be retained in that genus. According to Glaessner's (1969) diagnosis for the genus, *Zanthopsis* sensu stricto and *Zanthopsis vulgaris* share some characters, including a four-lobed front and a vaulted carapace; however, species of *Zanthopsis* sensu stricto possess large, nodular bosses or tubercles on the branchial regions of the carapace and exhibit fusion of abdominal somites 3–5. *Zanthopsis vulgaris* does not possess either characteristic.

McCoy (1849) erected the genus *Zanthopsis* and designated *Z. leachi* as the type species. He also described several other species of *Zanthopsis*, all of which possess nodular bosses on the dorsal carapace. Bell (1858) illustrated the type species and two of McCoy's species, *Z. bispinosa* McCoy and *Z. unispinosa* McCoy. Inspection of McCoy's (1849) descriptions and Bell's (1858) plates indicates that *Zanthopsis* sensu stricto and *Zanthopsis vulgaris* are not at all closely related. The carapace shape in *Zanthopsis* sensu stricto is rounded or oval; in *Zanthopsis vulgaris* the carapace is rounded-hexagonal. The carapace regions of *Zanthopsis* sensu stricto are indistinct and faintly marked by wide, shallow grooves. *Zanthopsis vulgaris* has well-defined carapace regions that are marked by narrow grooves. The carapace regions of the two taxa are completely different in terms of shape, ornamentation, and degree of inflation. The protogastric region of *Zanthopsis* sensu stricto is narrow and poorly delimited. In *Z. vulgaris*, those regions are broad, inflated, and well delimited by grooves on the lateral margins. The hepatic region is better developed, more inflated, and of an overall broader shape than in *Zanthopsis* sensu stricto. *Zanthopsis vulgaris* has one orbital fissure; members of *Zanthopsis* sensu stricto have none. The epibranchial region of *Z. vulgaris* is swollen and forms a transverse ridge; in *Zanthopsis* sensu stricto, this region does not appear to be differentiated at all. The branchial region of *Zanthopsis* sensu stricto is ornamented by large tubercles or bosses; there are no bosses on the branchial region of *Z. vulgaris*, which also has an overall larger and more inflated branchial region. The shape of the urogastric and cardiac regions are completely different. The urogastric region in *Z. vulgaris* is extremely constricted and flattened and the cardiac region is broadly triangular; both regions are very well defined. In *Zanthopsis* sensu stricto, these regions are not well defined and possess tubercles or bosses. The male abdomen of *Zanthopsis* sensu stricto exhibits fusion of the third through fifth somites, while in *Z. vulgaris*, these somites are free. For all of these reasons, *Zanthopsis vulgaris* is herein referred to the new genus *Pulalius* and is designated as the type species for that genus.

Three other species from the Tertiary of the west coast of North America have been referred to the genus *Zanthopsis*. *Zanthopsis sternbergi* Rathbun, from the Cretaceous of California (Rathbun, 1926), is known only from a claw, making confirmation of its placement in the genus difficult. *Zanthopsis hendersonianus* Rathbun from the Oligocene of Oregon and the Eocene of California (Rathbun, 1926) displays characteristics that place it within *Zanthopsis* sensu stricto. *Zanthopsis rathbunae* Kooser and Orr (*not* sensu Maury) resembles members of the Hepatinae Stimpson of the Calappidae de Haan and is currently being reevaluated by two of us (Schweitzer and Feldmann) to determine its generic and familial placement.

Some other species referred to *Zanthopsis* sensu stricto have been removed to other genera or families or should be reevaluated. *Zanthopsis peytoni* Stenzel and *Z. carolinensis* Rathbun may be compared with members of the genus *Harpactocarcinus* A. Milne Edwards. *Zanthopsis terryi* Rathbun and *Zanthopsis rathbunae* Maury were removed to the genus *Eriosachila* Blow and Manning by Blow and Manning (1996; Blow, personal communication, 1998). Both *Z. cretacea* Rathbun and *Z. kressenbergensis* Meyer possess a long lateral spine, which is not characteristic of members of either *Zanthopsis* sensu stricto or *Pulalius*, suggesting that their generic placement should be reconsidered.

Possession of a vaulted carapace with inflated regions; very small, blunt anterolateral teeth; a relatively simple arrangement of regions; and a distinctive transverse epibranchial ridge set *Pulalius* apart from all other members of the Xanthidae. Some other xanthid genera possess a more or less well-developed transverse ridge, and these were assigned to the subfamily Menippinae Ortmann by Sakai (1976). These genera include *Ozius* H. Milne Edwards, *Pseudozius* Dana, *Sphaerozius* Stimpson, and *Lydia* Gistel. However, members of this subfamily possess several characteristics that cannot accommodate *Pulalius*, including a carapace that is significantly wider than long or nearly circular instead of ovate-hexagonal as seen in *Pulalius*, carapace regions that are much less inflated than *Pulalius*, carapaces that are much less vaulted than *Pulalius*, more and larger anterolateral teeth than *Pulalius*, a branchial ridge that ends in the penultimate tooth instead of the last anterolateral tooth as in *Pulalius*, and better developed anterolateral and frontal teeth than in *Pulalius*.

Other families contain genera with transverse ridges on the dorsal carapace, but none can accommodate *Pulalius*. Members of the Portunidae typically possess a transverse ridge on the dorsal carapace, but portunids usually have a flattened dorsal carapace, a dentate front, and a dentate anterolateral margin with at least three well-developed spines; these characteristics are not seen in *Pulalius*. Further, in all but one subfamily of the Portunidae, the dactylus of the fifth pereiopod is paddlelike. In the new species to be described below, the dactylus of the fifth pereiopod is long and lanceolate.

The Retroplumidae Gill have transverse carapace ridges, but they are of an altogether different placement and conformation. Retroplumids have extremely wide orbits, a narrow front, and a flattened carapace, none of which are characteristic of *Pulalius*. Additionally, the carapace regions of *Pulalius* have an overall different conformation than members of the Retroplumidae.

Pulalius vulgaris appears to be superficially similar to some members of the Goneplacidae Dana. Goneplacids typically possess a quadrate carapace, a straight front, and a flattened dorsal carapace (Williams, 1984; Tucker and Feldmann, 1990), which are not characteristic of *Pulalius*. However, distinguishing between the Xanthidae and the Goneplacidae can be extremely difficult. Tucker et al. (1994) described sternal characteristics that can sometimes be used to distinguish between xanthids and goneplacids. In typical xanthids and some goneplacids, the sternum is narrow and the eighth thoracic sternite is not visible because the abdomen obscures it. In other goneplacids, the sternum is wider and a small part of the eighth sternite is therefore visible in ventral view (Tucker et al., 1994). The goneplacid species *Branchioplax washingtoniana* Rathbun, also known from Tertiary deposits of Washington, displays a conformation of the carapace regions that is very similar to that seen in *Pulalius vulgaris*. The sternum of *Branchioplax washingtoniana* is also xanthidlike because the eighth sternite is not visible in ventral view, and therefore cannot be used to distinguish between the two taxa. However, *Pulalius vulgaris* possesses a distinctly four-lobed front, inflated carapace regions, a rounded carapace, and a highly vaulted carapace, distinguishing it from *Branchioplax washingtoniana*, which has a straight front, flattened carapace regions, and a carapace that is rounded-hexagonal in shape. *Pulalius* can be differentiated from members of the goneplacid genus *Speocarcinus* Stimpson because the latter has a much less vaulted carapace, less inflated carapace regions, and a more square carapace. Additionally, *Speocarcinus* exhibits a distinctly goneplacidlike sternum in which the eighth sternite is clearly visible on either side of the abdomen, while *Pulalius* exhibits a typically xanthidlike abdomen and sternum. In summary, use of the sternum to differentiate between members of the Xanthidae and Goneplacidae must be used with extreme caution because the method does not work in all cases.

The new genus ranges from late Eocene to Oligocene rocks in British Columbia, Washington, and Oregon (Rathbun, 1926; Berglund, personal records). According to Berglund, members of the genus have been found in several rock units including the late Eocene Keasey Formation (Armentrout, 1987; Snavely, 1987), the late Eocene to early Miocene Lincoln Formation (Rau, 1964; Prothero and Armentrout, 1985; Armentrout, 1987; Babcock et al., 1994), the Oligocene Blakely and Marrowstone formations (Armentrout and Berta, 1977), the Eocene to Oligocene Makah Formation (Snavely et al., 1980), the Eocene ?Aldwell Formation at Pulali Point, Washington (Squires et al., 1992), and the Oligocene of Nootka Island, British Columbia (Jeletzky, 1973).

Pulalius dunhamorum, **new species**
(Fig. 9–11)

Diagnosis.—Carapace ovate; anterolateral and posterolateral margins convex, posterolateral margins especially so; regions inflated, especially the branchial regions; epibranchial region with prominent inflated ridge extending from last anterolateral spine to axial area; anterolateral teeth small, blunt, rounded.

Description.—Carapace ovate in outline, wider than long, maximum width about 1.2 times length, widest between last anterolateral spine, position of maximum width approximately 50% total length. Carapace strongly vaulted longitudinally, moderately vaulted transversely, vaulting most extreme at posterior part of mesogastric region.

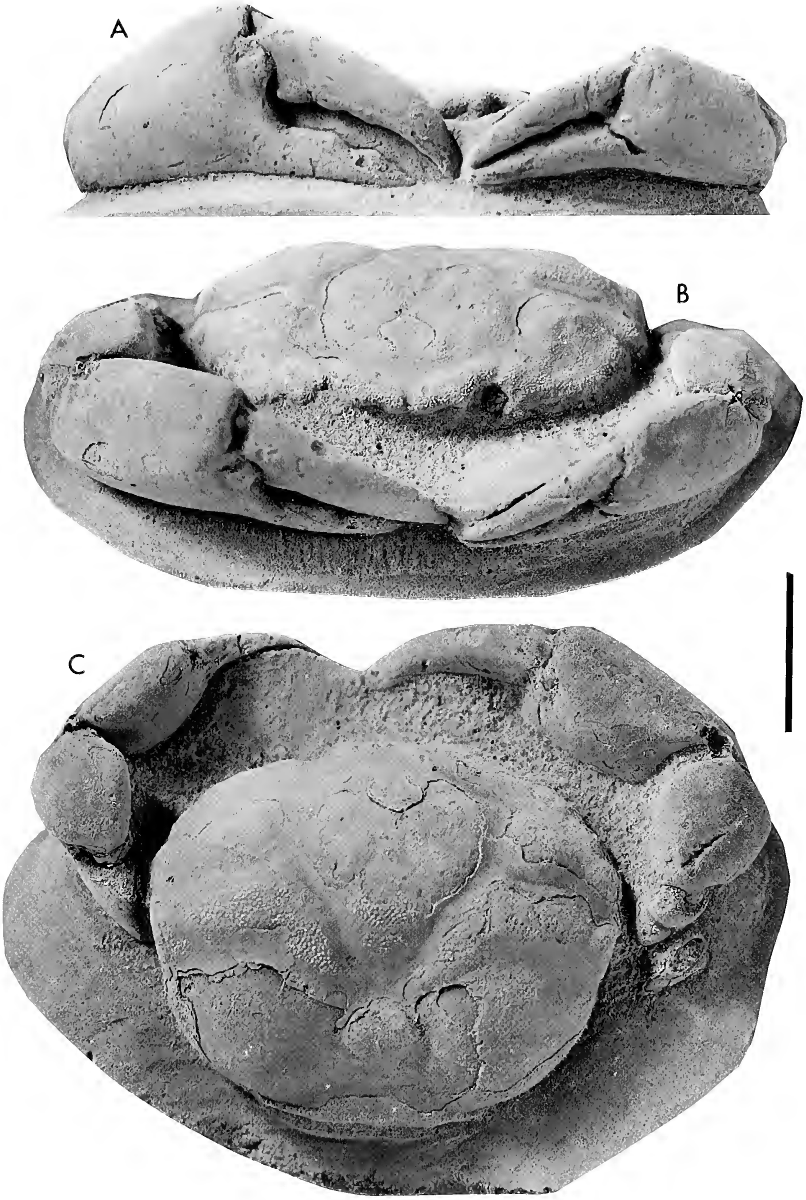


Fig. 9.—*Pulalius dunhamorum* new species, holotype, CM 45837. A. Anterior view showing chelipeds. B. Oblique anterior view showing orbits. C. Dorsal carapace. Scale bar = 1 cm.

Front approximately 0.25 maximum carapace width, produced beyond orbital teeth, sinuous in antero-oblique view, margin downturned; bearing four small, blunt teeth, outer teeth rounded, inner teeth small, rounded, closely spaced, separated by narrow, V-shaped medial notch, base of notch extending posteriorly into narrow sulcus. Orbits small, deep, slightly ovate in anterior view, directed forward and slightly upward; eyestalks appear to fill orbits; supraorbital margins raised with one closed fissure near midpoint.

Anterolateral margins with flanks turned under, very thick, sides nearly vertical at maximum width of carapace, becoming less so toward anterior; convergent anteriorly. Anterolateral margin bearing

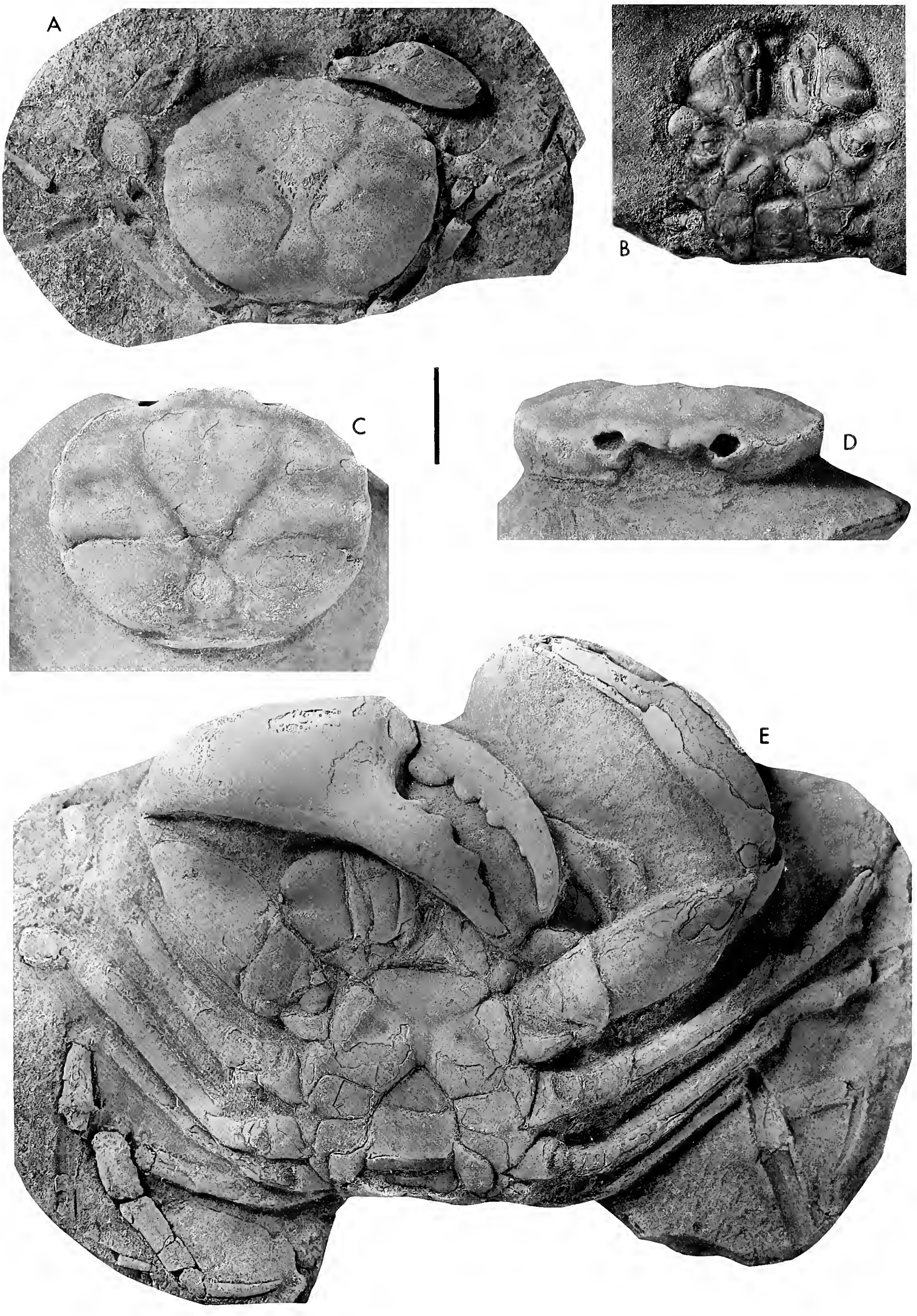


Fig. 10.—*Pulalius dunhamorum* new species. A. Dorsal carapace, CM 45840. B. Ventral surface of carapace, CM 45844. C. Dorsal carapace, CM 45839. D. Anterior view showing orbits, CM 45839. E. Venter and appendages, CM 45838. Scale bar = 1 cm.

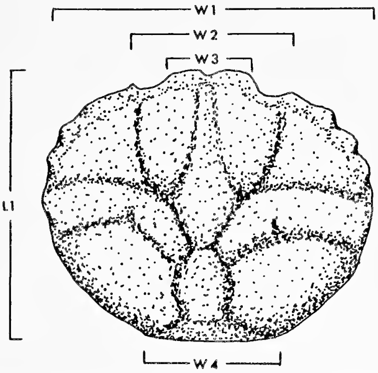


Fig. 11.—Line drawing of *Pulalius dunhamorum* showing position and orientation of measurements taken.

three blunt nodes; largest node at anterolateral angle located at termination of broad epibranchial ridge; nodes 1 and 2 smaller than third; nodes 1 and 2 separated by small triangular notch; nodes 2 and 3 separated by broad, shallow notch; nodes separated from extra-orbital angle by sinuous area, sometimes bearing one small, very blunt node. Posterolateral margins convex; posterior margin nearly straight, approximately 0.50 maximum carapace width.

Regions well defined by grooves; carapace surface finely granular except in grooves. Epigastric region small, weakly inflated; protogastric region longer than wide, separated from front by shallow postorbital furrow, narrowing distally into triangular point; hepatic region inflated, possessing bulbous swelling medially and flattening towards anterolateral margin; mesogastric region narrow anteriorly, widening posteriorly into a triangular area, lateral margins concave, posterior margin convex; urogastric region deeply depressed, narrowing distally, lateral margins very concave, highly restricted centrally; cardiac region moderately inflated, defined laterally by deep branchiocardiac grooves, narrowing distally, anterior portion of region most inflated and bearing two transverse pits; intestinal region poorly defined, flattened, broad, extending to posterolateral corner.

Cervical groove deep, well defined, interrupted axially by urogastric region; broad and shallow along anterior margin of epibranchial ridge, ending at base of second anterolateral node; branching at distal end into two short grooves anteriorly and posteriorly around second anterolateral node; posterior branch terminating at carapace margin between second and third anterolateral nodes; anterior branch extending through notch separating first and second anterolateral node onto subhepatic region.

Epibranchial region marked by prominent, inflated, arcuate, transverse ridge; extending from third anterolateral node anteriorly and then sharply posteriorly, terminating at lateral margin of urogastric region in sharp triangle. Branchial region strongly inflated, pentagonal, accentuating broadly rounded posterolateral margin of carapace.

Abdominal somites 1 and 2 approximately equal in width, somite 2 about twice as long as somite 1, lower margin of somite 2 convex, lower margin slightly sinuous; somite 3 widest of all somites, about 0.3 maximum carapace width, lateral corners rounded, upper margin slightly sinuous, posterior margin weakly concave; somites 4 and 5 about twice as wide as long; somite 4 slightly wider than somite 5, somite 4 widening posteriorly, lateral margins of somites 4 and 5 weakly concave, upper and lower margins of somite 4 and 5 nearly straight; somite 6 1.5 times as wide as long, margins nearly straight; telson equilaterally triangular, apices rounded; weak axial ridge extending from somites 1–6.

Sternum slightly longer than wide, widest at sternite 6, ovate; sternites 1 and 2 form equilateral triangle, surface weakly inflated, lateral margins slightly concave, apex sharp; sternite 3 with sinuous upper margin, lateral margins rounded, posterior margin converging distally, broad sulcus axially; sternite 4 with very concave anterior and posterior margins, with central and lateral depressions, blunt episternal projections; sternite 5 wider than sternite 4 and widest of all sternites, directed anterolaterally, upper and lower margins nearly straight, possessing sharp episternal projections; sternite 6 widening distally, directed slightly anterolaterally, upper and lower margins straight, with sharp episternal projections; sternite 7 directed slightly posterolaterally, upper and lower margins nearly straight, widening distally, with sharp episternal projections; sternite 8 about as wide as long, appearing to possess weak episternal projections, not well known; surface of all sternites granular.

Table 4.—*Measurements (in mm) taken on the dorsal carapace of specimens of* Pulalius dunhamorum. *Orientation of measurements is illustrated in Figure 11. L1 = maximum length, W1 = maximum width, W2 = fronto-orbital width, W3 = frontal width, W4 = posterior width.*

Specimen number	W1	W2	W3	W4	L1
CM 45837	36.5	16.0	9.2	17.0	29.7
CM 45845	36.0	17.6	—	15.6	30.3
CM 45839	32.6	14.8	8.2	14.1	27.1
CM 45844	26.0	12.5	7.6	12.6	21.6
CM 45843	36.1	17.0	9.4	8.6	30.0
CD 45838	46.8	—	—	17.3	38.8
CM 45842	31.7	14.8	8.6	14.0	28.3
CM 45840	27.9	13.0	7.0	12.8	23.2
CM 45841	36.7	17.7	9.3	13.2	31.1

Pterygostomial region triangular, incised by broad shallow groove extending from notch separating first and second anterolateral nodes; exopod of third maxilliped much longer than wide, outer margins nearly straight, widening slightly posteriorly, then converging to triangular point at posteriormost end; ischium of endopod somewhat longer than wide, upper margin nearly straight, outer margin slightly concave, inner margin weakly convex, lower margin weakly concave, narrow sulcus located about one-third the distance distally from inner margin; basis triangular, widening anteriorly.

Chelipeds unequal, both robust. Carpus of major cheliped longer than high, widening distally, distal margin nearly straight, upper margin very convex, lower margin concave, tapering to very narrow proximal margin, bulbous. Merus of major cheliped longer than high, lower margin weakly convex, appearing to be rather bulbous. Manus of major cheliped widening distally; lower margin extending nearly straight, then extending obliquely at propodus; outer surface highly vaulted transversely and longitudinally; upper margin weakly rounded, small blunt tooth at proximal corner; proximal margin sinuous, with broad inflated area centrally and blunt tooth at intersection with lower margin; distal margin sinuous, with trapezoidal projection centrally, distal margin extending obliquely between upper and lower margins.

Fixed finger of major cheliped slightly deflected; occlusal surface with four large, blunt teeth, first and third approximately equal in size, second largest and broadly triangular, fourth smallest, remainder of occlusal surface with small denticles; widest proximally and narrowing distally, tip upturned slightly, outer surface with setal pits arranged linearly below denticles, denticles also with setal pits.

Movable finger of major cheliped highly arched; narrowing distally; occlusal surface bearing at least three teeth, first tooth wide, blunt; second and third bluntly triangular, second larger than third, remainder of occlusal surface smooth or with small denticles. Each finger more darkly pigmented than remainder of carapace.

Minor chela similar in shape to major chela except not as bulbous and with more slender fingers; finger more weakly arched.

Basis of pereiopod 2 tubular; higher than long; merus much longer than high; carpus appearing to be longer than high. Basis of pereiopod 3 tubular, higher than long, distal margin concave; merus much longer than high, surface granular; ischium slightly longer than high; carpus longer than high, widening distally; manus longer than high. Basis of pereiopod 4 tubular, higher than long, distal margin concave; ischium not well known; merus much longer than high; carpus longer than high, widening distally. Basis and ischium of pereiopod 5 not known; merus much longer than high; carpus somewhat longer than high; propodus longer than high; dactylus much longer than high, lanceolate, tapering to sharp point distally.

Measurements.—Measurements of the dorsal carapace are given in Table 4, and orientation of measurements is illustrated on Figure 11. Measurements of the venter are given in Table 5, and measurements of the major and minor chelae are given in Table 6.

Types.—The holotype, CM 45837, and paratypes, CM 45838–45846, are deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Etymology.—The specific name honors Mr. and Mrs. George Dunham of Brinnon, Washington, who

Table 5.—*Measurements (in mm) taken on the sternum of specimens of* Pulalius dunhamorum. *L = length, W = width.*

Specimen number	Max. L of sternum	Max. W of sternum	Max. W of abdomen	Max. L of abdomen	W-telson
CM 45844	15.2	13.7	—	—	—
CM 45840	>14.2	14.5	8.7	9.1	5.0
CM 45838	27.8	22.8	14.2	13.1	8.1

kindly allowed collecting on their property and access to the cobble beaches of Pulali Point, Washington.

Remarks.—Ten specimens are herein referred to this species. The specimens are extremely well preserved, with some retaining cuticular material. At least three of the specimens appear to be corpses, based upon their possession of the venter, but others may also be corpses based upon retention of the chelae. All of the specimens were preserved in concretions. The nine specimens of *Pulalius dunhamorum* exhibit a range of variation in some characteristics. For example, some specimens, CM 45838 and CM 45842, possess a somewhat more hexagonal carapace than the other specimens. Additionally, the development of the anterolateral teeth ranges from weak to extremely reduced or almost nonexistent.

Pulalius dunhamorum can be differentiated from the only other species in the genus, *P. vulgaris*, in several ways. *Pulalius dunhamorum* possesses a more linear, well-developed epibranchial ridge while that of *P. vulgaris* is arcuate and discontinuous. The posterolateral margins of *P. dunhamorum* are shorter and much more convex and the anterolateral margins are also more convex than those of *P. vulgaris*. The carapace of *P. dunhamorum* is not as highly vaulted longitudinally and the anterolateral spines are not as well developed as in *P. vulgaris*. The urogastric region is more depressed in *P. dunhamorum* than in *P. vulgaris*. The overall shape of *P. dunhamorum* is rounder and more ovate than that of *P. vulgaris*, which has a more hexagonal carapace.

The new species has been reported only from the Pulali Point locality.

Family Carpiliidae Ortmann, 1893

Remarks.—Traditionally, *Carpilius* Leach, 1823, has been referred to the Xanthidae (Rathbun, 1930; Glaessner, 1969; Sakai, 1976; Manning and Holthuis, 1981; Dai and Yang, 1991). However, Guinot (1978) presented compelling arguments for separation of *Carpilius* and the related genera, *Palaeocarpilius* A. Milne Edwards, 1862, and *Ocalina* Rathbun, 1929, into a separate family, the Carpiliidae. We concur. In that same year, Collins and Morris (1978) also referred to the Carpiliidae and assigned two new species from Pakistan to their new genus

Table 6.—*Measurements (in mm) taken on the major and minor chelae of* Pulalius dunhamorum. *L = length.*

Specimen	Height	Length	L-Movable finger	L-Palm
CM 45838	19.0	40.4	26.2	29.2
CM 45837	>11.0	>30.0	19.7	23.1
CM 45845	12.3	27.7	16.8	20.8
CM 45838 (minor)	13.0	32.4	19.0	22.6
CM 45837 (minor)	10.4	25.7	15.4	17.7

Proxicarpilius Collins and Morris, 1978. To these four genera must be added *Eocarpilius* Blow and Manning, 1996 and *Harpactoxanthopsis* Via, 1959.

The characters of the dorsal carapace which unite these genera include a generally oval outline which is wider than long. The front is downturned and is either simple and triangular or undulatory, with a pair of inner orbital projections and a pair of generally smaller projections on either side of a shallow axial depression. The orbits are small, entire, and circular. The anterolateral margin may be smooth or may bear one or more blunt projections. The anterolateral corner is unmodified in some and bears a blunt projection extending onto the carapace as a subtle ridge on others. The carapace surface is generally smooth, the carapace regions are weakly defined or not discernable, and the carapace is strongly vaulted longitudinally. The characters of the appendages, sternum, and other features that define the family are given by Guinot (1978).

Genus *Carpilius* Leach *in* Desmarest, 1823

Type Species.—*Cancer maculatus* Linnaeus, 1758.

Remarks.—The Carpiliidae includes four genera known only from the fossil record and a single genus, *Carpilius*, that ranges into the Recent. The genera are distinguished from one another on the basis of the configuration of the front and on the nature of the anterolateral margin. In these regards, the specimens from Pulali Point must be assigned to *Carpilius*. The front bears four projections that extend forward and downward, very much like those of the type species, *C. maculatus*. The anterolateral margin is generally unmodified, although there is a very subtle angulation just in advance of the projection defining the anterolateral corner. The form of the anterolateral corner and the ridge projecting onto the carapace surface is nearly identical to those developed on extant species.

Recognition of the Pulali Point specimens as representatives of *Carpilius* provides the first authentic documentation of that genus in the fossil record. Although specimens from the Miocene of central Europe have previously been assigned to *Carpilius* (Müller, 1984), that species, *C. antiquus* Glaessner, 1928, has subsequently been assigned to *Eocarpilius* (Feldmann et al., 1998). Karasawa (1993) reported *Carpilius* from Miocene rocks of southwestern Japan, but that occurrence was based only upon a portion of a manus. Thus, the geologic range of *Carpilius* has been extended from Eocene to Recent.

Carpilius occidentalis, **new species**
(Fig. 12, 13)

Diagnosis.— Typical-sized *Carpilius* with subtle swelling on anterolateral margin just in advance of well-defined prominence on anterolateral corner; straight posterolateral margin as long as anterolateral margin. Gastric region weakly defined, branchiocardiac groove well defined for genus.

Description.—Moderate-sized carpiliid; carapace width approximately 1.4 times length, ovoid outline, flattened transversely, strongly arched longitudinally, regions weakly defined.

Front about 0.24 maximum width, downturned, bilobed axially, bounded by rounded inner orbital projections. Orbits smoothly rounded, complete, with subtle orbital rim. Fronto-orbital margin about equal in width to posterior margin, approximately 0.43 maximum width. Anterolateral margin smooth, with subtle rim, curvature increasing toward anterolateral corner which is marked by a swollen prominence extending onto carapace as a faint ridge. Less distinct swelling developed on anterolateral margin in advance of anterolateral corner. Maximum width developed at anterolateral corner situated

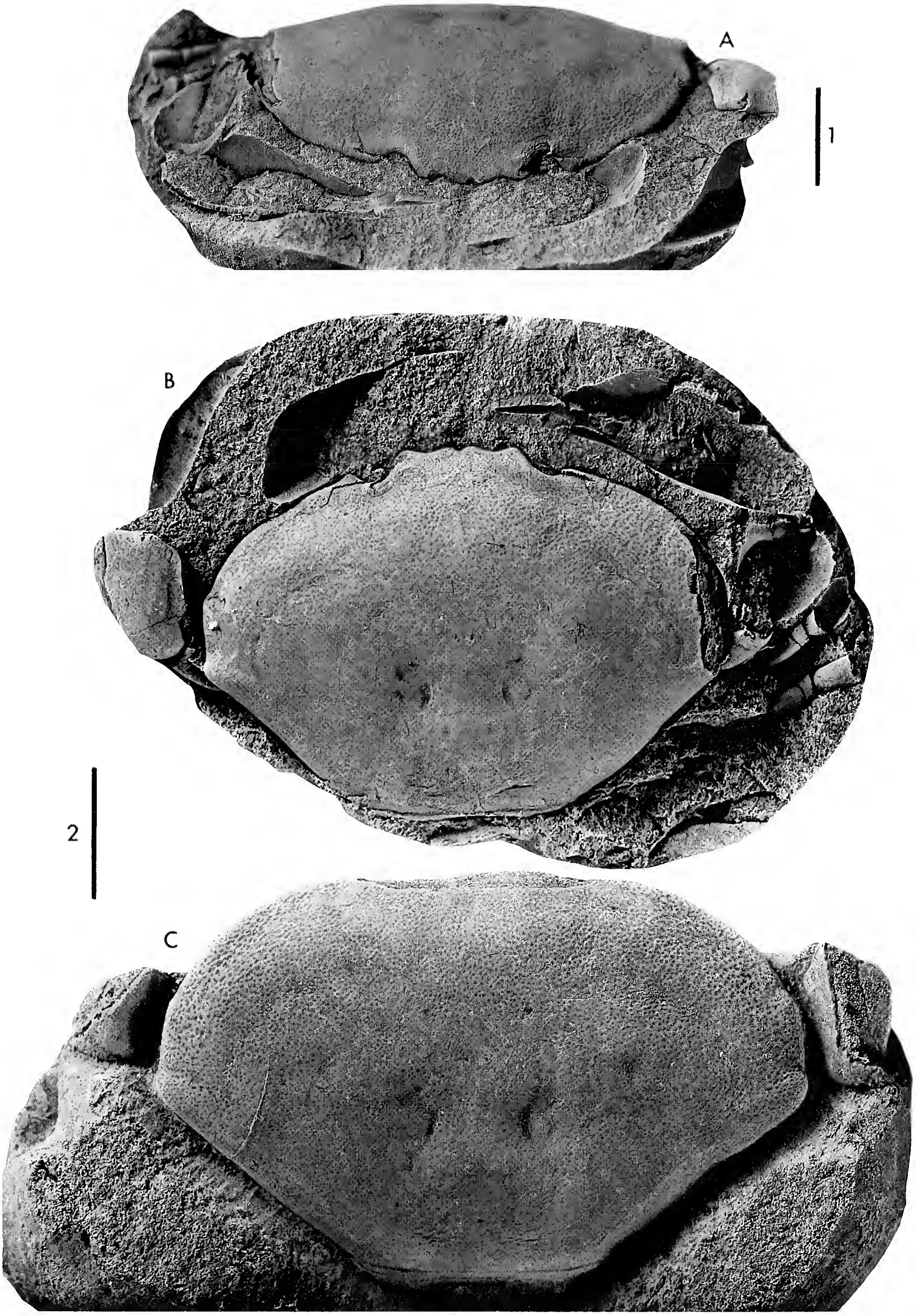


Fig. 12.—*Carpilius occidentalis* new species. A. Anterior view, holotype, CM 45847. B. Dorsal carapace, holotype, CM 45847. C. Dorsal carapace, CM 45848. Scale bar 1 for A and B and scale bar 2 for C. Scale bars = 1 cm.

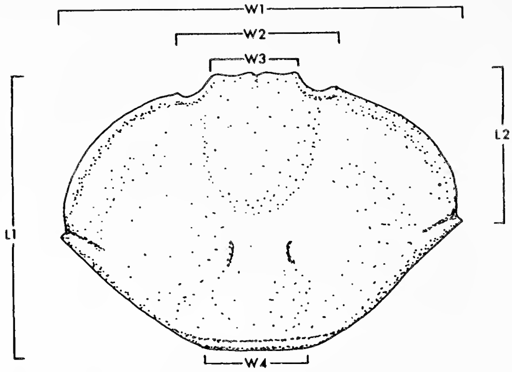


Fig. 13.—Line drawing of *Carpilius occidentalis* showing position and orientation of measurements taken.

at point about 0.66 maximum length. Posterolateral margin straight, intercepting straight posterior margin at about 140° angle. Posterior margin with narrow, distinct rim.

Carapace regions poorly defined as broadly domed surfaces and shallow grooves. Gastric region longer than wide, bounded by very shallow parabolic groove. Urogastric region about 0.13 maximum width, well defined by narrow, arcuate grooves laterally. Cardiac region about 0.24 maximum width, widest near anterior, tapering to indistinct intestinal region. Hepatic region separated from smooth branchial region by depression paralleling anterolateral margin.

Carapace surface with fine setal pits, more numerous and larger along anterior and anterolateral margins.

Measurements.—Measurements taken on specimens of *Carpilius occidentalis* are given in Table 7, and the orientation of those measurements is shown in Figure 13.

Types.—The holotype, CM 45847, and paratype, CM 45848, are deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Etymology.—The species takes its trivial name from its occurrence on the eastern Pacific rim.

Remarks.—Two specimens from the Pulali Point region can be referred to this species. Both are extremely well preserved; however, the front is broken away on the paratype. Fragments of the proximal elements of the pereiopods are preserved as is a portion of the right cheliped on the holotype. Unfortunately, preservation of this element is not sufficient to permit a good description. The ventral surface of this crab remains unknown.

Comparison with extant species within the genus permits distinguishing the Eocene form as a new species. The anterolateral corner of *C. occidentalis* is

Table 7.—*Measurements (in mm) taken on the dorsal carapace of specimens of* Carpilius occidentalis. *Position and orientation of measurements is illustrated in Figure 13. L1 = maximum length, L2 = length to maximum width, W1 = maximum width, W2 = fronto-orbital width, W3 = frontal width, W4 = posterior width.*

Specimen number	L1	L2	W1	W2	W3	W4
CM 45847	31.5	20.5	44.2	18.0	10.7	19.0
CM 45848	36.0	21.0	55.7	—	—	22.0

situated at about the midlength, and the posterolateral margins converge posteriorly to form an angle of about 98°. In all of the living species, the anterolateral corner is positioned in the posterior half of the carapace, and the posterolateral margins converge at angles between 110–118°. The curvature of the anterolateral margin of *C. occidentalis* is very much like that of *C. convexus* (Forskål); however, the point of inflection on the former species is a moderately well-defined prominence whereas none is present on *C. convexus*. The front on *C. occidentalis* bears four lobes, the axial pair being only slightly smaller than the inner orbital lobes. The axial region of *C. corallinus* (Herbst) is not bilobed; that region on the other two species is bilobed but the axial lobes are markedly smaller than the inner orbital lobes. The overall carapace surface is very smooth on all living species except *C. convexus*. On that species, the branchiocardiac groove is evident as a subtle demarkation that can be discerned between the gastric regions and the branchial regions. That same level of development is present on *C. occidentalis*.

In summary, the carapace morphology within the Carpiliidae has remained relatively conservative since the appearance of the family in the Eocene. The number of genera assigned to the family was greatest in the Eocene and has been reduced, possibly to a single genus, *Carpilius*, in modern environments. Sakai (1976) placed *Liagore* de Haan, 1833, with *Carpilius* in the Alliance Carpilioida. Guinot (1978), however, rejected that association and *Liagore* will be retained in the Xanthidae sensu lato until specimens can be examined in the light of the familial characters designated by Guinot.

Family Goneplacidae Macleay, 1838

Genus *Branchioplax* Rathbun, 1916

Branchioplax washingtoniana Rathbun, 1916

(Fig. 14A)

Branchioplax washingtoniana Rathbun, 1916:344. Rathbun, 1926:42, plate 9, fig. 6; Tucker and Feldmann, 1990:415, fig. 6, 7.1, 7.3.

Material Examined.—CM 45849–45851, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—The Pulali Point specimens are referred to this taxon based on their possession of a relatively square, equidimensional carapace; anterolateral teeth; well-defined regions, inflated branchial regions; and a straight front. The specimens conform well to the descriptions of the species provided by Rathbun (1916, 1926) and Tucker and Feldmann (1990).

Genus *Neopilumnoplax* Serène *in* Guinot, 1969

Neopilumnoplax hannibalanus (Rathbun, 1926)

(Fig. 14C)

Pilumnoplax hannibalanus Rathbun, 1926:37, 39, plate 10, fig. 1–4.
Neopilumnoplax hannibalanus (Rathbun): Tucker and Feldmann, 1990:418, fig. 7.2, 7.4, 8.

Material Examined.—CM 45855–45869, CM 45901, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—The Pulali Point specimens are referred to *Neopilumnoplax hannibalanus* based upon their possession of a straight front, flattened carapace, well-developed anterolateral teeth, prominent midorbital suture, arcuate posterolateral margins, and coalesced first and second anterolateral teeth. The specimens con-

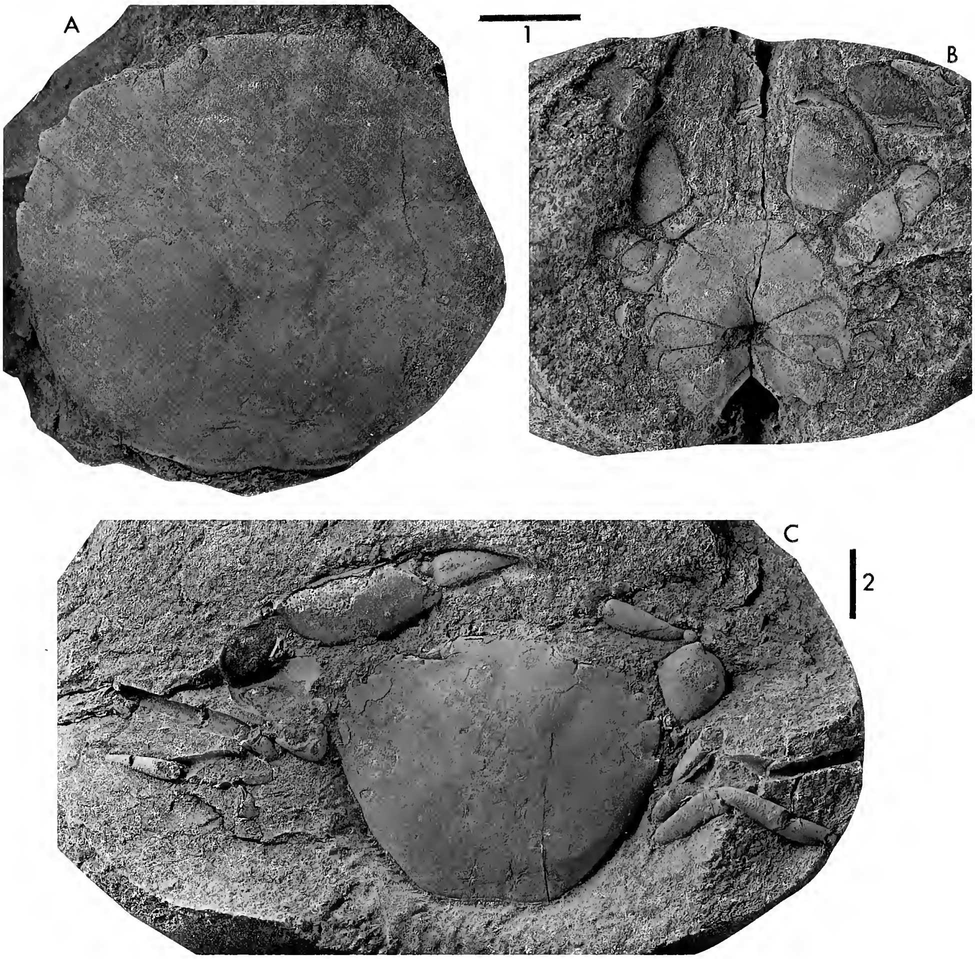


Fig. 14.—A. *Branchioplax washingtoniana* Rathbun, CM 45850. B. Venter of unknown goneplacid, CM 45852. C. *Neopilumnoplax hannibalanus* (Rathbun), CM 45855. Scale bar 1 for A and B and Scale bar 2 for C. Scale bars = 1 cm.

form very well to both Rathbun's (1926) description and the emended description of the species provided by Tucker and Feldmann (1990).

Differentiating between *Branchioplax washingtoniana* and *Neopilumnoplax hannibalanus* can be extremely difficult, as has been addressed by Tucker and Feldmann (1990). They suggested that *N. hannibalanus* has more posteriorly convergent posterolateral margins and more poorly marked regions than *B. washingtoniana*. Additionally, *B. washingtoniana* possesses much more inflated branchial regions than does *N. hannibalanus*, which provides the best means of differentiating the two taxa. *Neopilumnoplax hannibalanus* appears to have sharper, better developed anterolateral teeth than does *B. washingtoniana*, but this characteristic does not always hold and should be used with caution.

As has been discussed above, Tucker et al. (1994) provided a means by which some goneplacids could be distinguished from xanthids. Three of the goneplacid specimens in this study, CM 45852–45854, possess well-preserved sterna, and on these specimens, the eighth sternite is clearly obscured by the abdomen (Fig. 14B). Unfortunately, none of the three specimens exhibits dorsal carapace material, making them impossible to assign to a genus or species. However, the sterna correspond very closely to those illustrated by Tucker and Feldmann (1990) as belonging to the two species *Branchioplax washingtoniana* and *Neopilumnoplax hannibalanus*. Tucker and Feldmann (1990) suggested that the two taxa differ in the conformation of the sixth abdominal somite which has convex sides in *Branchioplax washingtoniana* and straight or concave sides in *Neopilumnoplax hannibalanus*. This character was not useful in assigning the three venters to a taxon, because the lateral margins are intermediate between the two conditions.

Section Thoracotremata Guinot, 1977
Superfamily Hexapodoidea Miers, 1886
Family Hexapodidae Miers, 1886

Remarks.—The Hexapodidae was raised to family level by Manning and Holthuis (1981) based upon the possession of three pairs of walking legs in this group instead of four as in other decapod families. They considered the Hexapodidae to be closely related to the Goneplacidae (Manning and Holthuis, 1981). In addition to loss of the fifth pereiopod, the eighth sternite is much reduced and is hidden by the seventh sternite and the posterior margin of the dorsal carapace (Gordon, 1971). Genera within the Hexapodidae are distinguished by the shape and degree of fusion of the abdomen, form of the third maxillipeds, shape of the eye, development of the sternal grooves of the abdomen, and the structure of the male pleopod (Manning and Holthuis, 1981). The specimens from Pulali Point are referred to the Hexapodidae because they possess four pairs of pereiopods and have no evidence of an eighth sternite.

Extant genera of the Hexapodidae include *Hexapinus* Manning and Holthuis, *Hexaplax* Doflein, *Hexapus* de Haan, *Lambdophallus* Alcock, *Paeduma* Rathbun, *Parahexapus* Balss, *Pseudohexapus* Monod, *Spiroplax* Manning and Holthuis, *Stevea* Manning and Holthuis, *Thaumastoplax* Miers, and *Tritoplax* Manning and Holthuis. Genera described from the fossil record include *Goniocypoda* Woodward, *Thaumastoplax*, *Hexapus*, *Stevea*, and *Prepaeduma* Morris and Collins. *Prepaeduma* possesses five pereiopods; Morris and Collins (1991) considered it to be an ancestor to *Paeduma* in which the fifth pereiopod was not yet fully suppressed. Beschin et al. (1994) doubted its placement in the Hexapodidae based upon its possession of five pairs of pereiopods; reevaluation of that genus by two of the authors (Schweitzer and Feldmann) is in progress.

Fossil hexapods have not previously been reported from North America. Fossil species of *Palaeopinnixa*, with the referral of several species to that genus to be discussed below, have been reported from Spain, Panama, Peru, Trinidad, and Argentina, (Rathbun, 1918; Woods, 1922; Via, 1966; Collins and Morris, 1976; Feldmann et al., 1995). *Hexapus nakajimai* Imaizumi has been described from the Miocene of Japan (Imaizumi, 1959), and *Hexapus pinfoldi* Collins and Morris has been reported from Pakistan (Collins and Morris, 1978). At least eight species of the hexapod genus *Goniocypoda* have been reported from England, Europe, Africa, and India (Woodward, 1867; Bittner, 1893; Carter, 1898; Glaessner, 1933; Remy and Tessier, 1954; Secretan, 1971; Crane, 1981; Crane and Quayle, 1986). The genus *Stevea* has been reported from the Eocene of Italy (Beschin et al., 1994).

Genus *Palaeopinnixa* Via, 1966

Type Species.—*Palaeopinnixa rathbunae* new name for *Pinnixa eocenica* Rathbun, 1926, by original designation. Via (1966) designated *Pinnixa eocenica* Rathbun, 1926 as the type species of his new subgenus *Pinnixa* (*Palaeopinnixa*). However, the referral herein of both *Thaumastoplax eocenica* Woods, 1922 and *Pinnixa eocenica* Rathbun, 1926 to *Palaeopinnixa* makes *Pinnixa eocenica* Rathbun a junior homonym. Therefore, the substitute name, *Palaeopinnixa rathbunae* is provided for Rathbun's (1926) species, which remains the type species for the genus as designated by Via (1966).

Included Species.—*Palaeopinnixa rathbunae* Rathbun, 1926 (formerly *Pinnixa eocenica*); *P. eocenica* Woods, 1922 as *Thaumastoplax*; *P. intermedia* (Collins and Morris, 1976), as *Thaumastoplax*; *P. mytilicola* Via, 1966; *P. perornata* Collins and Morris, 1976 (In the title for the original species description, the trivial name was erroneously spelled *porornata*. Derivation of the name as well as consistent spelling as *perornata* throughout the text indicate that *perornata* was the intended trivial name.); *P. prima* (Rathbun, 1918), as *Thaumastoplax*; *P. rocaensis* (Feldmann et al., 1995), as *Thaumastoplax*.

Diagnosis.—Carapace wider than long, length to width radio about 0.67, carapace widest just anterior to posterolateral reentrants; carapace rounded rectangular to ovoid, narrowing weakly anteriorly; carapace regions distinct; front widened distally, extending well beyond orbits, axially sulcate, frontal width to fronto-orbital width ratio about 0.42; orbits wider than high, with sinuous upper margins, moderately deeply excavated, fronto-orbital width to width ratio about 0.55; lateral rim absent or weakly developed; posterolateral reentrant well-developed; posterolateral width to maximum width ratio about 0.80; fronto-orbital width to posterior width ratio about 0.55; abdominal somites 3–5 fused in males; fourth sternite with anterior projections; third pereiopod longest.

Material Examined.—*Thaumastoplax intermedia*, In.60008 (holotype); *T. prima*, USNM 324227 (holotype); USNM 324228 (paratype); *T. eocenica* Woods, SM C 1394 (holotype); *Pinnixa (Palaeopinnixa) perornata*, In.61361 (holotype); *T. rocaensis*, GHUNLPam 7006 (holotype); GHUNLPam 7007–7009, 7026, 7027.

Discussion.—Via (1966) erected the subgenus *Palaeopinnixa* to embrace the new species *Pinnixa* (*Palaeopinnixa*) *mytilicola* as well as *Pinnixa eocenica* Rathbun which was designated as the type species for the subgenus. Newly collected specimens referrable to *Pinnixa eocenica* sensu Rathbun, described herein, possess four pairs of pereiopods and seven sternites; therefore, the subgenus *Palaeopinnixa* is removed from *Pinnixa* and the Pinnotheridae and is elevated to generic status. Because of the homonymy discussed above, the type species for the genus is *Palaeopinnixa rathbunae* new name.

Four fossil species previously assigned to *Thaumastoplax*, *T. intermedia*, *T. prima*, *T. eocenica* Woods, and *T. rocaensis*, are clearly congeneric with *Palaeopinnixa rathbunae* and *Pinnixa* (*Palaeopinnixa*) *mytilicola* and are therefore assigned to *Palaeopinnixa*. These fossil species possess all of the diagnostic characters of *Palaeopinnixa* including a rounded to ovoid carapace, distinct carapace regions, a front that is flared and axially sulcate, a well-developed posterolateral reentrant, and a posterior width-to-width ratio of about 0.80.

The new specimens cannot be referred to any of the genera previously known from the fossil record. Members of the genus *Goniocypoda* possess an extremely wide fronto-orbital margin which occupies more than 0.60 the maximum carapace width. Members of that genus also possess an extra-orbital tooth that can range from small to large; the fossils described here do not possess an extra-orbital tooth and have a fronto-orbital width to maximum width ratio of approximately 0.44. In the genus *Hexapus*, individuals possess deep sternal grooves, which the fossils here referred to *Palaeopinnixa* do not possess. Members of the genus *Stevea* have stridulating ridges on the pterygostomial region and exhibit fusion of somites 2–6; neither condition is exhibited on the new specimens.

The new specimens can be easily differentiated from most extant genera of the Hexapodidae. The sole extant species of *Thaumastoplax* has much smaller orbits and rostrum, a rectangular carapace, a convex posterolateral margin, and poorly defined carapace regions which clearly distinguish it from species of *Palaeopinnixa*. Members of *Lambdophallus* possess a well-developed sternal groove, which species of *Palaeopinnixa* do not possess. In the genus *Paeduma*, individuals exhibit fusion of somites 3 and 4 and somites 5 and 6, a pattern not seen in the Pulali Point specimens. Members of the two genera *Parahexapus* and *Pseudohexapus* possess a ridge that parallels the lateral margin of the carapace, a characteristic not seen in the specimens here referred to *Palaeopinnixa*. In the genus *Tritoplax*, the telson is distinctly trilobed; the telson in the specimens here referred to *Palaeopinnixa* forms an equilateral triangle. The male abdomen in members of the genus *Spiroplax* is very broad and exhibits somewhat convex lateral margins (Manning and Holthuis, 1981:177), while the male abdomen in the specimens described herein is narrow and has concave lateral margins. The sole species of *Spiroplax* has a much more rounded carapace than the new specimens. Additionally, the carapace is equidimensional in *Spiroplax*, while in the new specimens it is about 1.5 times as wide as long. Members of the two genera *Hexapinus* and *Hexaplax* are distinguishable from members of *Palaeopinnixa* because *Palaeopinnixa* has better developed carapace regions and a more rounded carapace.

Palaeopinnixa rathbunae **new name**

(Fig. 15–17)

Pinnixa eocenica Rathbun, 1926:34, plate 1, fig. 3, 4.
Pinnixa (*Palaeopinnixa*) *eocenica* Rathbun, 1926. Via, 1966:2, fig. 1.

Diagnosis.—Carapace subrectangular, with rounded anterolateral corners; branchial regions moderately well defined; orbits well developed, with sinuous upper margin; rostrum widening anteriorly.

Emendation to Description.—Carapace wider than long (L/W = 68.4%); surface finely granular, granules better developed on posterior of carapace; lateral sides steep; carapace convex longitudinally and weakly vaulted transversely; carapace regions weakly inflated; carapace grooves moderately to weakly developed.

Frontal margin about 0.18 maximum carapace width. Orbits well developed, directed forward, subrectangular in shape; upper margin sinuous, subtly rimmed. Rostrum about as wide as an orbit, subrectangular, widening anteriorly, sulcate medially, anteriormost edge flattened, lateral margins forming inner margins of orbits. Fronto-orbital width about 0.44 maximum carapace width.

Anterolateral margin rounded, continuous with lateral margin, weak ridge sometimes developed along edge of anterolateral and lateral margins, lateral sides steeply rounded, well developed. Posterolateral corners forming concave reentrants into carapace margin. Posterior margin about 0.84 maximum carapace width, very slightly sinuous.

Carapace grooves ranging from moderately defined to poorly defined. Cervical groove extending in broad sinuous U-shape from anterolateral margin posteriorly to axial region, moderately well developed posteriorly and weakly developed anteriorly.

Protogastric region moderately inflated, two small swellings located at base of rostrum; hepatic

Fig. 15.—*Palaeopinnixa rathbunae* new name, CM 45870. A. Dorsal carapace and appendages. B. Anterior view showing orbits. Scale bar = 1 cm.

region bounded by weakly developed grooves, somewhat flattened; branchial region moderately inflated, surface uneven with localized bulbous swellings, two swellings located on either side of the urogastric and cardiac regions, ornamented with granules, granules especially well developed posteriorly; metabranchial region flattened, not well ornamented, separated from branchial region by groove, groove well defined laterally and disappearing axially, groove extending from lateral margin axially and posteriorly.

Mesogastric region triangular, very narrow anteriorly, widening posteriorly, lateral margins concave, posterior margin convex, bounded by poorly developed grooves, grooves best developed posteriorly, two axial pits located on groove defining posterior margin. Urogastric region wider than long, constricted axially, upper margin concave, lower margin weakly concave, lateral edges bounded by rather deep, broad pits. Cardiac region subtriangular in shape, apex directed posteriorly; possessing three broad, weakly developed granules arranged in a triangular pattern, apex directed posteriorly; region weakly inflated.

Buccal frame rectangular; ischium of endopod of third maxilliped slightly longer than wide, narrowing anteriorly, lateral margins straight, anterior margin slightly convex, posterior margin sinuous; remainder of third maxilliped unknown. Subhepatic and sub-branchial regions finely granular; pterygostomial region finely granular, arcuate ridge paralleling entire length of lower margin, short ridge paralleling adaxial half of upper margin.

Sternum of male wider than long (L/W = 46.7%), semicircular in shape, lateral margins convex, widest at about midlength, narrowing anteriorly and posteriorly. Sternites 1–4 fused; broadly triangular; faint evidence of suture lines, suture between sternites 1 and 2 most distinct; surface finely granular; projection on anterior portion directed anteriorly, appearing to be associated with sternite 2, rounded and approximately equidimensional in shape; lower margin of sternite 4 with episternal projection, first pereiopod associated with sternite 4.

Sternite 5 wider than long, widest of sternites, finely granular, with episternal projections, lengthening laterally, associated with base of pereiopod 2. Sternite 6 wider than long but not as wide as sternite 5, lengthening laterally, with episternal projections, finely granular, associated with base of

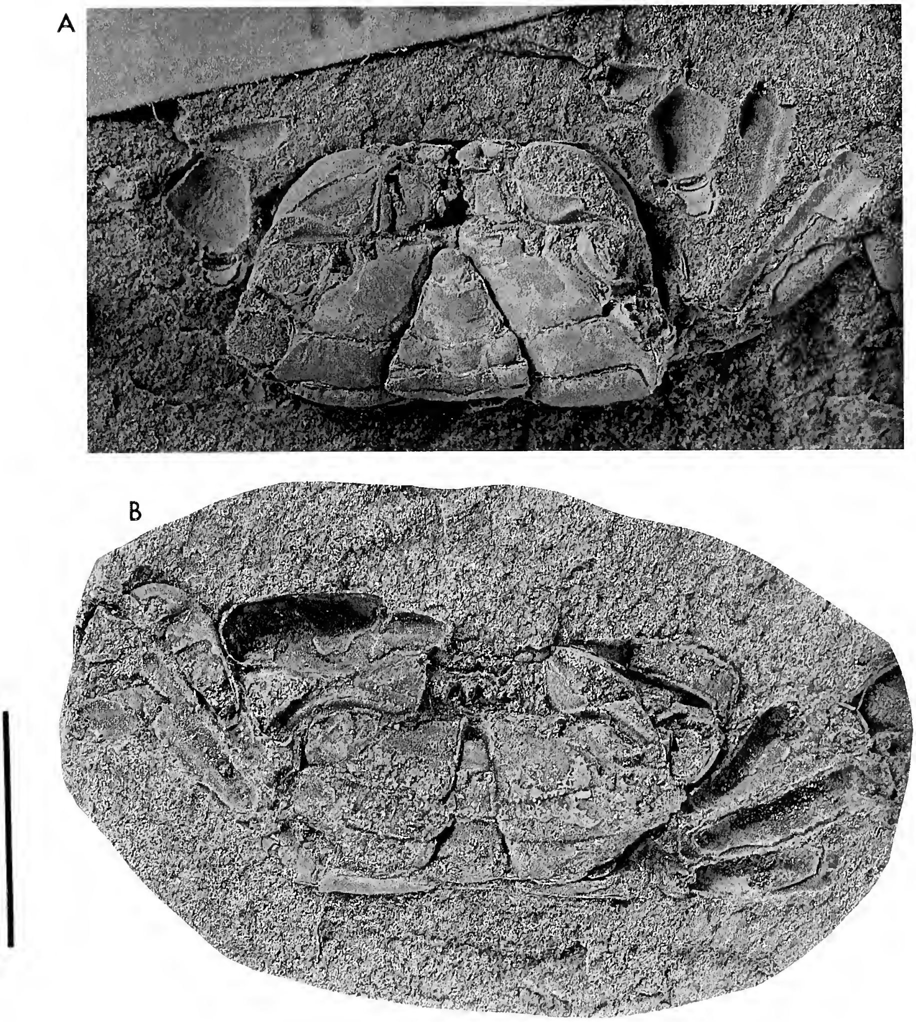


Fig. 16.—*Palaeopinnixa rathbunae*, new name. A. Venter of female, CM 45881. B. Venter of male, CM 45876. Scale bar = 1 cm.

pereiopod 3. Sternite 7 wider than long but not as wide as sternite 6, surface granular, lengthening laterally, associated with base of pereiopod 4. Sternite 8 and pereiopod 5 unknown.

Sternum of female wider than long (L/W = 45.3%); semicircular in shape, lateral margins convex; widening posteriorly, widest at posterior margin of carapace. Sternites 1–4 fused; broadly triangular; faint evidence of suture lines, suture between sternites 1 and 2 most distinct; surface finely granular; two anterior projections, directed anterolaterally, associated with sternites 2 and 3, projection on sternite 2 rounded and equidimensional, projection on sternite 3 longer and narrower; lower margin of sternite 4 with episternal projection, pereiopod 1 associated with sternite 4.

Sternite 5 of female wider than long, finely granular, with episternal projections, lengthening laterally, widest of all sternites, associated with base of pereiopod 2. Sternite 6 wider than long, almost as wide as sternite 5, with episternal projections, surface finely granular, associated with base of pereiopod 3. Sternite 7 wider than long but not as wide as sternite 6, surface finely granular, lengthening laterally, associated with base of pereiopod 4. Sternite 8 and pereiopod 5 unknown.

Abdomen an isosceles triangle in females, 1.2 times as long as wide, about 0.36 maximum width of sternum, straight-sided; telson isosceles triangular, apex appearing to be rounded, telson extending

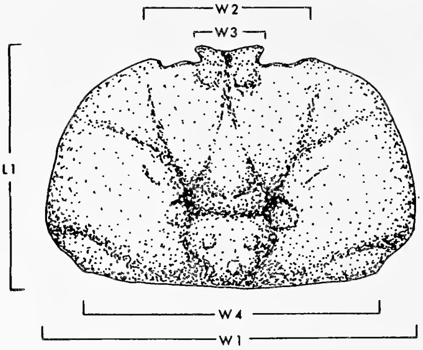


Fig. 17.—Line drawing of *Palaeopinnixa rathbunae*, new name, showing position and orientation of measurements taken.

slightly beyond suture of sternites 1 and 2; somites 5 and 6 fused, widening posteriorly, lateral margins slightly convex, lower margin convex, upper margin concave, about equidimensional when measured at maximum dimensions, possessing broadly rounded medial ridge; somite 4 wider than long, upper margin concave, lower margin convex, lateral margins slightly convex, widening posteriorly; somites 2 and 3 widest of somites; somite 3 much wider than long, upper margin slightly concave, lateral margins nearly straight, lower margin sinuous, widening posteriorly; somite 2 much wider than long, upper and lower margins sinuous, lateral margins weakly convex; somite 1 wider than long, narrowing posteriorly, upper margin sinuous, lower margin sinuous, lateral margins convex, medial swelling and weak lateral swellings; all somites except telson with rounded medial projection on lower margins, also with broad medial swellings and marginal swellings.

Abdomen of male narrowly triangular, approximately 1.65 times as long as wide, about 0.27 maximum sternal width, surface of somites granular, abdomen with weakly concave sides, widening posteriorly. Telson longer than wide, isosceles triangular in shape, apex rounded, extending beyond suture of sternites 1 and 2; somite 6 trapezoidal in shape, longer than wide, upper and lower margins nearly straight, lateral margins slightly concave; somites 3, 4, and 5 fused, fusion lines weakly developed, trapezoidal in shape, upper margin straight, lateral margins sinuous, weak medial swelling posteriorly and somewhat more well- developed lateral swellings posteriorly, lower margin weakly convex; somite 2 wider than long, upper margin weakly concave, lower margin weakly convex, lateral margins rounded, broad, gently swollen area medially; somite 1 poorly known.

Pereiopods ornamented with fine granules. Coxae of pereiopods 2–4 longer than wide, cylindrical. Merus of pereiopod 4 much longer than high, triangular in crosssection, lateral margins slightly sinuous; carpus about as long as high, widening distally, convex upper margin, concave lower margin, distal margin concave; propodus slightly longer than high. Merus of pereiopod 3 much longer than high, triangular in cross section, lateral margins slightly sinuous; carpus about as long as high, widening distally, convex upper margin, concave lower margin, concave distal margin, very short proximal margin. Merus of pereiopod 2 much longer than high, triangular in cross section, lateral margins slightly sinuous; carpus about as long as high, widening distally, convex upper margin, concave lower margin, distal margin concave. Chelipeds appearing to be unequal. Manus of major cheliped stout, longer than high, widening distally, surface finely granular, with sharp spine on lower proximal corner, spine extending posteriorly; carpus of cheliped about equidimensional, stout, bulbous; fingers arched, widest proximally and becoming narrow distally, appearing to possess moderately large denticles on occlusal surface. Manus of minor cheliped about equidimensional; fingers longer than manus, appearing to be finely granular, possessing moderately large denticles on occlusal surfaces; carpus equidimensional, stout, bulbous.

Measurements.—See Table 8 for measurements (in millimeters) taken on the dorsal carapace and Table 9 for measurements taken on the venter of specimens of *Palaeopinnixa rathbunae*. Position and orientation of measurements taken on the dorsal carapace are shown in Figure 17.

Material Examined.—CM 45870–45900, 45903, deposited in the Section of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, are referrable to this species.

Table 8.—*Measurements taken (in mm) on the dorsal carapace of* Palaeopinnixa rathbunae. *Position and orientation of measurements taken are illustrated in Figure 17. L1 = maximum length, W1 = maximum width, W2 = fronto-orbital width, W3 = frontal width, W4 = posterior width.*

Specimen number	L1	W1	W2	W3	W4	L2
CM 45897	11.1	16	9.3	3.6	13.3	10
CM 45899	>7.5	>12.2	—	—	10.2	>7.5
CM 45900	9.8	13.8	6	2.2	—	9
CM 45896	>10.3	15.9	—	—	—	>10.3
CM 45886	>9.0	14.3	—	—	—	>9.0
CM 45874	>11.0	16	—	—	13.9	>11.0
CM 45898	>11.0	15.7	—	—	—	11
CM 45872	8.5	12.7	5.7	—	9.9	8
CM 45888	—	16.4	7	3.2	—	—
CM 45891	>9.0	13.6	—	—	—	>9.0
CM 45870	12.2	16.9	7	3.3	13.8	>10.5
CM 45873	>9.8	>13.5	—	—	10.8	<9.8
CM 45885	8.6	12.9	6.2	1.8	10.4	8.3
CM 45895	>8.3	13.1	5.5	—	—	>8.3
CM 45887	>7.9	11.3	5.8	—	9.5	>7.7
CM 45883	10.3	16	6.7	1.9	12.3	9.7
CM 45884	>9.0	16	7.7	2.6	—	>7.7
CM 45889	10.6	15.9	7	2.5	—	9.7
CM 45871	11.1	16.5	7.5	3	13.6	10
CM 45892	>9.2	14.2	5.3	2.6	—	8.5
CM 45875	9.9	16	6.7	—	12.5	—
CM 45880	>10.0	16	7	—	13.6	>10.0
CM 45881	—	16.8	6.9	3.1	—	—
CM 45894	6.5	10	4.5	—	7.6	—
CM 45903	7.1	10.4	5	2.8	8	—
CSH 37	6.7	9.4	4.7	—	—	—
CSH 38	6.3	8.9	—	—	—	—
CSH 39	4	5.4	—	—	—	—

Two specimens, CM 45872 and CM 45873 were collected at the Pulali Point locality. Several of the specimens, CM 45871, 45876, 45877, 45879–81, 45883, 45887–89, 45891–93, 45896–99, and 45900 were collected from the Eocene Hoko River Formation at the RB32 locality of Berglund, located in the SW1/4, NW1/4, Sec. 4, T33N, R15W, Cape Flattery Quadrangle, Clallam County, Washington, 7.5 minute series, near Neah Bay. CM 45870, 45874, 45875, and 45878 were collected from the RB33 locality of Berglund, located in the W1/2, N1/4, Sec. 4, T33N, R15W, Cape Flattery Quadrangle, 15 minute series, near west Kydikabbit. CM 45884 and 45885 were collected from the RB31 locality of Berglund located in the E1/2, Sec. 4, T33N, R15W, Cape Flattery Quadrangle, Clallam County, Washington, in the intertidal zone west of Kydikabbit, Washington. CM 45882, 45894, and 45895 were collected from an unknown locality. CM 45890 and 45886 were reported as having been collected from the RB29 locality of Berglund; however, details are not available.

Table 9.—*Measurements (in mm) taken on the venters of* Palaeopinnixa rathbunae. *W1 = maximum width of sternum, L1 = maximum length of sternum, W2 = maximum width of abdomen, L2 = maximum length of abdomen.*

Specimen number	W1	L1	W2	L2	Sex
CSH 27	14.9	6.7	—	—	Female?
CSH 29	13.5	5.8	3.6	5.4	Male
CSH 30	14.7	7.4	3.9	7.0	Male
CSH 31	18.1	8.0	6.4	7.5	Female
CSH 28	16.1	7.5	5.9	7.3	Female

Remarks.—*Palaeopinnixa rathbunae* may be distinguished from other members of the genus in several ways. *Palaeopinnixa eocenica* possesses small orbits that are directly slightly axially; the orbits of *P. rathbunae* are larger and are directed forward. The front in *P. eocenica* is more narrow and less flared than that of *P. rathbunae*. The carapace regions of *P. eocenica* are poorly marked; in *P. rathbunae* the carapace regions are weakly but noticeably defined. *Palaeopinnixa eocenica* has a much more rounded carapace and more rounded lateral margins than does *P. rathbunae*, which has a more rectangular carapace. *Palaeopinnixa intermedia* Collins and Morris from the Miocene of Trinidad possesses a more rectangular carapace, straighter lateral margins, and narrower mesogastric, urogastric, and cardiac regions than does *P. rathbunae*. *Palaeopinnixa prima* Rathbun from the Oligocene of Panama possesses less clearly defined carapace regions than does *P. rathbunae*. *Palaeopinnixa prima* has a very sharp anterolateral margin and steep to slightly concave lateral sides, while *P. rathbunae* lacks a sharp anterolateral margin and has more rounded, slightly convex lateral sides. The metabranchial region in *P. rathbunae* is much more depressed and more clearly defined than that of *P. prima*. The lateral margins of the carapace of *Palaeopinnixa rocaensis* Feldmann et al., from the earliest Paleocene of Argentina, are much less rounded than those of *P. rathbunae*, which are markedly convex. Additionally, *P. rocaensis* achieves its maximum width at approximately the midlength; *P. rathbunae* reaches its maximum width about three-quarters the distance posteriorly on the carapace.

Although all of the specimens may be assigned to *Palaeopinnixa rathbunae*, there is a range of morphological variation in several aspects of the dorsal carapace. Development of the carapace grooves varies among specimens. Those specimens that appear to have well-developed grooves also are molds of the interior, suggesting that this apparent difference in development may be related to manner of preservation. The ridge paralleling the anterolateral and lateral margins is well developed in some specimens such as CM 45875 and absent in others such as CM 45870. This may be due to abrasion before or during burial, weathering of the specimen at surface conditions, or variation within the population. In the case of CM 45870, the carapace is badly weathered, perhaps accounting for the absence of the ridge. Ornamentation of the dorsal carapace is also variable, again probably due to both variation in the population and to weathering and abrasion of the specimens. Most of the specimens appear to be highly weathered and retain no ornamentation. Those that retain cuticle range from being finely granular to punctate. CM 45872 is finely granular on the posterior portion of the carapace, and CM 45870 possesses fine granules on the branchial region. While these ranges in variation exist, there seems to be no pattern in the variation and the magnitude of the variations is not sufficient to warrant removal of any of the specimens from this taxon.

Many of the specimens possess asymmetrical bulbous swellings on the dorsal carapace. In some specimens, the bulbous areas of the epibranchial regions are more well developed than in others. These swellings could be attributed to several factors. One is infestation by bopyrid isopods (Glaessner, 1969; Hessler, 1969; Overstreet, 1983), which could explain some of the asymmetries. Other cases can probably be explained by deformation or weak crushing of the carapace so as to slightly deform it.

The overwhelming majority of specimens possess some portions of the appendages suggesting that most of the specimens are corpses and that the animals were living near the site of deposition or were buried rapidly. The excellent preservation of some of the carapace material and appendages also supports this interpretation. However, the deformation of some of the carapaces suggests at the very least the material was crushed by compaction of the sediment.

Interestingly, there is a difference in the shape of the sterna of males and females as well as the typical differences in the shape of the abdomina. The sternum of the male is semicircular in shape and widest at the midlength while that of the female is widest at the posterior margin of the carapace. The sternites also appear to be wider in the females than in the males because more of the sternites are visible in ventral view in females than in males. In both males and females sternite 5 is widest and the sternum extends to the base of the buccal frame.

DISCUSSION

While an in-depth analysis of the biogeography of these decapods is premature, some overall patterns are clear. Most of the genera herein reported from the Pulali Point locality are well known and commonly reported from Tertiary rocks of the west coast of North America, including *Macroacaena*, *Laeviranina*, *Raninoides*, *Portunites*, *Pulalius*, *Branchioplax*, and *Neopilumnoplax*. *Carpilius* and *Palaeopinnixa* are the only genera that have not previously been reported from the west coast of North America.

Several members of the decapod fauna recovered from Pulali Point are known only from the Northern Hemisphere. Members of the genus *Macroacaena* have been reported from the Cretaceous and the Paleocene of Greenland and Japan, and the Eocene and Oligocene of Oregon and Washington (Tucker, 1995). *Portunites* has been reported from England, Europe, Japan, and the west coast of North America (Schweitzer and Feldmann, 1999), and *Pulalius* is known only from the west coast of North America. *Branchioplax* has been reported from western North America, Japan, and Europe (Karasawa, 1992) with a (very) questionable occurrence from Senegal (Remy and Tessier, 1954). These genera may have either a Tethyan or a north Polar distribution; Karasawa (1992) suggested that both *Portunites* and *Branchioplax* have a Tethyan distribution.

The closely related genera *Laeviranina* and *Raninoides* each have widespread distributions. *Laeviranina* is known only from fossil occurrences and has been reported from Europe, South America, North America, New Zealand, and Pakistan (Tucker, 1995). *Raninoides*, which ranges from the Eocene to the Recent, has a cosmopolitan range having been reported from the Atlantic, Pacific, and Indian oceans and the Caribbean and Central America. The oldest occurrence of *Laeviranina* is from the Paleocene of Alabama and Greenland, and the earliest report of *Raninoides* is from Eocene rocks of Japan (Tucker, 1995).

Carpilius has been reported from the fossil record in Japan and from the Pulali Point locality. However, the occurrence in Japan is based only upon a portion of a manus (Karasawa, 1993), so its use in biogeographic analysis awaits more complete material. The genus is currently known from the Indo-Pacific region and from the western Atlantic and Caribbean. *Neopilumnoplax* is known from the fossil record only on the west coast of North America and is currently found in the Indo- Pacific region, a similar biogeographic pattern to that of *Carpilius*.

The genus *Palaeopinnixa* has previously been reported from Eocene rocks of Panama, Peru, Trinidad, and the Paleocene of Argentina, and from Miocene rocks of Spain (Rathbun, 1918; Woods, 1922; Rathbun, 1926; Via, 1966; Collins and Morris, 1976; Feldmann et al., 1995). The first occurrence of the genus is in Paleocene rocks of Argentina, and the genus appears to have subsequently dispersed northward into the western Pacific Ocean during the Eocene and into the northeastern Atlantic Ocean by the Miocene.

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RHYSODINE BEETLES (INSECTA: COLEOPTERA: CARABIDAE): NEW SPECIES, NEW DATA. II

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Abstract

Seven new species of Rhysodini (Coleoptera: Carabidae) are described, *Kaveinga* (*Kaveinga*) *waai* (Moluccas), *Plesioglymmius* (*Juxtaglymmius*) *negara* (Malay Peninsula), *Omoglymmius* (*O.*) *emdomani* (New Guinea), *Rhyzodiastes* (*Temoana*) *riedeli* (New Guinea), *Rhyzodiastes* (*Temoana*) *mindoro* (Philippines), *Clinidium* (*Clinidium*) *onorei* (Ecuador), *Clinidium* (*C.*) *gilloglyi* (Panama). Descriptions are given for either males or females of the following five species, previously known from only one sex: *Omoglymmius* (*O.*) *pulvinatus* (Grouvelle), *Clinidium* (*C.*) *howdenorum* Bell and Bell, *Clinidium* (*C.*) *dormans* Bell and Bell, *Clinidium* (*C.*) *crater* Bell and Bell, *Clinidium* (*C.*) *spatulatum* Bell and Bell. An error in the description of *Clinidium* (*C.*) *boroquense* Bell is corrected. Range extensions or clarifications are given for the following 20 species: *Arrowina anguliceps* (Arrow), *Yamatosa niponensis* (Lewis), *Yamatosa draco* (Bell), *Yamatosa sinensis* Bell and Bell, *Plesioglymmius* (*Ameroglymmius*) *reichardti*, *Omoglymmius* (*Orthoglymmius*) *coomani* (Grouvelle), *Omoglymmius* (*O.*) *sakuraii* Nakane, *Omoglymmius* (*O.*) *semperi* Bell and Bell, *Omoglymmius* (*O.*) *hiekei* Bell and Bell, *Omoglymmius* (*O.*) *bucculatus* (Arrow), *Omoglymmius* (*O.*) *patens* Bell and Bell, *Omoglymmius*(*O.*) *pulvinatus* (Grouvelle), *Omoglymmius* (*O.*) *sedlaceki* Bell and Bell, *Rhyzodiastes* (*Temoana*) *convergens* Bell and Bell, *Clinidium* (*Arctoclinidium*) *rosenbergi* Bell, *Clinidium* (*C.*) *insigne* Grouvelle, Clinidium (*C.*) *oberthueri* Grouvelle, *Clinidium* (*C.*) *rossi* Bell, *Clinidium* (*C.*) *moldenkei* Bell and Bell, *Clinidium* (*C.*) *sulcigaster* Bell.

Key Words: Rhysodini, Rhysodina, Clinidiina, Omoglymmiina, new species, distributions

Introduction

Rhysodini is a taxon of about 350 beetles which live inside dead wood. They have been long interpreted as a separate family in Suborder Adephaga. It was recently demonstrated (Bell, 1998) that they are highly modified ground beetles (Carabidae) and belong in Subfamily Scaritinae. The sister group is Genus *Solenogenys* Westwood.

Adults are 4–10 mm long. All known species look red brown in bright light and piceous to black when seen in dimmer light. The general shape is like the smaller scaritine genera, especially *Clivina* Latreille but Rhysodini have many distinctive features, including a deep median pit communicating with an inner cavity in the head, moniliform antennae, and a condylelike neck. The pronotum has deep pits or longitudinal grooves. Males have calcars (anteriorly directed processes on middle and hind tibiae).

The mouthparts are highly unusual (Bell, 1994). The mentum covers the other mouthparts in ventral view and extends so far forward as to prevent any objects from coming between the mandibles. The leading edge of the mentum acts as a cutting edge as the insect thrusts itself forward between layers of wood fibers.

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The mandibles serve only as covers for the other mouthparts. The galea and laciniae of the maxillae form two pairs of stylets. The palpi are completely retractile.

Rhysodine beetles are limited to moist forest areas where their food source is thought to be the amoeboid stages of slime molds (Myxomycetes). About a third of the species have vestigial wings. There is no evidence that the fully winged species can fly very far. Nevertheless, rhysodines, including flightless groups, have been very effective in colonizing islands.

This is a second paper in the pattern of Bell and Bell (1993), extending our revision of the Rhysodini of the world. It contains descriptions of seven new species, descriptions of sexes not previously described for five species, significant locality data for additional species, and changes in keys to accommodate the new species. An error in the description of *Clinidium boroquense* is rectified, while that of *Plesioglymmius* (*Juxtaglymmius*) is altered to accommodate a second species, and a modified key to the subgenera of *Plesioglymmius* is presented.

Abbreviations used in the text are: BMNH, Natural History Museum, London, United Kingdom; CAS, California Academy of Sciences, San Francisco, California; CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; CMNO, Canadian Museum of Nature, Ottawa, Ontario, Canada; CNCO, Canadian National Collection, Ottawa, Ontario, Canada; CUIC, Cornell University, Ithaca, New York; MNHB, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; NMW, Naturhistorisches Museum Wien, Vienna, Austria; SMNS, Staatliches Museum für Naturkunde in Stuttgart, Germany; TAMU, Texas A & M University, College Station, Texas; UVM, University of Vermont, Burlington, Vermont. L/GW represents the ratio of pronotal length divided by its greatest width.

SYSTEMATIC ENTOMOLOGY

Subtribe Rhysodina

Kaveinga (*Kaveinga*) *waai*, **new species**

(Fig. 1A–C)

Type Specimens.—Holotype female, labelled "AMBON: Waai, Gg. Salahutu; 6.2: 300–600 m., Indonesia 1989; leg. Jäch" (NMW). "Ambon" refers to a political division, and not to the island. Waai is at 3°33′S, 128°18′E. Paratypes: two females, same data as holotype (NMW) (CMNH).

Etymology.—The specific epithet is derived from the name of the type locality.

Diagnosis.—This is the only species of *Kaveinga* sensu stricto which has several precoxal setae, and which has the outer pronotal carina much narrower than the inner one.

Description.—Length 6.7–7.0 mm. Antennal segment I pollinose above; segments II–V each with basal band of pollinosity; segments VII–XI with basal setae; segments VI–X with minor setae.

Head (Fig. 1A) as long as wide; clypeus broadly separated from median lobe by band of pollinosity; parafrontal bosses entirely pollinose; sides of median lobe deeply sinuate opposite temporal lobe; orbital groove dilated, as long as eye; temporal lobes slightly wider than long, their anteriomedial margins oblique, nearly straight, convergent posteriorly; medial angle rounded, scarcely overlapped by median lobe; two or three temporal setae, anteriormost seta at or in contact with orbital groove; pollinosity of postorbit well developed, with dorsal boundary opposite upper margin of eye; temporal lobe without overhang; no suborbital tubercle or gular ridge.

Pronotum (Fig. 1A) short; L/GW 1.05; widest near middle, sides curved, convergent to narrow apex; sides oblique, curved in posterior half, shallowly sinuate near posterior angle; latter obtuse; edge

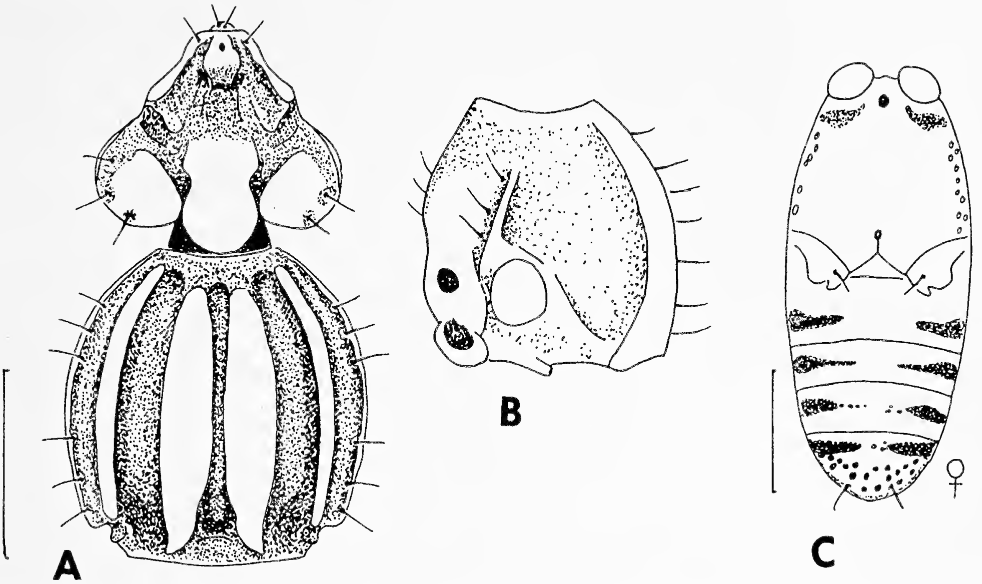

Fig. 1.—*Kaveinga* (sensu stricto) *waai*, n. sp. A. Head, pronotum, dorsal aspect. B. Prothorax, left ventrolateral aspect. C. Metasternum, abdomen, ventral aspect; female.

emarginate between hind angle and basal knob; latter rather prominent; paramedian grooves deep, pollinose; marginal grooves very broad; outer carina very narrow, about one-third of inner carina, much narrower than grooves on either side of it; anterior ends of inner carinae not abbreviated anteriorly by pollinosity; angular seta and about five marginals present; prosternum (Fig. 1B) with strong precoxal carinae, extended about 65% of distance to anterior margin; three to five precoxal setae; no transverse groove between carinae.

Elytra moderately broad; elytral intervals narrow, convex, outer ones subcarinate; strial punctures coarse; striae pollinose between punctures; posterior parts of outer striae deeply impressed; stria IV joined to III posteriorly; V and VI joined posteriorly; VII apparently joined to V + VI posteriorly; detached tip of VII marginal at apex of elytron; stria I with one seta at apex; stria II with one seta at apex, in some specimens also with one at base; stria IV with several (average seven) setae along its length, including one basal seta; detached apical part of stria VII with about seven setae. Abdominal sterna (Fig. 1C) III and IV with transverse grooves widely separated in middle; V with space between grooves occupied by a single line of punctures; VI with similar arrangement anteriorly, plus scattered, coarse punctures posteriorly; lateral pits in female not enlarged; front and middle femora partly pollinose; tibia of middle leg apparently minutely serrulate on lateral margin in profile view. Male unknown.

Distribution.—Known only from the type locality.

Remarks.—If a specimen were taken through our key to *Kaveinga* sensu stricto (Bell and Bell, 1979), it would trace to *K. abbreviata* (Lea), but the narrow outer carinae, the longer inner carinae, excavate marginal groove, and more numerous setae would easily separate it. The short pronotum and extensive pollinosity suggest that these two species are sister species. The key to *Kaveinga* sensu stricto (Bell and Bell, 1979:399) can be amended as follows:

3. remove K. abbreviata; substitute . . . . 3.1′
3.1(3). Outer carina as wide as inner; marginal groove narrow; pronotum with no lateral, one angular seta; parafrontal boss shining, glabrous . . . . *Kaveinga abbreviata* (Lea)
3.1′. Outer carina less than half as wide as inner; marginal groove very wide, with angular and about five marginal setae; parafrontal boss entirely pollinose . . . . *Kaveinga waai*, n. sp.

The presence of many pronotal and temporal setae would make this species trace to subgenus *Vakeinga* Bell and Bell. The presence of serrulations on the middle tibia, the absence of enlarged pits on the abdomen of the female, both diagnostic of *Kaveinga* sensu stricto, as well as the characters linking *K. waai* with *K. abbreviata*, suggest that the new species really belongs to the latter subgenus. A modified key to the subgenera of *Kaveinga* is therefore in order.

In the key to subgenera (Bell and Bell, 1979:390), substitute the following for couplet 3:

3(2′). Middle tibia not apparently serrulate in profile view of lateral surface; female with enlarged lateral pits on abdominal segments III and IV; prothorax without precoxal setae, but with postcoxal setae . . . . *Vakeinga*

3′. Middle tibia apparently serrulate in profile view of lateral surface; female without enlarged lateral pits on abdomen; prosternum with or without precoxal setae, but without postcoxal setae . . . . *Kaveinga* sensu stricto

Subtribe Omoglymmiina

Yamatosa niponensis (Lewis, 1888)

Additional Locality.—TAIWAN: Taichung, Pilushi, 2200-m series of 16 specimens, coll. Davidson, Young, Rawlins. May 22–23, 1988. (A second locality from Taiwan.) (CMNH).

Yamatosa draco (Bell, 1977)

Additional Locality.—CHINA: Sichuan, Gongga Shan, Hailuogou above camp 3, 3050–3200 m., 7-VII-1996. J. Farkac, B. Kabátek, A. Smetana. 29°35′N, 102°00′E. (A. Smetana personal collection.) This is the first record for China; previous records are from Bhutan and Pakistan. This is also the highest altitude from which rhysodines have been collected.

Yamatosa sinensis Bell and Bell, 1987

Additional Locality.—CHINA: Yunnan, Heishui—35–50 km N of Lijian, 27°13′N, 100°19′E. Five males, 15 females. Coll. E. Jendak and O. Sausa (NMW). Previously known only from Szechuan Province.

Plesioglymmius (*Ameroglymmius*) *reichardti* Bell and Bell, 1979

Additional Locality.—SURINAM: Saramacca, Kabo Agric. Sta., 3–7 VIII, 1980, M. I. Russell, under bark, dead tree. The first record from Surinam. Previously known from Venezuela (near the Orinoco River) and Brazil (Rio Madeira) (BMNH).

The discovery of a new species related to the subgenus *Juxtaglymmius*, but not conforming to the original description of that subgenus, necessitates a new definition of it, as well as a new key to the subgenera.

Subgenus *Juxtaglymmius*

Redescription.—Antennal segment XI longer than wide, with pointed apex (in some species the point represents a very reduced conical stylet); antennal basal setae very sparse, beginning on segments V or VII; segment I pollinose dorsally; segment II with basal pollinose band; segments III–XI without pollinosity; antennal lobes close together, either separated by one-half width of basal condyle of segment I or else in contact in midline, in form of median suture between them; clypeal setae absent;

median lobe of head small, narrow, elongate, or oval, strongly convex; medial angles of temporal lobes obtuse, narrowly separated at midline, margins oblique from medial angles to posterior angles; orbital groove, temporal setae absent; temporal lobe in form of long overhang in lateral view, separated by deep notch from suborbital tubercle; eye with posterior margin clearly anterior to middle of temporal lobe; ventral surface of head with gular shelf, extended between the two suborbital tubercles; pollinosity limited to margins of shelf; one pair of postlabial setae.

Paramedian groove limited to posterior two-thirds of pronotum, varied in form; base of elytron without tooth opposite interval I; striae shallow, finely punctured, pollinosity limited to punctures; apical impression of elytron small, limited to apices of striae I and II; apical tubercle not sinuate medially; metasternum with lateral band of very coarse punctures; punctures in midline present or absent; punctures of abdominal sterna III–V coarse, tending to form transverse line in each sternum; sternum VI with row of very coarse punctures parallel to posterior margin, with scattered punctures anterior to it; female known from only one species, with deepened lateral pits on sternum IV, and also moderately deepened on sternum V. Male with ventral tooth on anterior femur.

KEY TO SUBGENERA

1. Head with prominent suborbital tubercle on each side; in ventral view, these tubercles apparently prominent lateral angles on shelf extended across base of mentum; in lateral view, eye extended far posterior to middle of temporal lobe 2
1′. Head without suborbital tubercle; eye anterior to middle of temporal lobe . . . *Ameroglymmius*
2(1). Antennal lobes either contiguous in midline, or else narrowly separated by less than half width of median lobe; base of elytral interval not in form of tooth; temporal lobe in lateral view with strong overhang posteriorly . . . . *Juxtaglymmius*
2′. Antennal lobes in dorsal view separated by at least width of median lobe; base of elytral interval I in form of tooth; temporal lobe in lateral view not in form of overhang . . . . *Plesioglymmius* sensu stricto

KEY TO SPECIES OF *JUXTAGLYMMIUS*

1. Antennal lobes slightly separated, not extended to midline; basal impressions of pronotum preceded by row of coarse punctures . . . . *Plesioglymmius negara*, n. sp.
1′. Antennal lobes in contact at midline; basal impressions of pronotum preceded by linear groove . . . . *Plesioglymmius jugatus* Bell and Bell

Plesioglymmius (*Juxtaglymmius*) *negara*, **new species**
(Fig. 2A–D)

Type Specimen.—Holotype male, labelled "MALAYSIA:PAHANG, Taman Negara N.P., 12–14, 7, 1993, leg. H. Forster" (NMW).

Etymology.—The specific epithet is derived from the name of the type locality.

Diagnosis.—The separation of the antennal lobes and the coarse punctures forming the anterior end of the paramedian groove are diagnostic.

Description.—Length 4.9 mm. Antennal segments VII–X with basal setae; antennal lobes separated from one another by about half width of basal condyle of antenna (Fig. 2A); head (Fig. 2B) with median lobe elongate, narrow, nearly parallel-sided; medial angle of temporal lobe obtuse, margin posterior to it slightly emarginate; temporal lobe very finely punctate; orbital groove absent (Fig. 2C); temporal setae absent.

Pronotum (Fig. 2B) relatively elongate, L/GW 1.50, widest at middle; sides only slightly curved; median groove fine, linear except for anterior and posterior median pits; each paramedian groove represented by deep basal impression preceded by five or six coarse punctures in a line, ended anteriorly at anterior third of pronotum; marginal groove linear, fine; prosternum impunctate in midline, punctate laterally; pronotum sparsely punctate.

Elytron elongate; striae shallow, coarsely punctate, pollinosity limited to punctures; one seta in apical pit at apex of stria II; one seta at posterior end of stria IV; about nine setae in apex of stria VII. Metasternum impunctate in midline, with coarse lateral punctures. Abdominal sterna (Fig. 2D) with transverse row of punctures; sternum II with a shorter, more irregular row; sterna IV and V with

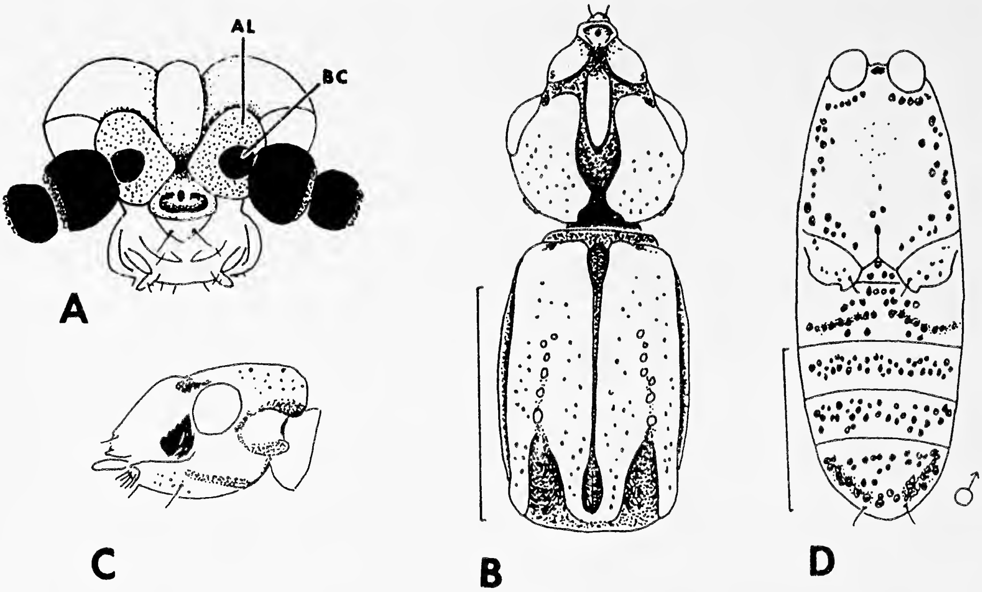

Fig. 2.—*Plesioglymmius* (*Juxtaglymmius*) *negara*, n. sp. A. Head, anterior aspect; AL, antennal lobe; BC, basal condyle. B. Head, pronotum, dorsal aspect. C. Head, left lateral aspect. D. Metasternum, abdomen, ventral aspect; male.

scattered punctures; sternum VI with coarse row parallel to posterior margin, with scattered punctures anterior to it; lateral pits very shallow in male; female unknown. Male with small ventral tooth on anterior femur; calcar of hind tibia with acute angle, raised well above tibial apex (more strongly so than in *P. jugatus*).

Distribution.—Known only from the type locality.

Arrowina anguliceps (Arrow, 1901)

Additional Locality.—INDIA: Tamil Nadu, Ootacamund Pykara, 11 km from Mysore. A. Riedel (Hendrich coll.). Previously known only from the Cardamum Mountains, further south.

Omoglymmius (*Orthoglymmius*) *coomani* (Arrow, 1942)

Additional Localities.—CHINA: Yunnan, 14–21 VI, 1993. 100 km W. Baoshan, Gaoligongshan Nat. Res. coll. E. Jendak and O. Sausa (NMW). THAILAND: (Northwest), 19°18′N, 97°59′E, Hae Hong Son, 1600–2000 m, Ban Huai Po. 9–16, 1991. S. L. Dembicky (NMW). This species was previously known only from Vietnam.

Omoglymmius (sensu stricto) *sakuraii* (Nakane, 1978)

Additional Locality.—TAIWAN: Taichung (same data as for *Y. niponensis* above). The type locality is Amami-O-Shima in the Ryukyus. The species has also been recorded from southern Japan (Kagoshima Prefecture, Kyushu Island) and Vietnam. The precoxal carina and other characters vary in this species, and we provisionally treat it as one variable species. The Taiwan specimens were in a very large (50 m) spruce (*Picea morrisonicola* Hayata) log (CMNH).

Omoglymmius (sensu stricto) *semperi* Bell and Bell, 1982

Additional Locality.—PHILIPPINES: Luzon, Laguna, Mt. Makiling, 3000 ft, 26 April, 1931, F. C. Hadden coll. (CAS). This is the first definite locality for the species.

Omoglymmius (sensu stricto) *hiekei* Bell and Bell, 1982

Additional Locality.—MALAYSIA: Sabah 60 km E of Kota Kinabalu, Crocker Mtns., Gunung Emas, 16–27 IV, coll. I. Janis (NMW). This puts the species on the island of Borneo. Previous records are from Luzon, Philippines.

Omoglymmius (sensu stricto) *bucculatus* (Arrow, 1901)

Additional Locality.—INDONESIA: Lombok: Sapit-Sembalun Bumbung, 14–16 Feb 1994. Bolm leg., 900–1500 m (SMNS). This is the first record of a rhysodine from Lombok. This species has previously been recorded only from Sumbawa.

Omoglymmius (sensu stricto) *patens* Bell and Bell, 1982

Additional Locality.—IRIAN JAYA: Manokwari, Ransiki, Mayuby, ca. 300 m, A. Riedel (Hendrich coll.). The known range of this species is on the north side of New Guinea, from Maffin Bay in the east to the east side of the Vogelkop Peninsula.

Omoglymmius (*Omoglymmius*) *pulvinatus* (Grouvelle, 1903)
(Fig. 3A–C)

Description of Female.—7.2 mm, labeled "W. Neuguinea/Pariai, Nabire Strass v. Nabire nach Ilasa, km 50, unter Rinde 29.9.90, leg. M. Balke, L. Hendrich" (collection of L. Hendrich, Berlin); head and pronotum (Fig. 3A and B) similar to male, anterior trochanter rounded, abdominal sterna (Fig. 3C) with lateral pit of sternum IV deep, but not much wider than that of male.

Range Extension.—IRIAN JAYA: Testega, Manokwari Province, 1100–1300 m elevation. A. Riedel (Riedel coll.); Nabire (Hendrich coll.). This species is perhaps confined to the Vogelkop Peninsula and south coast of Geelvink Bay.

Omoglymmius (*Omoglymmius*) *emdomani*, **new species**
(Fig. 4A–C)

Type Specimens.—Holotype female, labelled "Irian Jaya, Jayawijaya Prov. leg. A. Riedel 1993, Emdoman 900–1200 m., 29-IX-1993" (CMNH). The locality is in the mountainous interior of New Guinea, at about 4°S, 140°E. Paratype: female, mounted on same card as holotype. The holotype is the larger and darker specimen.

Etymology.—The specific epithet is derived from the name of the type locality.

Diagnosis.—An *Omoglymmius* sensu stricto with suborbital tubercles, the only such species with the antennal lobe entirely pollinose and with the median lobe shallowly emarginate posteriorly.

Description.—Length 6.5–8.2 mm. Antennal segments I–X punctate, XI impunctate; head (Fig. 4A) with length and width subequal; median lobe impunctate, truncate, slightly emarginate at apex, tip pollinose; frontal space broader than long; temporal lobe with anteriomedial margins slightly curved,

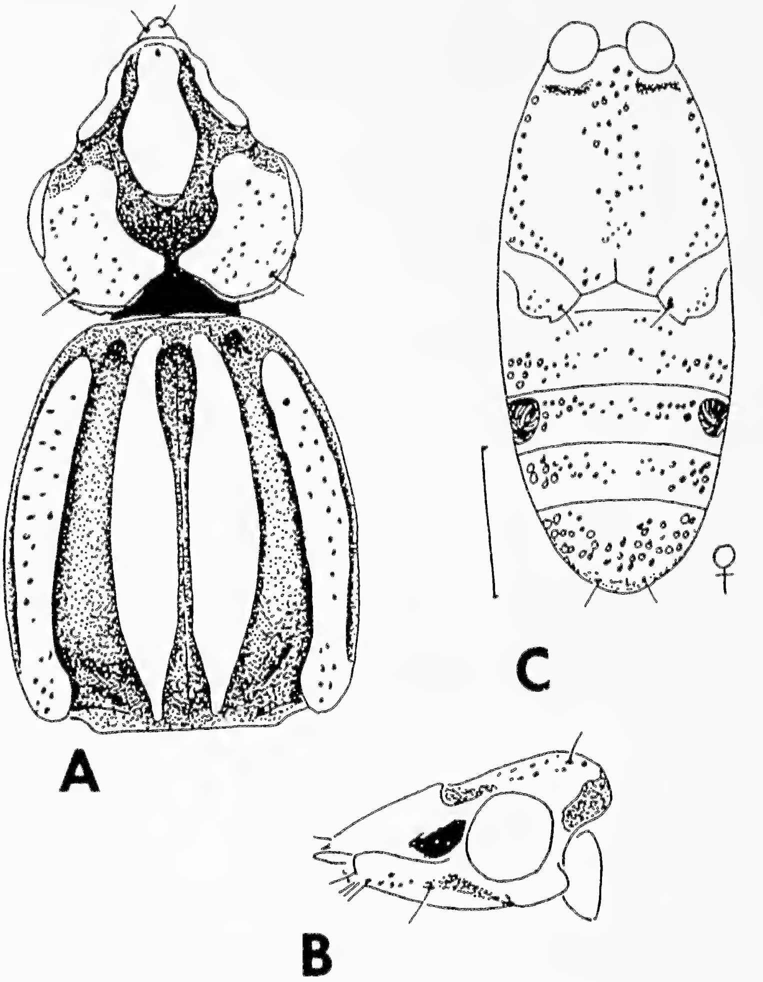

Fig. 3.—*Omoglymmius* (sensu stricto) *pulvinatus*, (Grouvelle). A. Head, pronotum, dorsal aspect. B. Head, left lateral aspect. C. Metasternum, abdomen, ventral aspect; female.

medial angles narrowly separated, slightly lobate; posteriomedial margins concave to posteriomedial angle, posterior margin transverse, temporal lobes margined posteriorly with pollinosity; medial slope of antennal lobes entirely pollinose, as are broad antennal grooves; orbital grooves broad, extended posteriorly nearly to posterior margin of eye; temporal lobe impunctate; temporal seta absent; eye large, round, prominent; suborbital tubercle rather large, about one-third as long as eye (Fig. 4B).

Pronotum (Fig. 4A) only moderately elongate, L/GW 1.17; pronotum almost quadrate but narrowed to anterior angles; lateral margins nearly straight; outer carina about three-fifths as wide as inner one at middle; medial margin of outer carina sinuate near base; marginal groove dilated, anterior half punctate; pronotum without setae; pronotal carinae impunctate; prosternum microsculptured in anterior half; precoxal carinae absent.

Elytra with striae shallowly impressed, intervals flat; strial punctures coarse, sparse; base of stria IV with pollinose scarp; transverse basal scarp pollinose from stria II–IV; stria IV with one seta at apex; subapical striole with one seta; stria VII with several setae near apex. Metasternum (Fig. 4C) with single row of punctures along each lateral margin, but without median row. Abdominal sterna III–V with coarse punctures in form of transverse row widely interrupted in midline; sternum VI with

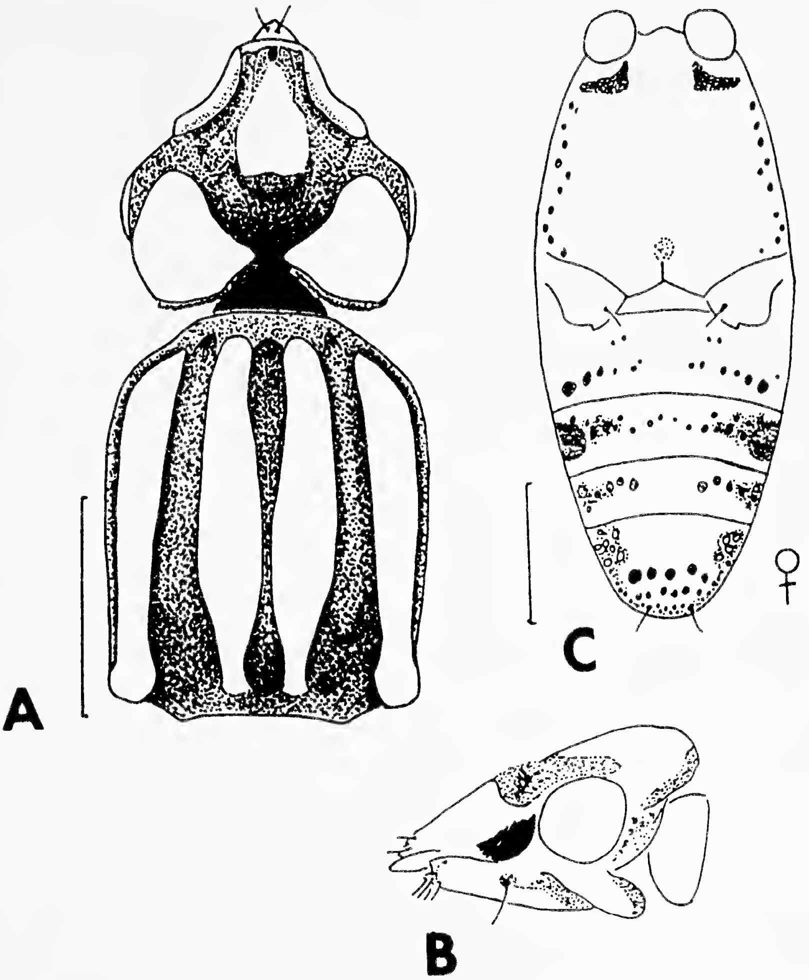

Fig. 4.—*Omoglymmius* (sensu stricto) *emdomani*, n. sp. A. Head, pronotum, dorsal aspect. B. Head, left lateral aspect. C. Metasternum, abdomen, ventral aspect; female.

scattered, very coarse punctures on posterior two-thirds; female with small but deep lateral pit on each side of sternum IV, without tooth on anterior femur; male unknown.

Distribution.—Known only from the type locality.

Remarks.—In the revised key to *Omoglymmius* sensu stricto, this species traces to couplet 74 (Bell and Bell, 1993). The latter couplet should be altered as follows:

74(73). Marginal groove of pronotum not dilated 75
74′. Marginal groove of pronotum dilated 74.1
74.1(74′). Inner carinae of pronotum impunctate but outer carinae coarsely punctate; one temporal seta present; pronotal margins curved . . . . *O. pulvinatus* (Grouvelle)
74.1′. Both carinae impunctate; temporal seta absent; pronotal margins nearly straight . . . . *O. emdomani*, n. sp.

Omoglymmius (sensu stricto) *sedlaceki* Bell and Bell, 1982

Additional Locality.—IRIAN JAYA: Manokwari Province, Anggi, Gunung Disbehey, 29.8.1991, 2000–2150 m, leg. A. Riedel (SMNS). Previous records of this species are from the highlands of northeastern New Guinea, and this is the first record from the western half of the island. The unity of this species is still in doubt. We found what appeared to be five distinct local forms in northeastern New Guinea which we designated by letters. The Anggi specimen is similar to our form E, from Sepalakambang, on the Huon Peninsula, from which it might differ only in having the median lobe of the head even narrower and more pointed. The status of these local forms remains in doubt, and they should be reexamined when more specimens are available.

Subtribe Clinidiina

Rhyzodiastes (*Temoana*) *riedeli*, **new species**

(Fig. 5A and B)

Type Specimen.—Holotype male, labelled "Irian Jaya: Baliem Dist., Ilugwa, Melanggama, Pass-Valley, 2100–2300 m., leg. A. Riedel, 9–10, IX, 1990" (Hendrich Colln.) (MNHB).

Etymology.—The specific epithet honors the collector, Alexander Riedel of Friedberg, Germany, who has sent us many interesting rhysodids from his collecting expeditions to Irian Jaya, New Guinea.

Diagnosis.—A species of *Rhyzodiastes* (*Temoana*) with antennal tufts beginning on segment V; marginal stria reduced to a row of punctures except near humerus and apex; sutural stria two-thirds length of elytra, pronotum rather short and subquadrate, and elytra without setae except near apex of marginal stria.

Description.—Length 7.0 mm. Tufts of minor setae on antennal segments V–X; basal setae of antennal segments absent; segments I–V with apical pollinose bands; apical stylet small, acute; head (Fig. 5A) about as long as wide; median lobe broad, triangular, its margins straight, apex slightly acute, opposite anterior third of eye; antennal lobe pollinose except for narrow lateral margin; temporal lobes widely separated from one another; orbital groove almost absent, represented only by very short narrow pollinose area opposite anterior end of eye; eye very narrow; temporal lobe with one seta in pollinose depression.

Pronotum (Fig. 5A) rather short, L/GW 1.21; subquadrate, sides only slightly curved, widest near middle, median groove deep, moderately narrow (but wider than in *R. raffrayi*), anterior pit slightly widened; median groove impressed beyond posterior pit to pronotal base; paramedian grooves with medial margins indistinct, lateral margins abrupt; outer carina broad, its width about half that of distance from paramedian groove to midline; outer carina of even width, truncate anteriorly and posteriorly; pronotal setae absent; marginal groove limited to posterior fourth of pronotum, visible only in lateral view.

Elytra only moderately elongate (shorter than in *R. raffrayi*), scarcely narrowed anteriorly; sutural stria impressed, impunctate, its apical third effaced; parasutural stria deep, entire, impunctate; intratubercular stria deep, entire, impunctate; marginal stria impressed only near humerus and apex, otherwise represented by widely spaced punctures; apical, subapical tubercles inflated, former extended to suture; elytra without setae except for four or five in apex of marginal stria. Metasternum not sulcate, its surface microsculptured, with bluish sheen. Abdominal sterna (Fig. 5B) with sterna III–VI with deep, pollinose transverse sulci broadly interrupted at midline; sternum VI with submarginal groove pollinose, joined at anterior ends to transverse sulci; lateral end of sulcus on sternum IV in form of a slightly enlarged pit in male; male with ventral surface of anterior femur with many small tubercles, with anterior trochanter acutely pointed ventrally; tibial spurs of middle and hind legs equal; calcars nearly triangular, but abruptly truncate apically; trochanter of middle leg with dorsal sinuation. Female unknown.

Distribution.—Known only from the type locality.

Remarks.—This species is closest to *R. raffrayi* (Grouvelle) and keys to that species in Bell and Bell (1985:12), except for the lack of setae in the parasutural stria. The two species are separated by the lack of most elytral setae in *R. riedeli*, and the quite different shapes of the pronota of the two species.

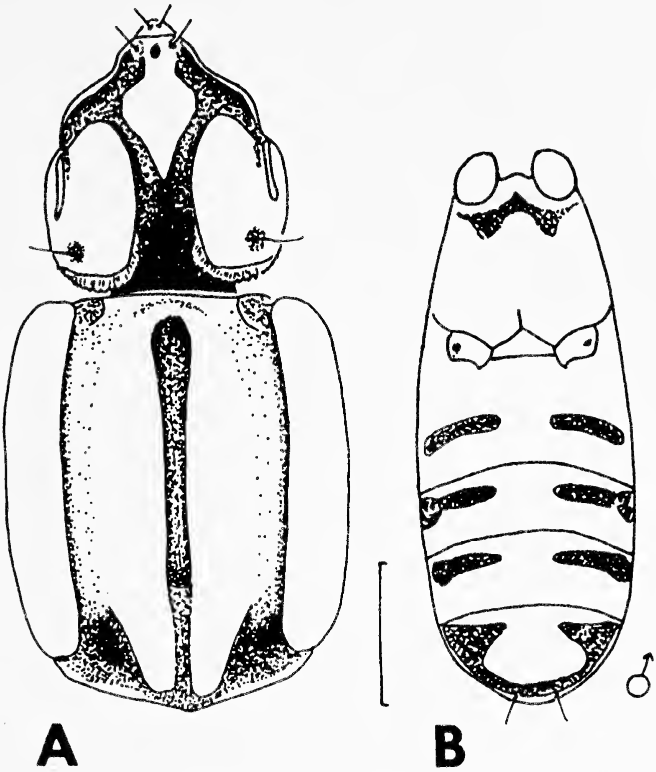

Fig. 5.—*Rhyzodiastes* (*Temoana*) *riedeli*, n. sp. A. Head, pronotum, dorsal aspect. B. Metasternum, abdomen, ventral aspect; male.

Rhyzodiastes riedeli is the second species of the genus found in New Guinea. It is a high-altitude species, while *R. guineensis* (Grouvelle) is a lowland species. *Rhyzodiastes guineensis* differs conspicuously in having a long, oval pronotum with a linear median groove, a complete orbital groove, the sutural stria completely lacking, and the tibiae incrassate. The two species do not appear to be closely related. The type locality of *R. riedeli* is high in the main central mountain range of New Guinea.

The key to the subgenus (Bell and Bell, 1985:12) should be altered as follows:

6(3′). Orbital grooves very much abbreviated or absent; temporal setae one or none 7
6′. Orbital groove complete at least to posterior margin of eye; temporal setae one or two 9
7(6). Lateral margins of pronotum nearly straight; outer carinae as far apart at apex of pronotum as at base; one temporal seta . . . . *Rhyzodiastes* (*Temoana*) *riedeli*, n. sp.
7′. Lateral margins of pronotum clearly convergent anteriorly; outer carinae much closer together anteriorly than posteriorly; temporal seta absent 7.1
7.1(7′). Orbital groove present, abbreviated opposite middle of eye; one temporal seta . . . . *R. mishmicum* (Arrow)
7.1′. Orbital groove absent 8

Rhyzodiastes (*Temoana*) *mindoro*, **new species**

(Fig. 6A and B)

Type Specimen.—Holotype female, labeled "Philippinen-Mindoro, 28 km. S. Calapan 1992, Balete 100–700 m. (19) leg. Jäch 27–29.11." (NMW).

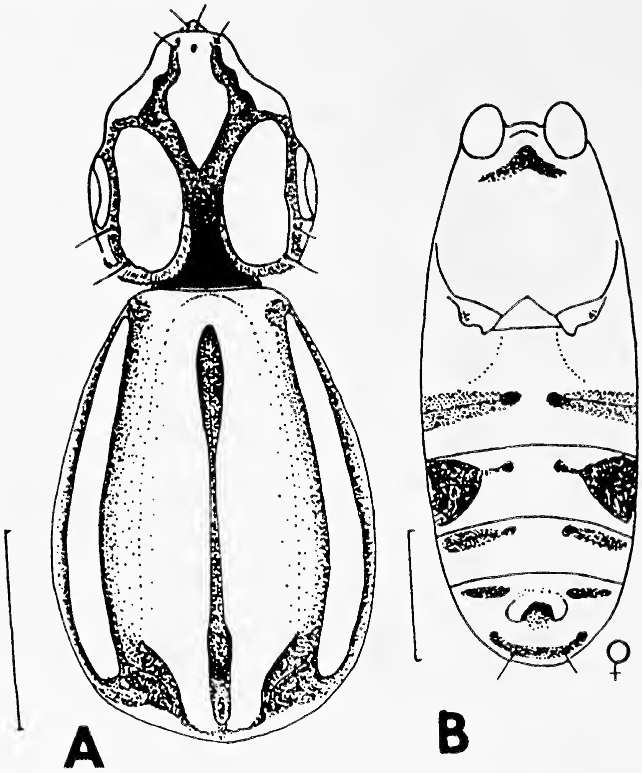

Fig. 6.—*Rhyzodiastes* (*Temoana*) *mindoro*, n. sp. A. Head, pronotum, dorsal aspect. B. Metasternum, abdomen, ventral aspect; female.

Etymology.—This specific epithet is derived from the name of the native island of the species.

Diagnosis.—A *Rhyzodiastes* (*Temoana*) with the characters of the *singularis* group (marginal stria entire, orbital groove complete, temporal setae present), with sutural stria impressed, and with two temporal setae, both in the pollinosity of the orbital groove. It differs from *R.* (*T.*) *bipunctatus*, since the latter species has the second temporal seta arising from a pit in the temporal lobe, well away from the margin. It resembles *R. rimoganensis* in having tubercles on sternum VI but differs from it by the presence of two temporal setae and by the linear median pronotal groove.

Description.—Length 7.5 mm. Antennal stylet short, conical; antennal segments short subcylindrical; tufts of minor setae on segments V–X; segments I and II partly pollinose, remaining segments glabrous; head (Fig. 6A) slightly longer than wide; median lobe short, triangular; antennal lobe glabrous, shining, well separated from median lobe; frontal grooves rather narrow pollinose; temporal lobe about twice as long as wide; medial margins curved evenly; orbital groove complete, with two temporal setae, anterior one at posterior end of eye, posterior near posteriolateral angle of head; eye crescentic, about three-fourths length of temporal lobe; posterior face of temporal lobe pilose.

Pronotum (Fig. 6A) elongate, L/GW 1.46, widest at posterior fourth, strongly narrowed anteriorly, rounded and narrowed posteriorly; median groove narrow in middle, dilated and tapered into anterior and posterior pits; paramedian groove with medial margin gradually sloped into disc, but lateral margin abrupt, pollinose scarp; medial margin of outer carina evenly curved; outer carina tapered, attenuate anteriorly, slightly narrowed posteriorly, rounded at base; marginal groove entire, visible in dorsal view; submarginal groove absent; pronotal setae absent; sternopleural groove absent.

Elytra moderately elongate, cauda absent; base of elytron deeply concave medial to base of parasutural stria, concavity densely pilose except narrow strip along suture; large scutellar pits opened into this depression; sutural interval nearly flat; sutural stria fine, impressed, finely punctate, apex outcurved, nearly extended to parasutural stria; second interval depressed; parasutural stria in form of medially facing scarp; intratubercular stria deep, entire; marginal deep, entire; submarginal impressed, ended opposite base of sternum VI; parasutural stria with one seta each near base and apex; marginal stria with four setae near apex; apical tubercle without setae. Metasternum not sulcate. Abdominal sterna (Fig. 6B) with transverse sulci of sterna III–VI broadly interrupted at midline, sulci pollinose, with distinct circular pit at medial ends; sternum IV with very large lateral pits (much larger than in *R.* (*T.*) *rimoganensis*); sternum VI with submarginal groove dilated, well separated from transverse grooves; posterior half of sternum VI impressed, bounded anteriorly by pair of tubercles; tibial spurs of middle and hind legs equal.

Distribution.—Known only from Mindoro Island in the Philippines.

Remarks.—The discovery of a member of this subgenus from the Philippines is not unexpected, as it has been found in all surrounding island groups. Other species probably await discovery in the Philippines.

To accommodate *R. mindoro*, and to make a better separation of *R. convergens*, the key to the subgenus (Bell and Bell, 1985:12) should be altered as follows:

11(9′). Metasternum with median sulcus; temporal lobe with one seta in orbital groove and one discal seta . . . . *R. bipunctatus* Bell and Bell

11′. Metasternum without median groove; temporal lobe without discal seta but with one or two in orbital groove 12

12(11′). Portion of median groove of pronotum between pits linear; orbital groove with two setae . . . . *R. mindoro*, n. sp.

12′. Median groove not as narrow; orbital groove with one seta 13

13(12′). Outer carinae of pronotum strongly tapered anteriorly 13.1

13′. Outer carinae not tapered anteriorly . . . . *R. mirabilis*

13.1(13). Median groove of pronotum narrow, although not linear, about one-tenth of width of pronotum . . . . *R. convergens* Bell and Bell

13.1′. Median groove broad 14

Rhyzodiastes (*Temoana*) *convergens* Bell and Bell, 1985

Additional Locality.—PAPUA NEW GUINEA: Manus I., 18-II, 1981, Bowar, 23 km W. of Lorengau, 230 m, rainforest fragment, 21, coll. W. L. Brown (CUIC). The species was previously known from New Britain, in the Bismarck Archipelago. This locality is in the Admiralty Islands, nearly 400 km distant, across deep waters. Although we are not naming the Manus specimen, we have some doubts about its identity with the New Britain species. The marginal groove of the pronotum is finer and fades out completely before the apex. The orbital groove is much finer and disappears opposite the posterior margin of the eye. In most of the type series of convergens, this groove is complete. In one paratype, however, it is as short as in the Manus specimen, although it is as broad as in the other New Britain specimens. The Manus specimen has a complete row of setae in the parasutural stria. We did not list such setae in the *convergens* description; however, on close examination, two of the types have a few setae in such a series, and they may have broken off in other specimens. There is no trace of the sinuation at the posteriomedial angle of the temporal lobe, but this is very reduced in some of the type series of *convergens*. We need a series of specimens from Manus before deciding whether its population merits a name. Whether the two populations are separate species or only incipient subspecies, they give the impression of being closely related populations just beginning to develop morphological differences after being isolated after a dispersal event. The key can be altered so as to separate

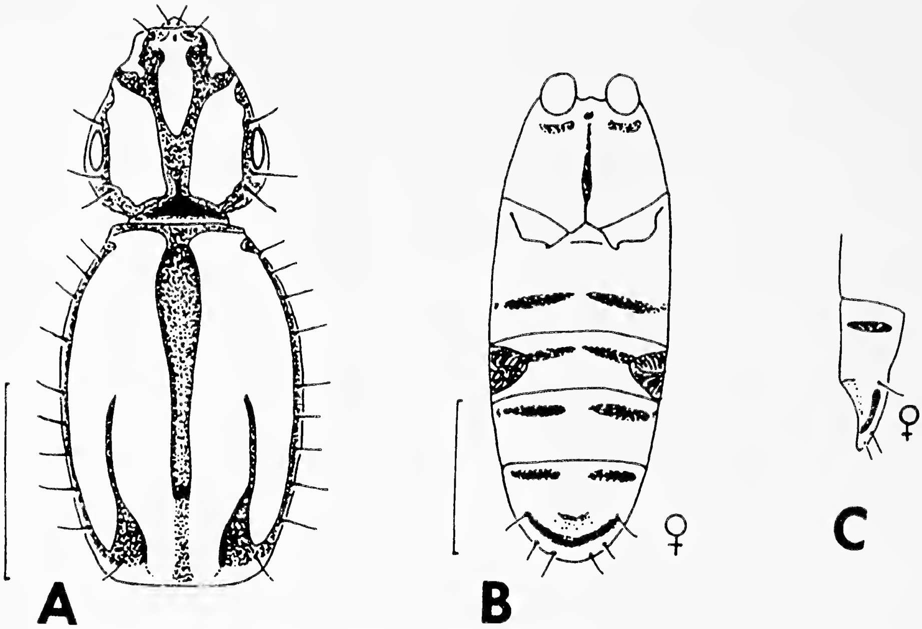

Fig. 7.—*Clinidium* (sensu stricto) *howdenorum*, Bell and Bell. A. Head, pronotum, dorsal aspect. B. Metasternum, abdomen, ventral aspect; female. C. Sternum VI, abdomen, left lateral aspect; female.

convergens (both populations) from related species. (See above under *Rhyzodiastes mindoro*.)

Clinidium (*Arctoclinidium*) *rosenbergi* Bell, 1970

Additional Locality.—ARKANSAS: Cross County, Village Street State Park, 29 VI, 1987, coll. Kovarik, one male, two females (TAMU). A new state record.

Clinidium (*Clinidium*) *insigne* Grouvelle, 1903

Additional Locality.—This species has previously been known only from the type locality, Cali, Colombia. Through the collecting efforts of Onore and associates, it is now revealed to occur in the northern half of the Andean part of Ecuador, south at least to Bolivar Province. Ecuadorean localities are Pichincha Province: Chiriboga, Est. Forestal "La Favorita," many specimens, several collectors; Palmeros, 26-VI-87, leg. Bustamente; Santo Domingo, 23-V-86, coll. P. Vega. Cotopaxi Province: Calupiña, VII-87, coll. Onore; Sigchos, VII-87, coll. Onore. Bolivar Province: Totoras, XII-87, coll. P. Mendoza (all specimens CMNH).

Clinidium (*Clinidium*) *howdenorum* Bell and Bell, 1985
(Fig. 7A–C)

Description of Female.—Three specimens, length 4.9–6.4 mm, labeled "Trinidad: Arima, Blanchisseuse Rd. 13.1 km n. of Arima, 29 Mar 1987, elev. 500 m. Trinidad Field Party, 1987, M. E. Carter, E. R. Hoebeke, J. K. Liebherr" (CUIC). Head and pronotum similar to male (Fig. 7A), but abdominal sterna (Fig. 7B) with transverse sulci of sterna III–VI narrowly interrupted in midline;

sternum IV with lateral pit large, deep, triangular; sternum VI (Fig. 7C) impressed posteriorly with slight transverse carina helping to define rudimentary median tubercle.

Remarks.—Hovorka (1997) recently described another new species of *Clinidium* (sensu stricto) from Ecuador, *Clinidium mareki.* The female of this species differs from *C. howdenorum* in having a pair of grooves on sternum VI which join together at the submarginal groove forming a characteristic V-shape.

Clinidium (*Clinidium*) *boroquense* Bell, 1970

Remarks.—The tufts of minor setae on the antenna are present on segments V–X, not VI–X as previously reported. Additional material has shown that precoxal setae are present, at least in some specimens. The antennal tufts take this species out of the Insigne group, as defined by Bell and Bell (1985). It belongs to the Guildingii group. The complete intercalary and intratubercular striae and absence of a longitudinal metasternal sulcus would put it in the Jamaicense section, but this is only doubtfully distinct from the Oberthueri section, in which the sulcus is very shallow in some species. Within the Jamaicense section, this species agrees with *C.* (*C.*) *trionyx* in the presence of precoxal setae, but the latter species has "false spurs" on the middle and hind tibiae, lacks discal strioles, and has the eye modified. *Clinidium boroquense* agrees with *C.* (*C.*) *jamaicense* and related species of Jamaica and Hispaniola in having narrow, elongate eyes and well-developed discal strioles, but the latter group of species lack precoxal setae and do not have the temporal lobes convergent posteriorly.

In the key in Bell and Bell (1985), *boroquense* should be removed from couplet 8, so couplet 7 leads directly to couplet 9. *Clinidium boroquense* would trace to couplet 18. At this point, those specimens with a precoxal seta would key to *C.* (*C.*) *humboldti* Bell and Bell, and those without a precoxal seta would probably trace to *C.* (*C.*) *jolyi* Bell and Bell. The key can be corrected as follows, using a new couplet 18, and renumbering the old one as 18.1.

18(15′).	Temporal lobes convergent posteriorly	*C. boroquense* Bell
18′.	Temporal lobes not convergent	18.1
18.1(18′).	Precoxal setae present	19
18.1′.	Precoxal setae absent	21

Clinidium (*Clinidium*) *spatulatum* Bell and Bell, 1985
(Fig. 8A–C)

Description of Male.—Length 6.4 mm. Head, pronotum, and abdomen (Fig. 8A and B) similar to female, but anterior tibia (Fig. 8C) with proximal tooth; anterior femur with raised carina; middle tibia with small acute calcars; hind tibia with short, rather blunt calcars.

Similar to *C. validum* Grouvelle male, except that the latter lacks the femoral carina and hind tibia has acutely pointed calcar. This specimen labeled "Panama: Darien, Estacion Ambiental Cana, 07°45.32′N, 77°41.07′W, Cerro Pirre, 1450 m., 6-VI-1996, R. S. Anderson, 96-112C, cloud forest litter" (CMNO).

The eye area of this specimen is heavily pigmented and almost invisible. This was true also of the holotype. In other members of this subgenus, paler (younger?) individuals may have unpigmented, obviously functional eyes, while the darker specimens have the area pigmented even more heavily than the rest of the exoskeleton.

Clinidium (*Clinidium*) *oberthueri* Grouvelle, 1903

Remarks.—The type locality of this species was simply "Ecuador." Bell and Bell (1985) listed three specimens from Papallacta, Napo-Pastaza Province. The

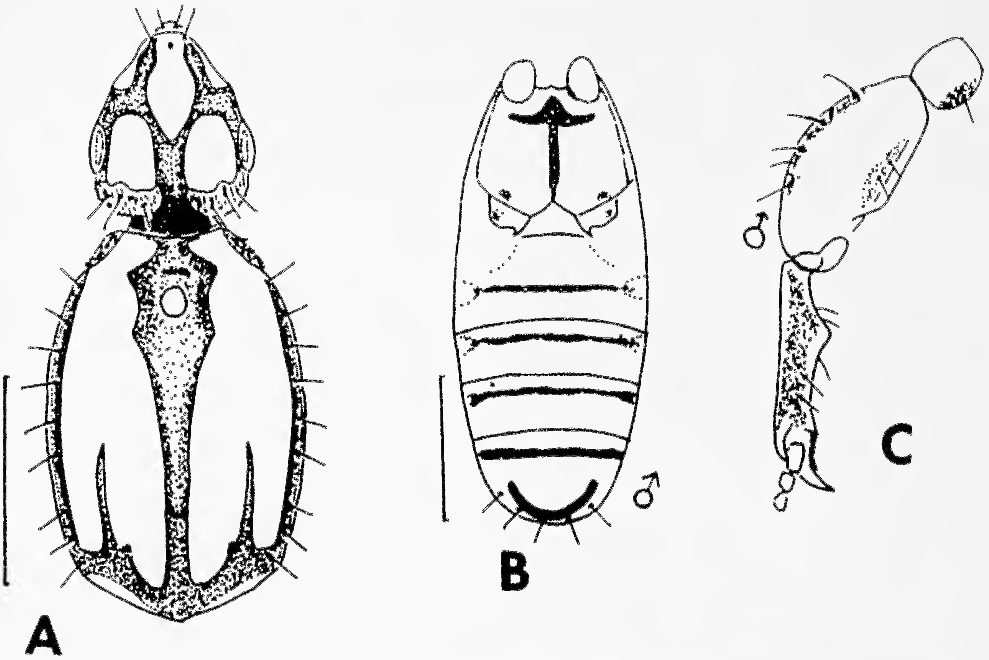

Fig. 8.—*Clinidium* (sensu stricto) *spatulatum* Bell and Bell. A. Head, pronotum, dorsal aspect. B. Metasternum, abdomen, ventral aspect; male. C. Anterior leg, tibia with proximal tooth, femur with raised ventral carina; male.

additional records below indicate that the range in Ecuador is similar to that of *C. insigne*, and that the species coexist in at least two localities.

Further locality records are: Napo-Pastaza Province: Cosanga, II-89, coll. G. Onore; km 36 via La Alegria La Bonita, 2100 m. Apr. 1-86, D. Bastidas (coll. P. Moret). Pichincha Province: Ayuriqui, 12-VII-87, M. Ferro; Palmeros, 26-VI-87, leg. Bustamente, Cotopaxi Province: Calupiña, III-87, G. Onore. Tungurahua Province: Tungurahua nord, P. Moret, 10-III-85, 3400 m. (coll. P. Moret). (All specimens CMNH except those cited as P. Moret.)

Clinidium (*Clinidium*) *rossi* Bell, 1970

Remarks.—This species was previously known from the type locality, Golfito, on the Pacific coast of Costa Rica. Additional records show that it occurs near the Atlantic coast, as well as in Panama. Costa Rica: Limón Province: Valle de la Estrella, Pandora, 17–20 Feb. 1984, H. & A. Howden (CMNO). Puerto Viejo Province: Sarapiqui, VIII-4-65, Raske (CNCO). Panama: Chiriqui Province: Dst. Renacimiento, Sta. Clara, 4400–4200 ft, July 5, 1976 (TAMU).

Clinidium (*Clinidium*) *dormans* Bell and Bell, 1985
(Fig. 9A and B)

Description of Female.—Length 5.8 mm, labeled "Panama: Chiriqui Prov., Reserva la Fortuna, Continent Divide Trail, 19–20 Apr., 1993 A. Gillogly" (TAMU). Head and pronotum (Fig. 9A) similar to male, but abdominal sterna (Fig. 9B) with lateral pit of sternum IV slightly deeper; sternum VI with five pairs of setae, two in submarginal groove, two on disc, and one in transverse sulci.

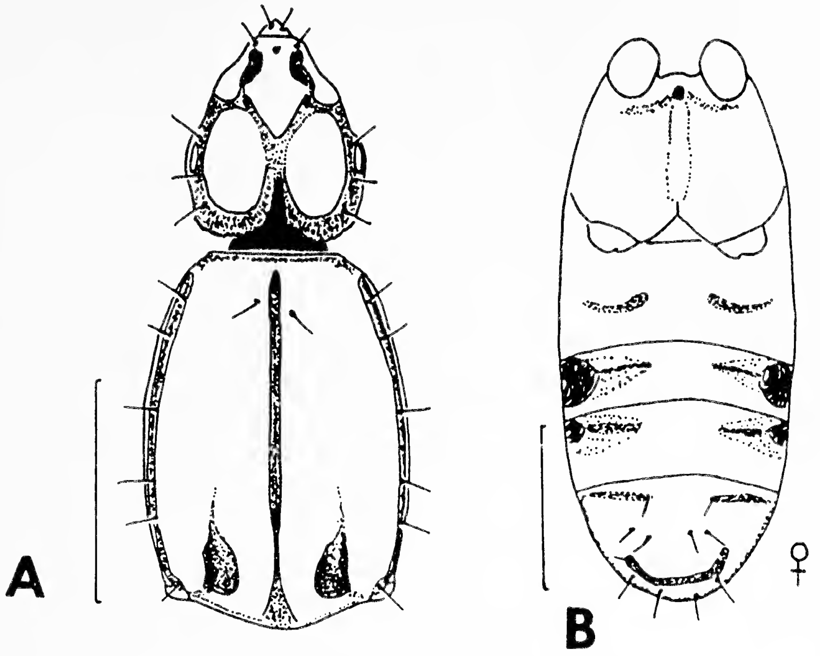

Fig. 9.—*Clinidium* (sensu stricto) *dormans* Bell and Bell. A. Head, pronotum, dorsal aspect. B. Metasternum, abdomen, ventral aspect; female.

Clinidium (*Clinidium*) *crater* Bell and Bell, 1985
(Fig. 10A–D)

Description of Male.—Series of seven; lengths 5.6–6.5 mm. Six females in the same series measure 6.0–6.8 mm; labeled "Panama, Pan. Pr., km 8, El Llano-Carti Rd., VI and VII (various dates), 1994, elev. 400 m., A. R. Gillogly" (UVM). Head and pronotum (Fig. 10A) similar to female; abdominal sterna (Fig. 10B) with transverse sulci of sterna III–V shallow, all equally narrowly interrupted in midline; lateral pits of sterna III–V equal, very shallow; sternum VI with transverse sulcus represented only by pair of coarse, shallow punctures on each side; some specimens with short, thin, curved, pollinose line transversely arranged in midline, anterior part of disc separated from posterior, sloped part; anterior femur (Fig. 10C) with ventral tooth; calcar of middle leg minute; calcar of hind leg small, acutely pointed (Fig. 10D).

Clinidium (sensu stricto) *onorei*, **new species**
(Fig. 11A and B)

Type Specimen.—Holotype male, labeled "Ecuador, Pichin (cha), Ayuriqui 12-VII-82. legit. M. Ferro ex copal, Hora P.M., haciendo galeria" (CMNH). Paratype: one female, same label as holotype (UVM).

Etymology.—The specific epithet is derived from the surname of Dr. Giovanni Onore, a Research Associate of Carnegie Museum of Natural History, whose energetic collecting and generosity with specimens has added much to our knowledge of Ecuadorian Rhysodini.

Diagnosis.—A *Clinidium* sensu stricto in the *rossi* section, combining a narrow median pronotal groove, a deep median metasternal groove, with a lack of setae in the sutural stria.

Description.—Length 5.6–6.0 mm; antennal stylet very slender, acute, about three-tenths of length

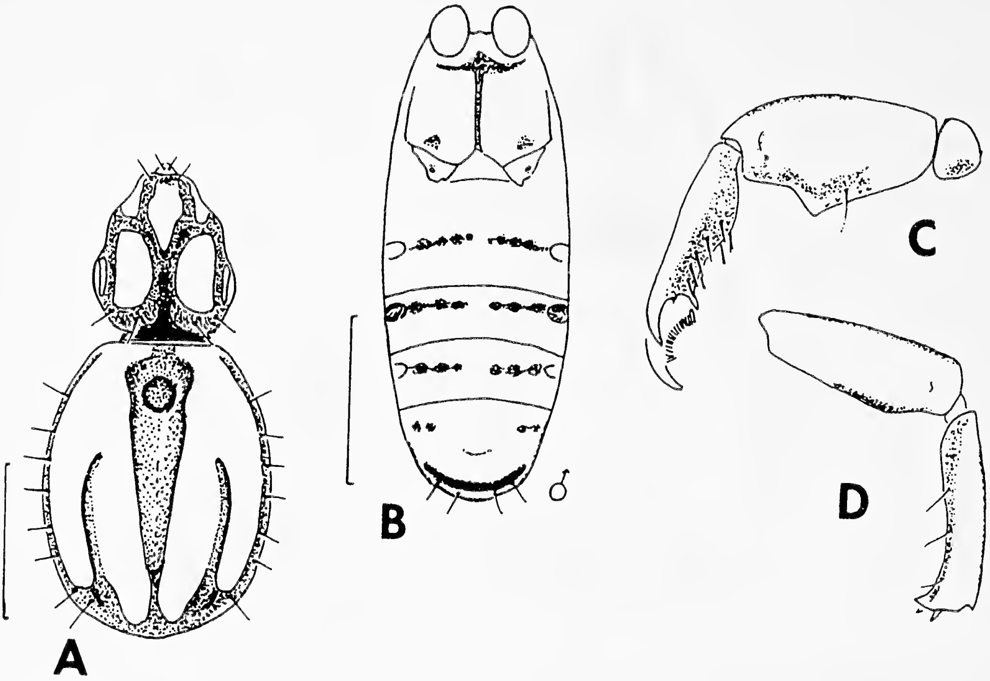

Fig. 10.—*Clinidium* (sensu stricto) *crater* Bell and Bell. A. Head, pronotum, dorsal aspect. B. Metasternum, abdomen, ventral aspect; male. C. Anterior leg, ventral tooth on femur; male. D. Hind leg, femur and tibia; male.

of antennal segment XI; tufts of minor setae on segments V–X; segments I–VII each with subapical pollinose ring; basal setae present on segments VI–XI or VII–XI. Head (Fig. 11A) slightly longer than wide; frontal grooves deep, narrow; median lobe short, triangular, its tip opposite anterior part of eye; medial margins of temporal lobes closest together posterior to tip of median lobe, divergent posteriorly; posteriomedial margins of temporal lobes very broadly bordered by pollinosity, pollinosity along lateral border of lobes also broad, irregular, curved around bases of temporal setae; four temporal setae (one anterior to eye, two opposite eye, one posterior to eye); two pairs of postlabial setae.

Pronotum (Fig.11A) moderately elongate; L/GW 1.44, widest posterior to middle; pronotum more narrowed anteriorly than in *segne* or *oberthueri*; median groove very narrow, its margins parallel, slightly widened between median pits, extremely narrow behind posterior median pit; basal impressions oblong; discal striole linear, nearly straight, about 0.45 of length of pronotum, marginal groove narrow, visible in dorsal view, eight to nine lateral setae; one seta posterior to each basal impression, one pair of discal setae; precoxal seta present; sternopleural suture faintly suggested.

Elytra moderately elongate; sutural, parasutural, intercalary striae complete, impressed; intratubercular stria complete apically, but not impressed, apical and subapical tubercles thus not differentiated; marginal stria impressed; sutural striae without setae; parasutural stria with one seta at base; intercalary stria with complete series of about 12 setae; series of five setae near apex of intratubercular seta and continued onto apical tubercle; marginal stria with complete series of about 16 setae. Metasternum (Fig. 11B) with deep, linear median groove. Abdominal sterna (Fig. 11B) with transverse sulci of sterna III–V represented by rows of coarse punctures, widely separated at middle; sternum VI with submarginal sulcus widely separated from transverse sulci; latter short but deep; lateral pit of sternum IV moderately large, shallower in male; Sternum VI with eight setae in two transverse rows, four anterior to submarginal groove, and four posterior to it; each tibia with two equal spurs, and an apical cusp (homologous to the "false spur" in some related species); male with both mesotibial and metatibial calcars cultrate.

Distribution.—Known only from the type locality.

Remarks.—The species is startlingly similar in general shape to the sympatric

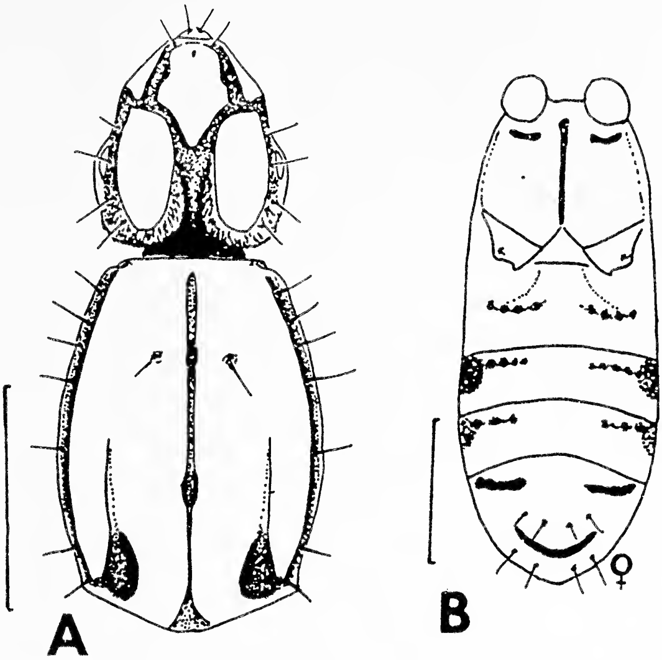

Fig. 11.—*Clinidium* (sensu stricto) *onorei*, n. sp. A. Head, pronotum, dorsal aspect. B. Metasternum, abdomen, ventral aspect; female.

C. oberthueri Grouvelle. The latter is easily distinguished by the separation of the subapical and apical tubercles, and by the setae in the sutural stria.

To accommodate *C. onorei*, substitute the following for couplets 26 and 27 in the key of Bell and Bell (1985:96):

26(25′). Sutural stria with five setae; female with brush of dense hairs at base of hind femur . . . . *C. segne* Bell and Bell
26′. Sutural stria without setae or with one basal seta 27
27(26′). Frontal grooves very shallow; antennal stylet minute, about one-tenth of length of antennal segment XI; pronotum without discal setae . . . . *C. dormans* Bell and Bell
27′. Frontal grooves deep; antennal stylet about one-third of length of antennal segment XI; pronotum with one pair of discal setae 27.1
27.1(27′). Median groove of pronotum dilated, its greatest width subequal to about half of distance to discal striole at this point; transverse sulci of abdominal sterna III–V impressed, continuously pollinose; female with anterior margin of subapical sulcus of sternum VI angulate at midline . . . . *C. kochalkai* Bell and Bell
27.1′. Median groove very narrow, at greatest width less than one-fifth of distance to striole; transverse sulci of abdomen formed of single rows of very coarse punctures, pollinosity limited to punctures; female with anterior margin of subapical sulcus unmodified . . . . *C. onorei*, n. sp.

Clinidium (sensu stricto) *moldenkei* Bell and Bell, 1985

Additional Locality.—PANAMA: Chiriqui Province, 2200 m, Las Nubes, Parque Amistad, 20 Dec. 1992, A. R. and T. Gillogly (TAMU). Bocas del Toro Province, Fortuna area, N. continental divide, 750 m, Aug. 6, 1993. A. R. Gillogly (TAMU). Previously known from Oso Peninsula of Costa Rica.

Clinidium (sensu stricto) *sulcigaster* Bell, 1973

Additional Locality.—PANAMA: Chiriqui Province: 1 km. n. of Jurutungo, 20-VI-1994, el. 1900 m, A. R. Gillogly (UVM). Previously known from Guatemala. This at present is the only species known to extend through the entire length of Central America.

Clinidium (*Clinidium*) *gilloglyi*, **new species**

(Fig. 12A–C)

Type Specimens.—Holotype male, labeled "Panama: Chiriquí Pr., 1 km SE Hornito 23-VII-1994, 1000 m. A. R. Gillogly" (CMNH). Paratypes: one female, one male same data as holotype (UVM).

Etymology.—The specific epithet is derived from the surname of the collector, Alan R. Gillogly, in appreciation of his efforts in sending us fine rhysodine material from Panama.

Diagnosis.—A *Clinidium* sensu stricto with the compound eye divided into two ocelluslike organs, and with tufts of minor hairs on antennal segments VII–X.

Description.—Length 6.0–6.6 mm. Antennal stylet compressed, chisel-like, obliquely truncate, length about one-third of length of last antennal segment. Minor setae present on segments VII–X; basal setae absent; segments I–X each with subapical pollinose ring; head (Fig. 12A) longer than broad; median lobe small, shield-shaped; frontal grooves broad, pollinose; antennal lobe small, separated from temporal lobe by broad, pilose postantennal area; frontal space moderately broad; medial margins of temporal lobes diverging slightly posteriorly; posterior margin of temporal lobe broadly pilose; orbital groove complete; three to five temporal setae in orbital groove; compound eye divided into two ocelluslike organs (Fig. 12B); two pairs of postlabial setae.

Pronotum (Fig. 12A) elongate, L/GW 1.48; widest near middle, sides curved; apex strongly narrowed, truncate, base slightly narrowed, curved; median groove open posteriorly, strongly dilated, margins of groove straight, slightly convergent posteriorly; anterior pit only slightly wider than median groove; discal striole straight, extended to middle of pronotum; marginal groove slightly dilated, visible in dorsal view; six to eight marginal setae, none medial to basal impression (such setae present in *C. argus*); sternopleural groove intact anteriorly; posterior half formed by line of three pits.

Elytra relatively long, narrow; sutural, parasutural striae deep, narrow, conspicuously punctate; intercalary stria wider, deeper than others; intratubercular fine, entire; marginal stria entire, strongly dilated posteriorly; preapical tubercle scarcely inflated; apical tubercle inflated; sutural, parasutural striae without setae; intercalary stria with series of eight setae; intratubercular stria with three setae opposite apical tubercle; apical tubercle with three or four setae; marginal stria with nine or ten setae. Metasternum (Fig. 12C) widely, shallowly impressed in midline, but without distinct median sulcus. Abdominal sterna (Fig. 12C) with transverse sulci rather broadly interrupted in midline, interruption about half length of sulcus on either side of it; transverse sulcus of sternum VI broadly separated from submarginal sulcus; lateral pit of sternum IV moderately large in female, shallower in male; sternum VI with one pair of apical setae; male abdomen without median pollinose areas, without paired tubercles; anterior femur of male without ventral tooth, but with slight ventral ridge; lateral pit of sternum IV in female large, nearly as long as sternum, that of male small; calcars triangular, that of hind tibia sinuate on dorsal margin.

Distribution.—Known only from the type locality. One other specimen is known from Veraguas Province, Panama, near Hato Chami, Cerro Colorado, 1400 m (TAMU).

Remarks.—The combination of divided eyes and minor setae on antennal segments VII–X has not been seen before in *Clinidium* sensu stricto, and prevents this species from keying out in Bell and Bell (1985:93–97). The minor setae send it ultimately to couplet 5, where it would match neither alternative. The eyes would send it to couplet 43, the *beccarii* group. The latter group appears to be its real kin; the head and pronotum are almost a perfect match for *C. argus* Bell and Bell. The *Clinidium* key should be altered as follows:

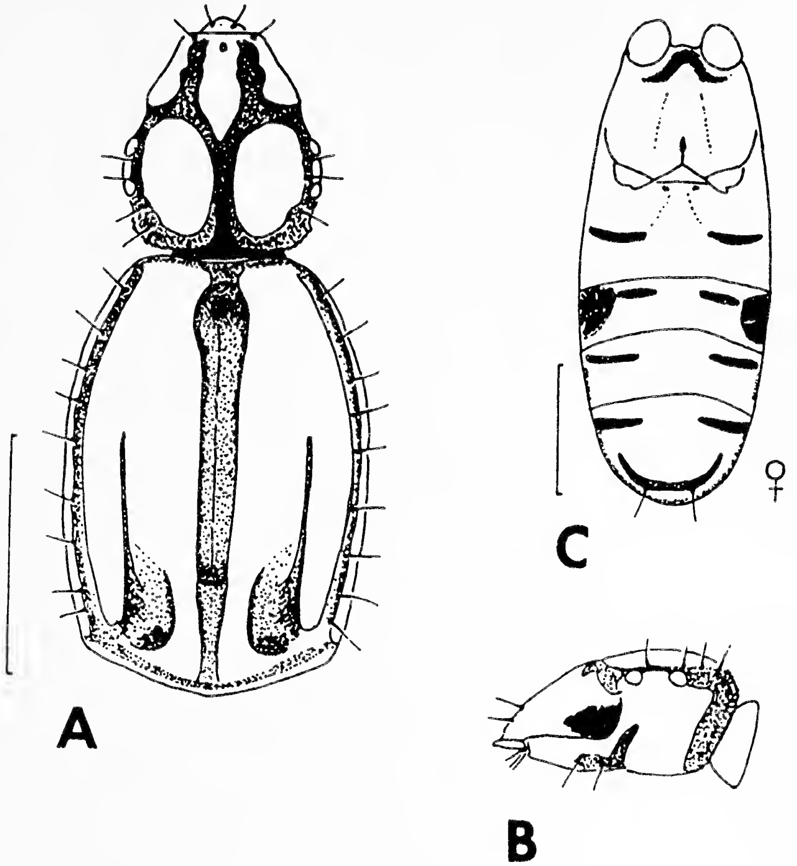

Fig. 12.—*Clinidium* (sensu stricto) *gilloglyi*, n. sp. A. Head, pronotum, dorsal aspect. B. Head, left lateral aspect. C. Metasternum, abdomen, ventral aspect; female.

2(1′). Eye not constricted in the middle nor divided into anterior, posterior halves; tufts of minor setae on antennae distinctly developed, on segments V–X, VI–X, or VII–X 3
2′. Eye either constricted at middle of length or else divided into anterior and posterior ocelluslike parts; tufts of minor setae either very inconspicuous on segments VII–X or else absent 43

C. gilloglyi will be included and the key to related species improved by substituting the following couplets in the same key:

43(2′). Discal striole of pronotum much closer to median groove than to lateral margin; antennal stylet very small . . . . *C. beccarii* Grouvelle
43′. Discal striole either closer to lateral margin than to median groove, or else equidistant between them; antennal stylet large, obliquely truncate, chisel-like 44
44(43′). Parasutural (second) stria with complete series of setae 45
44′. Parasutural stria without setae 46
45(44). Anterior median pit of pronotum about one-half of width of pronotum opposite it; anterior and posterior parts of eye small, close together; male with deep median sulcus on abdominal sterna I–III . . . . *C. sulcigaster* Bell
45′. Anterior median pit about one-fourth of width of pronotum; eye parts larger and further apart; male with only a slight suggestion of median groove . . . . *C. gilloglyi*, n. sp.
46(44′). Anterior part of sternopleural groove pollinose; median groove of pronotum as wide as

anterior pit, sides of groove parallel; male with pollinose strip in midline of abdominal sterna I–III . . . . *C. argus* Bell and Bell

46′. Anterior part of sternopleural groove glabrous, obsolete; anterior median pit much wider than median groove, latter tapered posteriorly; male abdomen without median pollinose strip . . . . *C. moldenkei* Bell and Bell

The inclusion of *C. gilloglyi* in the *beccarii* group alters the definition of the latter. The structure of the eye and the antennal stylet remain as group characters, but the new species has antennal tufts and the male lacks tubercles on abdominal sterna III and IV, so lack of tufts and presence of tubercles are removed from the list.

The close similarity between *C. gilloglyi* and *C. argus* suggests that these two species might be sister species. This would imply that the minor setae were lost independently in *C. argus* and in the ancestor of the remaining species. The paired abdominal tubercles, well developed in the latter species, are very small in *C. argus* and absent in *C. gilloglyi*, suggestive of a secondary loss in the latter species.

The discovery of *C. gilloglyi* in Panama gives added weight to the suspicion that the type of *C. argus*, supposedly from the Philippines, is probably mislabeled.

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THE MICROTINE RODENTS FROM THE PIT LOCALITY IN PORCUPINE CAVE, PARK COUNTY, COLORADO

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ABSTRACT

This report presents the results of an analysis of the microtine rodents from the Pit locality, one of four localities within Porcupine Cave that have a relatively long stratigraphic sequence. At 2900 m elevation, Porcupine Cave is the highest elevation site in North America to have produced a diverse microtine rodent assemblage. At least 11 species are distributed through 14 stratigraphic levels: *Phenacomys gryci, Phenacomys* sp., *Mimomys* (*Cromeromys*) cf. *M. virginianus, Ondatra* sp., *Allophaiomys pliocaenicus, Terricola meadensis, Mictomys* cf. *M. meltoni, Microtus paroperarius, Microtus* sp. (not *M. paroperarius*), *Lemmiscus curtatus*, and *Lemmiscus* sp. All but one of these (*Phenacomys* sp. not *P. gryci*) occur within a single stratigraphic level (level 4), making the assemblage of microtines unique in species composition and among the most diverse known from any fossil deposit. The diversity of the assemblage probably results from the location of the site within a topographically diverse ecotonal region that allowed sampling of a wide range of nearby microhabitats by the carnivores and raptors that initially collected the bones. The unique species assemblage is likely related to the high elevation of the site, which differentiates it physiographically from any other fossil deposit that has produced microtine rodents in abundant numbers, and perhaps because the Rocky Mountain backbone served as both a dispersal corridor and refugium as taxa adjusted biogeographic ranges in response to glacial-interglacial transitions and other climatic changes.

The particular assemblage of species, when compared with previously dated occurrences of microtine species, suggests that levels 4–8 of the excavation date to between approximately 750,000 and 850,000 YBP. This age assessment is consistent with paleomagnetic data which indicate that level 8 is older than the Bruhnes-Matuyama boundary (780,000 YBP). The microtine biochronology suggests that the upper levels of the Pit (levels 1–3), date somewhere between 250,000 and 780,000 YBP, but it is not yet possible to be more precise.

The new data presented herein are important in revising previously reported interpretations of the age of the Pit locality (e.g., the level 4/3 transition is now thought to be between 750,000 and 850,000 YBP rather than the previous interpretation of near 400,000 YBP). In addition, these data document the occurrence of a unique microtine species assemblage which has implications for biochronological schemes that rely on microtines, and provide a framework for interpreting the timing and effects of climate change on the other 70+ species that occur in this very important middle Pleistocene site.

KEY WORDS: Irvingtonian, Arvicolinae, biochronology, climate change

INTRODUCTION

Porcupine Cave is situated high in the Rocky Mountains in South Park, Park County, Colorado. At 2900 m elevation, it is one of the highest fossil vertebrate sites of Pleistocene age in North America, and has the most taxonomically diverse fauna of any high-elevation site on the continent. So far at least 80 species of

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mammals, birds, reptiles, and amphibians have been identified. Ongoing research in the cave continues to reveal a tremendous wealth of fossil vertebrate material, and the site is rapidly earning its place as the most important middle Pleistocene (Irvingtonian) locality in North America.

A history of the discovery and early investigations of Porcupine Cave was presented by Barnosky and Rasmussen (1988). Continuing investigations at the cave led to discovery of new localities and faunas, with a concomitant dramatic increase in the number of specimens recovered. In spite of these advances, the temporal span of the faunas, determination of the specific age of any given locality within the cave, and the correlation between discrete faunas and localities within the cave remain elusive goals. The most reliable age estimates were and are generated through analysis of the biochronologic implications of the fauna, despite efforts to apply paleomagnetic and electron-spin resonance dating techniques. Microtine rodents have been used for the last 50 years as a primary tool in construction of regional and continental scale biochronologies throughout the Holarctic, and biochronologic age estimates for the various deposits in Porcupine Cave are based on the stage of evolution and taxonomic composition of the microtines. The temporal resolutions reportedly obtainable through careful study of microtines in the Pliocene and Pleistocene range from on the order of hundreds of thousands of years to tens of thousands of years, making them a powerful tool for relative age determinations in a time period plagued by a lack of broadly applicable radiometric dating techniques and the difficulty of correlating to the geomagnetic polarity time scale (see below).

In this paper, we present a complete summary of the microtine rodent fauna from the Pit locality within Porcupine Cave that was excavated by the Carnegie Museum of Natural History from 1985 to 1990. Although work by the Denver Museum of Natural History continues in the cave today, the Pit excavation is now completed and that phase of the project is ended. Data from the Pit sequence provide a baseline against which other deposits in the cave can be evaluated as they are completely excavated and studied. The Pit locality represents one of only four excavation sequences within Porcupine Cave from which faunas can be placed in precise superpositional relationship. Our goals here extend beyond mere identification of species and documentation of the change in taxonomic composition in microtines at the site through time. We specifically address some of the problems encountered in attempts to place the Porcupine Cave faunas within the existing microtine rodent biochronological framework, present estimates of the temporal span of the Pit sequence, and discuss implications of these data for age determinations elsewhere. The data presented here represent a more complete summary of the fauna and update all previously published reports on microtine rodents from the Pit (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996*a*, 1996*b*; Bell, 1997, 1998).

Abbreviations

CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; DMNH, Denver Museum of Natural History, Denver, Colorado; KU, University of Kansas Museum of Natural History, Lawrence, Kansas; SBCM, San Bernardino County Museum, Redlands, California; UCMP, University of California Museum of Paleontology, Berkeley, California; USNM, United States National Museum, Washington, D.C.

Table 1.—*Institutional localities and locality numbers for vertebrate fossils recovered from different excavation units in Porcupine Cave. * denotes multiple discrete excavations from a single room; NA = locality number not assigned as of this writing; — = no collection housed at institution.*

Locality	CM	DMNH	KU	UCMP
Badger Room	1928	942/1351	—	V93176
Come-Along Room	—	1353	—	—
Cramped Quarters	—	1346	—	—
Crystal Room	—	1345	—	V94014
Damp Room	1929	NA	—	V93178
Ferret Room	1930	1342	—	V93179
Fissure Dump Pile	—	1348	—	—
Fissure Fill A	—	1344	—	V98022
Fissure Fill B	NA	—	—	NA
Generator Dome Room	—	1347	—	—
Gypsum Room	1926	—	—	V93174
Gypsum Room SE corner Site	—	1343	—	—
Gypsum Room Closet	—	—	NA	—
Memorial Day Room	—	1352	—	—
New Passage	1931	—	—	V93177
Pit*	1925	—	NA	V93173
Velvet Room*	1927	644	—	V93175
Velvet Room Mark's Sink	—	1349	—	—
Velvet Room Will's Hole	—	1350	—	—
PC General	1932	1354	—	V97002

The Localities in Porcupine Cave

At least 21 separate excavations in Porcupine Cave, conducted by parties representing four institutions (Table 1), have yielded vertebrate fossils. Most excavations were test pits or exploratory investigations, but as of 1998 four extensive excavations have been conducted (or are ongoing) in stratified deposits at least 1-m thick. One of these excavations was in the Pit locality, and the other three are located in the Velvet Room (Fig. 1). The first excavation within the Velvet Room was conducted by CM crews and was situated on a slightly elevated portion of the room along the northern wall. A second, more expansive excavation was opened by the DMNH on the west wall next to the entry passage into the room. This excavation is ongoing and continues to produce a wealth of material. A third excavation, which began as an exploration pit seeking a passage to another room, recently produced what appear to be some of the oldest vertebrate fossils from the cave. Detailed stratigraphic excavation of this pit, named Mark's Sink, was begun by DMNH crews during the 1996 field season.

Background and Previous Research

Since the first publication about Porcupine Cave fossils (Barnosky and Rasmussen, 1988), papers or theses have been completed about the carnivores from all localities within the cave (Anderson, 1994, 1996), the prairie dogs from the Pit (Rouse, 1997), and climatic implications of portions of the Pit fauna (Wood and Barnosky, 1994; Barnosky et al., 1996*b*).

In 1981, Don Rasmussen made the first systematic collection of vertebrate fossils from the cave (in the Gypsum Room). In 1985, small collections were made by Barnosky and Rasmussen in the Pit and Badger Room localities. Be-

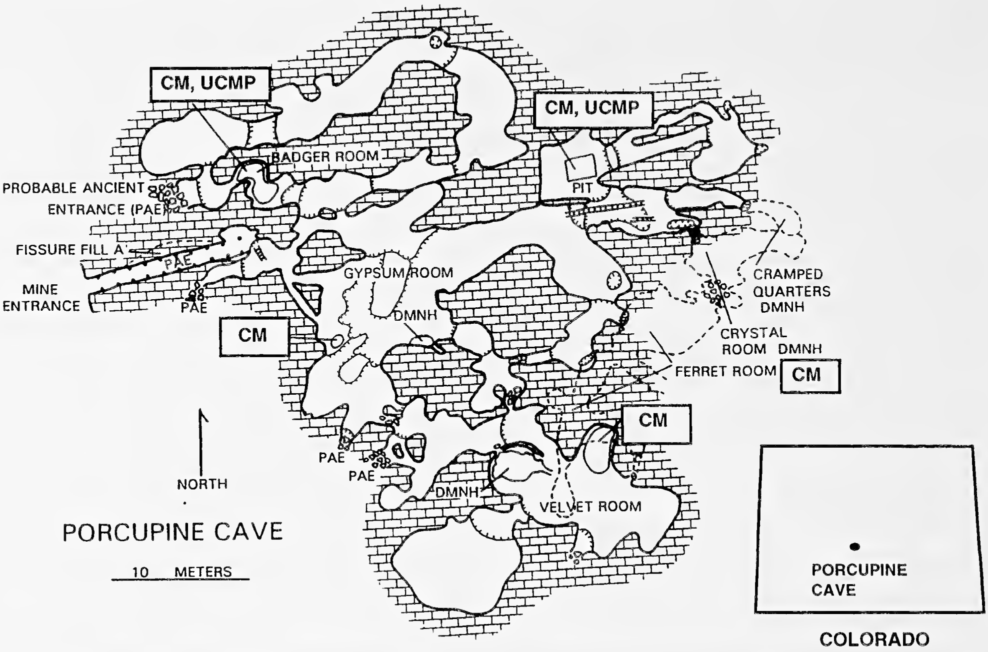

Fig. 1.—Location and map of Porcupine Cave. The map was produced by members of the Colorado Grotto of the National Speleological Society from a survey that took place in 1987 and was made available for this report by D. Rasmussen. Selected localities that have produced fossil vertebrates are labeled with the name of the institution that conducted excavations and at which specimens are deposited. Material in this report comes from the Pit locality, in which the location of the approximately 2 m × 4 m excavation is plotted.

tween 1986 and 1990, CM crews under the direction of Barnosky conducted full excavations in the Pit and the Velvet Room and made test excavations and/or surface collections in the Badger Room, Crystal Room, Damp Room, Gypsum Room, Ferret Room, Fissure Fill A, Fissure Fill B, and the New Passage Room. UCMP field parties (again directed by Barnosky) continued work on the localities originally worked by CM until 1993. In 1987, DMNH crews began a systematic study that included detailed mapping of the cave and all fossil vertebrate localities, additional test pit and surface sampling from known localities, the discovery and documentation of several new localities, and an extensive new excavation in the Velvet Room. The DMNH study still is underway. In 1994, a small team from KU conducted a limited excavation adjacent to the CM Pit excavations. Specimens from the various excavations are curated at CM, DMNH, UCMP, and KU.

Stratigraphy

The Pit locality (CM loc. 1925, UCMP loc. V93173) occurs in the northeastern part of the cave approximately 30 m from the modern cave entrance (Fig. 1). A grid system consisting of eight 0.91-m (3-ft) squares provided horizontal control of the excavation (Barnosky and Rasmussen, 1988:fig. 2). Each square was excavated by natural stratigraphic levels or 10-cm intervals (whichever was thinner) to an approximate depth of 235–252 cm where sediments terminated in a bedrock floor. Additional details of excavation and screening procedures were provided by Barnosky and Rasmussen (1988).

The stratigraphy in the Pit sequence consists primarily of alternating beds of homogenous, unindurated silts and fine sands ("loess" of Barnosky and Rasmussen, 1988) interbedded with more consolidated beds consisting primarily of hard clay nodules or concretions. At least the larger of the nodules appear to be formed around a center "core" consisting of a small piece of carbonate or bone. Some concretions effervesce readily and nearly completely disintegrate in hydrochloric acid, indicating carbonate cementation. The Pit stratigraphy is irregularly punctuated with flowstones of varying thickness, including one that appears to have been a stable surface for some length of time (designated as a "paleofloor"; level 8A). Two types of flowstone occurred in the excavation: apparently pure layers of calcium carbonate (generally less than 5 cm in thickness), and breccias tightly cemented by a calcium carbonate matrix. The breccias appear to have been indurated as calcium carbonate-laden waters trickled through them. Major sedimentological changes in the sequence were interpreted to be the result of climate change (Barnosky and Rasmussen, 1988) and subsequent faunal analyses supported this conclusion (Wood and Barnosky, 1994; Barnosky et al., 1996*b*; see below). Fourteen discrete stratigraphic levels were numbered sequentially from the top to the bottom of the section. Preliminary description of stratigraphic levels 1–9 was provided by Barnosky and Rasmussen (1988), but only levels 1–4 were entirely excavated at the time that report was written (lower levels were originally described based on samples from a bucket auger core). Figure 2 presents a schematic summary of the stratigraphic section in the Pit. Descriptions of levels listed here are in part taken from the discussion in Barnosky and Rasmussen (1988:274). Stratigraphic thickness is given as range of depth of level(s) below a permanent datum established at the surface of the Pit prior to excavation (datum = 0 cm). Color descriptions were obtained by matching samples to the Geological Society of America rock color chart (1984).

Levels 1–3.—Moderate yellowish brown dust with a flourlike consistency. Distributed in a cone that is 81-cm thick at the southeast corner of square 1 and tapers to 5-cm thick approximately 2 m to the northwest. Very soft. 0 cm below datum at the southeast corner of square 1 to −76 cm at the northwest corner of square 2 (Barnosky and Rasmussen, 1988).

Levels 4–5.—Consolidated clay, dark yellowish brown in color. Upper 15 cm composed of clay concretions (nodules) averaging 2–5 cm in diameter, grading downward to concretions averaging 1 cm in diameter. Distributed in a cone that is thickest in the vicinity of square 3 (63 cm) and tapers to the north, east, and west. Moderately hard. −76 to −139 cm. At the base of level 5 in square 2 a hard, indurated surface marked the end of the level and provided two paleomagnetic samples. Depths at the base of level 5 ranged from −112 cm in the southeast corner of square 2 to −117 cm along the west profile (Barnosky and Rasmussen, 1988).

Level 6.—The top of level 6 was a broad, indurated rocky surface no more than 5.08 cm thick. Below it was a moderately hard clay mixed with loose dust, similar in appearance to level 5, but with more white gypsum(?) crystals intermixed. The bottom of the level was marked by large chunks of white crystalline material and very soft, loose gray dust, with sparse pea-sized nodules, approximately 20% white crystalline flecks. In screenwashing, about one-half of residue

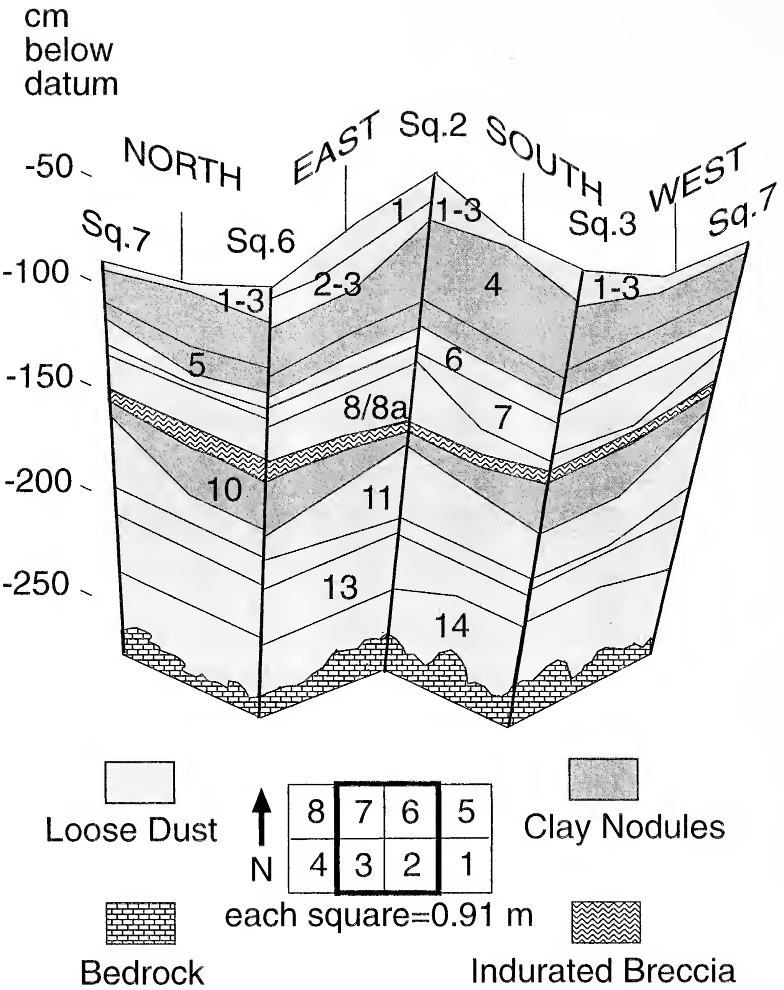

Fig. 2.—Fence diagram showing the basic stratigraphy of the Pit excavation. The excavation grid at the bottom is a plan view that enlarges the grid outline plotted on Figure 1. Squares 1, 2, 3, 5, 6, and 7 were excavated. The fence diagram shows schematic stratigraphy for the walls outlined in bold on the grid; numbers on the walls identify the various stratigraphic levels mentioned in the text. The north wall of the diagram shows the north wall of squares 7 and 6; the east wall is composed of squares 6 and 2; the south wall of squares 2 and 3; and the west wall of squares 3 and 7. Stratigraphic relationships became more complex in the center of the squares; see the explanation in the text and the diagonal cross section through square 2 that was illustrated as figure 2 in Wood and Barnosky (1994). Levels 1–3 were so thin and friable that they were not always differentiated in the areas of the excavation that show in the fence diagram; specimens from levels 1–3 in these areas were labeled "mixed level 1–3." However, in square 1 and other portions of squares 2, 3, 5, 6, and 7, levels 1–3 were much thicker and were easily differentiated by depth measurements; these areas provided the specimens that were stratigraphically assigned to level 1, 2, or 3. In general, layers identified as "loose dust" are thought to represent warm, arid climates (interglacials), and those labeled "clay nodules" and "indurated breccia" are thought to represent cool, moist climates (glacials).

was white crystalline fragments. Depths at base range from −114 cm in southern edge of square 2 to −130 cm in northeast corner of square 3.

Level 7.—Very soft, loose, gray dust with scattered pea-sized nodules; abundant white crystalline flecks concentrated at base of level. Depths at base of level range from −120 cm in northeast corner of square 6 to −145 cm at center of west wall (between squares 3 and 7).

Level 8.—Loosely consolidated gray dust mixed with nodules; laterally abuts or grades into level 8A.

Level 8A.—Indurated surface (paleo-floor), sitting on material similar to levels 1–3 but considerably more consolidated; two paleomagnetic samples were taken from here. Base depths ranged from −158 cm in southwest corner of square 6 to −145 cm in southeast corner of square 3.

Level 9.—Extremely well-cemented level with fractures (crevices); bone breccia in crevices in square 7; part of the bone breccia and paleo-floor is interpreted as a fossil woodrat nest based on the presence of abundant fossil fecal pellets; underlain in part by gypsum(?) powder. Depths at base ranged from −153 cm in northwest corner of square 7 to −162 cm in northeast corner of square 6.

Level 10.—Large (1–5 cm diameter) nodules similar to those in levels 4–5; reversely graded downwards to pea-sized nodules (0.5 cm diameter); a dusty matrix increasingly fills voids downwards until matrix becomes more abundant than nodules at base; in square 6, this level consists of a gypsum(?) powder (brown/white) similar to the matrix in which nodules are contained in the other squares; all overlying a hard flowstone. Depths at base of level 10 range from −168 cm in southeast corner of square 2 to −183 cm in center of the west profile (between square 3 and square 7).

Level 11.—Grayish-white dust; white gypsum crystalline flakes with more brown dust near the top; becomes whiter downwards. Bottom of level is defined by first occurrence of pinkish crystalline flakes. Only a slight color change breaks the level. Depths at base of level 11 range from −202 cm in southeast corner of square 2 to −212 cm in southwest corner of square 7 (−204 cm elsewhere).

Level 12.—Surface consists of pink crystalline flakes; this level is much more fine grained than level 11, with a higher percentage of clay-sized material. Almost 100% white powder. About 10–12-cm thick in square 3; base of level marked by mottled orangeish-brown material. Occasional large rock clasts (up to 14 cm in diameter). Depths at base of level 12 range from −214 cm on south wall to −212 cm in southwest corner of square 7 (no level 12 in square 7).

Level 13.—Mottled orangeish-brown material with occasional large rock clasts up to 14 cm in diameter; mostly largely devoid of bone. Depths at base range from −234 cm in northwest corner of square 7 to −231 in southeast corner of square 2.

Level 14.—Essentially the same lithology as level 13; an arbitrary level change, with possible slight darkening in color. Largely devoid of bone. Depth at base of excavation ranges from −235 cm in northwest corner of square 2 to −252 cm in southwest corner of square 6.

RESULTS

The Microtine Rodent Fauna

Microtine rodents constitute a major component of the specimens from the Pit locality. In their preliminary report on the fauna from Porcupine Cave, Barnosky

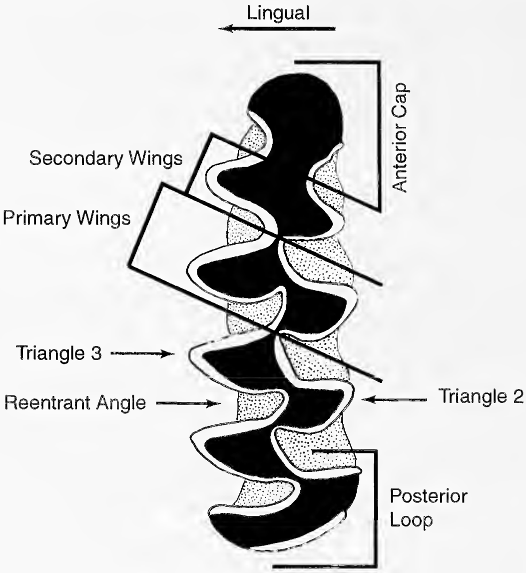

Fig. 3.—Lower right first molar of *Microtus* sp., illustrating the dental terminology used in the text.

and Rasmussen (1988) listed eight microtine rodent taxa, seven of which were recovered from sediments within the Pit sequence. The updated list of 11 taxa reported here reflects further investigation of the fauna from deeper stratigraphic levels in the Pit as well as refined taxonomic identifications of some previously reported material. Dental terminology is illustrated in Figure 3 and follows that of Repenning (1992) unless otherwise noted.

SYSTEMATIC ACCOUNTS

Family Muridae, Illiger, 1815
Subfamily Arvicolinae, Gray, 1821
Genus *Phenacomys*, Merriam, 1889
Phenacomys gryci, Repenning, 1987
(Fig. 4C)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155193 (left M_1, level 3); UCMP 155194 (left M_1, level 4); UCMP 155195 (right M_1, level 10).

Identification.—Molars rooted and lacking cementum in the reentrant angles; lingual alternating triangles and reentrants are asymmetrically elongated; usually only five triangles present on M_1, the fourth (second labial) usually preserving at least some indication of a "*Mimomys* kante" and the fifth (third lingual) broadly confluent with a highly variable anterior cap (Repenning et al., 1987; Repenning and Grady, 1988).

Discussion.–M_1s from the type population of *P. gryci* in the Fish Creek fauna of Alaska show a highly variable anteroconid complex (Repenning et al., 1987). USNM 264298 and 264299 (illustrated in Repenning et al., 1987:fig. 6D, E) show the closest resemblance to specimens identified from Porcupine Cave. The specimens from Porcupine Cave conform well with the diagnosis of *P. gryci*, but

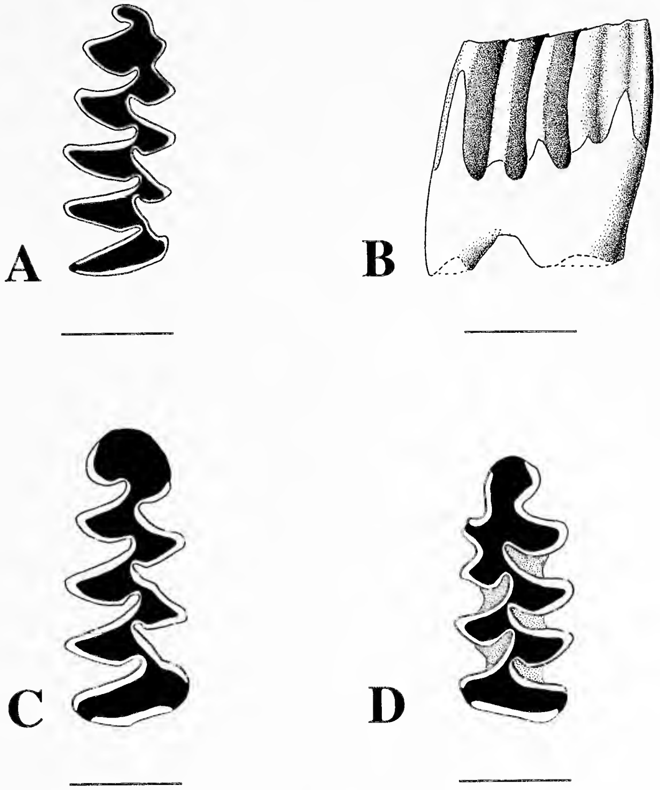

Fig. 4.—Lower first molars of microtine rodents from Porcupine Cave. A. Occlusal view of CM 66365, *Phenacomys* sp., right M_1. B. Labial view of CM 66365, *Phenacomys* sp., right M_1. C. Occlusal view of UCMP 155195, *Phenacomys gryci*, right M_1. D. Occlusal view of UCMP 155566, *Mimomys* (*Cromeromys*) cf. *M. virginianus*, left M_1. Scale bars = 1 mm.

show a very reduced (in one case absent) "*Mimomys* kante" structure on the fourth triangle. The type population from the Fish Creek fauna in Alaska is reported to date to approximately 2.4 Ma (Repenning et al., 1987). The species was also reported from the Froman Ferry sequence in Idaho, where its first appearance (at approximately 1.6 Ma) was used to define the beginning of the Irvingtonian component of that fauna (Repenning et al., 1995); it is also reported from Cathedral Cave in Nevada, in an Irvingtonian fauna with no precise age control (Bell, 1995).

Phenacomys sp. (not *P. gryci*)
(Fig. 4A, B)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): CM 66365 (right M_1, level 1); UCMP 155192 (right M_1, level 2).

Identification.—Molars rooted and lacking cementum in the reentrant angles; lingual alternating triangles and reentrants show pronounced asymmetrical elongation; five fully closed triangles on M_1, with a sixth well developed and confluent with a hooked anterior cap; no indication of a "*Mimomys* kante" structure.

Discussion.—These specimens differ from any known *P. gryci* in having a greater number of triangles on M_1. There are no intermediate forms between *P. gryci* and these *Phenacomys* specimens preserved in the Pit sequence and a direct ancestor-descendant relationship between these specimens and the older *P. gryci* cannot be demonstrated. Repenning and Grady (1988) relied upon labial dentine tract morphology on M_1 to diagnose three subgenera of *Phenacomys*. Our attempts to apply their methodology reveal that there may be greater variation in the morphology of dentine tracts on M_1 than was previously recognized. This, combined with the fact that on two occasions one of us (CJB) was unable to replicate subgeneric identifications made by Repenning, inspires conservatism in our identification of this material until a more thorough study of all known *Phenacomys* can be completed. Other Irvingtonian reports of *Phenacomys* include *P. brachyodus* from the Cheetah Room fauna in West Virginia (Repenning and Grady, 1988) and *Phenacomys* sp. from Cumberland Cave in Maryland (Guilday, 1971), the Little Sioux fauna in Iowa (Guilday and Parmalee, 1972; referred to as "County Line" fauna by Repenning, 1987) and from Wilson Valley in Kansas (Hibbard, 1944; Guilday and Parmalee, 1972; this appears to be the record referred to the "Cudahy fauna" by Hibbard, 1970 [see also Hibbard, 1976]). The genus is questionably reported from the SAM Cave fauna in New Mexico (Repenning, 1992: 33). Repenning (1987) listed *Phenacomys* sp. from the Java fauna in South Dakota but R. Martin (1989) identified this material as a new species of *Hibbardomys*.

Genus *Mimomys*, Forsyth-Major, 1902
Subgenus *Cromeromys*, Zazhigin, 1980
Mimomys cf. *M. virginianus*, Repenning and Grady, 1988
(Fig. 4D)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155188 (right M_1 fragment, level 5); UCMP 155189 (left dentary with M_{1-2}, level 6); UCMP 155191 (left M_1 fragment, level 8A); UCMP 155566 (left M_1, level 8A); UCMP 156158, 156159 (one left and one right M^1, level 5); UCMP 156160, 156161 (one left and one right M^1, level 7); UCMP 156162, 156163 (one left and one right M^1, level 10); UCMP 156164 (left M^2, level 5); UCMP 156165 (right M^2, level 7); UCMP 156166 (right M^2, level 8A); UCMP 155190 (left M^3, level 7); UCMP 156167 (right M_2, level 4); UCMP 156168 (left M_2, level 8A); UCMP 156169 (left M_3, level 8A).

Identification.—Molars rooted, with cementum in the reentrant angles; usually five triangles present on M_1, the fifth broadly confluent with a variable anterior cap; at least some expression of a "*Mimomys* kante" is present on M_1, and is frequently well developed in a position slightly anterior to the fourth triangle.

Discussion.—The status of the genus *Mimomys* in North America is a subject of some debate. In his long-standing effort to document intercontinental dispersal patterns, Repenning (1980, 1987; Repenning and Grady, 1988; Repenning et al., 1990) recognized the morphological similarities between North American and Eurasian forms and emphasized an Old-World/New-World connection by retaining the name *Mimomys* for the North American forms (although this is done in the absence of direct evidence for an immigrant status in North America of most of the taxa in question). An alternative view recognizes the unique morphological features (notably enamel microstructure or schmelzmuster) and emphasizes the endemic evolution seen within many of the North American lineages subsequent to their first appearance on the continent (von Koenigswald, 1980; von Koenigswald and Martin, 1984*a*; L. Martin, 1989). In the latter scheme, the different lineages traditionally recognized by Repenning as subgenera are elevated to full generic rank (*Cosomys, Ogmodontomys, Ophiomys, Cromeromys*).

The first report of a *Mimomys*-like microtine from the Pleistocene of North America was published in 1972 under the name *Mimomys monahani* (L. Martin, 1972). This species was later placed in the monotypic genus *Loupomys* based on the primitive nature of its enamel microstructure (von Koenigswald and Martin, 1984*a*); it is known only from the type locality in Nebraska. The presence of a *Mimomys*-like species in the Irvingtonian fauna of Hamilton Cave, West Virginia, was noted by Repenning and Grady (1988), who placed this material in a new species which they named *Mimomys virginianus*. A third record of a Pleistocene *Mimomys* came from the Java fauna in South Dakota (R. Martin, 1989) and also received a new name, *Mimomys dakotaensis*. The age of the Java fauna is somewhat problematic as it contains several taxa typical of the Blancan; R. Martin (1989) considered it to be earliest Pleistocene and Repenning et al. (1990, 1995) placed it in the Irvingtonian I microtine rodent division. Of the two *Mimomys* M_1s included in the Java fauna, one (designated as the holotype) is broken; the second is not illustrated or discussed. *Mimomys dakotaensis* is distinguished from *M. virginianus* by its size (larger than *M. virginianus*, although the measurement of only one specimen from Java was published), by having significantly less cementum in the reentrant angles and by the extremely high dentine tract at the position of the *Mimomys* kante. The amount of cementum in specimens from Porcupine Cave is more similar to that in *M. virginianus* than in *M. dakotaensis*. Tentative referral to *M. virginianus* is made pending detailed examination of the schmelzmuster of the Porcupine Cave material and comparisons with the complete Hamilton Cave sample (which is not published in its entirety; C. Repenning, personal communication). Other records of this species are from Cathedral Cave in Nevada (Bell, 1995, as "*Mimomys* [*Cromeromys*] sp.") and from several localities in the Yukon Territory (Repenning, personal communication).

Loupomys monahani, Mimomys virginianus, and *M. dakotaensis* share a remarkably similar morphological appearance, most notably in the presence of cementum in the reentrant angles (distinguishing these species from all other North American *Mimomys*-like taxa). However, the schmelzmuster of *Loupomys* appears to be quite primitive and is unique among North American microtines (von Koenigswald and Martin, 1984*a*). The schmelzmuster of *M. dakotaensis* was reported to be similar to that of typical European species of *Mimomys* (R. Martin, 1989); the schmelzmuster of *M. virginianus* and the Pit material has not been studied.

Mimomys virginianus was placed in the subgenus *Cromeromys* based on morphological similarity with Old World forms assigned to the genus *Cromeromys*; Repenning and Grady (1988:5) relegated *Cromeromys* to a subgenus to achieve "a more balanced classification" with other North American forms that were placed within various subgenera under the genus *Mimomys*. R. Martin (1989) refrained from placing *M. dakotaensis* within any subgenus, but the presence of cementum in the reentrant angles clearly argues for its alliance with *M. virginianus*. R. Martin's (1989) concern for subgeneric allocation of the North American *Mimomys* having cementum in the reentrant angles stemmed from the fact that Repenning and Grady (1988) did not distinguish *Mimomys* (*Cromeromys*) from *Mimomys* (*Pusillomimus*), a subgeneric designation proposed by Rabeder (1981).

Genus *Ondatra*, Link, 1795
Ondatra sp.

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155567 (broken juvenile right M_1, level 2); UCMP 155848 (right M^1, level 2); UCMP 155849 (left M^1, level 4); UCMP 155850 (right M^2, level 1 or 2); CM 66522 (left M^2, level 2); UCMP 155851 (left M^2, level 4); CM 45409 (right M^3, level 1); UCMP 155852, 155853 (one left and one right M^3, level 4); UCMP 155854 (left M^3, level 5); UCMP 155855 (right M^3, level 8A); UCMP 155856 (left M_2 fragment, level 4).

Identification.—Molars rooted, with reduced cementum in reentrant angles, often forming a "network" pattern in lateral view; this feature, combined with large size, distinguishes this genus from all other rooted microtines.

Discussion.—Muskrats are rare in the Pit fauna and unfortunately only one M_1 (the most important tooth for identifying *Ondatra* species) specimen is available. The Pit M_1 is badly broken and is from a juvenile, so identification to species cannot reliably be made. Muskrat specimens from Porcupine Cave were tentatively referred to *Ondatra* cf. *O. annectens* by Barnosky and Rasmussen (1988); this tentative identification may be correct, but definitive assignment to species must await recovery of additional material. All known Pleistocene muskrats were recently synonymizsed with the living species *Ondatra zibethicus* (R. Martin, 1993, 1996), yet formerly recognized species names were preserved and appended to the specific name to form a trinomial nomenclature indicative of what Martin calls "chronomorphs" (see also Krishtalka and Stucky, 1985).

Genus *Allophaiomys*, Kormos, 1933
Allophaiomys pliocaenicus, Kormos, 1933
(Fig. 5A, B)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155000–155005 (three right and three left M_1, level 4); UCMP 155006–155008 (two right and one left M_1, level 5); UCMP 155009, 155010 (two right M_1, level 6); UCMP 155564 (right M_1, level 6); UCMP 155011–155014 (two right and two left M_1, level 7); UCMP 155015 (right dentary with I_1 and M_{1-2}, level 8A); UCMP 155016 (right dentary with I_1 and M_{1-3}, level 8A); UCMP 155017 (left dentary with I_1 and M_{1-2}, level 8A); UCMP 155018, 155019 (one right and one left M_1, level 8A); UCMP 155020, 155021 (two right M_1, level 11).

Identification.—Rootless, ever-growing molars; M_1 with a posterior loop and three alternating closed triangles; primary wings well developed and broadly confluent with a very simple anterior cap.

Discussion.—*Allophaiomys* plays an important role in the biochronology of microtine rodents in Eurasia as well as in North America, where its complicated history was recently reviewed by Repenning (1992). In North America, its first appearance marks the lower boundary of the Irvingtonian I microtine rodent division east of the Rocky Mountains at approximately 1.9 Ma (Repenning, 1987; Repenning et al., 1990, 1995).

Allophaiomys pliocaenicus was originally described from Romania (Kormos, 1933) and is known from fossil faunas throughout much of the Holarctic (Repenning, 1992). Traditionally, *A. pliocaenicus* was viewed by most authors as a single extinct species that had an expansive geographic distribution across the Holarctic. More recently, evidence has come to light to suggest that its history, especially in Europe, may be much more complex than previously thought and that traditional treatments may actually be conflating members of a group of closely related sibling species (Agustí, 1992; Agustí et al., 1993; Nadachowski and Zagorodnyuk, 1996; see also R. Martin and Tesakov, 1988).

The oldest North American specimen associated with some form of external age control was recovered from a core drilled in the Hansen Bluff area of southern Colorado (Rogers et al., 1992). The first magnetic polarity sample taken from above the horizon in which the specimen was recovered (0.9 m above the specimen) was normal and interpreted to be the lowest record of the Olduvai event in the core; the first polarity sample from stratigraphically beneath the specimen (0.3 m below) was reversed. The specimen therefore dates to either the very base of the Olduvai Chron (at approximately 1.9 Ma) or just before it. The tooth in question is an isolated M_3 and cannot be positively identified as *Allophaiomys*. Repenning (1992:32) identified the specimen and argued that the existence of any other rootless microtine of that age and with that dental morphology (rootless and having cement in the reentrant angles) in North America was "unbelievable."

Other early North American records are from the Java fauna in South Dakota (considered to be earliest Pleistocene; R. Martin, 1975, 1989) and the Wellsch Valley fauna in Saskatchewan, Canada. The age of Wellsch Valley is not well established; the sediments record the 780,000 YBP Brunhes/Matuyama boundary and the fauna may be either latest Blancan or (more likely) earliest Irvingtonian in age (Churcher, 1984; Barendregt et al., 1991; Repenning, 1992).

Two records were discovered since the completion of Repenning's (1992) review of North American *Allophaiomys*: Cathedral Cave in Nevada (Bell, 1995) and the Little Dell fauna in northern Utah (Gillette et al., 1999). These records are significant in that they document for the first time the presence of *Allophaiomys* in faunas west of the Rocky Mountains, and lessen the distinction between Irvingtonian faunas from the western and eastern United States faunal regions proposed by Fejfar and Repenning (1992). The presence of this species in the Porcupine Cave faunal assemblage was first recognized by Keesing (1992).

Genus *Terricola*, Fatio, 1867
Terricola meadensis, (Hibbard, 1944)
(Fig. 5C, D)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155196 (left dentary with M_{1-2}, surface); UCMP 155197–155199 (two left and one right M_1, surface); UCMP 155200–155206 (four left and three right M_1, level 1); CM 45402–45404 (three left M_1, level 1); CM 45428, 45429 (two left M_1, level 1); CM 66307 (broken left M_1, level 1); CM 45405 (right M_1, level 1); CM 45430 (broken right M_1, level 1); CM 66199 (broken right M_1, level 1); UCMP 155207–155221 (five left and ten right M_1, level 2); UCMP 155222 (right dentary with M_{1-2}, level 2); CM 45431–45434 (four left M_1, level 2); CM 63601 (left M_1, level 2); CM 66542 (left M_1, level 2); CM 45435–45444 (ten right M_1, level 2); CM 45446, 45447 (two right M_1, level 2); CM 66530 (right M_1, level 2); CM 66560 (right M_1, level 2); CM 66571 (right M_1, level 2); UCMP 155223 (left M_1, level 3); UCMP 155224 (right dentary with M_1, level 3); UCMP 155225, 155226 (two right M_1, level 3); UCMP 155227 (right dentary with M_{1-2}, level 3); UCMP 155228 (left M_1, level 3); UCMP 155229 (right dentary with I_1 and M_{1-3}, level 3); UCMP 155230, 155231 (two2 right M_1, level 3); UCMP 155264 (left dentary with I_1 and M_1, level 3); CM 65558 (broken left M_1, level 3); CM 65563 (broken right M_1, level 3); CM 65587, 65588 (two right M_1, level 3); UCMP 155232–155243 (three left M_1, two broken left M_1, four right M_1, and three broken right M_1, level 4); UCMP 155565 (right M_1, level 4); UCMP 155244–155248 (two left M_1, one left M_1 fragment, and two right M_1, level 5); UCMP 155249–155252 (one broken left M_1 and three broken right M_1, level 6); UCMP 155253 (right M_1, level 7); UCMP 155847 (broken right M_1, level 8); UCMP 155254 (right M_1, level 8A); UCMP 155255 (left M_1, level 1–3 undifferentiated); UCMP 155256–155259 (four left M_1, level mixed).

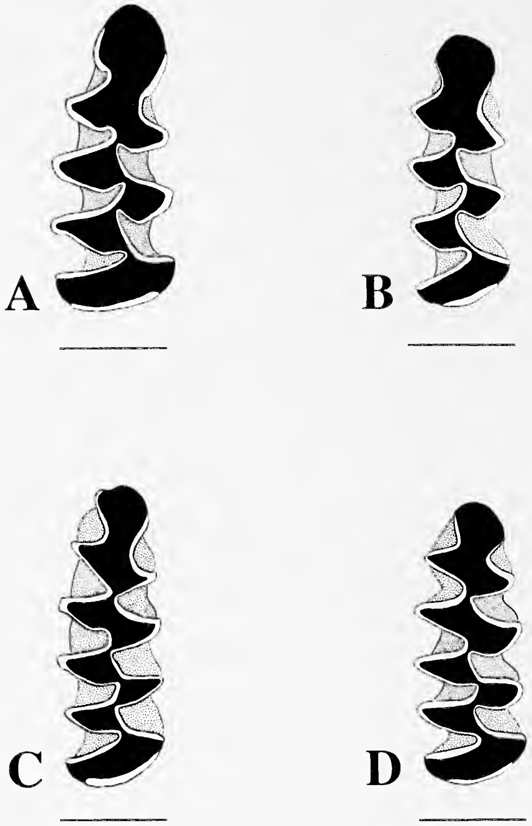

Fig. 5.—Occlusal view of right lower first molars of microtine rodents from Porcupine Cave. A. UCMP 155009, *Allophaiomys pliocaenicus*. B. UCMP 155012, *Allophaiomys pliocaenicus*. C. UCMP 155206, *Terricola meadensis*. D. UCMP 155227, *Terricola meadensis*.

Identification.—Rootless molars with cementum in the reentrant angles; M_1 with a posterior loop and three closed triangles; primary wings (triangles 4 and 5) are confluent in a rhomb which is either closed off from the anterior cap or connected to it via a narrow confluence; secondary wings well developed, with labial reentrant angle 4 and lingual reentrant angle 5 well developed.

Discussion.—Clear recognition of the morphological distinction between the dentition of pitymyines from that of *Microtus* dates back to Hinton (1923), but there is no consensus among modern microtine scholars as to the taxonomic treatment and systematic relationships of the group (Van Der Meulen, 1978; Repenning, 1983, 1992; R. Martin, 1987, 1993, 1995; Harris, 1988; Moore and Janecek, 1990). We follow Repenning (1992) in recognizing *Terricola* as a valid genus. Specimens of *Terricola* have been recovered from numerous localities throughout the western two-thirds of North America, but are not known from east of the Mississippi River (Repenning, 1983, 1992). The appearance of *Terricola meadensis* in the fossil record of North America at approximately 850,000 YBP is traditionally used to define the base of the Irvingtonian II microtine rodent division (Repenning, 1987; Repenning et al., 1990).

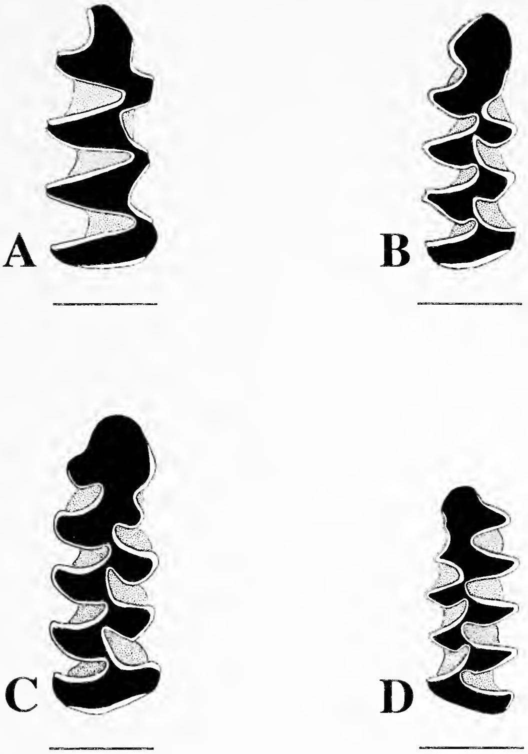

Fig. 6.—Occlusal view of lower first molars of microtine rodents from Porcupine Cave. A. UCMP 155177, *Mictomys* cf. *M. meltoni*, right M_1. B. UCMP 155262, *Lasiopodomys* morphotype of *Microtus paroperarius*, right M_1. C. UCMP 155562, *Microtus paroperarius*, right M_1. D. CM 66345, *M. paroperarius*, left M_1. Scale bars = 1 mm.

Genus *Mictomys*, True, 1894

Mictomys cf. *M. meltoni*, (Paulson, 1961)

(Fig. 6A)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155102 (right M_1, surface); CM 45414 (right dentary with I_1 and M_{1-2}, level 1); CM 45415 (left M_1, level 1, specimen missing); CM 45416 (left M_1, level 1); UCMP 155103 (right dentary with I_1 and M_{1-2}, level 2); CM 45509, 45510 (two right M_1, level 2); UCMP 155104 (broken left M_1, level 2); UCMP 155105 (left M_1, level 3?); UCMP 155106 (left M_1, level 3); UCMP 155107 (left M_1 fragment, level 3); UCMP 155108 (left M_1, level 3); UCMP 155109 (left M_1 fragment, level 3); UCMP 155110 (left M_1, level 3); UCMP 155111 (right M_1, level 3); UCMP 155112 (right dentary with I_1, M_{1-2}, and M_3 fragment, level 3); UCMP 155113 (right M_1 fragment, level 3); UCMP 155841, 155842 (two left M_1, level 3); CM 65572 (right M_1, level 3); UCMP 155114–155120 (seven left M_1, level 4); UCMP 155121 (broken left M_1, level 4); UCMP 155122, 155123 (two left M_1, level 4); UCMP 155563 (left M_1, level 4); UCMP 155124–155127 (two left M_1 fragments and two right M_1 fragments, level 4); UCMP 155128–155134 (seven right M_1, level 4); UCMP 155135–155137 (three broken right M_1, level 4); UCMP 155138–155141 (four right M_1, level 4); UCMP 155142, 155143 (two right M_1 fragments, level 4); UCMP 155144–155150 (two left M_1, three right M_1, and two right M_1 fragments, level 5); UCMP 155151 (left dentary with M_{1-2}, level 5); UCMP 155844 (right M_1, level 5); UCMP 155845 (broken right M_1, level 5); UCMP 155846 (broken left M_1, level 5); UCMP 155152–155157 (three left M_1, one right M_1, one left M_1 fragment, and one right M_1 fragment, level 6); UCMP 155158–155161 (one right M_1, three broken right M_1, level 7); UCMP 155162 (right dentary fragment with broken M_1, level 7); UCMP 155163, 155164 (two right M_1 fragments, level 7); UCMP 155165 (left M_1, level 7); UCMP

155843 (left M_1, level 7); UCMP 155166–155171 (five left and one right M_1, level 8); UCMP 155172–155177 (two left M_1, two right M_1, and two left M_1 fragments, level 8A); UCMP 155178–155182 (three left and two right M_1, level 10); UCMP 155183–155185 (one right M_1 and two right M_1 fragments, level 11); UCMP 155186 (left dentary with M_{1-2}, level 1–3 undifferentiated); UCMP 155187 (left M_1, level mixed); CM 45417 (left M^1, level 1); UCMP 155568 (right M^1, level 3); UCMP 155569–155594 (11 left and 15 right M^1, level 4); UCMP 155595–155609 (seven left and eight right M^1, level 5); UCMP 155610–155616 (five left and two right M^1, level 6); UCMP 155617–155620 (two left and two right M^1, level 7); UCMP 155621–155625 (two left and three right M^1, level 8); UCMP 155626–155633 (six left and two right M^1, level 8A); UCMP 155634–155637 (four left M^1, level 10); UCMP 155638–155641 (one left and three right M^1, level 11); UCMP 155642 (right M^1, level 12); UCMP 155644, 155645 (one left and one right M^2, level 2); CM 65577 (left M^2, level 3); UCMP 156170 (right M^2, level 3); UCMP 155646–155653 (five left and three right M^2, level 4); UCMP 155655–155665 (seven left and four right M^2, level 4); UCMP 155666–155676 (seven left and four right M^2, level 5); UCMP 155677–155681 (one left and four right M^2, level 6); UCMP 155682–155687 (six right M^2, level 7); UCMP 155688–155690 (one left and two right M^2, level 8); UCMP 155691–155694 (two left and two right M^2, level 8A); UCMP 155695–155697 (three left M^2, level 10); CM 45418, 45419 (one left and one right M^3, level 1); UCMP 155698 (left M^3, level 3); UCMP 155699–155715 (five left and 12 right M^3, level 4); CM 45511 (right M^3, level 5); UCMP 155716–155720 (two left and three right M^3, level 5); UCMP 155721–155727 (three left and four right M^3, level 6); UCMP 155728–155733 (three left and three right M^3, level 7); UCMP 155734–155736 (one left and two right M^3, level 8); UCMP 155737 (left M^3, level 8A); UCMP 155738 (right M^3, level 9); UCMP 155739 (right M^3, level 10); UCMP 155740, 155741 (two right M^3, level 11); UCMP 155742 (left M^1 or M^2 fragment, level 8A); UCMP 155743 (upper molar fragment, level 4); UCMP 155744, 155745 (two left M_2, level 3); UCMP 155746–155764 (11 left and eight right M_2, level 4); UCMP 155765–155770 (four left and two right M_2, level 5); UCMP 155771–155775 (four left and one right M_2, level 6); UCMP 155776–155780 (one left and four right M_2, level 7); UCMP 155781–155786 (two left and four right M_2, level 8); UCMP 155787 (left M_2, level 10); UCMP 155788–155790 (two left and one right M_2, level 11); UCMP 155792 (right M_3, level 2); UCMP 155793 (right M_3, level 3); UCMP 155794–155802 (three left and six right M_3, level 4); UCMP 155803–155805 (two left and one right M_3, level 5); UCMP 155806–155809 (one left and three right M_3, level 6); UCMP 155810–155812 (one left and two right M_3, level 7); UCMP 155813 (right M_3, level 8A); UCMP 155814, 155815 (one left and one right M_3, level 10).

Identification.—Rootless molars with cementum in at least the lingual reentrant angles of lower molars; as noted by von Koenigswald and Martin (1984*b*), the axis of the lower tooth row is shifted to the labial edge; M_1 with a posterior loop, two closed but not alternating triangles, and a moderately variable anterior cap; the first labial triangle of M_1 (triangle 2 in other microtines) is absent due to flattening of the first labial reentrant angle; enamel is positively differentiated, with the anterior enamel band thicker than the posterior enamel band on each triangle; posterior border of the first triangle is convex anteriorly or flat.

Discussion.—*Mictomys kansasensis* was named from the Kentuck assemblage in Kansas (Hibbard, 1952) and was diagnosed primarily by the posteriorly extended margin of the lower incisor to a position about equal to the posterior edge of M_3. *Mictomys meltoni* was described from the Cudahy ash pit fauna in Kansas (Paulson, 1961) and diagnosed by a combination of characters including positively differentiated enamel, lack of a cementum-filled labial reentrant on M_3, a posterior extension of the lower incisor to a point just anterior to the anterior border of M_3, and a first triangle of M_1 with an anteriorly convex (rather than concave) posterior wall. The *Mictomys* material from Snowville, Utah (Repenning et al., 1987; Repenning and Grady, 1988), consists of two specimens (left and right partial dentaries), both cataloged under UCMP 124887. The left dentary retains all teeth, the right is missing the M_3. In all cheek teeth, enamel is positively differentiated and the posterior border of the first triangle is concave anteriorly. The schmelzmuster of these specimens has never been examined and their specific affinity remains uncertain; they were previously regarded as representing the final (and unnamed) intermediate step in the evolution of bog lemmings towards the extant *M. borealis* (Repenning and Grady, 1988).

The majority of the Porcupine Cave M_1 specimens have a convex or flat posterior margin on the first triangle, similar to that described for *M. meltoni*, but the expression of this character in *M. kansasensis* has not been explored. Examination of resin casts of four M_1s of this species from the Wathena fauna (Van Der Meulen, 1978) in Kansas indicate that this morphology is at least sometimes present in populations of *M. kansasensis*. In the few Porcupine Cave jaws of *Mictomys* which preserve the necessary region, the posterior margin of the incisor terminates at a point anterior to the M_3, similar to the condition in the extant *M. borealis* and in *M. meltoni*. Some variation in the expression of this character was noted by Repenning and Grady (1988), and its reliability as a definitive character to distinguish *M. meltoni* and M. *kansasensis* remains to be proven.

Specimens from Porcupine Cave have not as yet been subjected to an examination of schmelzmuster, which may be the only reliable way to consistently distinguish *M. meltoni* and *M. kansasensis* (von Koenigswald and Martin, 1984*b*). Triangles of M_1 of *Mictomys kansasensis* are reported to have an extremely thin posterior enamel margin that consists almost exclusively of radial enamel (the exception to this being at the extreme lingual border of the triangle where some lamellar enamel is present; von Koenigswald and Martin, 1984*b*). The only comparison of the schmelzmuster of M_1 in these two species of *Mictomys* was restricted to one specimen of *M. kansasensis* from each of three localities and one specimen of *M. meltoni* from Cudahy ash pit (von Koenigswald and Martin, 1984*b*). This analysis does not establish a range of variation in enamel microstructure within a population and further analysis of multiple specimens from a single stratigraphic horizon would be necessary to increase confidence in the use of this character to discriminate between species. The importance of studying multiple specimens from a single locality cannot be overstated. Few studies of schmelzmuster in microtines have utilized more than one or two specimens from a given locality, but a recent study of fossil remains of *Microtus henseli* from Sardinia demonstrates that when sample size is increased, increased variation in enamel microstructure pattern is evident (Mezzabotta et al., 1995).

Based on the morphology of the first triangle on M_1, the posterior margin of the lower incisor, and the measurements presented by Wood and Barnosky (1994) for these specimens, we tentatively refer the Porcupine Cave material to *Mictomys* cf. *M. meltoni*. A more definitive identification must await a thorough reexamination of all Irvingtonian *Mictomys*.

Genus *Microtus*, Schrank, 1798
Microtus paroperarius, Hibbard, 1944
(Fig. 6B–D)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): CM 66345 (left M_1, level 1); UCMP 155081–155084 (one left and three right M_1, level 1); UCMP 155085 (right dentary with M_{1-2}, level 2); CM 45482–45484 (two left and one right M_1, level 2); UCMP 155086–155089 (two left and two right M_1, level 3); UCMP 155090 (left M_1, level 3?); CM 45507 (left M_1, level 3); CM 65559 (broken left M_1, level 3); UCMP 155091–155095 (three left and two right M_1, level 4); UCMP 155262 (right M_1, level 4); UCMP 156152 (right M_1, level 4); UCMP 155096 (right M_1, level 5); UCMP 155098, 155099 (one left and one right M_1, level 7); UCMP 155562 (right M_1, level 7); UCMP 155100 (left dentary with I_1 and M_{1-2} level mixed); UCMP 155101 (right M_1, level mixed).

Identification.—Rootless molars with cementum in the reentrant angles; M_1

with a posterior loop followed by four closed alternating triangles; a fifth triangle well developed, but confluent with the anterior cap; triangle 2 smaller than triangle 1 on M_1.

Discussion.—This species was originally diagnosed by Hibbard (1944) by the presence of a posterior loop and four closed triangles on M_1, with a fifth triangle confluent with the anterior cap, and with the cap showing evidence of lingual reentrant angle 5 and labial reentrant angle 4. A subsequent analysis of new material collected from the type locality resulted in an amended diagnosis (Paulson, 1961) in which 20% of the population was said to have a closed fifth triangle. Subsequent authors have followed Paulson's amended diagnosis of the species and many descriptions of fossil populations included a percentage of M_1 with a closed fifth triangle (although Paulson's figure of 20% appears to be an artifact of his sampling; Bell, 1997; Bell and Repenning, 1999). Until recently, this practice met with no difficulty because in all reported occurrences *M. paroperarius* was the only *Microtus* species presumed to be present (although the presence of a second species of *Microtus* in the Cudahy fauna in Kansas is now suspected; Bell, 1997; Bell and Repenning, 1999). With the discovery of this species in the Porcupine Cave assemblage (Barnosky and Rasmussen, 1988) a new challenge is faced. The Porcupine Cave assemblage contains numerous specimens of *Microtus* that cannot be assigned to *M. paroperarius*. For the purpose of this report, all specimens identified as *M. paroperarius* conform with Hibbard's (1944) primary criterion in the original diagnosis: the fifth triangle is confluent with the anterior cap. We recognize the possibility that some small percentage of the specimens we identify as "*Microtus* sp." may actually be *M. paroperarius*, but we can find no way to reliably separate them at this time. Five specimens of *M. paroperarius* were previously reported from the Pit locality, with an average length of 2.61 mm (Barnosky and Rasmussen, 1988). In our larger sample size from the Pit locality ($n = 22$) the average length measurement is 2.64 mm. It is interesting that none of the Porcupine Cave material approaches the large size reported for teeth of *M. paroperarius* from the basal portions of the Hansen Bluff sequence in southern Colorado (Rogers et al., 1985; Repenning, 1992:57).

A single specimen from the Pit excavation (UCMP 155262) has a relatively primitive morphotype resembling that of *Lasiopodomys deceitensis*. The name *Lasiopodomys* is applied to three living species found in Russia and China (Musser and Carleton, 1993) and to numerous fossil populations throughout the Holarctic (Repenning, 1992). The species here called *L. deceitensis* was described under the name *Microtus deceitensis* from the Cape Deceit fauna in Alaska (Guthrie and Matthews, 1971). This form was given the new name combination by Repenning (1980; following a precedent set by Erbaeva [1976] for fossil forms in Asia) and taken by him (Repenning, 1992) as "typical" of *Lasiopodomys*. In Repenning's usage, *Lasiopodomys* is retained as a name for "intermediate forms that have been assigned either to more primitive *Allophaiomys* or to the more advanced *Microtus*" (Repenning, 1992:47).

Most Irvingtonian records of *Lasiopodomys deceitensis* are from localities in the eastern United States, including Hamilton Cave, West Virginia (Repenning and Grady, 1988), Hanover Quarry, Pennsylvania (Guilday et al., 1984), the County Line fauna in Illinois (Miller et al., 1994), and a population interpreted to be intermediate in stage of evolution between *Lasiopodomys* and *Microtus paroperarius* from Cumberland Cave, Maryland (Repenning, 1992). A very low percentage (0.6%) of the M_1 with four closed triangles from the type locality of

Fig. 7.—Occlusal view of lower first molars of *Microtus* sp. from Porcupine Cave. A. UCMP 155042, left M_1. B. CM 45502, right M_1. C. UCMP 155045, right M_1. Scale bars = 1 mm.

the Cudahy fauna also are *Lasiopodomys* morphotypes, but these are interpreted as specimens of *Microtus paroperarius* with relatively primitive morphologies (Bell, 1997; Bell and Repenning, 1999). There are now three localities from the southwestern United States containing specimens potentially referable to *Lasiopodomys.* A single specimen from the Anza-Borrego Desert in southern California was described and illustrated by Repenning (1992:50, fig. 11A). A single specimen from Cathedral Cave in Nevada and this record from the Pit locality in Porcupine Cave constitute the only other records in western North America south of Beringia. It is difficult to interpret the Anza-Borrego specimen since it is an isolated find not associated with any other microtine rodent material. Both of the cave faunas, however, have extensive microtine rodent faunas that include *Microtus paroperarius.* This is significant since the only difference in the M_1 of *Lasiopodomys* and that of *M. paroperarius* is the development of secondary wings and at least incipient constriction between the fifth triangle and the anterior cap (dimension B–B′ of Repenning, 1992) in the latter. The specimens from Cathedral and Porcupine caves are here interpreted as simple morphotypes of *Microtus paroperarius.*

Microtus sp. (not *M. paroperarius*)
(Fig. 7A–C)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155022 (left M_1, surface); UCMP 155023 (left dentary with I_1 and M_{1-2}, west of square 1 towards ladder); UCMP 155024 (left M*1*, south extension); UCMP 155025–155036 (seven left and five right M_1, level 1); CM 45485 (left M_1, level 1); CM 45497 (left M_1, level 1); CM 66319 (broken left M_1, level 1); CM 66338 (left M_1, level 1); CM 45486 (right M_1, level 1); CM 45498 (right M_1, level 1); CM 45502 (right M_1, level 1); CM 65232 (right M_1, level 1); CM 66276 (right M_1, level 1); CM 66303 (right M_1, level 1); CM 66348 (right M_1, level 1); CM 66284 (broken left M_1, level 1); UCMP 155037 (broken right M_1, level 1); CM 66202 (broken right M_1, level 1); UCMP 155038 (right M_1, level 1); UCMP 155039–155054 (six left and ten right M_1, level 2); UCMP 155055 (right dentary with M_{1-2}, level 2); UCMP 155056 (right dentary with M_{1-2}, level 2); UCMP 155261 (right dentary with M_1, level 2); UCMP 156153 (right dentary with I_1–M_2, level 2); UCMP 155057 (left M_1, level 2); CM 45487, 45488 (two left M_1, level 2); CM 45503 (left M_1, level 2); CM 63606 (left M_1, level 2); CM 66534 (left M_1, level 2); CM 66593 (left M_1, level 2); CM 45445 (right M_1, level 2); CM 45489–45494 (six right M_1, level 2); CM 45499 (right M_1, level 2); CM 66567 (right M_1, level 2); CM 66569 (right M_1, level 2); UCMP 155058 (left dentary with I_1 and M_1, level 3); UCMP 155059–155061 (three right M_1, level 3); UCMP 155062, 155063 (two left M_1, level 3?); UCMP 155064 (left M_1, level 3); CM 45495, 45496 (one left and one right M_1, level 3); UCMP 155561 (right M_1, level 3?); UCMP 155065–155067 (two left and one right M_1, level 4); UCMP 156154–156156 (two left and one right M_1, level 4); UCMP 155068, 155069 (one left and one right M_1, level 5); UCMP 155070 (right M_1, level 6); UCMP 155071, 155072 (two left M_1, level 1–3 undifferentiated); UCMP 155073, 155074 (two right dentaries with M_{1-2}, level 1–3 undifferentiated)); UCMP 155075–155079 (three left and two right M_1, mixed level); CM 45500, 45501 (two right M_1, level mixed); UCMP 155080 (juvenile right M_1, level 1).

Identification.—Rootless molars with cementum in the reentrant angles; M_1 with a posterior loop followed by at least five closed alternating triangles; triangle 2 distinctly smaller than triangle 1 on M_1; secondary wings extremely well developed.

Discussion.—There are at least 12 *Microtus* species extant in North America that have M_1 with five or six closed alternating triangles. These species include *M. breweri, M. californicus, M. chrotorrhinus, M. longicaudus, M. mexicanus, M. miurus, M. montanus, M. oregoni, M. pennsylvanicus, M. richardsoni, M. townsendii,* and *M. xanthognathus* (Hall, 1981). Quaternary paleontologists have been struggling to discover means of reliably distinguishing these species in the fossil record, but little progress has been made. The application of discriminant analysis and morphometrics to *Microtus* samples in New Mexico showed some promise for distinguishing the five species included in the analysis (Smartt, 1972, 1977), but no such study has yet been conducted that includes all North American taxa.

Some studies focused on certain morphological features such as size or the complexity of M^3 as an aid in identification of *Microtus* species. The size criterion was used in conjunction with cranial characters from partial skulls and dental variation to identify the remains of *M. xanthognathus* in the eastern United States (Guilday and Bender, 1960; Hallberg et al., 1974; Guilday et al., 1977, 1978), but these studies did not consider *M. richardsoni*, another large species from the northwestern United States. Similarly, the presence of M^2 with an additional posterior dentine field is often regarded as positive evidence of the presence of *M. pennsylvanicus*, yet this morphological feature is irregularly expressed in a number of different North American species, and is a regular feature in at least two others (Bell, 1997; Bell and Repenning, 1999). A careful reading of the literature on North American Quaternary *Microtus* demonstrates that modern geographic distribution plays an important role in the taxonomic identification of fossil material, if only in the choice of taxa to exclude from possible consideration. This practice can result in faulty conclusions regarding the biogeographic and temporal history of *Microtus* species in North America, and leads to potentially misleading information that is then incorporated into biochronologies and other paleobiological applications.

One specimen listed above (CM 45445) was previously reported as *Pitymys meadensis* (= *Terricola meadensis* by our usage; Barnosky and Rasmussen, 1988). The specimens listed above also include specimens previously reported as *Microtus montanus/M. longicaudus* (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996*b*). Preliminary identification of *M. pennsylvanicus* in the Porcupine Cave Velvet Room fauna was made on the basis of the presence of M^2 specimens showing a well-developed posterolingual dentine field (Barnosky and Rasmussen, 1988; the species is included in the faunal list in their table 2, p. 270, but is not discussed in the text). In light of the small number of specimens with this morphology in the sample, and the infrequent occurrence of this structure in at least five species of *Microtus* in North America (Bell, 1997; Bell and Repenning, 1999), this identification is no longer is considered conclusive. It is possible that *M. pennsylvanicus* occurs in the Porcupine Cave fauna, but this cannot be verified with the material at hand. Living specimens were trapped in the vicinity of the cave by members of the DMNH Department

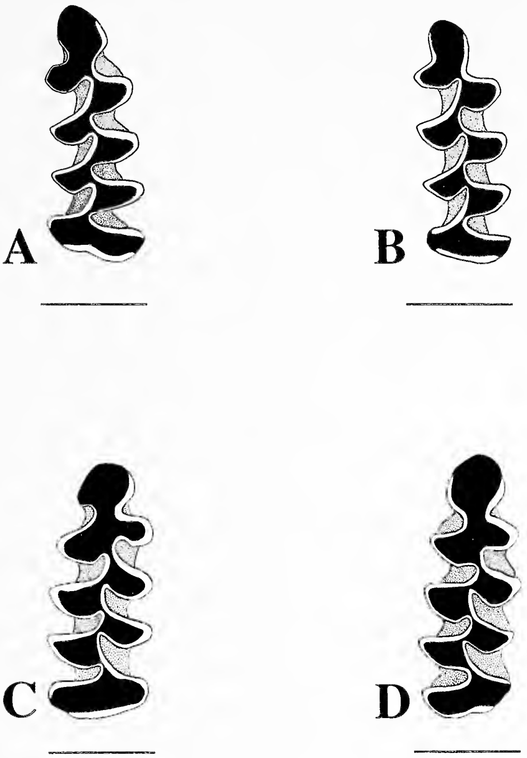

Fig. 8.—Occlusal view of lower first molars of microtine rodents from Porcupine Cave. A. UCMP 155273, *Lemmiscus curtatus*, left M_1. B. UCMP 155310, *L. curtatus*, left M_1. C. UCMP 155382, *Lemmiscus* sp., right M_1. D. UCMP 155343, *Lemmiscus* sp., right M_1. Scale bars = 1 mm.

of Zoology in June 1988; *M. montanus* and *M. longicaudus* are also reported to occur in the vicinity of the cave (Armstrong, 1972).

Genus *Lemmiscus*, Thomas, 1912

Lemmiscus curtatus, (Cope, 1868)

(Fig. 8A, B)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155265 (right dentary with I_1 and M_{1-2}, surface); CM 45457 (left dentary with I_1 and M_1, level 1); CM 45458, 45459 (two right dentaries with I_1 and M_1, level 1); UCMP 155266–155290 (11 left M_1, two broken left M_1, and 12 right M_1, level 1); CM 45461 (left M_1, level 1); CM 66239 (left M_1, level 1); CM 66242 (left M_1, level 1); CM 66277 (broken left M_1, level 1); CM 66279 (left M_1, level 1); CM 66283 (left M_1, level 1); CM 66304 (left M_1, level 1); CM 66310 (left M_1, level 1); CM 66330 (left M_1, level 1); CM 66343 (left M_1, level 1); CM 66346, 66347 (two left M_1, level 1); CM 45465 (right dentary with M_{1-2}, level 1); CM 66190 (broken right M_1, level 1); CM 66201 (right M_1, level 1); CM 66220 (right M_1, level 1); CM 66267 (broken right M_1, level 1); CM 66268 (right M_1, level 1); CM 66281 (broken right M_1, level 1); CM 66282 (right M_1, level 1); CM 66301 (right M_1, level 1); CM 66308 (right M_1, level 1); CM 66323, 66324 (two right M_1, level 1); CM 66328 (right M_1, level 1); CM 66334 (right M_1, level 1); UCMP 155291–155295 (two left M_1, two right M_1, and one broken right M_1, level 2); CM 66572 (left M_1, level 2); CM 66597 (left M_1, level 2); CM 66562 (right M_1, level 2); CM 66570 (right M_1, level 2); CM 66581 (right M_1, level 2); UCMP 155296, 155297 (one left and one right M_1, level 3); CM 45468, 45469 (two left M_1, level 3); CM 65578 (left M_1, level 3); CM 45471, 45472 (two right M_1, level 3); UCMP 155298–155309 (seven left M_1, two right M_1, and three broken right M_1, level 4); UCMP 155310–155312 (two left and one right M_1, level 5); UCMP 155313 (right M_1, level 6); UCMP 155314 (broken left M_1, level 6); UCMP 155315 (broken left M_1, level 7); UCMP 155316, 155317 (two left M_1, level 8); UCMP 155318 (right M_1, level 9); UCMP 155319 (broken right M_1, level 10); CM 65169 (left dentary with I_1 and M_{1-2}, level 1–3 undifferentiated); UCMP 155320 (left dentary with M_{1-3}, level 1–3 undifferentiated); UCMP 155321 (left dentary with M_{1-2}, level 1–3 undifferentiated); UCMP 155322 (right M_1, level 1–3 undifferentiated); UCMP 156157 (right M_1, level 1–3 undifferentiated); UCMP 155323 (left dentary with I_1 and M_{1-2}, south of extension area); UCMP 155324–155328 (two left M_1, one broken left M_1, and two right M_1, Pit undifferentiated); UCMP 155407, 155408 (one left and one right M^2, surface); UCMP 155409–155423 (ten left and five right M^2, level 1); UCMP 155494 (left M^2, level 1); UCMP 155424–155427 (one left and three right M^2, level 2); UCMP 155428 (left M^2, level 3); UCMP 155429–155457 (12 left and 17 right M^2, level 4); UCMP 155458–155471 (seven left and seven right M^2, level 5); UCMP 155472–155478 (three left and four right M^2, level 6); UCMP 155479, 155480 (one left and one right M^2, level 7); UCMP 155481, 155482 (one left and one right M^2, level 8); UCMP 155483–155486 (four right M^2, level 8A); UCMP 155487–155489 (one left and two right M^2, level 10); UCMP 155490 (right M^2, level 11); UCMP 155491 (left M^2, Pit undifferentiated); UCMP 155495, 155496 (one left and one right M^3, surface); CM 45410–45413 (two left and two right M^3, level 1); CM 66191 (left M^3, level 1); CM 66260 (left M^3, level 1); CM 66286 (left M^3, level 1); CM 66265 (right M^3, level 1); CM 66286 (right M^3, level 1); UCMP 155497–155501 (four left and one right M^3, level 1); UCMP 155502–155504 (one left and two right M^3, level 2); UCMP 155505 (right M^3, level 3); UCMP 155506–155525 (seven left and 13 right M^3, level 4); UCMP 155526–155533 (four left and four right M^3, level 5); CM 45473 (left M^3, level 5); UCMP 155534–155537 (one left and three right M^3, level 6); UCMP 155538, 155539 (two left M^3, level 7); UCMP 155540–155542 (three left M^3, level 10); UCMP 155543 (left M^3, Pit undifferentiated).

Identification.—Rootless molars with cementum in the reentrant angles; M_1 with a posterior loop and five or six closed alternating triangles (in most specimens, triangle 6 is confluent with the anterior cap); incipient development of a seventh triangle is very rare; triangle 2 of M_1 as large as or larger than triangle 1. M^3 of *Lemmiscus* is diagnostic in having an anterior loop, usually two alternating triangles, and an elongated posterior loop. M^2 with anteroposteriorly enlarged lingual reentrant angle.

Discussion.—*Lemmiscus curtatus* is reported from numerous Rancholabrean localities in the western United States (Kurtén and Anderson, 1980; Barnosky and Rasmussen, 1988; Harris, 1993; Bell and Mead, 1998), but is rare from sites of Irvingtonian age (the only other locality of that age being Cathedral Cave in Nevada [Bell, 1995], and possibly the Kennewick Road Cut in Washington [Rensberger et al., 1984; Rensberger and Barnosky, 1993]). M^2 and M^3 specimens listed in the material above probably include specimens from individuals showing the primitive morphology of M_1 described below under "*Lemmiscus* sp."

Lemmiscus sp.
(Fig. 8C, D)

Material.—Specimens from the Pit (UCMP V93173, CM 1925): UCMP 155333–155338 (two left and four right M_1, level 1); UCMP 155339 (right dentary with I_1 and M_{1-2}, level 1); CM 45460 (left M_1, level 1); CM 45462 (left M_1, level 1); CM 66214 (left M_1, level 1); CM 45463, 45464 (two right M_1, level 1); CM 65233 (right M_1, level 1)); CM 65481 (right dentary with M_{1-2}, level 2); UCMP 155340–155343 (two left and two right M_1, level 2); CM 66547 (left M_1, level 2); CM 45466, 45467 (two right M_1, level 2); CM 66588 (right M_1, level 2); UCMP 155344–1553478 (one left and three right M_1, level 3); UCMP 155348 (left M_1, level 3?); UCMP 155349 (left dentary with M_{1-3}, level 3); UCMP 155350, 155351 (two right M_1, level 3); CM 45506 (broken left M_1, level 3); CM 65556 (left M_1, level 3); CM 45470 (right M_1, level 3); CM 65562 (right M_1, level 3); CM 65579 (right M_1, level 3); UCMP 155352–155373 (nine left and 13 right M_1, level 4); UCMP 155374 (broken right M_1, level 4); UCMP 155375–155378 (four right M_1, level 5); UCMP 155379, 155380 (one left and one right M_1, level 6); UCMP 155381 (right M_1, level 7); UCMP 155382, 155383 (two right M_1, level 8);

UCMP 155384, 155385 (one left and one right M_1, level 10); CM 65053 (right dentary with I_1 and M_{1-3}, level 1–3 undifferentiated).

Identification.—Rootless molars with cementum in reentrant angles; M_1 with posterior loop and four closed triangles, fifth triangle open and confluent with anterior cap; only labial secondary wing (triangle 6) is developed; otherwise similar to *L. curtatus.*

Discussion.—Specimens of *Lemmiscus* with a more primitive (four closed triangles) morphology on M_1 were first described from the basal sections of the Kennewick Roadcut in Washington; higher in the same section, specimens with the typical *L. curtatus* morphology were present (Rensberger et al., 1984; Rensberger and Barnosky, 1993). *Lemmiscus* specimens from SAM Cave in New Mexico only show the primitive morphology and are reported to date to between approximately 870,000 YBP and 875,000 YBP (Repenning, 1992). In both the Kennewick locality and the Pit sequence in Porcupine Cave, there is evidence to suggest that the *Lemmiscus* populations in these areas were undergoing progressive morphological evolution in which the complexity of the M_1 was increasing (by the closing off of triangle 5). Under such circumstances, the loss of individuals showing the primitive morphology would represent a pseudoextinction as opposed to the loss of an actual species (Archibald, 1993). It is not certain whether this primitive morphology merits recognition as a separate species. Until very recently the primitive morphology of *Lemmiscus* was known only from Irvingtonian or early Rancholabrean faunas in Porcupine Cave, Kennewick, Cathedral Cave, and SAM Cave. However, several specimens were recently identified from the microtine rodent fauna from Snake Creek Burial Cave (Bell and Mead, 1998), a late Pleistocene locality in the central Great Basin radiocarbon-dated between 9460 ± 160 and 15,100 ± 700 YBP (Mead and Mead, 1989). This is the only record of the primitive morphotype from sediments of late Rancholabrean age, and it was not found in a survey of several hundred specimens of modern *L. curtatus* (A. Barnosky and C. Bell, unpublished data). For the present, we simply refer to these specimens as *Lemmiscus* sp., but recognize that they may represent a primitive morphotype of *Lemmiscus curtatus.*

One of the specimens listed above (CM 45506) was previously reported as *Microtus paroperarius* (Barnosky and Rasmussen, 1988).

Chronological Control

For much of the Irvingtonian mammal age, radiometric dating techniques for vertebrate fossils in cave deposits are limited to uranium series dating or stratigraphic association of fossiliferous deposits with a volcanic ash. Further complications in chronological ordering of faunas from this time stem from the difficulty in correlating faunas with the geomagnetic polarity time scale. Most Irvingtonian vertebrate faunas are from caves or thin stratigraphic sections, conditions under which sequences of magnetic reversal events are not frequently detectable. In such circumstances, paleomagnetic signatures are most useful to determine whether a fauna is older than the Brunhes/Matuyama boundary (dated approximately 780,000 YBP); a reversed signature indicates that the fauna is older than 780,000 YBP. In short stratigraphic sequences where only normal polarity is recorded, it is impossible to say on the basis of paleomagnetic data alone whether the fauna is in the Brunhes Chron (and therefore younger than 780,000 YBP) or whether

Table 2.—*Amino acid racemization results from samples taken from within Porcupine Cave. Relative ages are expressed as a numeric sequence, with 1 being the oldest, and 3 the youngest. Absolute age estimates were generated from a rate constant calculated using a mean annual temperature in the cave of 51°F. Absolute age estimates are here considered to be in error; see text for discussion.*

AAR sample and locality	D/L ratio	Relative age	Absolute age estimate
Badger Room; 2 teeth	0.241	1	82,334 YBP
Gypsum Room; horse tooth	0.170	2	52,666 YBP
Pit, level 2; broken horse tooth	0.250	1	86,165 YBP
Pit, level 6; 2 rodent incisors	0.249	1	85,738 YBP
Velvet Room (CM), level 1; horse tooth	0.1002	3	24,000 YBP

the fauna is encased in pre-780,000 YBP sediments deposited during a normal polarity subchron within the Matuyama Chron (e.g., Jaramillo or Cobb Mountain).

At Porcupine Cave, radiometric dating has not yet been possible, although the recent discovery of a degraded ash bed within the DMNH Velvet Room excavation may provide an opportunity for K-Ar dating. Adequate samples of the ash have not yet been collected or submitted for analysis (D. Rasmussen, personal communication, 1997). A horse molar (from levels 1–3 mixed) and flowstone samples from the base of level 5 were submitted for uranium-series and electron spin resonance dating, but results are pending. Other attempts to establish non-biostratigraphic age control at Porcupine Cave included amino acid racemization and paleomagnetic analyses.

Amino Acid Racemization.—Five samples of bone (taken from the Pit, Badger Room, Gypsum Room, and CM Velvet Room excavations) were submitted to the Amino Acid Dating Laboratory at Scripps Institution of Oceanography at the University of California at San Diego for amino acid racemization in order to determine relative ages of the localities (see Table 2). D/L enantiomeric ratio results (from aspartic acid) indicate that the specimens from the Badger Room and the Pit are the oldest of those analyzed. The Gypsum Room sample was next oldest, and the Velvet Room sample was the youngest. The Velvet Room sample was taken from the highest stratigraphic level within the CM excavation, and it is not known whether the lower stratigraphic levels from the CM Velvet Room excavation might overlap the younger units of the Pit. The relative ages as determined by amino acid racemization are more or less consistent with relative ages determined from biochronologic age assessments for the various localities, but absolute age estimates derived from amino acid racemization (Table 2) are not in accordance with approximate ages derived from biochronology. Absolute age estimates were derived according to the calculations discussed by Bada (1985) with rate constant (k_i) evaluations based on modern mean annual temperature values in the cave measured at 10.5°C. There is an order of magnitude difference between biochronologic age estimates based on microtines and the absolute ages of localities calculated by amino acid racemization. This extreme difference is probably the result of a number of factors. First, fossil bone does not represent a closed system with respect to amino acid racemization. Free amino acids from the surrounding environment (e.g., sediment) can be added to fossil bones after burial; these free amino acids usually result in lower D/L ratios, and age estimations that are consequently too young (Bada, 1985). Secondly, the age calculation is only as good as the rate constant evaluation, which in this case was derived from an assumption of a stable temperature of 10.5°C within Porcupine

Cave over the last several hundred thousand years. Clearly, if the deposits represent glacial-interglacial transitions as discussed by Barnosky and Rasmussen (1988), Wood and Barnosky (1994), and Barnosky et al. (1996*b*), stable temperatures through time would not be the case. Finally, although previous studies indicate that after 80,000 to 100,000 years aspartic acid in fossil bones should be completely racemized, fossil bones from Olduvai Gorge (dated by other means at close to 600,000 YBP) still yielded aspartic acid ratios of approximately 0.075, indicating that secondary aspartic acid was introduced in significant quantities from sediments and groundwater (Bada, 1981, 1985). We believe that a similar situation is likely to have occurred in Porcupine Cave and for the present, reject the absolute age estimates derived from amino acid racemization.

Paleomagnetics.—Paleomagnetic samples were taken from the base of level 5 and from levels 8A and 14 in the Pit sequence and were analyzed by V. A. Schmidt at the University of Pittsburgh Paleomagnetic Laboratory shortly before he died. Unfortunately, no viable paleomagnetic samples were obtained from higher stratigraphic levels due to the friable nature of the sediment. Results of the paleomagnetic analyses provided by Schmidt are difficult to interpret. Analysis of the sample taken from the base of level 5 was equivocal. The data suggest that levels 8 and 14 record mostly reversed polarities, but there are significant components of intermediate and, to a lesser extent, normal components that make a definitive reversed interpretation for these levels problematic. It is likely that at least some of these sediments reliably record a reversed field and that at least the lower levels of the Pit sequence (below level 7) can be considered to be older than 780,000 YBP (Barnosky et al., 1996*b*).

Biochronology.—The taxonomic composition of the microtine rodent fauna from the Pit sequence poses a challenging problem for biochronologic age estimation. At least 11 microtine rodent species are present in the fauna as a whole; as many as ten of these species occur within a single stratigraphic level (e.g., level 4; see Table 3) and seven or eight taxa are typical for most of the levels in the Pit (these figures are based on consideration of non-M_1 teeth for both *Mimomys* and *Ondatra*; see Table 3). Such diversity is rare within North American microtine rodent faunas and the taxonomic associations in Porcupine Cave are not found anywhere else on the continent. This particularly intriguing aspect of the Pit fauna complicates attempts to place the sequence within the existing microtine rodent biochronology.

Previous age estimations for the upper stratigraphic levels in the Pit (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994) were derived from preliminary analysis of the microtine rodent fauna and were based upon the standard biochronological framework outlined by Repenning (1987) and Repenning et al. (1990). In these schemes, the presence of *Lemmiscus* and specimens referred to *Microtus pennsylvanicus* argued for an age no older than 400,000 YBP for stratigraphic levels reported to containing these taxa.

In 1992, a significant change in the microtine biochronology was necessitated with the recognition of *Lemmiscus* in the fauna from SAM Cave, New Mexico, which dates to between 870,000 and 875,000 YBP (Repenning, 1992). In the preliminary analysis of the SAM Cave fauna, the relatively primitive morphotypes of *Lemmiscus* were interpreted to represent a gradual transition within that fauna from *Allophaiomys* into *Lemmiscus*. It was this hypothesis that led to the suggestion that the *Allophaiomys* morphotypes from Porcupine Cave might possibly be three-triangle morphotypes of *Lemmiscus*. This suggestion was published as an

Table 3.—*Stratigraphic distribution by level of* M_1 *specimens of microtine rodent species in the Pit sequence in Porcupine Cave. Left and right sides are distinguished (L/R). S = Surface of excavation; x = genus present in level, but not represented by* M_1 *specimens; — = taxon not present in level.*

Species	S	1	2	3	4	5	6	7	8	9	10	11
Mictomys cf. *M. meltoni*	0/1	2/1	1/3	7/4	13/18	4/7	4/2	2/7	9/3	x	3/2	0/3
Lemmiscus curtatus	0/1	26/28	4/6	4/3	7/5	2/1	1/1	1/0	2/0	0/1	0/1	—
Lemmiscus sp.	—	5/8	3/6	4/8	9/14	0/4	1/1	0/1	0/2	—	1/1	—
Terricola meadensis	3/1	12/6	11/26	4/10	5/8	3/2	1/3	0/1	0/2	—	—	—
Allophaiomys pliocaenicus	—	—	—	—	3/3	1/2	0/3	2/2	2/3	—	—	0/2
Microtus sp.	1/0	12/15	13/24	3/4	4/2	1/1	0/1	—	—	—	—	—
Microtus paroperarius	—	2/3	2/2	4/2	3/3	0/1	—	1/2	—	—	—	—
Mimomys cf. *M. virginianus*	—	—	—	—	x	0/1	1/0	x	2/0	—	x	—
Phenacomys sp. (not *P. gryci*)	—	0/1	0/1	—	—	—	—	—	—	—	—	—
Phenacomys gryci	—	—	—	1/0	1/0	—	—	—	—	—	0/1	—
Ondatra sp.	—	x	0/1	—	x	x	—	—	x	—	—	—

alternative hypothesis by Wood and Barnosky (1994) and Barnosky et al. (1996*b*), but these authors preferred an interpretation in which *Lemmiscus* in the fauna was restricted to a primitive four-triangle morphotype (as a possible new species of *Lemmiscus*) and a more typical five-triangle morphotype similar to the modern *L. curtatus*, with three-triangle specimens representing a true population of *Allophaiomys*. After a challenge to the interpretation of an *Allophaiomys-Lemmiscus* ancestor-descendaent relationship in SAM Cave, a more detailed analysis of the fauna by C. A. Repenning failed to show a transition in morphology from a three-triangled population to a four-triangled population and the hypothesis presented by Repenning (1992) is now rejected on grounds of a more thorough analysis (Bell, 1998). We follow Barnosky et al. (1996*b*) in considering the three-triangle M_1 in the Pit sequence to represent a valid population of *Allophaiomys pliocaenicus*. The earliest *Lemmiscus* known are from SAM Cave, New Mexico, and are dated between 870,000 and 875,000 YBP. These specimens all display a primitive morphology in which the fifth triangle on M_1 is confluent with the anterior cap. Similar morphotypes are found in the basal (undated, but probably early Rancholabrean) sections of the Kennewick Road cut locality (Rensberger et al., 1984; Rensberger and Barnosky, 1993), and are known from a late Rancholabrean locality in eastern Nevada (Bell and Mead, 1998).

The most serious difficulty in determining an age for the different stratigraphic levels within the Pit sequence is the apparent coexistence of taxa which before have never been found in direct stratigraphic association, and are not known to occur contemporaneously elsewhere. In the case of the lower stratigraphic levels, there is independent evidence from paleomagnetic analyses that level 8 and below are older than the Brunhes/Matuyama boundary at approximately 780,000 YBP. Above level 8, external age control is unavailable, and age determination must be based on faunal composition.

There are three species from the Pit sequence (*Phenacomys gryci, Mimomys* cf. *M. virginianus*, and *Allophaiomys pliocaenicus*) that argue for a greater antiquity than previously considered possible for this deposit. At least one species (*Lemmiscus curtatus*) would appear to indicate a younger age.

Phenacomys gryci was previously reported from three other localities. In the Fish Creek fauna in Alaska (the type locality) it was determined to date to approximately 2.4 Ma (Repenning et al., 1987). In Froman Ferry, Idaho, specimens of *P. gryci* were recovered from a much younger sequence spanning 1.6 to 1.5 Ma (Repenning et al., 1995). *Phenacomys gryci* first appears in the Pit sequence in level 10, is absent until level 4, and makes its last appearance in level 3 (Table 3).

Mimomys (*Cromeromys*) *virginianus* is currently known only from the type locality in the Cheetah Room fauna of Hamilton Cave, West Virginia, which is reported to date to between 850,000 and 820,000 YBP (Repenning and Grady, 1988; Repenning 1992). A similar species described from the Java fauna in South Dakota is considered by most authors to be early Irvingtonian in age (R. Martin, 1989; Repenning, 1992). Both of these previous North American records are from pre-Brunhes age localities. *Mimomys* cf. *M. virginianus* is present in low abundance in the Pit and is represented by M_1 specimens only in levels 8, 6, and 5; other teeth document its presence in levels 10, 7, and 4 as well (see Table 3).

The earliest well-dated occurrence of *Allophaiomys pliocaenicus* in North America is from a drill core at the base of Hansen Bluff, Colorado, where a single specimen was recovered from a horizon at or near the lower boundary of the

Olduvai magnetic polarity Chron at about 1.9 Ma (Repenning, 1992; Rogers et al., 1992). Specimens are also reported from early Irvingtonian faunas at Java, South Dakota, and the Wellsch Valley fauna in Saskatchewan. The youngest reported occurrence is from the Cheetah Room fauna in Hamilton Cave (840,000 YBP) or possibly from Cumberland Cave in Maryland (830,000 YBP); in any event no records from North America are known to date younger than 825,000 YBP (Repenning, 1992). *Allophaiomys* occurs in levels 11 and 8–4 in the Pit sequence.

Microtus paroperarius first appears in faunas reported to date between 830,000 and 840,000 YBP; Repenning and Grady (1988) suggested an evolutionary transition out of *Lasiopodomys* in the vicinity of Hamilton Cave, West Virginia, sometime around 840,000 YBP. It is known from three other localities reportedly dating to about 830,000 YBP (Cumberland Cave, Maryland; County Line, Illinois;, and the base of the Hansen Bluff sequence in Colorado). Because of its presumed endemic evolution in the eastern United States, *M. paroperarius* was never proposed as a defining taxon at the base of the Irvingtonian II microtine rodent division (traditionally drawn at 850,000 YBP based on the first appearance of presumed immigrants), but it has played a role in characterizing faunas of this age in the eastern and central United States (Repenning, 1987, 1992; Repenning et al., 1990). Its youngest reported occurrence is in Salamander Cave, South Dakota (323,000 to 252,000 YBP; Mead et al., 1996). *Microtus paroperarius* is absent from the lower stratigraphic levels in the Pit, but makes its first appearance in level 7, and persists through level 1.

Terricola meadensis, which is present in Porcupine Cave Pit from levels 1 through 8, currently is used as the primary defining taxon for the base of the Irvingtonian II microtine rodent division. Its earliest occurrence is dated at approximately 820,000 YBP near the base of the Hansen Bluff sequence in Colorado; an undated, but apparently early, occurrence was reported from the Anza-Borrego Desert (Repenning, 1992). The youngest report of *T. meadensis* may be in the Kennewick locality in Washington state, where it comes from deposits estimated to be not much older than 328,000 YBP based on rates of formation of pedogenic calcretes (Rensberger and Barnosky, 1993), or from Salamander Cave, where it may be as young as 252,000 (Mead et al., 1996). However, living populations of the Jalapan pine vole in Mexico (*Terricola quasiater, Pitymys quasiater*, or *Microtus quasiater*, depending on whose taxonomy is followed) have a dental morphology indistinguishable from *T. meadensis* (Repenning, 1983).

The primitive morphotypes of *Lemmiscus* mentioned above first appear in level 10 of the Pit sequence and persist throughout the section. Specimens with a more complex morphology similar to that seen in living *L. curtatus* also make their first appearance in level 10 and persist to the top of the sequence. The specimens from Porcupine Cave represent the earliest known record of *Lemmiscus curtatus*; the oldest previously reported record is probably from the Kennewick fauna in Washington (Rensberger et al., 1984; Rensberger and Barnosky, 1993).

Attempts to place the Pit sequence into the existing biochronological framework for microtines forces changes in the accepted temporal ranges of several taxa. The most anomalous occurrence is that of *Phenacomys gryci*. This is in part explained by the fact that so little is known about this species. The youngest known occurrence of 1.5 Ma at Froman Ferry is still much older than the maximum temporal range of most other taxa in the Pit. It is noteworthy that the Pit specimens are, without exception, among the most advanced morphotypes known

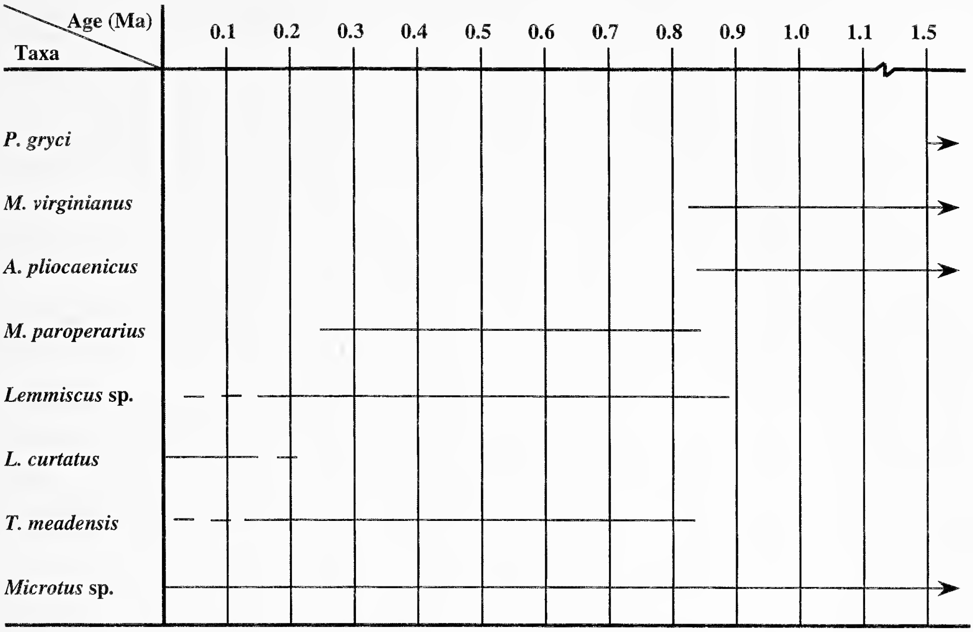

Fig. 9.—Temporal ranges of selected microtine rodent taxa in North America, based on previously reported faunas and correlations. Data summarized from Repenning (1987, 1992), Repenning and Grady (1988), Repenning et al. (1990, 1995), Mead et al. (1996), Bell (1998), and Bell and Mead (1998).

for this species. Although they do fall within the morphological variation displayed in the type population (Repenning et al., 1987), the extremely complex anterior cap morphologies seen in the Fish Creek sample are conspicuously absent from the Pit sample. It is possible that as more becomes known of this species and its evolution in North America, more sense may be made of the material from the Pit. For now, we consider these specimens to represent the youngest occurrence of the species, and count them among the most advanced morphotypes described.

Setting *Phenacomys gryci* aside, plots of oldest and youngest reported occurrences elsewhere in North America of the other species in the fauna reveal only a narrow temporal range during which potential sympatric associations could be expected (Fig. 9). At some time near 850,000 YBP, both *Allophaiomys* and *Mimomys* (*Cromeromys*) disappear from the North American fauna. At approximately the same time (within 20,000 years or so to either side) *Microtus paroperarius*, the primitive morphotypes of *Lemmiscus* sp., and *Terricola meadensis* all appear for the first time. If an age of 850,000 YBP is accepted for stratigraphic levels in which sympatric associations of *Allophaiomys, Mimomys, Microtus paroperarius*, the primitive morphotypes of *Lemmiscus* sp., and *Terricola* are found, then the middle sections of the Pit sequence (levels 4, 5, and 7) would date to that time.

It is unclear whether this age estimation is inconsistent with paleomagnetic data because of the confusing paleomagnetic signature from level 5, which contained some reversed component, but also contained a nearly equal proportion of normal signatures. By level 8, a predominance of reversed signatures is consistent with an age of older than 780,000 years.

The presence of both normal and reversed paleomagnetic signatures in level 5, and to a lesser extent in level 8, may indicate that the middle section of the Pit actually records the transition from the Matuyama Chron (reversed) to the Brunhes Chron (normal). The magnetic signature of sediments deposited immediately preceding, during, and immediately after this event might be expected to be somewhat erratic (Opdyke and Channell, 1996). If levels 4 through 8 in the Pit do capture the magnetic transition, then an age of around 750,000 to 780,000 YBP would be applied to that part of the sequence. This would require younger occurrences of *Allophaiomys* and *Mimomys* than are elsewhere known (by approximately 70,000–100,000 years). This explanation would nicely reconcile the biochronological and paleomagnetic data.

An estimation of 750,000–780,000 years for levels 4 through 8 still requires a very significant change in the accepted temporal range of *Lemmiscus curtatus* (which is present in the Pit as low as level 10). Any interpretation of the age of the Pit sequence will involve moving the first appearance datum of this species back into the Irvingtonian because of its presence in the largely reversed sediments below level 8.

Temporal ranges of other species in the Pit fauna are not affected by this age interpretation. Five-triangle *Microtus* were present in North America on the west coast by as early as 1.4 Ma in the Anza-Borrego Desert (Zakrzewski, 1972; Repenning, 1992), and probably earlier than that time, if Beringian immigrant status for the southern California populations is to be believed. Without reliable species identification of the *Mictomys, Ondatra*, and *Phenacomys* specimens not referable to *P. gryci*, evaluations of their temporal span cannot be made. It is interesting to note that these more advanced morphotypes of *Phenacomys* do not appear in the Pit sequence until very near the top of the section (level 2; see Table 3). *Ondatra* is in such low abundance in the Pit that any statements regarding its status would be premature.

If the magnetic reversal in the Pit sequence represents the change from the base of the Jaramillo into the middle Matuyama instead of the Brunhes/Matuyama boundary, then an age of about one million years would apply to sediments in level 8 of the Pit. This interpretation is rejected based on the biochronological evidence. An age interpretation of approximately one million years would better explain the presence of *Mimomys* and *Allophaiomys* in the Pit sequence, but would force a much older age for the first appearance of *Microtus paroperarius, Terricola*, and both species (or morphotypes) of *Lemmiscus*.

If the 252,000 YBP dates for *Microtus paroperarius* and *Terricola meadensis* from Salamander Cave (Mead et al., 1996) are correct, then the higher stratigraphic levels of the Pit sequence (levels 1–3) probably are no younger than approximately 250,000 YBP. The potential temporal span of levels 1–3 is between 250,000 and 750,000 YBP. At present, a more precise age assessment of these levels cannot be provided.

DISCUSSION AND CONCLUSION

The microtine rodent fauna from the Pit locality in Porcupine Cave is one of the most taxonomically diverse in North America. It seems likely that the high diversity and anomalous taxonomic associations are somehow related to the extremely high elevation of Porcupine Cave. At least three factors may have contributed to the unique assemblage found in the Pit.

Taphonomic Pathways

It is possible that the taphonomic pathways responsible for the introduction of bones and teeth into the site may have sampled taxa from a variety of microhabitats within the hunting ranges of the carnivores and raptors that apparently collected most of the bones. The cave sits along a ridge overlooking a valley within South Park, and a view from the top of the ridge today reveals an impressive diversity of microhabitats and elevations within a relatively short distance from the modern entrance. The taphonomic pathways that brought skeletal material inside the Pit apparently included hunting of small mammals by predators, deposition of raptor pellets or fecal material near the cave entrance, and collection of and hoarding in their nests of the bone-laden pellets by woodrats (genus *Neotoma*; Barnosky and Rasmussen, 1988; Barnosky et al., 1996*b*). Several lines of evidence substantiate this taphonomic interpretation. Abundant *Neotoma* skeletal remains and fossilized woodrat midden matrix and fecal pellets in the Pit deposits demonstrate the presence of these animals in and around the cave throughout the period during which fossils were preserved. Predominance of the kind of small-mammal bones (jaws, broken skulls, isolated teeth, disarticulated postcranial elements, etc.) and bone-breakage patterns (e.g., teeth etched by digestive juices and skulls missing their posterior half) commonly preserved in raptor pellets and carnivore scat (Andrews, 1990) suggests that significant portions of the vertebrate fossils from the cave were derived from these sources. In addition, observation of modern *Neotoma* middens inside Porcupine Cave revealed that they contain mummified *Neotoma* carcasses, raptor pellets, and carnivore scat with skeletal representation similar to that found in the fossil deposits, and modern cow teeth similar in size to the fossil ungulate teeth that occur in the Pit deposits. Observations by other authors also demonstrate the penchant of *Neotoma* for collecting plant and animal remains (including raptor pellets and carnivore feces) from within the region immediately surrounding their nests (Betancourt et al., 1990).

Detailed study of *Neotoma cinerea* accumulations indicate that fossil deposits generated by woodrat activities such as occurred at Porcupine Cave reliably record the taxonomic composition and probably relative abundance of small mammal communities through time (E. Barnosky, 1992, 1994; Hadly, 1999). Therefore, it seems reasonable to assume that at least part of the diversity in Porcupine Cave is simply a reflection of relatively complete sampling of the taxa living within the immediate vicinity of the site.

Introduction of Allocthonous Taxa

The contribution of fossil remains from relatively distant areas is more difficult to assess. Raptorial birds and mammalian carnivores can introduce into cave deposits materials from distant locations, but most commonly their prey comes from within a 5-km radius (Hadly, 1999). The abundant carnivore remains in Porcupine Cave (Anderson, 1996) demonstrate that badgers, ferrets, other mustelids, wolves, coyotes, and foxes were present and probably contributing to the deposition of vertebrate materials near, and in some cases (e.g., the Badger Room) in, the cave.

Although transport of animal remains from within South Park seems likely, there is little evidence to support the hypothesis that materials were transported from long distances. A lower elevation (2300 m) fauna from Hansen Bluff, approximately 120-km south of Porcupine Cave, was described in detail by Rogers et al. (1985). Of the six microtine rodents described from that locality, five are present in the Pit sequence in Porcupine Cave. The single exception is a reported occurrence of *Clethrionomys* sp. from locality PP2 near the base of the Hansen Bluff sequence. Because of the significance of this record, both for interpretation of the Porcupine Cave fauna and because of its importance for the definition of the Irvingtonian II microtine rodent division (Repenning, 1987; Repenning et al., 1990), we asked C. A. Repenning to reexamine the specimen and confirm the identification. Closer inspection revealed that the specimen is a rooted microtine molar, but is badly broken and lacks cementum in the reentrant angles. All known specimens of living and fossil *Clethrionomys* have pronounced cementum in the reentrant angles, and the material from Hansen Bluff is here transferred to *Phenacomys* (of unknown specific affinity).

The fact that all the microtines from Hansen Bluff are represented in Porcupine Cave is interesting, but not necessarily surprising; *Mictomys meltoni, Terricola meadensis, Ondatra annectens* (in Porcupine Cave as "*Ondatra* sp."), *Microtus paroperarius*, and *Microtus* sp. are all known from lower elevations in the Great Plains. Comparison of the faunal lists from Porcupine Cave (Barnosky and Rasmussen, 1988) and Hansen Bluff (Rogers et al., 1985) reveals an overall similarity in the taxonomic composition of other small mammal species from the two localities, but two important exceptions occur. The heteromyid genera *Perognathus* and *Dipodomys* are present in the Hansen Bluff sequence (at 2300-m elevation), but are conspicuously absent from Porcupine Cave (all of the excavations within the cave produced only one heteromyid specimen—an isolated molar of *Dipodomys* sp.). The historical distribution of heteromyids in Colorado includes records from at least as high as 2530 m for both *Perognathus* and *Dipodomys* (Armstrong, 1972); a very early report (Coues and Yarrow, 1875) of *Dipodomys ordii* taken from approximately 2804 m in the vicinity of Twin Lakes was considered doubtful by Armstrong (1972). If raptors or carnivores were bringing in materials from lowland localities farther south or east, heteromyid remains would be expected in the Pit deposit.

Dispersal Corridors

The position of the cave high in the Rocky Mountains may offer at least a partial explanation of the anomalous assemblage of microtine rodents. It is possible that Porcupine Cave is situated near an ancient dispersal corridor along which microtine species may have expanded their ranges from further to the north. This hypothesis was proposed by Barnosky et al. (1996*b*) as an explanation for what appeared to be an anomalously early occurrence of *Microtus montanus/M. longicaudus*. Although these specimens are here identified simply as *Microtus* sp., they do appear rather abruptly in the Pit sequence at level 6 and persist through the younger levels, increasing in relative abundance upsection (Fig. 10). Unfortunately, the specific affinities of these specimens cannot be determined with the material at hand, but it is possible that the dispersal of *Microtus* species with an M_1 with five closed triangles into the Rocky Mountain region was from north or south along a mountain corridor. Fossil material of five-triangle *Microtus* is known from earlier deposits in southern California (Zakrzewski, 1972; Repenning, 1992) and also from the roughly contemporaneous Irvington gravels in north-central

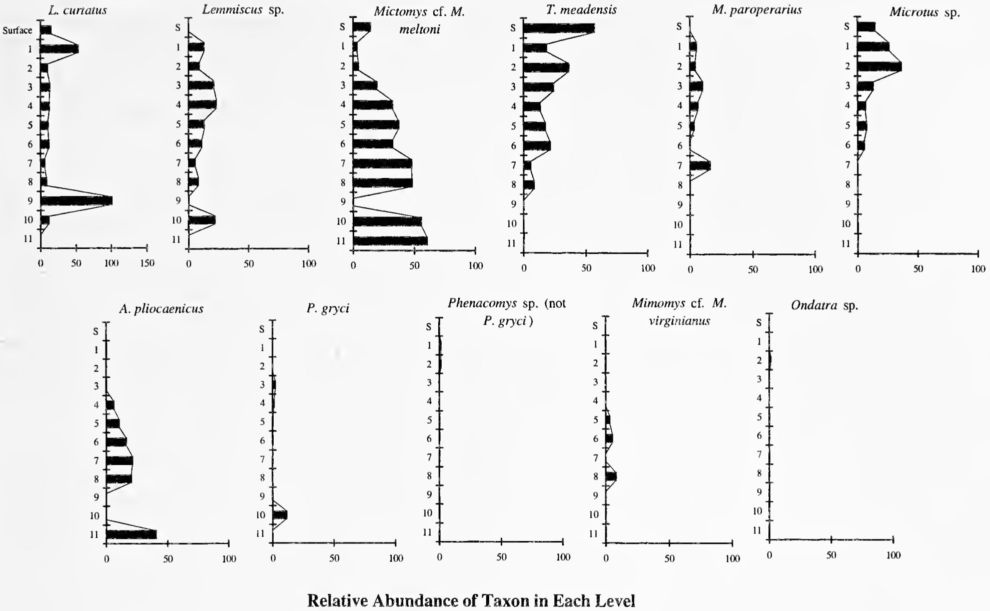

Fig. 10.—Relative abundance of microtine rodent taxa from the Pit excavation in Porcupine Cave.

California at a slightly lower latitude, and significantly lower elevation, than that at Porcupine Cave (Savage, 1951). Similarly, the relatively late appearance in the Pit sequence of *Phenacomys* not referable to *P. gryci* may indicate utilization of a Rocky Mountain dispersal corridor (although the referral of the Hansen Bluff "*Clethrionomys*" to *Phenacomys* could indicate its presence in Colorado at a slightly earlier date).

More importantly, if the age interpretation given above is correct, the appearance of *T. meadensis* in the Pit sequence ranks as one of the earliest occurrences of the species in North America (Repenning, 1992), and certainly the *Lemmiscus curtatus* record is the oldest known from the continent. *Terricola meadensis* has long been regarded as an immigrant and used as a defining taxon for the beginning of the Irvingtonian II microtine rodent division. The proposed immigration date of this species at 850,000 YBP is based on its earliest occurrence at Hansen Bluff at about 830,000 YBP (Repenning, 1987; Repenning et al., 1990). The approximately contemporaneous first occurrence in two Colorado faunas, at Hansen Bluff and in the Pit (level 8), provides support for a Rocky Mountain dispersal route for this species. One problem with this interpretation is the occurrence of *Terricola* at a relatively early age in southern California. A single specimen was reported from reversely magnetized sediments of unknown age in the Anza-Borrego Desert, (Repenning, 1992). One of us (CJB) recently identified an additional (and potentially early) occurrence from the Elsinore Fault Zone in Riverside County, California (SBCM locality 5.6.301; the fauna contains 15 M_1 specimens of *T. meadensis*).

The Pit sequence unquestionably records the earliest appearance of M_1 showing the morphology of the extant *Lemmiscus curtatus*. Prior to its discovery in Porcupine Cave, all records were of Rancholabrean age, the oldest probably from the Kennewick locality in Washington state (Rensberger et al., 1984; Rensberger and

Barnosky, 1993). The place and time of origin and evolution of *Lemmiscus curtatus* remain unknown, but there is an indication in both the Porcupine Cave Pit sequence and in the Kennewick sequence that the earlier individuals with an M_1 with four closed triangles evolved into the more complex five-triangle forms.

Faunal Response to Climate Change

It is possible that the region around Porcupine Cave served as a high-elevation refugium for some microtine rodent taxa that appear to have been extirpated elsewhere at earlier times. This hypothesis would apply specifically to *Allophaiomys* and *Mimomys*, which elsewhere in North America disappear from faunas between 820,000 and 840,000 YBP, and possibly to *Phenacomys gryci*, the latest occurrence of which is 1.56 Ma elsewhere. The refugium hypothesis would gain support if it could be shown that the appearance (or persistence) of some taxa in Porcupine Cave was correlated with climate change in the region.

Changes in the lithology of sediments within the Pit sequence were previously interpreted to reflect climate change, with the nodule layers representing wetter (and presumably glacial) periods and the fine "loess" deposits representing drier (presumably interglacial) periods (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996*b*). At least two such sedimentological changes are recorded within the Pit sequence (Fig. 2). If this interpretation is correct, the level 10/9 transition probably represents a change from glacial to interglacial conditions, as does the transition between levels 4 and 3 (Fig. 2, 10). Previous analyses of faunal change across sedimentary boundaries focused on the level 4/3 transition since this was the only portion of the Pit collection that had been adequately studied. In addition to the physical changes in the sediments from level 3 to 4, changes in faunal composition across the stratigraphic levels support the idea that the differences in lithology reflect climatic change. Three faunal groups (squirrels, microtines, and reptiles) from levels 1 through 6 now have been studied in sufficient detail to permit some tentative conclusions about faunal response to climate change in the Porcupine Cave region.

In an analysis of the upper stratigraphic levels of the Pit (levels 1–5), Wood and Barnosky (1994) presented dramatic faunal evidence in support of major environmental change at the level 4/3 transition; levels 1–3 were composed of nearly uniform, fine dust and levels 4 and 5 predominantly of reversely graded clay nodules (with a change in nodule size defining the break between the levels). Wood and Barnosky (1994) focused on changes in relative abundance in two groups, sciurid rodents and microtine rodents (in the latter case drawing upon a greater sample size than that reported by Barnosky and Rasmussen [1988] but less than that reported here). Although in most cases all taxa analyzed were recovered from all stratigraphic levels, and changes in relative abundance were detected within the homogenous sediment types (levels 1–3 and 4 and 5 respectively), the most dramatic changes were seen at the level 4/3 transition. Among the sciurids, a sharp decline in relative abundance of *Marmota* (from 81.7% to 17.4%) occurs concomitantly with increases in both *Cynomys* (from 1.4% to 16.3%) and *Spermophilus* (from 16.9% to 66.3%). Assuming the environmental preferences of these genera have remained the same since the deposition of fossils in the Pit, this change in the sciurid rodent fauna supports an interpretation of decreased precipitation across the level 4/level 3 boundary because *Marmota* today prefers wetter climates than do *Cynomys* and most species of *Spermophilus*

(Wood and Barnosky, 1994). The persistence of *Marmota* during effectively drier climatic conditions might lend some support to the refugium hypothesis, since its presence indicates that some mesic microhabitats remained within an overall drier climatic regime.

Because reptile and amphibian fossils can in some instances provide information on climate change (Holman, 1995), we examined the reptile and amphibian fossils from the Pit sequence across the level 4/level 3 transition. Reptile and amphibian fossils are relatively rare in all stratigraphic levels of the Pit, and most of the remains are isolated vertebrae of small snakes, rendering estimates of number of individuals impossible. Nonetheless, an interesting change in the taxonomic composition of the herpetofauna is clear. The oldest snakes appear in level 8A (seven vertebrae) and are then sporadically encountered in other stratigraphic levels (three vertebrae in level 7, one in level 6, five in level 4, three in level 3, six in level 2, and three in level 1). All of the snakes below level 3 are identified as natricines and probably represent fossils of *Thamnophis*, a widespread genus throughout North America today whose members inhabit a wide variety of habitats and elevations (Stebbins, 1985). *Thamnophis* is not uncommon in the immediate vicinity of Porcupine Cave today. Natricines also are present in levels 1–3 (nine vertebrae), but one colubrine fossil and two crotalid fossils (probably representing *Crotalus*) are also present. Neither of these latter taxa are known in the vicinity of the cave today (R. Finley, personal communication). Two other fossils, from a sceloporine lizard and a pelobatid toad, cannot be placed in precise stratigraphic levels, but their state of preservation and color more closely resemble that of fossils from levels 1–3 than that of fossils from deeper levels. The change in reptile diversity is probably correlated with increased temperatures around the cave during the interglacial recorded in levels 1–3. In addition, the interglacial recorded in the upper levels of the Pit was possibly warmer than the present interglacial, since modern herpetofaunal diversity in the vicinity of the cave is lower than that recorded in the upper levels of the Pit.

The changes in relative abundance and taxonomic diversity in the reptile and squirrel components of the fauna support the conclusion that a change from a glacial period to an interglacial period is recorded at the level 4/3 transition. This transition records a change from relatively cooler, wetter (probably glacial) conditions (level 4) to warmer, drier (probably interglacial) conditions (level 3) that were probably warmer than current conditions. Previously, the putative glacial-interglacial transition demonstrated by the level 4/3 boundary was thought to correspond with oxygen-isotope stages near stage 12 (glacial) and stage 11 (interglacial) (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996*a*, 1996*b*). However, the new biochronologic and paleomagnetic interpretations presented here suggest the level 4/3 transition corresponds to a part of the oxygen-isotope curve that dates between 750,000 and 850,000 YBP. The istotope excursion from (glacial) stage 22 to (interglacial) stage 21 occurred about 875,000 YBP; and from (glacial) stage 20 to (interglacial) stage 19 about 800,000 YBP. At about 740,000 YBP, there was a significant warming event indicated by the isotope excursion from (cold) stage 18 to (warm) stage 17 (Raymo et al., 1997). It presently is impossible to say which of these warming events is recorded by the Porcupine Cave Pit record, but it seems likely that one of them is.

Other clay-dust transitions (probably indicating changes from cool, mesic to warm, dry conditions) in the Porcupine Cave Pit sequence (e.g., level 10 to 9; see Fig. 2) are older than the level 4/3 transition, but probably still within the

780,000-900,000 range. This conclusion is based on the stratigraphic position of these levels below sediments with a magnetically reversed signature, the species assemblage of microtine rodents, and the rapid sedimentation rates in Holocene deposits in which *Neotoma* nests played a major role. An example of such rapid sedimentation rates was provided by Hadly (1996, 1999) who reported accumulation rates in Lamar Cave, Yellowstone Park, which produced 2 m of fossiliferous deposit similar to the Porcupine Cave deposit within 3000 years.

The distribution of microtine rodent taxa within the stratigraphic levels of the Pit (Table 3) and the changes in their relative abundance (Fig. 10) are difficult to explain in terms of climate change. Sample sizes are too low in levels 10, 9, and 8 for any meaningful statements to be made about faunal response to the climatic transitions recorded in the sediments from those levels. The sample size for the level 4/3 transition is adequate, but relative abundances for many of the taxa are either stable (*Lemmiscus curtatus, Lemmiscus* sp.) or appear to reflect continuance of trends begun prior to the major sedimentary change (*Allophaiomys, Mictomys, Terricola*; see Fig. 10). One possible exception is *Microtus* sp. which begins a sharp increase in relative abundance in level 3, but the major jump in relative abundance is actually between levels 3 and 2, where sediments do not record a major climatic change. It may be that the small mammals began responding to the climate change prior to its reaching the threshold that caused a change in sediment deposition, which would explain the earlier inception and continuation of relative abundance trends across the sedimentary change at the level 4/3 boundary.

These more complete data force slight modifications to the previous interpretations of changes in relative abundance of microtine rodent taxa in the Pit (Barnosky and Rasmussen, 1988; Wood and Barnosky, 1994; Barnosky et al., 1996*a*, 1996*b*), but the substantive conclusions of these earlier reports are upheld. Previous discussions of changes in the microtine rodent fauna indicated that *Allophaiomys* made its last appearance in the Pit in level 4, suggesting that the local extirpation of this species (and quite possibly its extinction from North America, as the Pit records represent the youngest known specimens of the species) corresponded with a major sedimentary change indicative of changing climate (Wood and Barnosky, 1994; Barnosky et al., 1996*a*, 1996*b*). This hypothesis is supported by our further examination of the fauna. In addition, although no M_1 specimens of *Mimomys* cf. *M. virginianus* are present in level 4, there is an isolated M_2 representing this genus (and presumably the same species as is represented by the M_1 material). The presence of this specimen in level 4 suggests the possibility that *Mimomys* also was driven to extinction by the climate change recorded at the level 4/level 3 transition.

The Possible Influence of Elevation

Although relatively little is known about *Mimomys* (*Cromeromys*) in North America, the existing records (Cheetah Room in West Virginia, Porcupine Cave, the Java fauna in South Dakota, and Cathedral Cave in Nevada) suggest that the animal favored relatively high elevations or high latitudes. This raises the interesting question about the potential influence of high elevation on biochronological frameworks. It has long been recognized that both living and extinct faunas could be partitioned into broad geographic provinces based on their occurrence at differing latitudes (Brown and Gibson, 1983). Faunal provinces of relatively limited geographical extent are recognized in the late Pleistocene of North America (Graham, 1979; L. Martin and Hoffmann, 1987; Rogers et al., 1990; FAUNMAP Working Group, 1996). Fejfar and Repenning (1992) proposed a series of provincial designations specifically applied to microtine rodents (microtine rodent faunal regions). The proposed regions correspond to both latitudinal and longitudinal differences in the distribution of fossil microtine rodents. The validity of these regions is sometimes difficult to assess, but in principle the concept appears sound. There is increasing evidence to support the idea that different biochronologies must be applied to different geographical regions (intracontinental as well as intercontinental). Differences in the taxonomic composition of microtine rodent faunas on either side of the Rocky Mountains led Repenning et al. (1995) to argue for the recognition of different temporal boundaries for the Irvingtonian I microtine rodent division in the eastern versus western United States. The challenge in implementing such regional biochronologies lies in the adequate establishment of reliable, independent chronologies for the different proposed regions, and, especially in the case of the Irvingtonian, simply in identifying a sufficient number of localities to permit regional faunal patterns to appear.

The unique species assemblage character of the Porcupine Cave microtine fauna suggests the possibility that age relations of faunas from high elevations may not be readily interpreted in terms of biochronologies established based on examinations of low-elevation sites. Much of the microtine rodent biochronology in North America west of the Mississippi River was developed based on faunas from relatively low elevations. The difficulties in determining the age of various stratigraphic levels within the Pit sequence may be a result of differences in Irvingtonian community composition between high-elevation sites like Porcupine Cave and contemporaneous low-elevation sites, just as is the case today (Armstrong, 1972). For the present, Porcupine Cave stands alone as a representative of a high-elevation Irvingtonian microtine rodent fauna. Future discovery and investigation of high-elevation sites in western North America may begin to provide the data required to construct an independent biochronology. Any efforts to construct such a biochronology must ultimately be anchored by reliable external age control.

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NEW LOWER MISSISSIPPIAN TRILOBITES FROM THE CHOUTEAU GROUP OF MISSOURI

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Abstract

Reexamination of existing trilobite collections from the Kinderhookian (Lower Mississippian) Chouteau Group of central and northeastern Missouri indicates that two different suites of trilobites are present in these two areas of the state. Moreover, the study of these collections has led to the erection of a new genus and four new species. The new genus, *Ameropiltonia*, is based on a new species, *A. lauradanae*. This genus and species is commonly confused with *Breviphillipsia sampsoni* (Vogdes). *Elliptophillipsia rotundus*, n. sp., differs from the type species of this genus by possessing a rounded frontal lobe to the glabella. The other new species, *Perexigupyge chouteauensis* and *Richterella hessleri*, are present in the Compton Limestone of Marion and Ralls counties of northeastern Missouri.

Variations in trilobite species found in the Compton Limestone of central Missouri and the northeastern part of the state are interpreted to be environmentally related. It appears that the lime mudstone and wackestone lithologies characteristic of the Compton Limestone of central Missouri were deposited in a low-energy, subtidal shelf setting. The lime packstone-grainstone strata of northeastern Missouri are interpreted to have formed as a tidal sand belt on the eastern margin of the Burlington shelf.

Key Words: Missouri, trilobites, Mississippian, Kinderhookian, Chouteau

Introduction

Trilobites are well known from the Lower Mississippian (Kinderhookian) Chouteau Group of Missouri. Vogdes (1888, 1891), Branson and Andrews (1938), Hessler (1963, 1965), and Brezinski (1986, 1988*a*) are several of the more salient references dealing with trilobites from the Kinderhookian strata of Missouri. Collection of new material and reevaluation of preexisting collections have brought to light a number of previously undescribed species and a new genus. Moreover, reexamination of known collections indicates that broadly distributed biofacies were present during the Kinderhookian. These regional trilobite biofacies parallel distinct lithofacies within the Chouteau Group. The purpose of this paper is to briefly describe the lithofacies and associated trilobite faunas present in the Chouteau Group of Missouri, and to describe a new genus and four new species of trilobites.

The trilobites described in this report were recovered from three localities. Locality 1 is located in central Missouri along the abandoned MKT Railroad right-of-way, at the base of the river bluffs of the Missouri River, one mile north of the town of Easley, Boone County. The remaining two localities are located in northeastern Missouri. Locality 2 is along County Road 183, one mile south of Warren, Marion County. Locality 3 is located along the spillway of the Clarence Cannon Dam, Ralls County.

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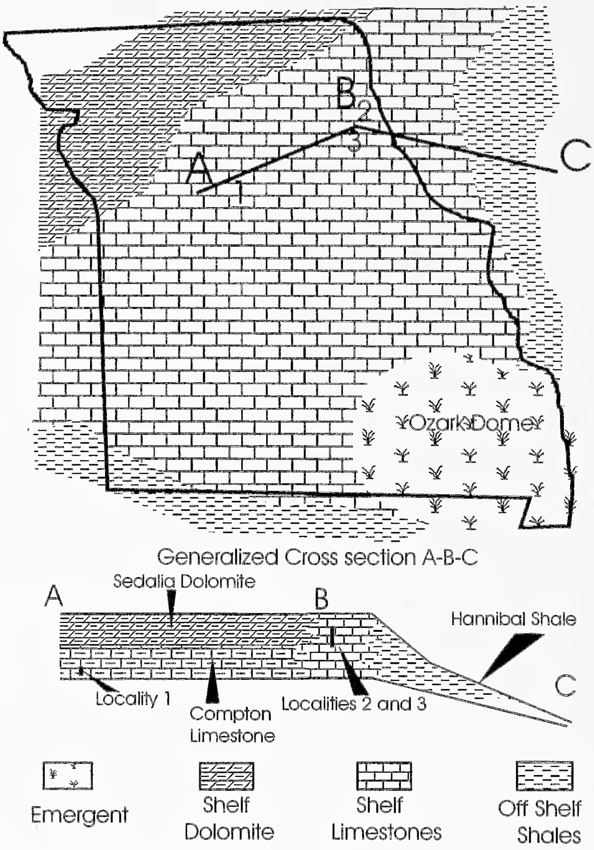

Fig. 1.—Generalized early Mississippian paleogeography of Missouri (modified from Lane and De Keyser, 1980:fig. 8). Location of the three trilobite localities (labeled 1–3) used in this study with their relative stratigraphic position illustrated on cross section. Cross-section A–B–C section line illustrates relative stratigraphic distribution of formations within the Chouteau Group of Missouri, modified from Thompson (1979). No vertical scale implied.

Morphological terminology used in this paper follows that described by Whittington (1997). Collections utilized in this study were made by J. L. Carter, A. Kollar, and the author and are reposited in the invertebrate fossil collections of Carnegie Museum of Natural History (CM).

REGIONAL FACIES

The Kinderhookian strata of Missouri is a complex mosaic of intertonguing limestone, dolomite, and shale that were lumped together as the Chouteau Group by Thompson (1979). The composite units include the Northview Shale, Sedalia Dolomite, Compton Limestone, and Hannibal Shale (Fig. 1). The composite units that make up the Chouteau Group, and especially the Compton Limestone, exhibit a broad facies change from central to eastern Missouri (Thompson, 1979). In central Missouri (Boone and Pettis counties), where the trilobite faunas have been well described (Branson and Andrews, 1938; Hessler, 1963, 1965; Brezinski, 1986, 1988*a*), the main fossiliferous unit, the Compton Limestone, consists of nodular- to medium-bedded, argillaceous, fossiliferous, lime mudstone to wackestone. King (1980) interpreted this lithology as having formed in an open shelf environment of deposition, below storm wave base. Trilobites characteristic of this facies include *Breviphillipsia sampsoni* (Vogdes), *Comptonaspis swallowi* (Shumard), *Griffithidella welleri (Branson and Andrews), Dixiphopyge armatus*(Vogdes), and *Ameropiltonia lauradanae*, n. gen. and n. sp. Uncommon faunal components include *Proetides colemani* Hessler, *Elliptophillipsia rotundus*, n. sp., and *Brachymetopus brezinskii* Hahn and Hahn.

To the east, in Marion and Ralls counties (Fig. 1), the lime wackestone of the Compton Limestone is replaced through lateral facies change. In this area an unnamed Compton Limestone equivalent consists of medium-bedded, locally cross-bedded, highly fossiliferous lime packstone to grainstone. The unnamed Compton equivalent appears to have been deposited at a much higher energy level than the nodular-bedded wackestone of the central part of the state. This is indicated by the lack of carbonate mud and the presence of cross-bedded grainstones. This regional facies variation is interpreted to represent the change from subtidal, low-energy, carbonate mud deposition of the inner shelf to tidally influenced, sand deposition of the outer shelf. Consequently, the grainstone facies within the Chouteau of northeastern Missouri are interpreted as representing a shelf margin shoal deposits.

The trilobite fauna present in the packstone-grainstone facies of the Compton Limestone of northeastern Missouri is quite different than that of the argillaceous, lime mudstone-wackestone of central Missouri. In northeastern Missouri the most common trilobites include *Griffithidella newarkensis* Hessler, *Proetides insignis* (Winchell), *Richterella snakedenensis* Hessler, and *Perexigupyge chouteauensis*, n. sp. A rarer component is *Richterella hessleri*, n. sp. This fauna is interpreted to have inhabited high-energy environments of deposition rather than the quieter subtidal environments which existed in central Missouri.

In western Illinois, the equivalent Chouteau Limestone undergoes an additional facies change and rapidly thins eastward (Lineback, 1969). In what is now the Mississippi River Valley, the grainstone facies is replaced by a thin (< 3 m) dark-gray, bioturbated, lime wackestone. Brezinski (1998) interpreted this facies as having formed in a deep-water, sediment-starved setting. The depth of the water in this basinal environment may have exceeded 180 m (Lineback, 1969).

The trilobite fauna from the Chouteau Limestone of Illinois differs from either of the Chouteau lithofacies observed in Missouri. The Illinois fauna consists of *Pudoproetus chappelensis (Hessler), Griffithidella doris* (Hall), *Phillibole planucaudus* (Brezinski), and *Thigriffides roundyi* (Girty). Brezinski (1998) proposed that the Illinois fauna was similar to that found in the Welden Limestone of Oklahoma and the Chappel Limestone of Texas because these areas shared a similar depositional setting. These interpreted deep-water species are generically different from the fauna found within the presumed shelf deposits of Missouri.

SYSTEMATIC PALEONTOLOGY

Order Proetida Fortey and Owens, 1975
Family Phillipsiidae Oehlert, 1886
Genus *Ameropiltonia*, **new genus**

Type Species.—*Ameropiltonia lauradanae*, n. sp.

Other Species Assigned.—Only the type species is currently assigned.

Diagnosis.—Exoskeleton highly vaulted, covered with coarse tubercles. Cephalon strongly arched in transverse and longitudinal profile. Genal angle rounded. Glabella parallel-sided to mildly forward-tapering, reaching to overhanging anterior border. Pygidium semicircular, ribs sharply overhanging pleural furrows, interpleural furrow lacking.

Remarks.—In his erection of the genus *Breviphillipsia*, Hessler (1963) designated *Phillipsia sampsoni* Vogdes as the genotype (i.e., type species). As a type species, *B. sampsoni* has been somewhat of an enigma because Hessler (1963:pl. 61 and 62) included a number of specimens that differ considerably from the holotype. It appears that all of the specimens, except the holotype, that Hessler assigned to *B. sampsoni* differ in various characters from the holotype of *Phillipsia sampsoni*. The holotype (Hessler, 1963:pl. 61; fig. 15–17, 21) has a forwardly tapering, broadly rounded glabella that is mildly constricted at γ. The anterior facial sutures diverge from γ to β, and the posterior segment has a relatively long and straight ϵ to ζ section. The anteriorly rounded glabella extends to the anterior border furrow, but not to the anterior margin, and the pygidium has a well-defined interpleural furrow which gives the pygidial ribs anterior and posterior bands. Furthermore, the glabella is covered with small granules and the pygidium has no prosopon. Most of the coarsely ornamented specimens illustrated by Hessler (1963:pl. 61, fig. 22, 23, 27, 28; pl. 62, fig. 1) are not assignable to *B. sampsoni*. The disparity of shape of the glabellae among the specimens suggests that the coarsely ornamented specimens do not even belong to the genus *Breviphillipsia*. The species *B. sampsoni* is herein restricted to those specimens from central Missouri similar to the holotype in that they exhibit the tongue-shaped glabella that extends to the anterior border furrow and a pygidium that exhibits both pleural and interpleural furrows. Thus, most fossils referred to *B. sampsoni* (see Levi-Setti, 1975; Brezinski, 1986:fig. 4) belong to both a different genus and species. A new genus, *Ameropiltonia*, is established to include species from the Compton Limestone of Missouri that exhibit the coarsely tuberculate prosopon.

Comparison.—*Ameropiltonia* is similar to *Piltonia* in shape of the glabella, ornamentation, and outline and character of the pygidium. It is distinguished from the latter genus by the lack of a preglabellar field, anterior facial sutures that trace very close to the dorsal furrow rather than diverge anteriorly, and a shorter pygidium that has fewer rings and ribs. American representatives of *Piltonia* such as *P. tuberculata* (Meek and Worthen, 1870) and *P. eurybathrea* (Hessler, 1963) have much longer pygidia, a short preglabellar field, and anterior facial sutures that diverge moderately from γ to β. Another closely related genus, *Eocyphinium*, has a forwardly expanding glabella and longer pygidia than *Ameropiltonia*.

Range.—Late Kinderhookian.

Ameropiltonia lauradanae, **new species**

(Fig. 2A–E)

Breviphillipsia sampsoni Hessler, 1963:pl. 61, fig. 13, 19, 20 (not pl. 61, fig. 15–17, 21, 22, 27, 28; pl. 62, fig. 1); Hahn and Hahn, 1972:120–121; Brezinski, 1986:fig. 4.1, 4.5, 4.8.

Diagnosis.—Highly vaulted species with coarse tuberculation. Glabella outline quadrate, slightly anteriorly tapering to parallel-sided, broadly rounded anteriorly, strongly arched in longitudinal and transverse profile, overhanging anterior margin. Dorsal furrow deep, narrow. Palpebral lobes small, anteriorly located. Pygid-

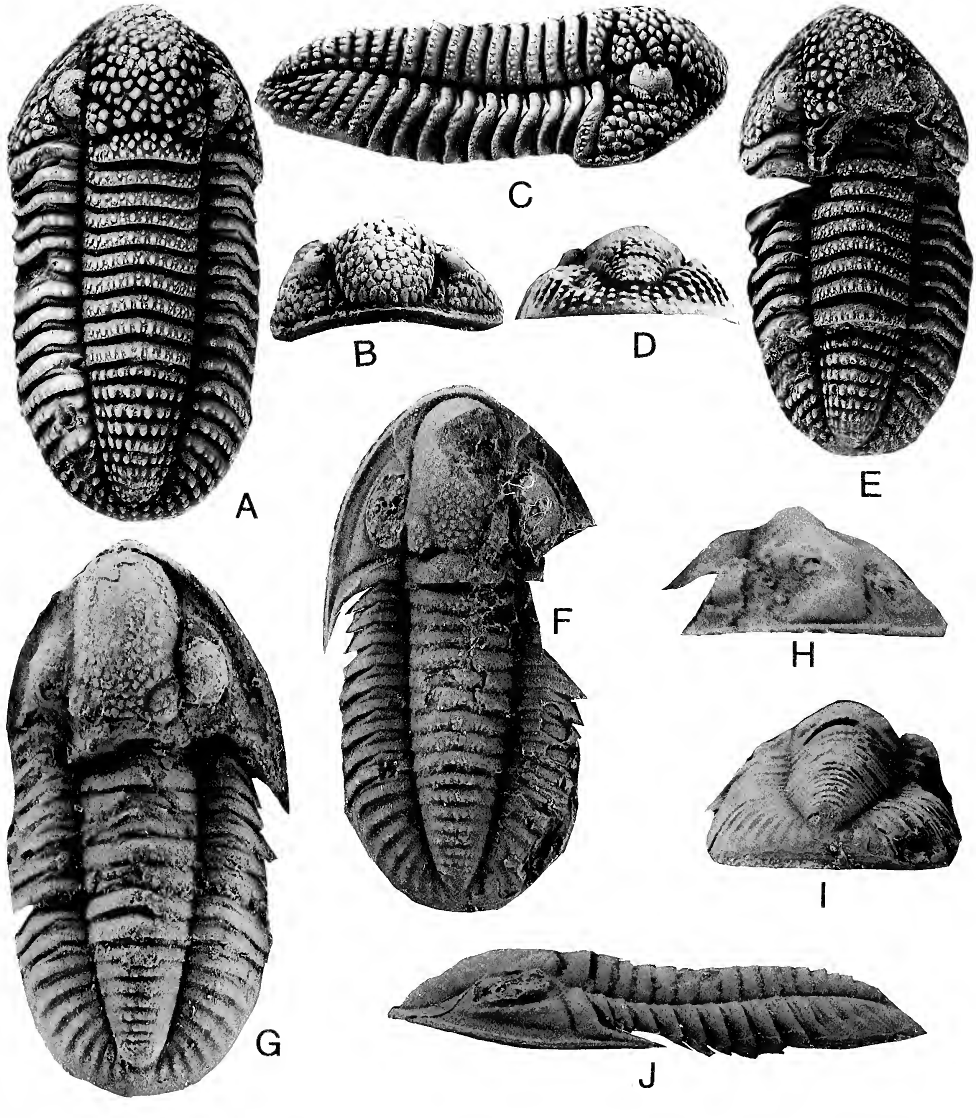

Fig. 2.—A–E. *Ameropiltonia lauradanae*, n. gen. and n. sp. A–D. Holotype specimen from the Compton Limestone, Boone County, Missouri, Locality 1, CM 45115, × 3.5. D. Paratype specimen from Locality 1, CM 45116, × 3.0. F–J. *Elliptophillipsia rotundus*, n. sp. F, H-J. Holotype specimen from the basal Compton Limestone, Boone County, Missouri, Locality 1, CM 45118, × 4.0. G. Paratype specimen, CM 45119, × 4.0.

ium highly vaulted, with robust, wide, rounded axis, and deeply incised pleural furrows.

Holotype.—A complete exoskeleton from the Compton Limestone at locality 1, Boone County, Missouri, CM 45115, collected by the author.

Paratypes.—A partial exoskeleton and a pygidium from locality 1, CM 45116 and 45117, collected by the author.

Description.—Exoskeleton outline oval, vaulting high. Cephalon outline parabolic, genal angle sharply rounded. Glabella with straight sides, nearly parallel to very slightly forward-tapered, broadly rounded anteriorly; sides vertical, mildly arched crest in transverse profile; strongly longitudinally arched. Frontal lobe with prosopon of coarse polygonal tubercles, meeting and/or overhanging anterior border. S1 narrow, deep, straight; S2–S4 marked by separation of the coarse prosopon. L1 outline triangular. Dorsal furrow deepest between eyes, shallowest anteriorly. Occipital furrow deep, sinuous, overhung by L1. Occipital lobe wide at axial line. Palpebral lobes small, crescentic, ornamented by a line of tubercles along outer edge. Anterior branch of facial sutures parallel and close to sides of glabella, sharply rounded at β. Posterior branch of facial sutures with a short straight section at ϵ. Eyes small, reniform, with vertical sides, and a row of tubercles at the base. Librigenae descending steeply from eye to narrow, shallow, lateral border furrow. Lateral border sharply crested, underturned on its outer edge, with a row of small tubercles on its inner edge. Posterior border furrow deep, relatively wide. Posterior cephalic border wide, with a row of posteriorly directed tubercles at crest.

Thorax of nine equal tergites. Axial lobe robust, rings wide, semicircular in transverse profile ornamented with two rows of small tubercles. Ring furrows deep, narrow, sinuous. Dorsal furrow, deep, relatively straight. Pleural fields proximally flattened, sharply curved at fulcrum, nearly vertical at distal ends. Pleural tips sharply angular.

Pygidium outline semicircular, highly vaulted. Axis robust, wide, semicircular in transverse profile, mildly arched in longitudinal profile, sharply rounded at posterior terminus, not reaching posterior of pygidium, composed of ten to 11 rings. Rings wide, sharply crested, ornamented with a row of coarse tubercles that are posteriorly directed, deep. Ring furrows deep, straight to slightly bowed forward over axis. Pleural fields strongly arched in transverse profile, mildly arched in longitudinal profile, composed of ten to 11 ribs that extend behind the axis. Posteriormost ribs defined by rows of tubercles. Anterior ribs wide, sharply crested, and ornamented with a row of coarse tubercles that overhang very deep pleural furrows that extend to and overhang margin.

Remarks.—Brezinski (1986:fig. 4) interpreted variations in coarseness of the prosopon within *Breviphillipsia sampsoni* as the result of phenotypic plasticity of individuals occurring in different depositional environments. The taxonomic refinement and reassignment in the current paper suggest otherwise. The shape of the glabella and presence of interpleural furrows on the individuals illustrated in figures 4.3 and 4.4 suggest that these specimens may be assignable to *Breviphillipsia.* Figures 4.1, 4.5, and 4.8 lack interpleural furrows, and thus appear to be assignable to *Ameropiltonia.* It is not clear now whether the coarsely ornamented specimens illustrated by Hessler (1963:pl. 61, fig. 22, 27, 28; pl. 62, fig. 1) are compacted specimens assignable to *A. lauradanae* or to a different species of *Ameropiltonia.*

Distribution.—Chouteau Formation of Boone County, Missouri; Cuyahoga Formation of Ohio.

Etymology.—Named for Laura Dana Brezinski.

Genus *Elliptophillipsia* Hessler, 1963
Elliptophillipsia rotundus, **new species**
(Fig. 2F–J)

Diagnosis.—Glabella long, broadly rounded in the frontal lobe, slightly constricted at the palpebral lobes. Anterior border narrow, sharply rounded at crest. S1 arcuate; L1 suboval.

Holotype.—A nearly complete exoskeleton from the basal Compton Limestone at locality 1, Boone County, Missouri (see Brezinski, 1986:location 1), CM 45118, collected by the author.

Paratypes.—A partial exoskeleton and a cranidium, from the same locality, CM 45119, 45120, collected by the author.

Description.—Exoskeleton outline elliptical, vaulting low. Cephalon outline parabolic. Glabella long, narrow, slightly constricted between anterior end of palpebral lobes, broadly rounded in the frontal lobe, exhibiting granular prosopon. S1 relatively deep, arcuate; L1 suboval. S2–S3 faint. Occipital furrow straight, shallow, narrow; occipital lobe wide at axial line. Dorsal furrow relatively deep, slightly sinuous. Anterior border narrow, sharply crested; anterior border furrow deep in front of glabella and much shallower in front of anterior fixigenae. Palpebral lobes large, about one-quarter of total cranidial length, anteriorly located. Anterior section of the facial sutures straight, slightly anteriorly divergent; posterior section with a long straight section at ϵ. Eyes large, about one-third of total cranidial length, outline hemispherical; ocular platform narrow, flat. Lateral border furrow broad, deep, shallowing and narrowing posteriorly, extending well out onto genal spine. Border sharply crested, narrow. Posterior border furrow shallow, narrow; posterior border wide, evenly convex. Genal spine short, stout.

Thorax of nine subequal segments. Axis wide, evenly arched in transverse profile, rings wide, furrows narrow. Dorsal furrow narrow, relatively deep. Pleural fields narrow, flat adjacent to dorsal furrow, gently arched at fulcrum, descending to sharply rounded pleural tips.

Pygidium short, outline semicircular, vaulting low. Axis narrow, sharply posteriorly tapering, acutely rounded at terminus, approximately 0.8 total pygidial length. Axis semicircular in transverse profile, straight in longitudinal profile, composed of nine rings ornamented at crest with a row of small granules. Ring furrows shallow, narrow, deepest over axis. Dorsal furrow narrow, relatively deep. Pleural fields mildly arched in transverse profile, flat in longitudinal profile, composed of eight to nine ribs. Anterior ribs composed of a broad anterior band and a short, narrow posterior band. Posterior ribs not separated into bands. Border narrow, flat.

Remarks.—*Elliptophillipsia rotundus*, n. sp., differs from *E. ellipticus* (Meek and Worthen) by having a constriction to the glabella between the palpebral lobes, and a frontal lobe that is rounded. The holotype of *Elliptophillipsia ellipticus* (see Hessler, 1963:pl. 62, fig. 16, 17, 21) has a forward-tapering glabella that is squared off in front, and an anterior border furrow that is wider and deeper. No other North American Carboniferous trilobite genus displays such an axial elongation to the glabella.

The long, tongue-shaped glabella of *Elliptophillisia rotundus* is similar to that seen in the European genus *Linguaphillipsia*. *Linguaphillipsia* differs from *Elliptophillipsia* by having an elongate pygidium.

Distribution.—Late Kinderhookian of Boone County, Missouri, and Jersey County, Illinois.

Etymology.—*Rotunda*, Latin, refers to the rounding of the anterior of the glabella.

Genus *Perexigupyge* Brezinski, 1988*b*
Perexigupyge chouteauensis, **new species**
(Fig. 3A–G)

Diagnosis.—Glabella tongue-shaped, widest between the palpebral lobes. Pygidium outline semicircular, evenly convex, low relief.

Holotype.—A fragmentary cranidium, from the grainstone facies of the Compton Limestone, at locality 2, Marion County, Missouri, CM 45121, collected by the author.

Paratypes.—Four pygidia and an external and internal mold of a cranidium from localities 2 and 3 of Marion and Ralls counties, Missouri, CM 45122, 45123, collected by A. Kollar, J. L. Carter, and the author.

Description.—Cranidium low in relief and vaulting. Glabella long, smooth, tongue-shaped, widest between the palpebral lobes, tapering forward to about γ, rounded anteriorly, extending to broad, shallow, anterior border furrow. Anterior border rounded. S1 short, shallow, arcuate; S2 short, perpendicular to shallow dorsal furrow; S3 slightly anteriorly directed adaxially. L1 small, oval, incompletely isolated from frontal lobe. L2–L3 small, faint. Palpebral lobes long, narrow. Anterior branch of facial sutures with a long, straight section, diverging moderately from γ to β, sharply rounded at β. Occipital furrow narrow, deep, straight. Occipital lobe wide, flat.

Pygidium outline semicircular, vaulting low. Axis short, narrow, mildly arched in transverse profile, straight in longitudinal profile, strongly posteriorly tapering, sharply rounded at terminus, reaching 0.75 total pygidial length, composed of 11 to 12 smooth, wide (transverse) rings. Ring furrows shallow,

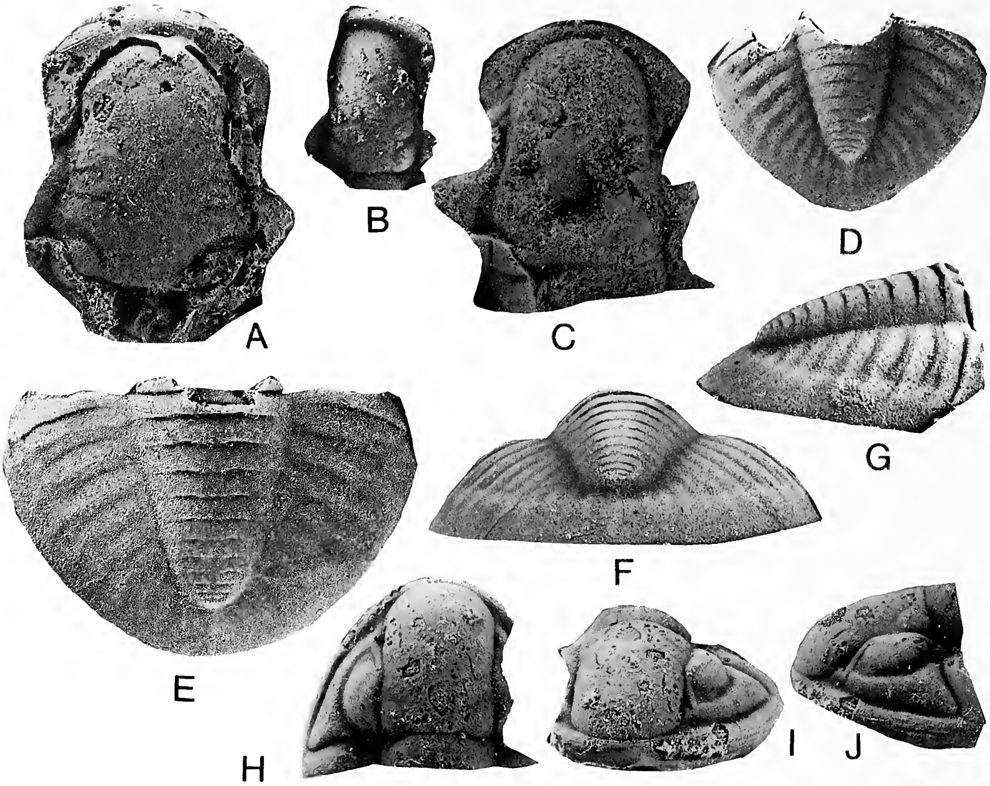

Fig. 3.—A–G. *Perexigupyge chouteauensis*, n. sp. A. Partially exfoliated holotype cranidium, Locality 2, Marion County, Missouri, CM 45121, × 4.0. B. Cast of external mold of partial paratype cranidium, CM 45122a, × 4.0. C. Internal mold of paratype cranidium, CM 45122b, × 3.5. D. Nearly complete paratype pygidium, CM 45123a, × 3.0. E–G. Dorsal, posterior, and lateral views of paratype pygidium, CM 45123b, × 4.0. H–J. *Richterella hessleri*, n. sp., partial holotype cephalon from Locality 2, Marion County, Missouri, CM 45124, × 3.5.

narrow, straight, shallower laterally. Pleural fields mildly arched in transverse profile, straight in longitudinal profile, composed of eight to nine ribs. Ribs consist of broad, slightly elevated anterior bands, and narrower, lower, posterior bands. Interpleural furrows shallow. Anterior bands extend onto border nearly to margin. Border relatively wide and of equal width along entire margin, exhibits same slope as pleural fields. Margin sharply underturned.

Remarks.–Perexigupyge chouteauensis, n. sp., differs from *P. hodgesi* Brezinski, 1988, by having a cranidium with much lower relief, and a glabella that is tongue-shaped rather than nearly cylindrical. The pygidium of *P. chouteauensis* is much lower in relief, and has more poorly defined pygidial rings and ribs. *Perexigupyge gerki* Brezinski, 1988, is similar to *P. chouteauensis* with the forwardly tapering glabella, but differs from the latter species by having a more triangular outline to the glabella, narrower, more forwardly located palpebral lobes, and more arcuate trace to the anterior facial sutures which causes them to appear more broadly divergent. The low relief and vaulting of *P. chouteauensis* is similar to species of *Spergenaspis* as illustrated by Brezinski (1987). Indeed, the shape of the glabella and smoothness of the pygidium are suggestive of a species of *Spergenaspis*. However, *P. chouteauensis* lacks a preglabellar field which characterizes *Spergenaspis*, and possesses the extension of the anterior band of the pygidial ribs onto the border, a character present in *Perexigupyge*. It seems plausible, inasmuch as both genera tend to be present in similar environmental settings, that morphological convergence occurred between these two genera. Conversely, it is possible that *Spergenaspis* descended from *Perexigupyge*.

Distribution.—Present in the late Kinderhookian of Marion and Ralls counties, Missouri.

Etymology.—Named for the Chouteau Group from which the type material was collected.

Genus Richterella Hessler, 1965
Richterella hessleri, **new species**
(Fig. 3H–J)

Diagnosis.—Cranidium moderately vaulted, glabella smooth, with parallel sides and a slight constriction between the palpebral lobes, anterior border very narrow, rounded, border furrow absent. Palpebral lobes narrow, facial sutures with short posterior section, and long, straight, slightly diverging anterior section.

Holotype.—An incomplete cephalon from the grainstone facies of the Compton Limestone of locality 2, Warren, Marion County, Missouri, CM 45124, collected by the author.

Description.—Cephalon semicircular to slightly parabolic in outline, moderately vaulted, relief low. Cranidium longitudinal profile flat becoming more strongly arched anteriorly, evenly rounded in transverse profile. Glabella with nearly parallel sides, a very slight constriction between the palpebral lobes. S1 shallow, arcuate; L1 suboval. S2 straight, shallow; L2 subrectangular. S3 and L3 obsolete. Frontal lobe bluntly rounded anteriorly, meeting a very narrow, rounded border. Anterior branch of facial sutures long, straight, only slightly diverging from γ to β, sharply rounded at β. Posterior section of facial sutures with a short, straight, parallel section, otherwise posteriorly diverging. Occipital furrow shallow, narrow, straight except where overhung by L1; occipital lobe broad, flat. Dorsal furrow, narrow, relatively deep between eyes, shallower forward. Palpebral lobes long, narrow. Eyes large, with distinct, deep, ocular furrow that widens in front of the eye. Genal fields smooth, slightly inflated, steeply descending into deep, narrow, lateral border furrow that becomes broader and shallower anteriorly. Lateral border narrow in dorsal view, relatively broad, evenly rounded in lateral view, with faint terrace lines. Posterior border furrow, deep, narrow, directed to the posterior laterally; posterior border wide, evenly rounded.

Remarks.—*Richterella hessleri*, n. sp., is diagnosed by the shape of the glabella which is parallel-sided, and by the bluntly rounded frontal lobe and narrow anterior border. *Richterella hessleri* can be distinguished from *R. snakedenensis* Hessler,1963, by the more posterior location of the palpebral lobes, medially constricted glabella, and wider anterior border in the latter species. The shape of the glabella is similar to *Perexigupyge hodgesi* Brezinski, 1988. *Richterella hessleri* can be distinguished from *P. hodgesi* by the presence of an anterior border furrow, and by the more distinctively deeper dorsal, occipital, and glabellar furrows in the latter species.

Distribution.—Known from the late Kinderhookian Chouteau Group of Marion County, Missouri.

Etymology.—Named in honor of R. R. Hessler who erected the genus *Richterella*.

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    Smith, J. P. 1976. Review of Eocene Mammals. Unpublished Ph.D. Dissert., University of California, Berkeley, California.
6) Book:
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7) Journal articles with usual volume and issue number:
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REASSESSMENT OF THE NORTH AMERICAN PELOBATID ANURAN *EOPELOBATES GUTHRIEI*

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ABSTRACT

Eopelobates guthriei Estes, 1970, is based on a partial skull and associated right scapula from the Early Eocene Wind River Formation (Lysitean), Fremont County, Wyoming. Reexamination of the holotype and only known specimen reveals that it should no longer be regarded as *Eopelobates* because it lacks characters considered to be diagnostic of that genus. Comparison to other pelobatids indicates it is most similar to *Scaphiopus* and *Spea* in possession of an elongate postchoanal ramus of the vomer. It compares more closely with *Scaphiopus* in its lack of hypossification of cranial bones and possession of a long, low, arcuate ventral flange of the pterygoid. There is no evidence to suggest that it represents a new genus, but because it is not known if the postcranial skeleton was specialized for burrowing, as in *Scaphiopus* and some other pelobatids, it is only tentatively referred to *Scaphiopus* as cf. *S. guthriei* (Estes, 1970). Two derived characters distinguish cf. *Scaphiopus guthriei* from other *Scaphiopus*: 1) frontoparietal narrowest just posterior of the supraorbital flange and 2) otic ramus of squamosal long and thin. Assuming assignment to *Scaphiopus* is correct, then the temporal range for *Scaphiopus* can be extended back from the Middle Oligocene to the Lower Eocene.

KEY WORDS: Anura, Pelobatidae, *Eopelobates*, *Scaphiopus*, Lower Eocene

INTRODUCTION

In 1929 Parker named and described *Eopelobates anthracinus* as the generic holotype for *Eopelobates* on the basis of a single specimen that was collected from strata now considered to be uppermost Oligocene in age (von Koenigswald et al., 1992) from Rott, near Bonn, Germany. Since Parker's (1929) description of *E. anthracinus*, seven other species from North America, Europe, and Asia have been included in this genus. However, the generic assignment of most of these taxa has been either changed or questioned. *Eopelobates bayeri*, from the Oligo-Miocene of the Czech Republic, is regarded as either very closely related to *E. anthracinus*, differing only in its larger size (Špinar and Roček, 1984; Roček, 1995), or synonymous with *E. anthracinus* (Sanchíz, 1998). *Eopelobates leptocolaptus* and *E. sosedkoi* from the Upper Cretaceous of Mongolia and Uzbekistan, respectively, have been reassigned to the gobiatid *Gobiates* (Špinar and Tatarinov, 1986; Roček and Nessov, 1993). Roček (1981), in a monographic study of *Pelobates fuscus*, observed that both *Pelobates* and *Eopelobates* have a frontoparietal derived from three ossifications, the typical paired elements with the addition of a median element situated posterior to them. The three ossifications are easily identified in tadpoles, but in adults the only indication of the presence of the posteromedial element is that it prevents the median suture from reaching the posterior end of the frontoparietal complex. On the basis of this character, Roček (1981) suggested that only two species, *E. anthracinus* and *E. bayeri*, should be retained in the genus *Eopelobates*. Published information about the frontoparietal of *E. hinschei* from the Middle Eocene of Geiseltal, Germany (Kuhn, 1941; Estes,

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1970), led Roček (1981) to suspect that the posteromedial element is absent in this taxon, and thus it should not be regarded as *Eopelobates*. In addition, Sanchíz (1998) maintained that although the species is valid, it lacks a diagnosis and is in need of restudy. More recently, Wuttke (1988) has reidentified *Propelodytes wagneri*, from the Middle Eocene of Messel, Germany, as *Eopelobates wagneri*.

Two species of *Eopelobates* have been described from North America: *E. guthriei* from the Lower Eocene Wind River Formation of Wyoming (Estes, 1970) and *E. grandis* from the Lower Oligocene Chadron Formation of North Dakota (Zweifel, 1956). Roček (1981) concluded that both species are not *Eopelobates* but rather may be more closely related to the North American spadefoots *Scaphiopus* and *Spea*. This conclusion was based on his determination from published descriptions and illustrations that the frontoparietals of *E. guthriei* and *E. grandis* also lack the posteromedial element, the quadratojugal is absent in *E. guthriei* and possibly misidentified in *E. grandis*, and the columella is present in *E. guthriei*. These are characters which all occur in *Scaphiopus* and *Spea* but not *Eopelobates* (Roček, 1981).

The purpose of this study is to provide a revision of *E. guthriei* that considers the more recent published information about this genus and pelobatids in general. Minor preparation of the holotype and only known specimen has also revealed a feature important to its taxonomic assignment. A redescription and reassessment of *E. grandis* is being prepared separately.

The correct identification of North American *Eopelobates* is important for understanding pelobatid evolutionary history and paleobiogeography. *Eopelobates* has been thought to be a primitive pelobatid that is ancestral to the spadefoots (Parker, 1929; Estes, 1970; Špinar, 1972; Savage, 1973), and Estes (1970) speculated that *E. guthriei* was close to the origin of spadefoots. The timing and place of divergence of spadefoots has changed in accordance with new additions to the fossil record, but, in general, the Eocene-earliest Oligocene was considered to be an important time for spadefoot evolution and dispersal (Savage, 1973; Estes, in Sage et al., 1982). More recently, Sage et al. (1982) have suggested that the modern spadefoots (*Pelobates*, *Scaphiopus*, and *Spea*) diverged during the Cretaceous, and the spadefoot morphotype then subsequently underwent little change. Their divergence time was based on immunological evidence.

ABBREVIATIONS

Anatomical.—a, angular; c, choana; co, columella; cp, crista parotica; fo, fenestra ovalis; fp, frontoparietal; ipfm, impression of pars facialis of maxilla; jf, jugular foramen; m, maxilla; md, mandible; n, nasal; op, otic plate of squamosal; pa, parasphenoid; pcv, postchoanal ramus of vomer; pf, prootic foramen; pfm, pars facialis of maxilla; pm, premaxilla; ppm, palatine process of maxilla; pt, pterygoid; q, quadrate; s, sphenethmoid; sc, scapula; sq, squamosal; v, vomer; vf, ventral flange of pterygoid.

Institutional.—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

DESCRIPTION AND COMPARISON OF "*EOPELOBATES*" *GUTHRIEI*

The holotype and only known specimen of "*Eopelobates*" *guthriei* (MCZ 3493) consists of a moderate-sized, incomplete skull and associated incomplete

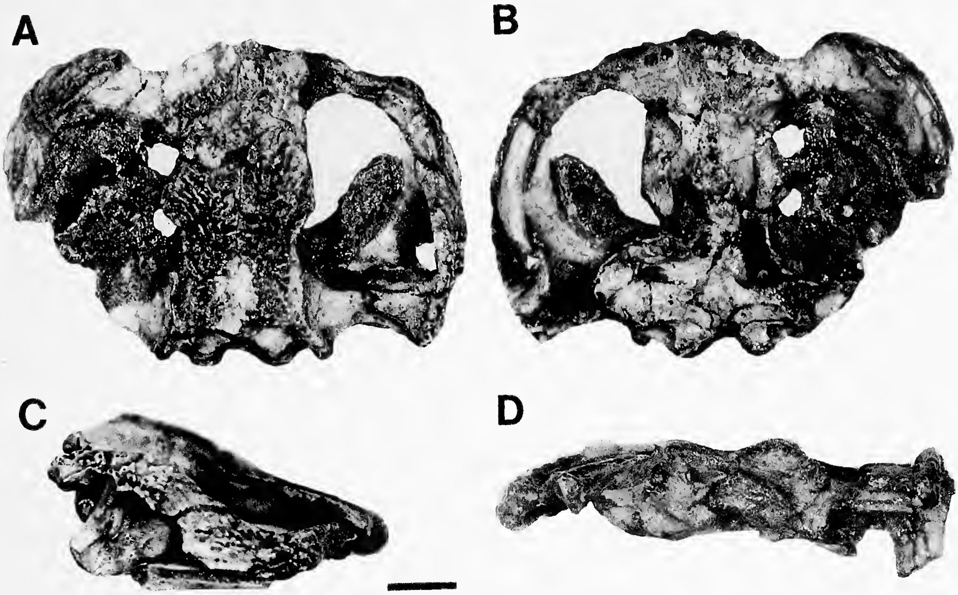

Fig. 1.—Photographs of holotype of cf. *Scaphiopus guthriei*, MCZ 3493. A, dorsal view; B, ventral view; C, right lateral view; and D, occipital view. Scale bar = 5 mm.

right scapula (Fig. 1, 2) collected from the Lower Eocene Lysite Member of the Wind River Formation in the Wind River Basin, Fremont County, Wyoming. The skull is missing bones of the snout, left temporal region, and most of the lower jaws; the preserved bones are in articulation or are very closely associated. Distortion of the right temporal region has resulted in anterior rotation of the otic plate of the squamosal away from the dorsal surface of the right exoccipital-prootic complex. The ventral ramus of the squamosal is missing its base and is pushed inward. Also, the medial ramus of the right pterygoid is not preserved in articulation with the exoccipital-prootic complex.

Estes (1970) argued that the flattened, medially concave dorsal skull roof was not an artifact of preservation but was natural and similar to the skull of other *Eopelobates*. Evidence that the skull was dorsoventrally compressed does exist, however. The left maxilla is not preserved in near vertical orientation but, rather, slopes outward. In conjunction with this, the lateral process of the nasal, which bears evidence of crushing by the numerous cracks running through it, is flattened and oriented horizontally instead of a more vertical orientation. The anterior portion of the left frontoparietal is more depressed than the right, and the dorsal edge of the right squamosal is preserved at the same level as the right frontoparietal rather than at a more ventral level. Additionally, the long axis of the occipital condyles is oriented horizontally instead of having the typical, for pelobatids, transverse orientation.

The undistorted skull roof of MCZ 3493 probably resembled that of *Scaphiopus skinneri* from the Middle Oligocene of North Dakota (Estes, 1970) in being flat and sloping slightly downward anteriorly. It should be noted that currently known specimens of *Eopelobates* are all preserved as flattened skeletons, so the outline of their dorsal skull roof cannot be accurately determined.

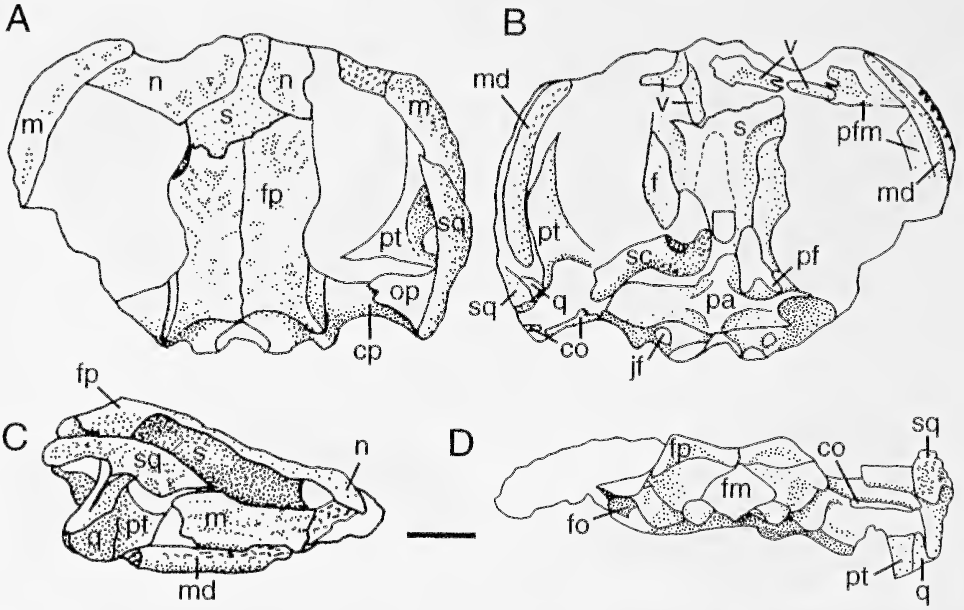

Fig. 2.—Diagrammatic drawings of holotype of cf. *Scaphiopus guthriei*, MCZ 3493. A, dorsal view; B, ventral view; C, right lateral view; and D, occipital view. Scale bar = 5 mm.

Dermal ornamentation occurs on the frontoparietals, nasals, maxillae, and squamosal. Although the dermal ornamentation is somewhat eroded and covered by matrix in places, it can be discerned that it consists of a system of grooves and ridges bearing tubercles, as well as being slightly reticulated in places. This ornamentation pattern most closely resembles that occurring in *Scaphiopus holbrooki*. Špinar and Roček (1984) used as a diagnostic character of *Eopelobates* the presence of a posteromedial element in the frontoparietal, resulting in a frontoparietal complex that is derived from the fusion of three ossifications. A frontoparietal complex derived from three ossifications also occurs in *Pelobates* (Roček, 1981). In contrast, the frontoparietals of MCZ 3493 are paired (Estes, 1970); the median suture clearly extends the entire length between the two halves, indicating that a posteromedial element is absent. The subrectangular frontoparietals bear supraorbital flanges (otic processes in Estes, 1970) that reach their greatest width at approximately one-third their length from the anterior end. The frontoparietal is waisted and narrowest just posterior to the supraorbital flange. At the posterolateral corner of each frontoparietal the posterolaterally oriented posterior tip caps a small boss on the dorsal surface of the exoccipital-prootic complex. This boss was referred to as the paroccipital process by Estes (1970), which is misleading because the paroccipital process is part of the opisthotic, a bone that is absent in anurans. Anteriorly, the right frontoparietal seems to be complete, but the left is not. The posterior edges of the nasals are irregular, which suggests that some bone is missing, although Estes (1970:fig. 13B) illustrates them as being complete. The exposed dorsal surface of the sphenethmoid bears faint impressions of what probably were the posterior and medial edges of the nasals. These impressions suggest that the complete nasals allowed considerably less dorsal exposure of the sphenethmoid than that illustrated by Estes (1970:fig. 13B).

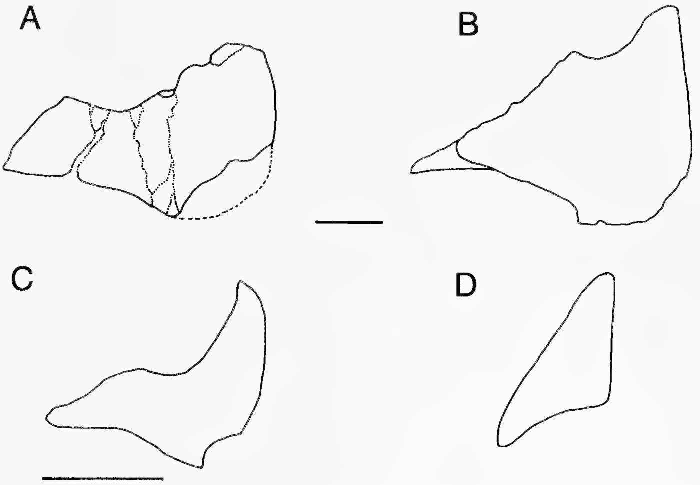

Fig. 3.—Comparison of some pelobatid nasal bones. A, cf. *Scaphiopus guthriei*, holotype, MCZ 3493; B, *Scaphiopus holbrooki*, CM 32300; C, *Spea bombifrons*, CM 48932; D, *Eopelobates bayeri* (from Špinar, 1972). Scale bars = 2 mm. No scale for D.

Flattening of the left nasal has distorted its shape somewhat. Its short lateral process is preserved in articulation with the maxilla. Bone making up the somewhat concave anterolateral edge of the nasal is rounded, indicating that the shape of this edge is not the result of breakage. It is apparent that the anterolateral margin of the nasal was not straight but was probably concave as in *Scaphiopus*, *Spea,* and *Pelobates* (Fig. 3). A straight anterolateral margin coupled with a long and slender lateral process is considered a diagnostic character for *Eopelobates* (Špinar and Roček, 1984). All that remains of the right nasal is its posteromedial corner.

Only the posterior end of the right maxilla is preserved, and its posterior process is broken off. The left maxilla is missing its anterior and posterior ends. Small, bicuspid, pedicellate teeth are preserved along the pars dentalis of the left maxilla, and a few tooth bases are preserved on the right. Bicuspid, pedicellate teeth occur in *Eopelobates* (Wuttke, 1988), as well as in other pelobatids.

The right squamosal is nearly complete, missing only the base of its ventral ramus, and the left squamosal is absent. The zygomatic ramus is deep proximally, bearing a concavity along its ventral margin, and tapers distally where it articulates with the zygomatic process of the maxilla. The otic ramus becomes deeper distally, although it is not as deep as and is only slightly shorter than the zygomatic ramus. It bears a longer and deeper concavity on the ventral margin than that occurring on the zygomatic ramus. The otic plate, which has rotated anteriorly from its articulation with the crista parotica, extends slightly beyond the midpoint between the frontoparietal and lateral edge of the skull and does not contact the frontoparietal, as occurs in most megophryines. A dorsal process, which in all *Pelobates* species except *P. fuscus* articulates with the superior lateral process of the frontoparietal (Roček, 1981), is absent. In *P. fuscus* a ligament bridges the squamosal and frontoparietal (Roček, 1981). The quadrate forms a wedge between the pterygoid and ventral ramus of the squamosal. A quadratojugal is not preserved. As noted by Estes (1970), it was either absent or was lost during dis-

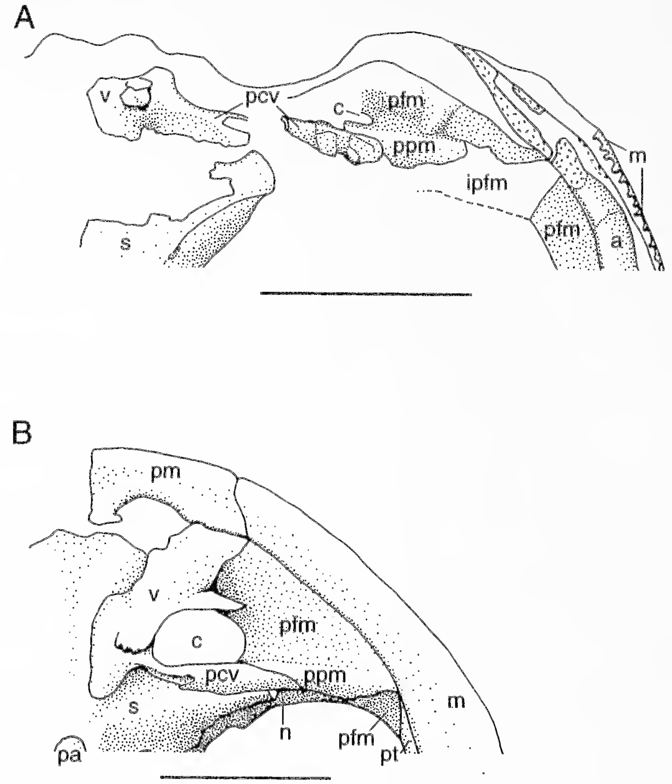

Fig. 4.—Comparison of vomer region of palate. A, cf. *Scaphiopus guthriei*, holotype, MCZ 3493; B, *Scaphiopus holbrooki*, CM 18719. Note that dorsoventral compression of skull figured in A has caused lateral displacement of part of the postchoanal ramus of the vomer and jaw elements. Scale bars = 5 mm.

placement of the posteroventral corner of the maxilla and ventral ends of the squamosal and quadrate. Among pelobatids only *Scaphiopus* and *Spea* lack a quadratojugal.

The sphenethmoid (ethmoid in Estes, 1970) is incompletely preserved, lacking the right lateral process, most of the anterior process, and portions of the ventral and anterior surfaces of the left lateral process. All that remains of the right vomer is the proximal portion of the postchoanal ramus and bone forming the posteromedial border of the internal nares. The somewhat more complete left vomer (Fig. 4A) has a raised area medial to the postchoanal ramus that Estes (1970) suggested was the vomerine tooth plate. The lateral end of the postchoanal ramus ends in a break, and lateral to this is a thin, fragmented rod of bone identified as a probable palatine by Estes (1970). It should be noted that discrete palatines (neopalatine of Trueb, 1993) do not occur in any known pelobatid (Cannatella, 1985). Various authors have argued that in pelobatids each palatine fuses with either the postchoanal ramus of the vomer (Roček, 1981) or the maxilla (Kluge, 1966; Zweifel, 1956). A study on the development of *Spea bombifrons* by Wiens (1989) revealed that the elongate postchoanal ramus of the vomer arises from either the vomer ossification or an independent ossification. Wiens (1989) also observed that the palatine process of the pars facialis of the maxilla does not represent a palatine fused with the maxilla, but rather is derived from the maxillary ossification. In MCZ 3493 the broken medial end of the "palatine" is preserved in line with the broken lateral end of the postchoanal ramus, and the gap that separates them was filled with glue. Removal of matrix along the anterior edge of the lateral portion of the "palatine" reveals that it is continuous with the pars facialis of the maxilla, indicating that it is the palatine process of the maxilla rather than a discrete palatine. An impression posterior and lateral to the palatine process indicates that a wedge of the pars facialis is missing. The remaining portion of the "palatine" consists of a thin bone that is sutured to the pars facialis of the maxilla. This piece of bone is assumed to be the rest of an elongate postchoanal ramus of the vomer for several reasons: it is preserved sutured to the pars facialis of the maxilla; its broken end is close in size to the broken, lateral end of the postchoanal ramus of the vomer; and it is preserved in alignment with and separated only by a small gap from the rest of the postchoanal ramus. Presumably, this separation occurred when the skull was flattened. The only pelobatid genera possessing an elongate postchoanal ramus of the vomer that articulates with the palatine process of the maxilla are *Scaphiopus* (Fig. 4B) and *Spea* (Cannatella, 1985). The anterior portion of both vomers is missing.

The three rami of the pterygoid are broad proximally and taper distally. As in *Scaphiopus*, a long, low, arcuate ventral flange runs along the lateral edge of the pterygoid, extending from the base of the anterior ramus to near the tip of the posterior ramus (Fig. 5). The anterior ramus of the pterygoid articulates with the medial edges of the zygomatic ramus of the squamosal and maxilla. The dorsal margin of the distal end of the medial ramus is broken off. Matrix and the overlying right lateral ala of the parasphenoid obscure the ventral portion of the distal end of the medial ramus.

The prootic foramen is widely emarginate as in other pelobatids, except *Spea*, where it is completely surrounded by bone. The occipital condyles appear to be widely separated, but this is probably the result of dorsoventral compression and bone loss. The right occipital condyle is kidney shaped, whereas the left has a more circular outline due to bone loss along the medial margin of the condyle. The shape and position of the right occipital condyle indicates that the condyles were probably narrowly separated, which is typical for pelobatids (Lynch, 1971). A columella is present, as noted by Estes (1970).

A crushed, incomplete right scapula, mistakenly identified as a left by Estes (1970), is exposed in medial aspect and rests against the anterior edge of the right lateral ala of the parasphenoid. Most of the anterior half of the scapula is preserved, but missing are all of the pars glenoidalis except for its base, the distalmost edge of the scapular blade, and the posterodistal corner of the scapula. Enough of the scapula is preserved to determine that it is long. As in other pelobatids, the scapula bears a large and bulbous pars acromialis, which indicates that the clavicle articulated with its ventral edge rather than its anterior edge. When the clavicle articulates with the anterior edge of the scapula, the pars acromialis narrows considerably distally. Although only the base of the pars glenoidalis is preserved, it was obviously a distinct process that was separated from the pars acromialis by a cleft. The anterior edge of the scapula is strongly concave and lacks an anterior lamina (Estes, 1970), as in *Scaphiopus* and *Spea*. Presence of an anterior lamina was demonstrated by Henrici (1994) to be a synapomorphy of *Eopelobates*, *Macropelobates*, and *Pelobates*.

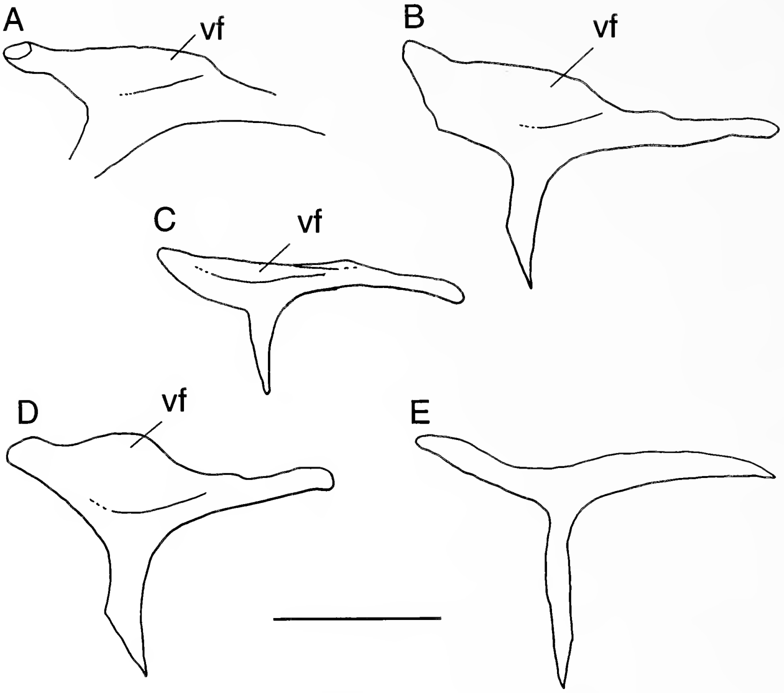

Fig. 5.—Comparison of some pelobatid pterygoid bones. A, cf. *Scaphiopus guthriei*, holotype, MCZ 3493; B, *Scaphiopus holbrooki*, CM 18719; C, *Spea bombifrons*, CM 48932; D, *Pelobates cultripes*, CM 55769; E, *Leptobrachium hasselti*, FMNH 131998. Anterior is to the right and medial to the bottom of the page. Scale bar = 5 mm.

DISCUSSION

Estes (1970:313) assigned MCZ 3493 to *Eopelobates* based on its possession of " . . . a concave skull roof, approximately subequal orbital and temporal openings, as well as the distinctive shape of the squamosal and ethmoid." As noted in the description, dorsoventral compression of the skull of MCZ 3493 most likely caused the skull roof to appear concave. Also, as previously mentioned, all known specimens of *Eopelobates* are preserved as flattened skeletons, and the configuration of their dorsal skull roof cannot be accurately determined. The other characters used by Estes (1970) are either not preserved or are not diagnostic at the generic level. The sphenethmoid of MCZ 3493 is incomplete anteriorly, making comparison to other pelobatid sphenethmoids impossible. Estes (1970) observed that the orbital and temporal openings are of subequal size in *Megophrys* and *Eopelobates*, whereas in pelobatines the orbit is enlarged and the temporal area reduced. However, this character is difficult to interpret and varies intergenerically. The shape of the squamosal is diagnostic at the species level for at least *Pelobates* and *Scaphiopus* and thus is not a useful character for differentiating pelobatid genera.

Four of the characters currently considered as diagnostic for *Eopelobates* (Špinar and Roček, 1984; Sanchíz, 1998) can be analyzed in MCZ 3493. Polarity of these characters is based on the phylogenetic analysis of pelobatoids in Henrici (1994) or outgroup comparison (using methodology of Wiley et al., 1991) in which pelodytid and pipoid anurans comprise the outgroup. The characters are as follows: 1) frontoparietal is derived from three ossifications (derived state); 2) frontoparietal does not contact squamosal (primitive state); 3) nasal has a straight anterolateral margin and a long, slender lateral process (derived state); and 4) dermal sculpturing is pitted and lacks tubercles (state indeterminate). The first character also occurs in *Pelobates*, the second occurs in *Macropelobates*, *Scaphiopus*, and *Spea*, and the latter two characters appear to be unique. The first of these characters, incorporation of a posteromedial element into the frontoparietal complex, warrants further discussion, because it has had some bearing on theories of anuran phylogeny. Roček (1981) homologized the posteromedial element with the median extrascapular of *Eusthenopteron*, considered it to be a primitive character, and used it to form the basis of a phylogeny that placed *Eopelobates* and *Pelobates* outside of Salientia (sensu Sanchíz, 1998). Milner (1988) pointed out that the occurrence of an extra ossification wedged between the parietals and postparietals, which he identified as the interparietal, is not unprecedented and observed its occurrence in several temnospondyls. He (Milner, 1988:63) suggested that the interparietal " . . . is a recurrently occurring derived condition" and further stated that the posteromedial element in *Eopelobates* and *Pelobates* is either a neomorph or a character reversal and, thus, is derived and most likely defines a subclade within Pelobatidae. The phylogeny of Pelobatoidea proposed by Henrici (1994) supports Milner's theory that the occurrence of the posteromedial element in the frontoparietal complex of *Eopelobates* and *Pelobates* is derived and represents a synapomorphy of a subclade within Pelobatidae.

Of the four diagnostic characters, MCZ 3493 is similar to *Eopelobates* and other pelobatines except *Pelobates* only in the primitive character of lack of contact between frontoparietal and squamosal. It differs from *Eopelobates* in three of these characters: 1) frontoparietal is paired (primitive state); 2) anterolateral margin of nasal is not straight but probably was concave, and the lateral process is short (Fig. 3; primitive state); and 3) dermal sculpturing consists of ridges and grooves, which are arranged in a slightly reticulated pattern in places, and tubercles (state indeterminate). Another distinction from *Eopelobates*, as well as *Macropelobates* and *Pelobates*, is the absence of an anterior lamina of the scapula. Presence of an anterior lamina was determined by Henrici (1994) to be a synapomorphy of *Eopelobates*, *Macropelobates*, and *Pelobates*. Based on these differences, it is apparent MCZ 3493 should not be regarded as *Eopelobates*.

Comparison of MCZ 3493 to other pelobatids reveals that it most closely resembles *Scaphiopus* and *Spea* in possession of an elongate postchoanal ramus of the vomer that articulates with the palatine process of the maxilla (Fig. 4). Among pelobatids this character is unique for *Scaphiopus* and *Spea* and has been regarded as one of several synapomorphies uniting them (Cannatella, 1985; Henrici, 1994; Maglia, 1998). It should be mentioned that besides pelobatids, the postchoanal ramus of the vomer is known to articulate with the palatine process of the maxilla in at least some species of *Discoglossus*: *D. sardus* (Púgener and Maglia, 1997) and *D. pictus* (pers. obs.). However, in these species of *Discoglossus* the postchoanal ramus is not elongate, in contrast to that of *Scaphiopus*, *Spea*, and MCZ 3493.

The skull of MCZ 3493 compares more closely with *Scaphiopus* than with *Spea*. *Spea* exhibits cranial hypossification that is evidenced by the loss of dermal ornamentation, reduced ossification of the frontoparietals and nasals which allows dorsal exposure of the frontoparietal fontanelle and sphenethmoid, and reduction of the otic plate and the zygomatic and otic rami of the squamosal with consequent loss of contact between the squamosal and maxilla (Kluge, 1966; Wiens, 1989; Maglia, 1998). This hypossification of the skull does not occur in MCZ 3493 or other pelobatids and is thought to be paedomorphic in *Spea* (Wiens, 1989). *Scaphiopus* and MCZ 3493 possess a similarly shaped ventral flange of the pterygoid that is long, low, and arcuate, and differs from the low, straight ventral flange in *Spea*, and the prominent, short ventral flange in *Pelobates* and *Eopelobates* (Fig. 5). *Leptobrachium* and presumably other megophryines lack a ventral flange. Maglia (1998), in a cladistic analysis of extant pelobatoids, considered the presence of a ventral flange to be derived and its absence to be primitive. It stands to reason, then, that the different shapes of the ventral flange in pelobatids represent independently derived states.

Because there is no evidence suggesting that MCZ 3493 represents a new genus, it is tentatively referred to *Scaphiopus* on the basis of the following characters: 1) presence of an elongate postchoanal ramus of the vomer that articulates with the palatine process of the maxilla, 2) lack of hypossification of cranial bones, and 3) presence of a long, low, arcuate ventral flange of the pterygoid. It is acknowledged, however, that the first character is based on somewhat fragmentary evidence. This, together with the lack of a postcranial skeleton for MCZ 3493, which in *Scaphiopus* and some other pelobatids is specialized for burrowing, is the reason for only tentatively referring MCZ 3493 to *Scaphiopus*. Confident generic assignment of MCZ 3493 must await discovery of more complete specimens to determine if it has a postcranial skeleton similar to *Scaphiopus*. Assuming assignment to *Scaphiopus* is correct, then two unique characters distinguish it from other species of this genus. These represent two of the three characters used by Estes (1970) in his diagnosis of MCZ 3493 as a new species of *Eopelobates*, but are described here using different terminology: 1) frontoparietal is waisted and narrowest just posterior of the supraorbital flanges and 2) otic ramus of squamosal is relatively thin and almost as long as the zygomatic ramus. These characters are unique among pelobatids and, based on comparison to pelodytids and pipoids, are judged to represent the derived state in cf. *S. guthriei*.

Several assumptions can be made about pelobatid evolution and paleobiogeography if assignment of MCZ 3493 to *Scaphiopus* is correct. The temporal range of *Scaphiopus* can now be extended back from the Middle Oligocene to the Early Eocene. The currently known first occurrences of extant and extinct spadefoots indicates that their dispersal across Laurasia must have occurred very early in the Paleogene, if not earlier. In addition to the Early Eocene record of *Scaphiopus*, the oldest-known record of *Pelobates* is *P. decheni* from the Late Eocene of Belgium (Böhme et al., 1982). Additionally, the oldest known record for the extinct spadefoot, *Macropelobates*, is *M. osborni* from the Early Oligocene of Mongolia (Noble, 1924). Unfortunately, the fossil record of spadefoots is too sparse to allow speculation on their center of origin or dispersal routes. Finally, the presence of extant spadefoots in both North America and Europe by the Late Eocene adds support to the theory of Sage et al. (1982) that they are an ancient and morphologically stable group that most likely diverged during the Cretaceous.

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HOMOLOGY AND PHYLOGENETIC IMPLICATIONS OF SOME ENIGMATIC CRANIAL FEATURES IN GALLIFORM AND ANSERIFORM BIRDS

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ABSTRACT

Two landmarks of the temporal region of the skull in most birds are the zygomatic process (processus zygomaticus) and the postorbital process (processus postorbitalis). The morphology and homology of these processes in gallinaceous birds (Galliformes) and waterfowl (Anseriformes), however, are not clear. Anseriformes usually are said to lack a processus zygomaticus. By contrast, the processus zygomaticus of many Galliformes often is described as connected to the tip of the processus postorbitalis, forming a temporal arch. Olson and Feduccia (1980*a*) cited these cranial differences as evidence opposing a hypothesis of sister relationship between the two orders, an hypothesis having a substantial history of advocacy (Seebohm, 1889; Shufeldt, 1901; Delacour, 1954; Johnsgard, 1965; Cracraft, 1981*a*, 1986; Schulin, 1987). Dzerzhinsky (1982, 1995) contradicted the proposal by Olson and Feduccia (1980*a*), interpreting the two processes as completely fused in Anseriformes, forming a unique "sphenotemporal process," which he averred to have been derived evolutionarily from the condition found in the Galliformes.

In the present study, we examined skulls and jaw muscles of juvenile and adult specimens of selected taxa from both orders to test these opposing hypotheses, and found that: (a) the processus zygomaticus is small or lacking in adult Galliformes, and absent in all Anseriformes; (b) the processus zygomaticus is connected to the tip of the processus postorbitalis by an ossified aponeurosis of m. adductor mandibulae externus (aponeurosis zygomatica) in adults of most galliforms, whereas the aponeurosis zygomatica of anseriforms has a linear origin along the os squamosum as far as the processus postorbitalis; the aponeurosis zygomatica is ossified in Anhimidae and unossified in Anatidae; (c) a laterally exposed fossa of the temporal region (fossa musculorum temporalium) is reduced in Galliformes and absent in Anseriformes; (d) pars superficialis and pars zygomatica of m. adductor mandibulae externus are shifted rostrad in Galliformes and Anseriformes, and (e) pars articularis of m. adductor mandibulae externus is much enlarged in both orders. Based on these observations, we conclude that the parts of musculus adductor mandibulae externus of Anseriformes have been misinterpreted in a number of previous studies, perhaps reflecting confusion about associated processes and fossae. These findings are interpreted with respect to the homology of the osteological features and their associated muscles. The distribution of the included states supports the growing consensus for a sister relationship between the Galliformes and Anseriformes.

KEY WORDS: Anseriformes, cranium, Galliformes, homology, myology, osteology, processus postorbitalis, processus zygomaticus

INTRODUCTION

Historical Background

A series of classic, nineteenth-century works—e.g., Blanchard (1859), Eyton (1867), Fürbringer (1888), Seebohm (1888, 1889, 1890, 1895), Gadow and Se-

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lenka (1891), Gadow (1892, 1893), and Beddard (1898)—mark the advent of important contributions of comparative anatomy to an understanding of the evolutionary relationships of birds. Despite diverse, intensive study of avian osteology and myology since that time (e.g., Hofer, 1945, 1950, 1955; Starck and Barnikol, 1954; Yudin, 1961, 1965; Burton, 1984), however, a number of features of the avian skull have proven problematic for systematists, including the processus basipterygoidei of the os parasphenoidale (Weber, 1993), the os lacrimale (Cracraft, 1968), and the os pterygoideum (Hofer, 1945; Jollie, 1957; Weber, 1993). In recent decades (Hennig, 1966; Wiley, 1981), with the development of explicit methodologies for the reconstruction of evolutionary relationships based on anatomical characters, the elucidation of the homologies and transformations of anatomical structures is recognized to be of paramount importance (Nelson, 1994; Doyle, 1996; Sanderson and Hufford, 1996).

Two features of the avian skull—the processus postorbitalis and the processus zygomaticus (Fig. 1)—serve as landmarks for the structure and function of the jaws (Bühler, 1981) but have proven problematic for systematists concerned with the Anseriformes. In most birds, the processus postorbitalis provides the dorsal attachment for the ligamentum postorbito-mandibulare, a structure important in several aspects of cranial kinesis (Kripp, 1933; Zusi, 1962, 1967; Bock, 1964); the processus zygomaticus supports the origin of a major aponeurosis of the external adductor muscle of the mandibula. Absence of the processus postorbitalis is unusual and typically associated with a reduction or loss of the ligamentum postorbito-mandibulare. Absence of the processus zygomaticus, however, does not necessarily signify a change in the musculus adductor mandibulae externus. In the Anseriformes, the processus postorbitalis and adjacent fossae are uniquely modified among extant birds (Fig. 2), and the processus zygomaticus is essentially absent in Anseriformes (e.g., Gadow, 1892; Olson and Feduccia, 1980*a*). The processus postorbitalis has become an integral part of a reconstruction of the regio temporalis (Fig. 1) on the lateral surface of the neurocranium, that part of the skull enclosing the brain and sensory capsules (de Beer, 1937; ICVGAN, 1983; Baumel and Witmer, 1993). In Anseriformes, the stout, rostrally oriented processus postorbitalis also serves as origin for a part (pars zygomatica) of musculus adductor mandibulae externus that is independent of the processus postorbitalis in most avian taxa (Fig. 1). Thus the profound modification of these structures in waterfowl is of considerable functional and phylogenetic interest.

Conformation of the regio temporalis and mandibular rami reflects the structure of the primary, superficial adductor acting on the mandibula, m. adductor mandibulae externus (abbreviated hereafter as AME). This complex, multipennate muscle consists of two or more parts, each of which is more or less distinct and associated with one or more aponeuroses that provide extensive surface for the attachment of muscle fibers (Fig. 3). Despite several thorough anatomical surveys of the avian cranium (Lakjer, 1926; Hofer, 1950; Starck and Barnikol, 1954; Weber, 1993), delimitation of the parts of AME is somewhat arbitrary for many taxa because the fibers of one part may blend imperceptibly with those of another and some aponeuroses are shared by two or more parts. Disagreements about terminology and homology of the parts of AME in the Anseriformes are considerable (e.g., Lakjer, 1926; Starck and Barnikol, 1954; Dzerzhinsky, 1982; Weber, 1996).

These complexities notwithstanding, selected aspects of the AME and osteological features of the regio temporalis have figured prominently in studies of a

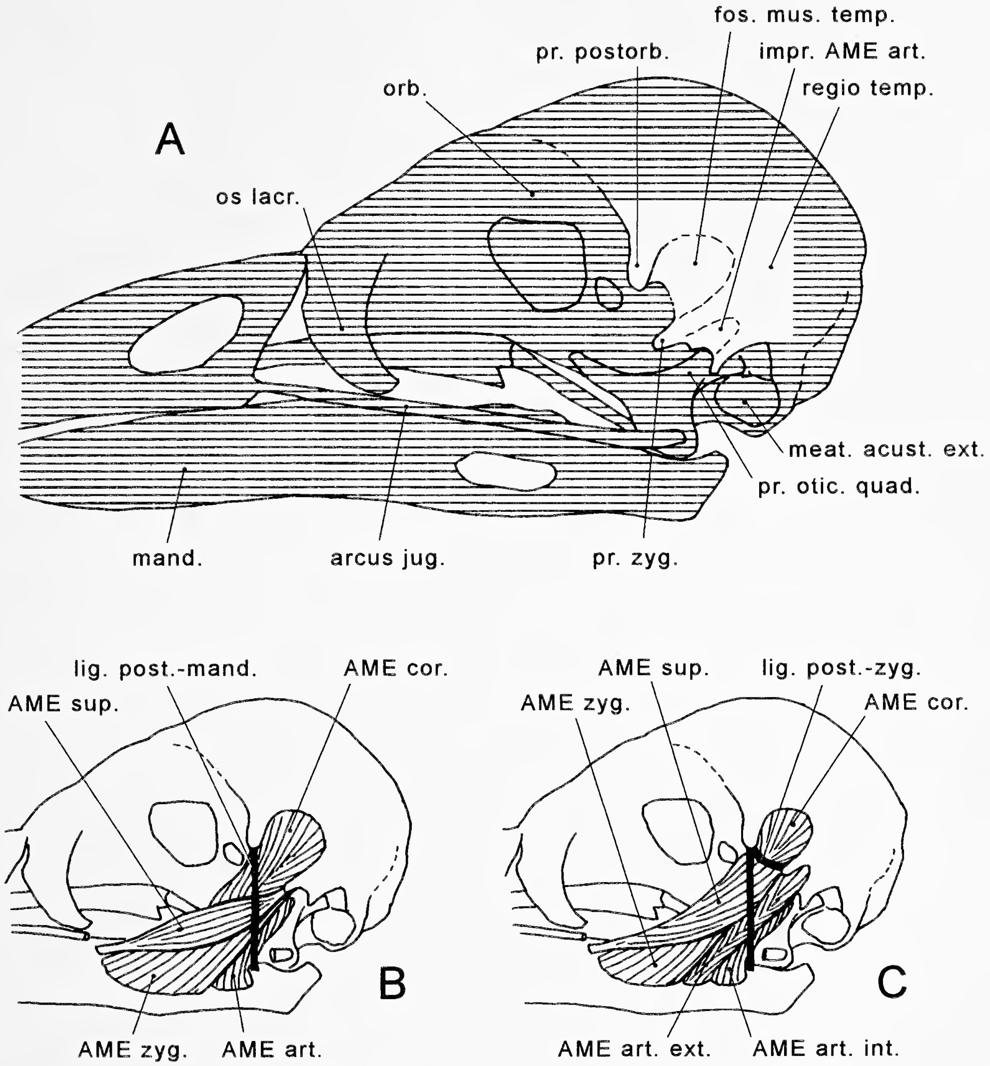

Fig. 1.—Diagrams of facies lateralis cranii of a hypothetical bird showing: (A) critical osteological features highlighted in the clear rectangle; and (B, C) critical myological features. See Methods for list of abbreviations used here and in the following figures.

diversity of avian orders (e.g., Möller, 1932; Hofer, 1945, 1950; Fiedler, 1951; Barnikol, 1952, 1953; Bas, 1954, 1955; Fisher and Goodman, 1955; Bams, 1956; Simonetta, 1960*a-b*, 1963, 1968; Zusi and Storer, 1969; Merz, 1963; Van der Klaauw, 1963; Yudin, 1965; Bock and McEvey, 1969; Richards and Bock, 1973; Burton, 1974*a-c*, 1984; Morioka, 1974; Bhattacharyya, 1980, 1989; Cracraft, 1982; Johnson, 1984; Zusi and Bentz, 1984; Van Gennip, 1986; Elzanowski, 1987; Zusi, 1993; Dzerzhinsky, 1999), including members of the Galliformes (Burggraaf, 1954; Burggraaf and Fuchs, 1954, 1955; Fuchs, 1954, 1955; Jollie, 1957; Fujioka, 1963; Dzerzhinsky and Belokurova, 1972; Dzerzhinsky, 1980; Weber, 1996) and Anseriformes (Davids, 1952; Starck and Barnikol, 1954; Good-

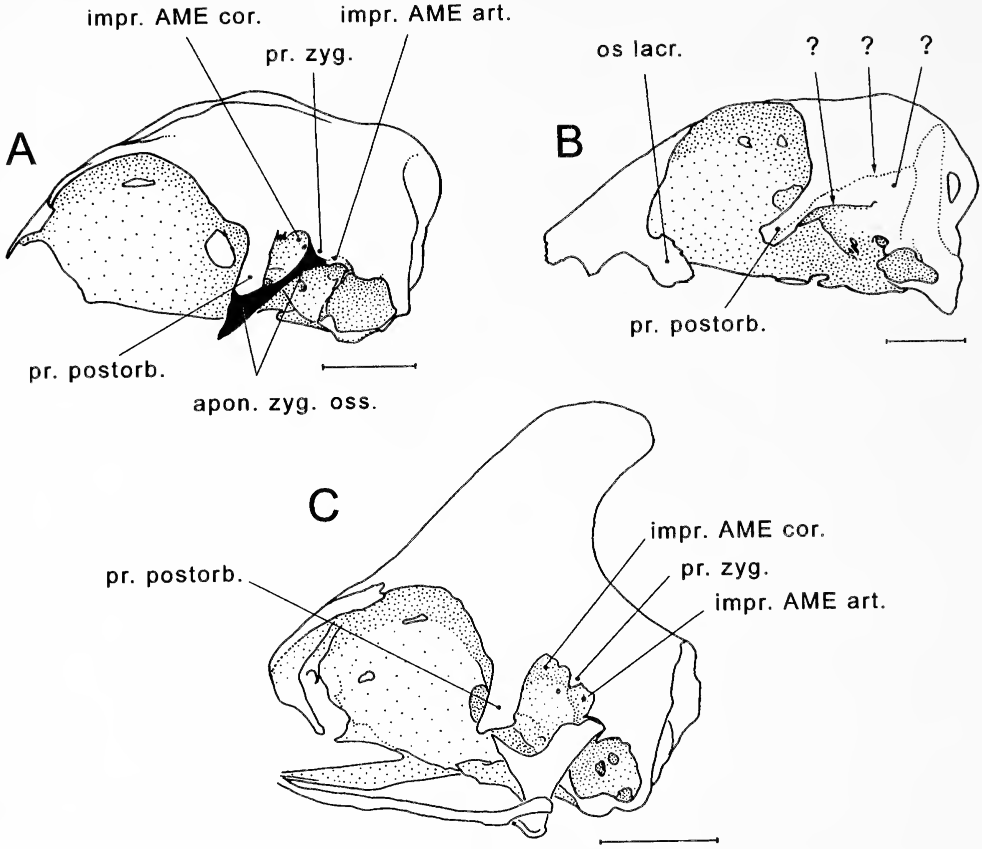

Fig. 2.—Facies lateralis cranii of: (A) an adult specimen of *Meleagris gallopavo* (USNM 556372), (Galliformes: Meleagrididae); (B) an adult specimen of *Sarkidiornis melanotos* (USNM 490276), (Anseriformes: Anatidae); and (C) an adult specimen of *Numida meleagris* (USNM 430657), Galliformes: Numididae). Features unlabelled or controversial in the literature are indicated by question marks. Scale bar = 1 cm.

man and Fisher, 1962; Zweers, 1974; Dzerzhinsky, 1982; Jäger, 1990). In addition to comparatively traditional studies, the complex has been examined with respect to structural details and functional roles of the constituent parts (e.g., Gans and Bock, 1965; Bock, 1964, 1968; Zweers, 1974; Dzerzhinsky, 1982).

The processus zygomaticus of Galliformes was described as well developed by Gadow (1892), Shufeldt (1909), and Baumel and Witmer (1993), but as absent or vestigial by Verheyen (1956). Starck and Barnikol (1954) found that the process zygomaticus was small in juvenile *Gallus*, and that the aponeurosis of AME, pars zygomatica, originating on the processus, ossified during maturation; they then referred to the combined process and ossified aponeurosis as the zygomatic process. Hofer (1950) considered the processus zygomaticus to be strong in *Meleagris* and *Tetrao*, taxa in which the aponeurosis zygomatica is ossified, but interpreted the processus to be lacking in *Numida*, in which the aponeurosis is not ossified (Fig. 2). Traditionally, the processus zygomaticus was said to be lacking in Anseriformes (e.g., Gadow, 1892; Olson and Feduccia, 1980*a*).

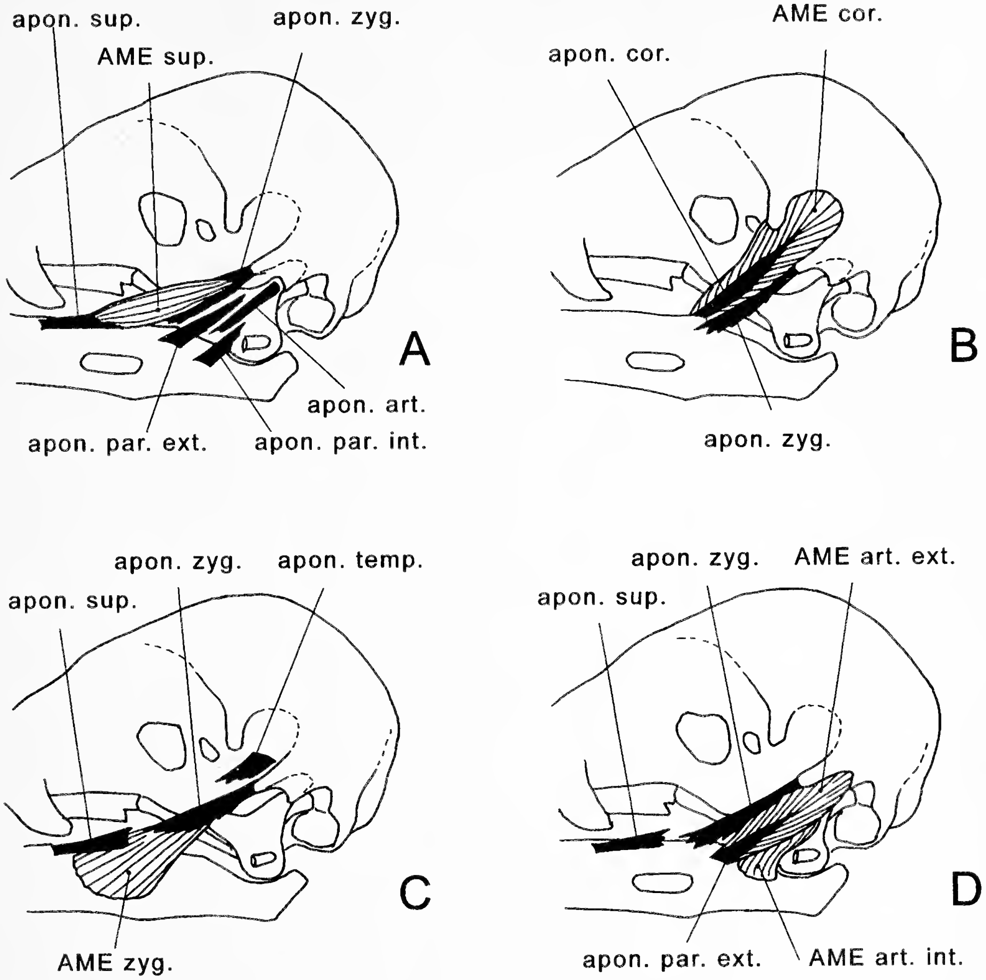

Fig. 3.—Diagrams of m. adductor mandibulae externus (AME) complex of a hypothetical bird: (A) AME superficialis; (B) AME coronoidea; (C) AME zygomatica; and (D) AME articularis. Aponeuroses shown in black.

Olson and Feduccia (1980*a*:4) argued against a close relationship between the Galliformes and Anseriformes, stating that " . . . the tip of the postorbital process fuses with that of the zygomatic process in Galliformes, leaving a foramen, whereas in the Anseriformes the zygomatic process is absent." This anatomical interpretation was part of a larger proposal in which the hypothetical "transitional shorebirds" (purportedly exemplified by the fossil *Presbyornis*) were considered ancestral to several modern orders (Livezey, 1997*a*), including waterfowl (Feduccia, 1977, 1978, 1980*a-b*, 1994, 1995, 1996; Olson and Feduccia, 1980*b*). By contrast, Dzerzhinsky (1995:327-328) concluded that " . . . in the Anseriformes, the [ossified muscular aponeurosis from the zygomatic process] fuses to the postorbital process over its entire caudoventral border to form a complete sphenotemporal process . . . ." Dzerzhinsky (1995) considered the "sphenotemporal process" of the Anseriformes to be derived from the condition characteristic of the

Galliformes, bolstering his argument for a sister relationship between the two orders. Still other workers simply omitted these disputed features from consideration with respect to either order (Livezey, 1986; Cracraft, 1986, 1988; Ericson, 1996, 1997).

Objectives of Study

In this paper we interpret the homologies of osteological features unique to the Anseriformes through comparative study of skeletal and spirit (fluid-preserved) specimens of juvenile and adult examples of anseriform and galliform birds. Of primary concern are the nature of the processus zygomaticus, homologues of the aponeurosis zygomatica of AME, and the relationship of both with the processus postorbitalis in Anseriformes. This examination is associated with several new proposals regarding nomenclature for selected anatomical features. Finally, a comparison of the Anseriformes and Galliformes provides a perspective on the evolutionary derivation of the condition of these features in waterfowl.

MATERIALS AND METHODS

Specimens and Related Data

Criteria for Determination of Age.—Although none of the museum specimens studied herein was of known age in relation to hatching, we use the terms *chick, juvenile, immature* and *adult* as progressive stages of development based on size and degree of fusion of suturae cranii. Chicks are birds within a few days of hatching with fully evident suturae cranii. Juveniles are larger, even approaching full size, and their neurocranial suturae are variously unfused. Immatures are essentially full size with the suturae cranii fused except for those between the processes frontales of the ossa nasales and the neurocranium. In adults all neurocranial suturae are fused; only those between the processes nasales of the paired premaxillae may remain distinct. Adults often display a more robust skull than that of immatures.

Osteological Specimens.—Comparisons of adult skeletons of Galliformes and Anseriformes were based on the entire skeleton collection of USNM, as well as selected taxa from other museums (AMNH, BMNH, YPM). Taxa in which adult specimens were compared with one or more specimens of chicks, juveniles, or immatures are as follows: Galliformes: Megapodiidae—*Megapodius freycinet, Leipoa ocellata*; Cracidae—*Ortalis vetula, Penelope jacuacu, P. superciliaris, P. purpurascens, Crax rubra, C. alector, C. fasciolata, Aburria pipile*; Meleagrididae—*Meleagris gallopavo*; Tetraonidae—*Lagopus lagopus, L. mutus, Tetrao tetrix, Bonasa bonasia, B. umbellatus, Centrocercus urophasianus*; Phasianidae—*Alectoris chukar, Francolinus adspersus, F. capensis, F. sephaena, F. pondicerianus, F. francolinus, Arborophila crudigularis, A. brunneopectus, Bambusicola thoracica, Ithaginia cruentatus, Lophura leucomelanos, Gallus domesticus, Crossoptilon crossoptilon, Catreus wallichii, Chrysolophus pictus, C. amherstiae, Pavo cristatus, P. muticus*; Numididae—*Numida meleagris*; Odontophoridae—*Callipepla squamata, Lophortyx californica, Colinus virginianus*. Anseriformes: Anhimidae—*Chauna torquata*; Anatidae—*Dendrocygna bicolor, Anser caerulescens, A. canagicus, Branta canadensis, B. bernicla, Cygnus atratus, C. bewickii, C. columbianus, Tachyeres pteneres, T. patachonichus, Tadorna radjah, T. tadorna, Casarca ferruginea, Chloephaga hybrida, C. picta, Heteronetta atricapillus, Oxyura jamaicensus, Anas platyrhynchos, Aythya americana, Somateria* *mollisima, Histrionicus histrionicus, Melanitta perspicillata, M. fusca, Clangula hyemalis, Bucephala clangula, B. islandica, Mergus merganser, M. serrator.*

Spirit Specimens.—Spirit specimens (adults unless specified) dissected for comparison of jaw muscles were as follows: Galliformes: Megapodiidae—*Megapodius freycinet*; Cracidae—*Ortalis vetula*; Meleagrididae—*Meleagris gallopavo*; Tetraonidae—*Dendragopus canadensis*; Phasianidae—*Alectoris graeca, Gallus domesticus, Francolinus capensis*; Numididae—*Numida meleagris*; Odontophoridae—*Lophortyx gambelii.* Anseriformes: Anhimidae—*Chauna torquata*; Anseranatidae—*Anseranas semipalmata* (chick); Anatidae—*Dendrocygna bicolor* (chick), *D. autumnalis, Anser albifrons, Anas crecca, A. versicolor* (chick), *A. acuta* (chick), *Mergus merganser.*

Nomenclature and Classification of Galliformes and Anseriformes

For the Galliformes, we adopted the families recognized by Sibley and Monroe (1990), except that we elevated the three major groups included by them in Phasianidae (Tetraonidae, Meleagrididae, and Phasianidae sensu stricto) to family rank, as accorded them by Peters (1934) and Wetmore (1951), and used by del Hoyo et al. (1994).

For purposes of reference in comparative descriptions, tables, and figures, we adopted the higher-order, phylogenetic classification of waterfowl proposed by Livezey (1997*a-b*). The essentials of this framework are as follows:

- Order Anseriformes (Wagler, 1831).—Waterfowl
  - Suborder Anhimae Wetmore & Miller, 1926
    - Family Anhimidae Stejneger, 1885.—Screamers
      - Genus *Anhima* Brisson, 1760.—Horned screamer
      - Genus *Chauna* Illiger, 1811.—Crested screamers
  - Suborder Anseres Wagler, 1831.—True waterfowl
    - Superfamily Anseranatoidea (Sclater, 1880)
      - Family Anseranatidae (Sclater, 1880)
        - Genus *Anseranas* Lesson, 1828.—Magpie goose
    - Superfamily Anatoidea (Leach, 1820).—Typical waterfowl
      - †Family Presbyornithidae Wetmore, 1926
        - Genus *Presbyornis* Wetmore, 1926
      - Family Anatidae Leach, 1820.—True ducks, geese and swans

Myological Technique

Dissection of jaw musculature was performed by RLZ on one specimen of each taxon. The specimens, of varying age and provenance, had been fixed in formalin and preserved in alcohol. Attention was focussed on m. adductor mandibulae externus, the muscle most often associated with the cranial features of concern in this paper. Although this muscle is largely superficial and readily accessible, an understanding of its complexity could be gained only through knowledge of its internal structure of aponeuroses and associated muscle fibers. After illustrating the superficial aspect of the muscle, all fibers were removed systematically, leaving intact the complex of interdigitating, aponeurotic origins and insertions. The identity of the major aponeuroses (coronoidea, superficialis, zygomatica, paracoronoidea externa and interna, and articularis—Fig. 3) could then be determined in most instances and the different taxa compared. Uncertainties were resolved by inspection of the opposite muscle, usually with only partial dissection.

Anatomical Nomenclature

General Nomenclatural References.—Osteological and arthrological nomenclature, respectively, followed Baumel and Witmer (1993) and Baumel and Raikow (1993), much of which remained unchanged from the first code proposed by the International Committee on Avian Anatomical Nomenclature (ICAAN); in the latter, osteology was treated by Baumel (1979*a*), arthrology by Baumel (1979*b*), and myology by Vanden Berge (1979). The two codes prepared by the ICAAN were paralleled by standards for veterinary anatomists (Komárek, 1979; Komárek et al. 1982), which in turn were intended to stabilize names used most frequently by avian anatomists in recent decades (e.g., Bellairs and Jenkin, 1960; Berger, 1960, 1966). Osteological features labeled using ICAAN nomenclature were figured in substantial detail elsewhere (Butendieck, 1980; Butendieck and Wissdorf, 1982).

Myological Nomenclature.—Weber (1996) recently compiled a synonymy of terms used in major myological studies of the cranium and mandibula. In this paper, myological nomenclature (listed below) for parts of AME mainly follows Weber (1996), with any synonyms from Vanden Berge and Zweers (1993) given in parentheses:

M. adductor mandibulae externus (AME)
  pars coronoidea (rostralis; temporalis, or rostralis temporalis)
    caput temporale
    caput mediale
  pars superficialis (lateralis)
  pars zygomatica (ventralis; medialis)
  pars articularis (profunda; caudalis)
    caput interna
    caput externa
M. pseudotemporalis superficialis
M. adductor mandibulae posterior (adductor mandibulae caudalis)
M. depressor mandibulae

The parts of AME will be abbreviated throughout the paper as AME coronoidea, AME superficialis, AME zygomaticus, and AME articularis, and the heads of the latter as AME articularis internis and AME articularis externis.

The name m. adductor mandibulae posterior was used traditionally until the compilation by Vanden Berge (1979), in which the term "posterior" was changed routinely to "caudal." Under this nomenclatural convention, the name for this muscle became M. adductor mandibulae caudalis. However, recognizing the possibility of confusion with AME articularis (also called AME caudalis; see above), Vanden Berge and Zweers (1993) proposed a new name—"M. adductor mandibulae ossis quadrati"—while retaining "adductor mandibulae caudalis" as an acceptable alternative. We retain the traditional name (m. adductor mandibulae posterior) in the present study because it is used universally in the pertinent literature on galliforms and anseriforms.

Each of the parts of m. adductor mandibulae externus (AME) is built around one or more major aponeuroses (as well as some smaller, unnamed aponeuroses), an architecture first emphasized for establishment of homologies by Barnikol (1952) and that is evolutionarily conservative despite many adaptive modifications among avian taxa exhibited in the avian jaw mechanism (Starck and Barnikol, 1954; Zusi, 1962; Dzerzhinsky and Podanova, 1974; Dullemeijer, 1951, 1952; Weber, 1996). We use the following designations for the aponeuroses of the parts of the AME, largely after Weber (1996):

AME coronoidea.—aponeurosis coronoidea and aponeurosis temporalis;
AME superficialis.—aponeurosis superficialis; Weber (1996) included AME superficialis under AME zygomatica, but we provisionally recognize it here pending a broader comparison of avian taxa;
AME zygomatica.—aponeurosis zygomatica;
AME articularis.—aponeurosis paracoronoidea externa, aponeurosis paracoronoidea interna, and aponeurosis articularis.

Arthrological Nomenclature.—With respect to nomenclature of ligaments and joints, we mainly follow Baumel and Raikow (1993). However, in reference to the complex of ligamenta included by those authors under the name "ligamentum postorbitale," we distinguish three separate ligamenta for purposes of this study, thereby formalizing the substantial variations in attachments noted for this complex (e.g., Lebedinsky, 1921; Zusi and Storer, 1969; Elzanowski, 1987; Jäger, 1990): ligamentum postorbito-mandibulare (connecting processus postorbitalis with the mandibula), ligamentum postorbito-jugale (connecting processus postorbitalis with the arcus jugalis), and ligamentum postorbito-zygomaticum (connecting processus postorbitalis with the processus zygomaticus). The last of these three names is synonymous with the "ligamentum zygomaticum" provisionally recognized by Elzanowski (1987) and Weber (1996). Although this complex is extremely variable among taxa and the included ligaments vary in discernability within the fascia temporalis in which they are sometimes imbedded (Hofer, 1950; Barnikol, 1953; Bas, 1954; Zusi, 1975; Elzanowski, 1987; Weber, 1996), we concluded that separate, completely descriptive names for these important ligamenta were critical for the clarity of comparative descriptions.

Osteological Nomenclature.—A term of long-standing in osteological nomenclature of most tetrapods is "fossa temporalis" or "temporal fossa," traditionally associated with the origin of AME coronoidea. However, among birds, this sometimes prominent feature of the regio temporalis marks the origins of more than one muscle. For this study, it was critical to ascertain by dissection the relationships of specific muscles associated with specific osteological features of the neurocranium, and in this context a vague term encompassing a series of distinct, nonhomologous states was not only useless but also misleading. Accordingly, the "fossa temporalis" of birds has relevance for comparative study only as a broad, topographic area—a variably differentiated site of origin for one or more unspecified mandibular muscles. For this reason, we propose the explicitly descriptive "fossa musculorum temporalium" (new term), for "fossa for muscles of the temporal region," as a replacement for the misleading, traditional name.

The fossa musculorum temporalium of a given species could comprise the impressiones deriving from one or more of four muscles—AME coronoidea, m. pseudotemporalis superficialis, AME articularis externus, and even m. depressor mandibulae; the term "impressio temporalis" was proposed by van Gennip (1986) for the scar of a portion of m. depressor mandibulae in the Rock Dove (*Columba livia*). In addition, included muscles may occupy different portions of the fossa without osteological delimitation of the subdivisions. We recommend reference to the impression of the pertinent muscle whenever it is known (e.g., impressio m. AME coronoidea).

A more obscure term in avian osteology is "fossa subtemporalis" or "subtemporal fossa." Typically occupied by AME articularis externus, this concavity also has been cited as the position of origo m. depressor mandibulae (Baumel and Witmer, 1993). Some authors (e.g., Vickers-Rich et al., 1995) regarded the confluence of impressiones AME coronoidea and articularis as the temporal fossa in *Megalapteryx* (Dinornithiformes), worsening the ambiguity of the term with respect to the homologies of the impressiones involved. Consequently, we abandon the term fossa subtemporalis and refer to this feature using a directly descriptive alternative—impressio AME articularis.

Abbreviations Used To Label Figures

Abbreviations of anatomical terms used in the accompanying figures are listed below in alphabetical order:

AME art.—musculus adductor mandibulae externus, pars articularis
AME art. ext.—musculus adductor mandibulae externus, pars articularis, caput externa
AME art. int.—musculus adductor mandibulae externus, pars articularis, caput interna
AME cor.—musculus adductor mandibulae externus, pars coronoidea
AME sup.—musculus adductor mandibulae externus, pars superficialis
AME zyg.—musculus adductor mandibulae externus, pars zygomatica
apon. art.—aponeurosis articularis
apon. par. ext.—aponeurosis paracoronoidea externa
apon. par. int.—aponeurosis paracoronoidea interna
apon. cor.—aponeurosis coronoidea
apon. sup.—aponeurosis superficialis
apon. temp.—aponeurosis temporalis
apon. zyg.—aponeurosis zygomatica
apon. zyg. oss.—aponeurosis zygomatica ossificans
arcus jug.—arcus jugalis
arcus suborb.—arcus suborbitalis
crist. AME art.—crista musculi adductoris mandibulae externus, pars articularis
crist. zyg.—crista zygomatica
fos. mus. temp.—fossa musculorum temporalium
impr. AME art.—impressio musculi adductoris mandibulae externus, pars articularis
impr. AME cor.—impressio musculi adductoris mandibulae externus, pars coronoidea
lam. parasph.—lamina parasphenoidalis
lig. lac.-mand.—ligamentum lacrimo-mandibulare
lig. post.-mand.—ligamentum postorbito-mandibulare
lig. post.-zyg.—ligamentum postorbito-zygomaticum
lig. suborb.—ligamentum suborbitale
m. add. mand. post.—musculus adductor mandibulae posterior
mand.—mandibula
meat. acust. ext.—meatus acusticus externus
orb.—orbita
os front.—os frontale

os lacr.—os lacrimale
os lat.-sphen.—os laterosphenoidale
os par.—os parietale
os squam.—os squamosum
pr. otic. quad.—processus oticus quadrati
pr. postorb.—processus postorbitalis
pr. zyg.—processus zygomaticus
regio temp.—regio temporalis
rost. parasph.—rostrum parasphenoidale
sut. front.-squam.—sutura fronto-squamosa
sut. lat.-squam.—sutura laterospheno-squamosa
tuber.—tuberculum

Concepts and Diagnosis of Homology

General Principles and Terms.—The concept of the homologue, first defined by Owen (1843) as "... the same organ in different animals under a variety of form and function" (*fide* Panchen, 1994), originated and principally remains within the context of comparative anatomy (Boyden, 1943, 1947; Patterson, 1982; Van Valen, 1982; Young, 1993; Sluys, 1996). Despite the antiquity and generally narrow context of the concept, the issue of homology and its practical application remain the subject of substantial controversy (Rieppel, 1980, 1992, 1994; Roth, 1984, 1988, 1991; Sattler, 1984). Subsequently, however, the concept and criteria for the diagnosis of homology have been recognized as equally vital and challenging for phylogenetic interpretation of characters as diverse as DNA sequences (Patterson, 1988; Mindell, 1991; Hillis, 1994; Brower and Schawaroch, 1996), proteins (Fitch, 1970), metric abstractions (Bookstein, 1994; Fink and Zelditch, 1995; Zelditch et al., 1995, 1998; Adams and Rosenberg, 1998; Rohlf, 1998; Swiderski et al., 1998; Zelditch and Fink, 1998), and behavioral repertoires (Wenzel, 1992; Greene, 1994). In that Owen (1843) originally contrasted "analogues"—phylogenetically independent structures having common functions in different taxa—from "homologues," it is not surprising that an emphasis on function persists in the diagnosis of homology and the utility of characters for phylogenetic reconstruction (Bock, 1967, 1977, 1979, 1989; but see Cracraft, 1981*b*). In its most essential form, the definition of homologues is structures having a common evolutionary origin (Simpson, 1959; Bock, 1963*a*); an important implication of this definition is that homologues would share ontogenetic bases (Wagner, 1989*a-b*, 1994; Goodwin, 1994; Hall, 1994, 1995).

These theoretical essentials of homology, however instructive, provide little in the way of practical methodology for the recognition of homologues in a phylogenetic context. In this work, we essentially applied the three classical criteria of Remane (1952, 1956): (1) similarity of position; (2) quality of resemblance (see also Inglis, 1966); and (3) continuance of similarity through intermediate forms (Wiley, 1981). Problems of homology do not increase necessarily with the complexity of the characters in question; in fact, structural detail often provides the distinctions essential to diagnosis of homology, rendering many anatomical systems more amenable to such determinations than simple features such as sequence data (Wägele, 1995; McShea, 1996).

Specific Criteria Applied.—Use of published descriptions of jaw muscles is complicated by different terminologies and different judgments about homologies.

We hypothesize homologies from similarity in external and internal structure of muscles, and location of muscles in relation to each other and to associated bony features. Within a phylogenetic context, inference of homology assumes an iterative nature, in which *a priori* assessments of homology can be questioned on the basis of the most parsimonious interpretation of the totality of evidence (Stevens, 1984; Bryant, 1989; de Pinna, 1991; Haszprunar, 1992, 1998; Lipscomb, 1992; Coddington, 1994; McKitrick, 1994; Brooks, 1996; Hawkins et al., 1997; but see Lauder, 1994). The confirmatory advantages of this process hinge on the validity of the delimitation of characters and composite states (Pogue and Mickevich, 1990; Barriel and Tassy, 1993). In this work, we emphasize the primary assessment of homology by comparative study, relegating most phylogenetic implications of this study to companion works (Livezey, 1997*a*, 1998).

Innervation is not included here because the muscles under discussion—parts of the AME—are supplied mainly by branches of nervus trigeminus mandibularis; this complex varies sufficiently within species (Barnikol, 1953, 1954) to suggest that data from single specimens could be misleading. Available information on the associated systema cardiovasculare (Baumel, 1993) also provided no critical, ancillary clues to homology of subdivisions of the AME (e.g., Richards, 1968).

Examination of crania of very young birds was critical for discernment of most or all suturae cranii. Therefore direct study of prepared skeletons and fluid-preserved specimens of juveniles was performed for as many relevant taxa as possible, supplemented by reference to the literature on the ontogeny of cranial elements and overlying musculature in a diversity of avian taxa (e.g., Edgeworth, 1907; Jollie, 1957; Hogg, 1978). Although all parts of the AME are derived from a single primordium (McClearn and Noden, 1988), the study of juveniles provided additional insight into the structure of AME in that parts of this complex were clearly separable even in early developmental stages.

Changes in aspects of osteological or myological features during development per se, however, were not used to infer directions of evolutionary change among taxa, but instead as a means for delimitation of homologous anatomical structures that are rendered less distinguishable in adults through variation in function and selection pressures (Hanken and Hall, 1993). The relevance of such information to the polarity of character states (i.e., the "ontogenetic criterion") remains controversial (Nelson, 1978; Alberch, 1985; de Queiroz, 1985; Kluge and Strauss, 1985; Kraus, 1987; Mabee, 1989, 1993; Wheeler, 1990; Williams et al., 1990; de Pinna, 1994; Meier, 1997). In the present paper, references to phylogenetic position and polarity were based on previous works in which outgroup comparisons were employed (Livezey, 1986, 1989, 1991, 1995*a-c*, 1996*a-c*, 1997*a-c*, 1998).

Pertinent Anatomical Issues

Processus Postorbitalis.—The processus postorbitalis usually arises from the caudolateral border of the orbita. With few exceptions, the processus postorbitalis is largely derived from the os laterosphenoidale, with variable contribution from the rostral portion of the os squamosum in most neognathous taxa. Typically the processus is oriented roughly perpendicularly to the long axis of the mandibula and it serves as origin for the ligamenta postorbito-mandibulare, postorbito-jugale, and ligamentum suborbitale, which extend ventrally to the mandibula and arcus jugalis and rostrally to the os lacrimale or os ectethmoidale, respectively. In some taxa, the complex of ligamenta arising from the processus postorbitalis includes, in addition to the comparatively conspicuous ligamentum postorbito-mandibulare, a variably distinct component (ligamentum postorbito-zygomaticum) that attaches on the processus zygomaticus (Starck and Barnikol, 1954). The ligamenta arising from the processus postorbitalis may be slender or absent, and the processus postorbitalis correspondingly reduced.

Therefore the processus postorbitalis may support the complex comprising the ligamenta postorbitalia as well as the ligamentum suborbitale. These ligamenta ossify in some taxa such that, in adult birds, the processus postorbitalis may appear to be extended ventrally by dorsal ossification of the ligamentum postorbito-mandibulare, rostrally by partial or complete ossification of the ligamentum suborbitale, or caudally by ossification of the ligamentum postorbito-zygomaticum.

Processus Zygomaticus.—This processus of the os squamosum is located on the regio temporalis of the cranium between the processus postorbitalis and the meatus acusticus externus, in many taxa immediately rostral or dorsal to the meatus. Oriented rostroventrally, or sometimes extended laterally, it supports the aponeurosis zygomatica of AME zygomatica; in some taxa this aponeurosis becomes ossified at its base, effectively extending the processus. Although the AME zygomatica and aponeurosis zygomatica are usually present in birds, the processus zygomaticus may be absent or reduced to an indistinct crista in some taxa (e.g., Sulidae, Phalacrocoracidae, Ardeidae, Phoeniculidae).

Fossa Musculorum Temporalium.—Usually this impressio is occupied largely or wholly by the AME coronoidea in neognathous birds, but in paleognathous birds the area supports m. pseudotemporalis superficialis wholly or in part (Hofer, 1945; Webb, 1957; Elzanowski, 1987; Weber, 1996). Additional complexity of the muscles associated with this fossa were noted above.

Impressio AME Articularis.—This variably distinct depression, sometimes termed "fossa subtemporalis," lies caudal or ventral to the fossa musculorum temporalium in some taxa, and is partly delimited by the processus zygomaticus and the meatus acusticus externus. Occasionally it has been regarded as part of fossa musculorum temporalium. This impressio is occupied by AME articularis externus.

AME.—This complex muscle (Fig. 1, 3) arises variously from the fossa musculorum temporalium, processus zygomaticus, processus oticus quadrati, and impressio AME articularis in most birds. Pars coronoidea usually occupies part or all of the fossa musculorum temporalium and facies lateralis of aponeurosis temporalis and inserts on aponeurosis coronoidea of the mandibula. Pars zygomatica originates mainly from the medial surface of aponeurosis zygomatica and has a fleshy insertion on the lateral surface of the mandibula. Pars superficialis originates from the lateral surface of aponeurosis zygomatica and, in some taxa, from the fascia temporalis, ligamentum postorbito-mandibulare, and the ligamentum postorbito-zygomaticum. It inserts rostrally on aponeurosis superficialis and the adjacent mandibular surface. Caput interna of pars articularis originates from aponeurosis articularis and the processus oticus of os quadratum and inserts on aponeuroses paracoronoidea interna and externa and on the adjacent portion of the mandibula; some taxa have a caput externa of AME that originates from the impressio AME articularis and on part of the lateral surface of aponeurosis zygomatica, and inserts mainly on aponeurosis paracoronoidea externa and on the mandibula.

In the absence of the processus zygomaticus, we consider the point of attachment of the aponeurosis zygomatica, which lies between the fossa musculorum temporalium and origo AME articularis, to be homologous among taxa. Although aponeurosis zygomatica is the major aponeurosis of AME zygomatica, it also receives fibers rostrolaterally from AME superficialis, dorsomedially from AME coronoidea, and ventrolaterally from AME articularis. Association with these three parts of the AME is characteristic of the aponeurosis zygomatica in various neognathous birds, whether the aponeurosis occurs as an extension of processus zygomaticus or originates from the cranium in the absence of the processus. Within a few orders (e.g. Pelecaniformes, Ciconiiformes, Coraciiformes, Passeriformes), the AME articularis externus and its impressio on the cranium are enlarged in some taxa, occupying a significant portion of the regio temporalis immediately caudal to fossa musculorum temporalium (Fiedler, 1951; Barnikol, 1952; Richards and Bock, 1973).

RESULTS

Processus Zygomaticus

Galliformes.—We found the processus zygomaticus to be present in most chicks and juveniles as an inconspicuous crista or tuberculum on the ventrolateral facies of os squamosum, between the processus postorbitalis and meatus acusticus externus (Fig. 4). The crista is typically oriented obliquely on a parasagittal plane along the ventral edge of os squamosum, and aponeurosis zygomatica arises from it as a flat band passing rostroventrally.

Anseriformes.—We found no clear evidence of a processus zygomaticus on the os squamosum in juveniles, immatures, or adults of many Anseriformes; in some taxa, however, a tuberculum on the crista of origin of the aponeurosis zygomatica at its caudal extremity may represent the processus (Fig. 5F). However, the conformation of the rostral portion of os squamosum resembles a processus in some juvenile anatids. Os squamosum borders the entire length of the processus postorbitalis at sutura laterospheno-squamosa in anhimids, and its basal (dorsal) one-half in anatids. In most Anatidae, the processus postorbitalis is strongly angled rostroventrad, and sutura laterospheno-squamosa conforms to this orientation of the processus, as seen in immature specimens (Fig. 5). Furthermore, sutura fronto-squamosa of anatids is located closer to the dorsal limit of the processus postorbitalis than in galliform birds, and in some anatids the sutura lies only slightly above the processus postorbitalis (Fig. 5). In the latter case, the dorsoventrally compressed, anterolateral facies of os squamosum, in combination with its sometimes pointed rostral extremity, offers a spurious resemblance to a processus zygomaticus in direct association with the processus postorbitalis.

Ossification of Aponeuroses

Galliformes.—Our survey of skeletal specimens of Galliformes of all age classes revealed that almost all chicks and juvenile specimens, and some immatures, lacked ossification of aponeurosis zygomatica as indicated by its absence from prepared skeletons. Occasional specimens of chicks and juveniles had tiny splints of ossified aponeurosis attached to the zygomatic process by syndesmosis or synostosis. By contrast, ossified portions of the aponeurosis were an integral part of most immature and all adult specimens of many galliform taxa (Fig. 4, 6).

During development, ossification of the aponeurosis begins basally and extends rostrad to the level of the processus postorbitalis or beyond, but never to the

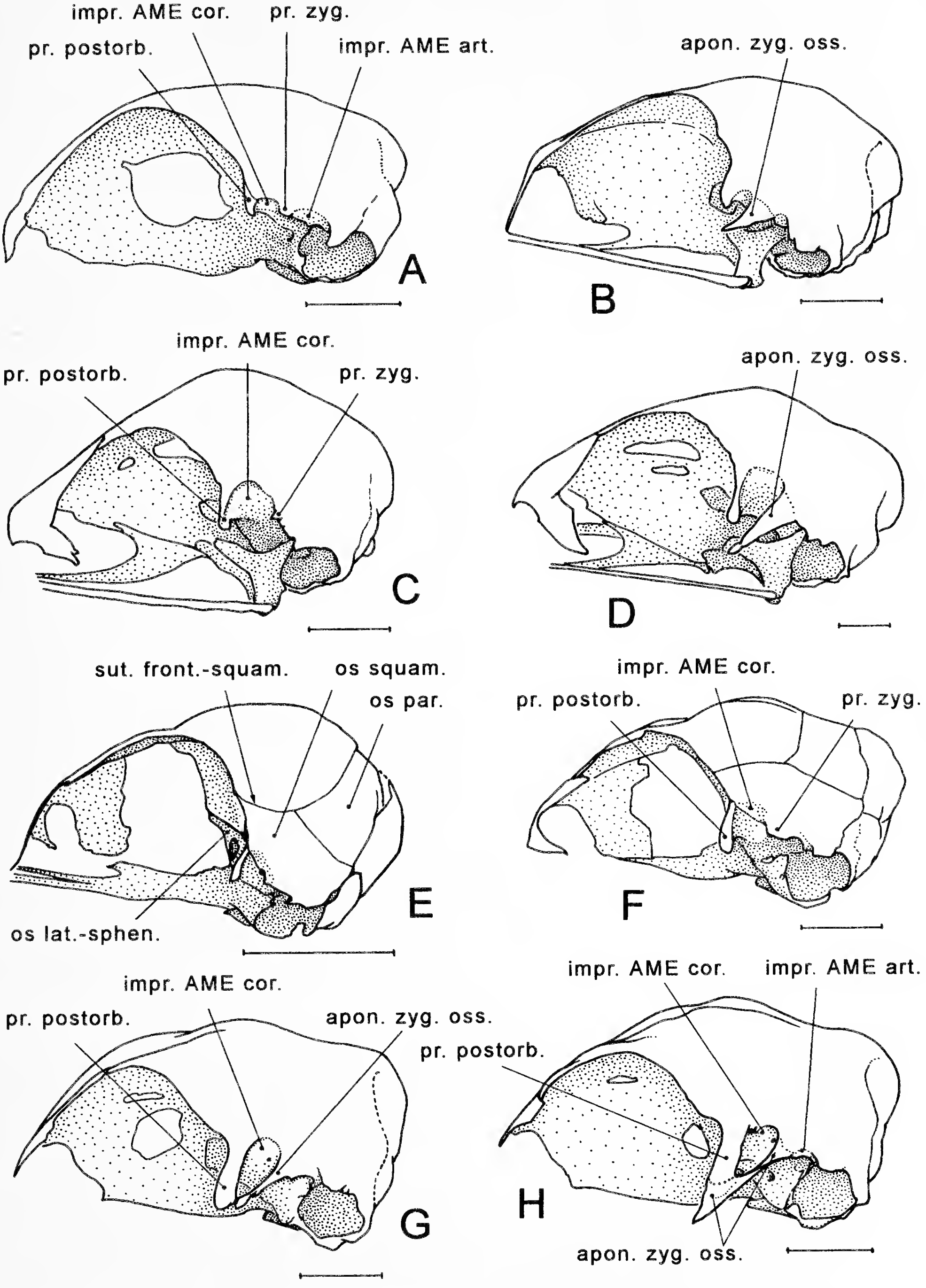

Fig. 4.—Facies lateralis cranii of selected Galliformes: (A) *Leipoa ocellata* (USNM 346351), immature (Megapodidae); (B) *L. ocellata* (USNM 345086), adult (Megapodidae); (C) *Penelope jacquacu* (USNM 345564), immature (Cracidae); (D) *P. purpurascens* (USNM 613959), adult (Cracidae); (E) *Meleagris gallopavo* (USNM 611021), chick (Meleagrididae); (F) *M. gallopavo*, juvenile (USNM 501018); (G) *M. gallopavo* (USNM 556388), immature (Meleagrididae); and (H) *M. gallopavo* (USNM 556372), adult (Meleagrididae). Scale bar = 1 cm.

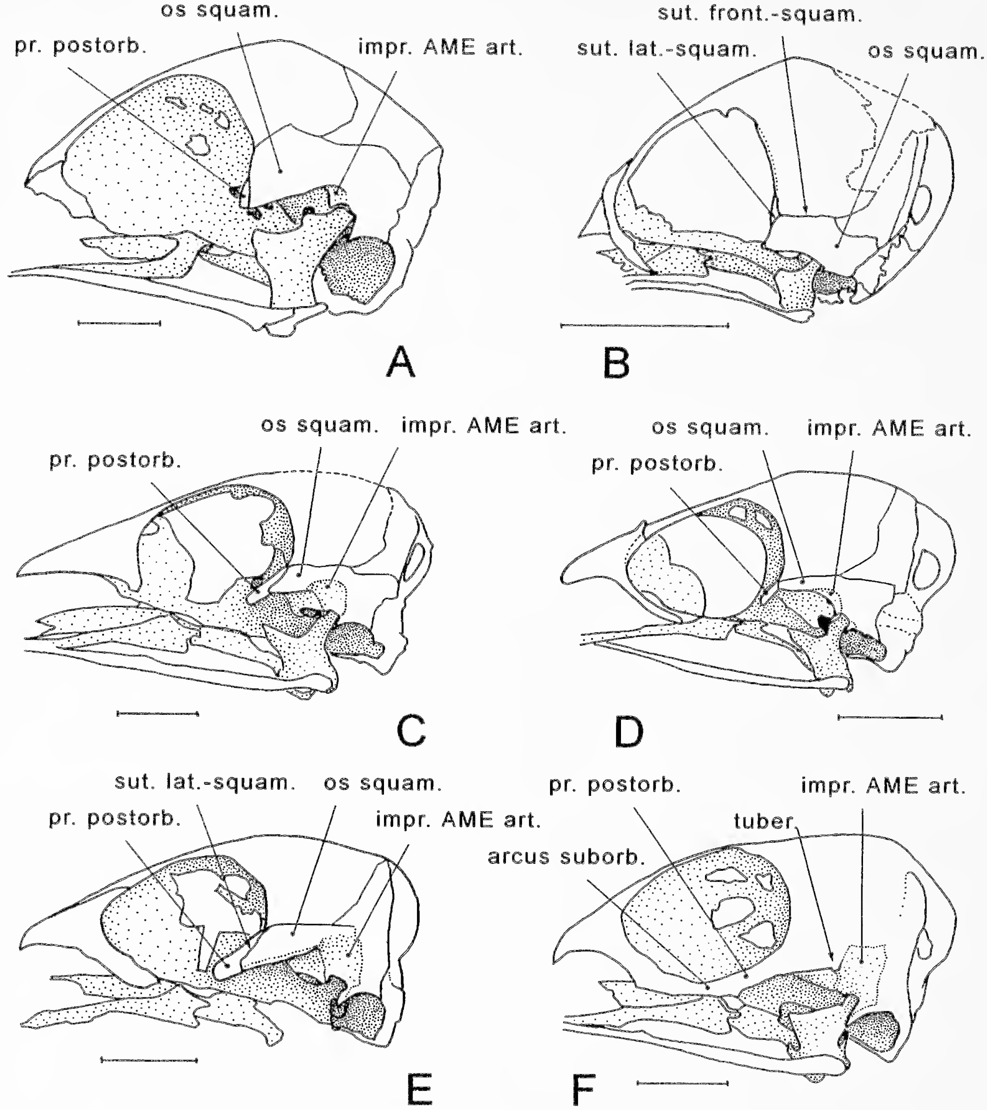

Fig. 5.—Facies lateralis cranii of selected Anseriformes: (A) *Chauna torquata* (BMNH 1954·5·3), juvenile (Anhimidae); (B) Anatinae sp. (AMNH 8737), chick (Anatidae); (C) *Anas platyrhynchos* (BMNH 1986·48·1), juvenile (Anatidae); (D) *Clangula hyemalis* (AMNH 6046), juvenile (Anatidae); (E) *Dendrocygna bicolor* (USNM 501992), juvenile (Anatidae); and (F) *D. javanica* (USNM 343514), adult (Anatidae). Scale bar = 1 cm.

rostral extremity of the aponeurosis. The juncture of aponeurosis zygomatica ossificans with processus zygomaticus is usually synostotic, but occasionally the juncture is syndesmotic even in adults, indicating the limited extent of the processus. Typically, the aponeurosis zygomatica ossificans is markedly flattened lateromedially or in a ventrolateral-dorsomedial plane, but instead it may be irregular, with longitudinal plicae (e. g., *Aepypodius*, *Chauna*; Fig. 7). In the latter case, the delimitation of the processus from a stout, ossified aponeurosis in adults

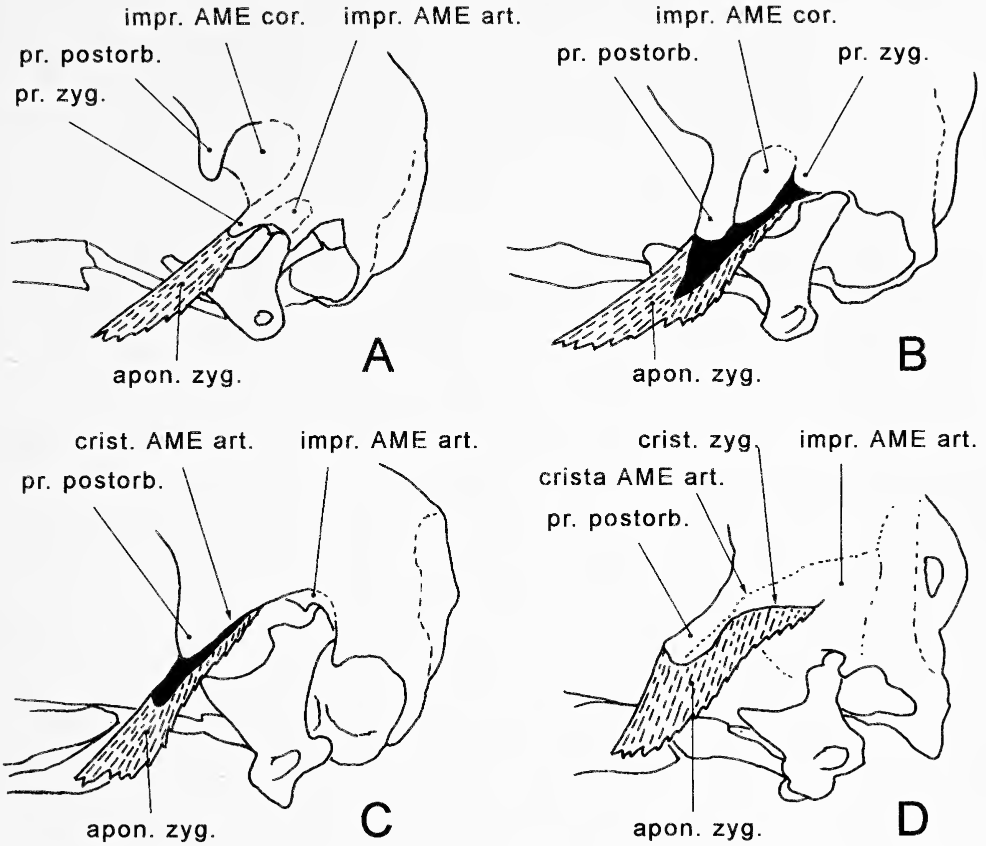

Fig. 6.—Diagrams of the typical arrangement of the aponeurosis zygomatica of: (A) a generalized neornithine bird; (B) a galliform; (C) an anhimid; and (D) a member of the Anseres. Membranous portion is cross-hatched, ossified portion is shown in black.

is more difficult, but the longitudinal patterning of robust and complicated aponeuroses is continuous with their ossified portion (Zusi, personal observation). Although no juvenile of *Aepypodius* was examined, we compared adults of *Alectura lathami* with the illustration of a juvenile (Weber, 1996:fig. 3). The aponeurosis zygomatica ossificans of adult *A. lathami* resembles that of *Aepypodius*, but the processus zygomaticus of the juvenile is a robust tuberculum as in other megopodes. Aponeurosis zygomatica, whether or not ossified, may have no connection with the processus postorbitalis (Megapodiidae). However, in most taxa this aponeurosis is anchored to the processus by a connection with ligamentum postorbito-zygomaticum, which is ossified in adults of most galliforms (Phasianidae, Tetraonidae, Meleagrididae, Odontophoridae, and some Cracidae).

Anseriformes.—In the anhimid *Chauna*, the aponeurosis zygomatica has a linear attachment along lamina lateralis cranii from a point rostral to meatus acusticus externus to, or nearly to, the processus postorbitalis, where the aponeurosis passes medial or ventromedial to the terminus of the processus (Fig. 7). Rostral to the processus postorbitalis, the aponeurosis is free from the cranium (Fig. 6). In adults the aponeurosis is ossified to a point level with, or more often, rostral

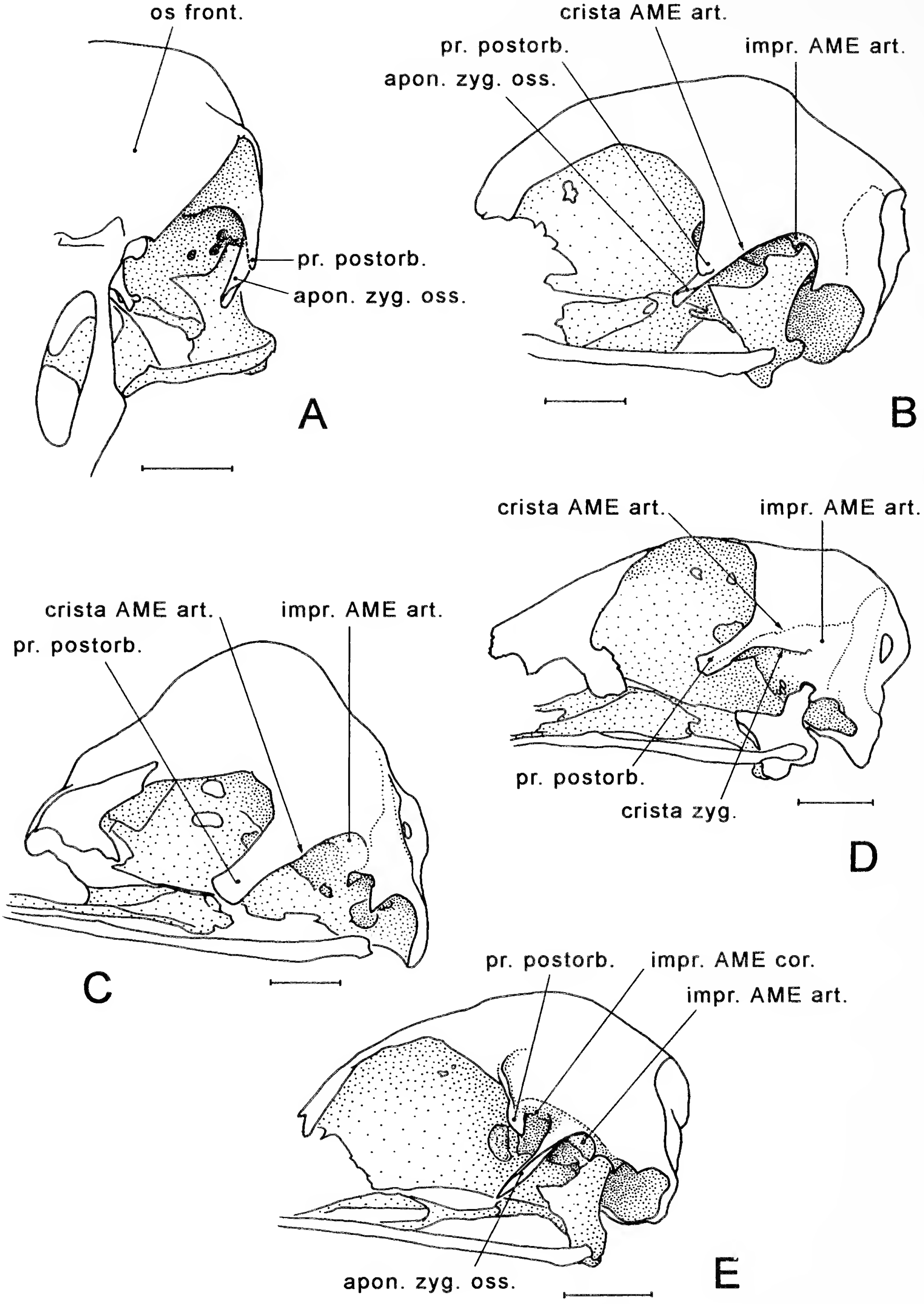

Fig. 7.—Facies rostrolateralis cranii (A) and facies lateralis cranii (B-E) of adult specimens of: (A, B) *Chauna torquata* (USNM 614547), (Anseriformes: Anhimidae); (C) *Anseranas semipalmata* (USNM 347638), (Anseriformes: Anseranatidae); (D) *Sarkidiornis melanotos* (USNM 490276), (Anseriformes: Anatidae); and (E) *Aepypodius arfakensis* (YPM 7594), (Galliformes: Megapodiidae). Scale bar = 1 cm.

to the processus postorbitalis, but as in galliform birds, the rostral-most portion of the aponeurosis does not ossify.

Anatids show little or no ossification of aponeurosis zygomatica (Fig. 6). The caudal-most portion of the aponeurosis arises on the cranium from the rostral limit of impressio AME articularis or sometimes within the impressio, and continues rostrad along a linea or weak crista as far as the apex of the processus postorbitalis; beyond the processus the aponeurosis extends rostroventrad toward the mandibula, independent of the cranium. Ossification, if any, produces a low, irregular crista (crista zygomatica) where the aponeurosis meets the cranium (Fig. 6).

Processus Postorbitalis and Processus "Sphenotemporalis"

Galliformes.—The processus postorbitalis of Galliformes is well developed, straight, and oriented approximately ventrad or somewhat rostrad, and continuous with the margo (rima) caudalis of the orbita. The processus arises largely from the os laterosphenoidale, and meets os squamosum only at its dorsal limit. The ligamentum postorbitale-mandibulare is strong and unossified except at its extreme dorsal limit in some Tetraonidae.

Anseriformes.—In the Anhimidae, the processus postorbitalis is not well defined as a process in lateral view, but in rostral perspective it constitutes a ventrally directed hook of os laterosphenoidale (Fig. 7). Caudal to the apex of the processus postorbitalis, the lamina lateralis cranii is undercut ventrally, forming an overhanging crest that extends caudodorsally from the processus postorbitalis. Dorsal to this crista AME articularis (new term), the regio temporalis forms a wedge-shaped area defining an angle of 60–70° and delimited by the caudal contour of the orbita and by crista AME articularis (Fig. 7). Dzerzhinsky (1982) termed this wedge the "sphenotemporal process." Aponeurosis zygomatica lies adjacent and medial to crista AME articularis, arising along the facies medialis of the crista as far as the apex of the processus postorbitalis, to which it passes ventromediad.

The skull of a large anhimid chick (*Chauna*) exhibits a sutura laterospheno-squamosa that borders the processus postorbitalis for almost its full length. By contrast, in chicks and immatures of the Anatidae, os squamosum borders only the base of the processus postorbitalis (Fig. 5). A processus zygomaticus is not visible in any anseriform, and the aponeurosis zygomatica takes its caudalmost point of origin well caudal to the processus postorbitalis (Fig. 6). These facts suggest that the "sphenotemporal" process was formed (in an evolutionary sense) not by fusion of processes, but more likely by medial retreat of impressio AME coronoidea and rostral extension of origo aponeurosis zygomatica to the processus postorbitalis.

Anseres differ from anhimids in several respects. First, the processus postorbitalis of os laterosphenoidale extends well beyond os squamosum (Fig. 5). Second, the processus postorbitalis usually extends rostrad to form the caudoventral margin of the orbita, and the sutura laterospheno-squamosa often is angled correspondingly. Third, the homologue of the crista AME articularis of anhimids is not a well-defined crest in Anseres (except *Anseranas*), but rather a faint linea or crest extending caudad from margo caudoventralis of the processus postorbitalis roughly parallel to crista zygomatica and continuous with the margo dorsalis of impressio AME articularis. Aponeurosis zygomatica attaches just medial or ven-

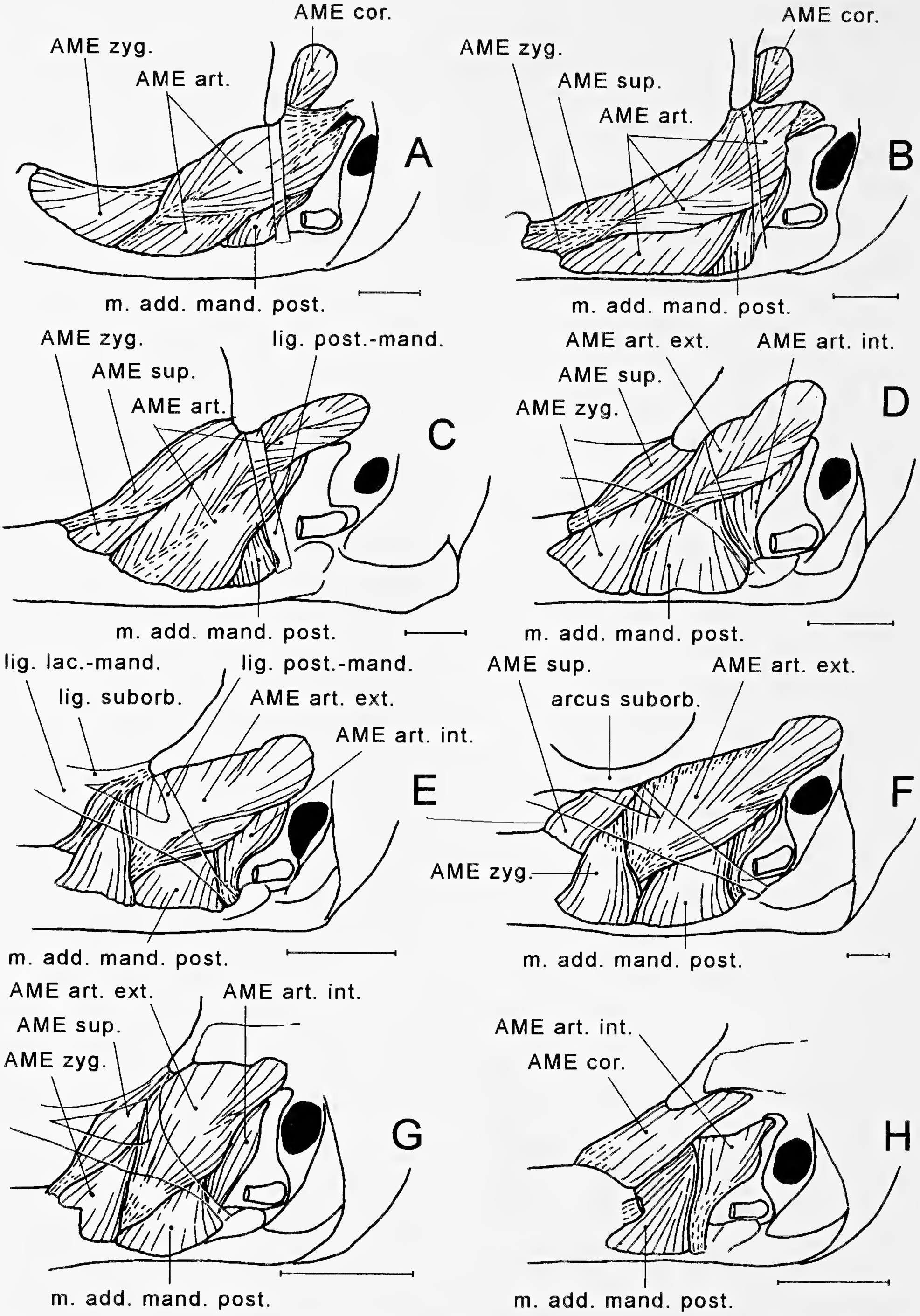

Fig. 8.—Detailed illustrations of the AME complex (left lateral views) of: (A) *Ortalis vetula* (USNM 344381), adult (Galliformes: Cracidae); (B) *Alectoris graeca* (USNM 540255), adult (Galliformes: Phasianidae); (C) *Chauna torquata* (USNM 508682), adult (Anseriformes: Anhimidae); (D) *Anseranas*

tromedial to crista AME articularis (Fig. 6, 7). Fourth, the aponeurosis zygomatica is unossified or forms only a roughened crista along its origin on os squamosum.

M. Adductor Mandibulae Externus

Our findings on the structure of AME in terms of muscle fibers and aponeuroses agree essentially with those of Weber (1996) for the Megapodiidae, Dzerzhinsky (1980) for the Cracidae, and Dzerzhinsky and Belokurova (1972) for the Tetraonidae. Also, our inferences concur in large part with those by Davids (1952) and Zweers (1974) for the Anatidae, and with those by Dzerzhinsky (1982) for the Anhimidae. However, our interpretations of homology of muscle parts differ from the conclusions of those authors to varying degrees.

We applied the following anatomical generalizations derived from the literature on avian jaw musculature to the interpretation of structure in Galliformes and Anseriformes: (a) muscle fibers from all four parts of AME originate on aponeurosis zygomatica in the Galliformes, Anseriformes, and other avian orders (Fig. 3); (b) by contrast, fibers to aponeurosis superficialis represent largely AME superficialis, those to aponeurosis coronoidea represent mainly AME coronoidea, and those to aponeuroses paracoronoidea externa and interna represent primarily AME articularis; (c) some fibers of AME superficialis are inseparable from some fibers of AME coronoidea and AME zygomatica; and, (d) similarly, fibers of AME zygomatica blend with those of AME articularis. Based on the above conventions, we conclude that AME articularis is much enlarged in galliform and anseriform birds, and that AME zygomatica and AME superficialis are thereby displaced rostrally (Fig. 8). Although our interpretations differ radically from those of Lakjer (1926) and his followers (see below and Table 1), they agree substantially with those of Dzerzhinsky (1982) and Weber (1996).

In anseriforms, AME superficialis and AME zygomatica are distinct and typical in form except that both arise from aponeurosis zygomatica rostral to its attachment on the processus postorbitalis, and from an additional, short aponeurosis arising on that processus. Unique to adult specimens of *Dendrocygna* is an ossified ligamentum suborbitale, a structure fused with the tip of the processus postorbitale and os lacrimale, and forming an arcus suborbitalis (Shufeldt, 1914; Schiøler, 1926; Livezey, 1995*b*). In adults, some fibers of AME superficialis arise from the arcus rostral to the processus postorbitalis (Fig. 8).

The interpretation of homologies within galliformes is clouded by certain specializations. AME superficialis and AME zygomatica are variously developed or merged within Galliformes, but, except for the Megapodiidae, their origins from aponeurosis zygomatica are supported by the processus postorbitalis, as they are in the anseriforms. These combined muscle parts blend also with AME articularis externus in phasianid galliforms. Commensurate with the blending of muscle parts are modifications of aponeuroses superficialis and paracoronoidea externa, which form a continuous sheet that inserts along the facies lateralis of the mandibula

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semipalmata (USNM, uncataloged), chick (Anseriformes: Anseranatidae); (E) *Dendrocygna bicolor* (CM 2117), chick (Anseriformes: Anatidae); (F) *D. autumnalis* (CM 5247), adult (Anseriformes: Anatidae); (G) *Anas versicolor* (USNM 345162), chick (Anseriformes: Anatidae); and (H) *Anas acuta* (USNM 225218), chick (Anseriformes: Anatidae), with AME superficialis, zygomatica, and articularis externa removed. Scale bar = 5 mm.

Table 1.—*Anatomical nomenclatures applied to the m. adductor mandibularis externus complex (AME) of selected non-anseriform and anseriform birds by Lakjer (1926), Starck and Barnikol (1954), and the present study.*

Non-anseriform birds		Anseriform birds	
Lakjer (1926)[a]	Present study[b]	Lakjer (1926)[c]	Present study[d]
III profundus[e]	AME coronoidea	[absent]	
I superficialis	AME superficialis	I superficialis a	AME articularis externus
III profundus[f]	AME articularis	I superficialis b	AME zygomatica
II medialis	AME zygomatica	I superficialis c	AME superficialis
		III profundus	AME articularis internus
		II medialis	AME coronoidea
Starck and Barnikol (1954)[g]	Present study[b]	Starck and Barnikol (1954)[h]	Present study[d]
Aponeurosis 1 portion	AME coronoidea	Aponeurosis 1 portion (right)	AME articularis externus (part)
		Aponeurosis 1 portion (middle)	AME zygomatica
		Aponeurosis 1 portion (left)	AME superficialis et coronoidea
Aponeurosis 2 portion	AME zygomatica et superficialis	Aponeurosis 2 portion	AME articularis externus (part)
Aponeurosis 3 portion	AME articularis internus et externus	Aponeurosis 3 portion	AME articularis internus

[a] *Cepphus grylle.*

[b] *Cepphus grylle.*

[c] *Melanitta nigra.*

[d] *Anseranas semipalmata, Dendrocygna bicolor, D. autumnalis, Anser albifrons, Anas versicolor,* and *A. acuta.*

[e] Labelled "rostr" in some figures.

[f] Labelled "kaud" in some figures.

[g] Various non-passeriform taxa.

[h] *Anas platyrhynchos.*

and merges with aponeurosis paracoronoidea interna in at least some members of all galliform families.

Impressio AME Coronoidea

Galliformes.—The impressio AME coronoidea is variable in size but always limited in extent among galliform birds, and it occupies the lamina lateralis cranii between the processus postorbitalis and processus zygomaticus. In many taxa, but most prominently in the Megapodiidae, the fossa is barely perceptible in lateral view and the impressio is rotated mediad, occupying portions of ossae squamosum and laterosphenoidale (Fig. 4, 7, 9). In those taxa characterized by an ossified ligamentum postorbito-zygomaticum, the fossa is partially enclosed laterally (Fig. 4).

Anseriformes.—Most waterfowl lack a laterally exposed impressio AME coronoidea. Instead, the impressio occupies a comparatively medial position, and is largely or completely overhung by crista AME articularis (Anhimidae, Anseranatidae) or crista zygomatica (most Anatidae). From a ventrolateral perspective, impressio AME coronoidea is visible at the junctura of the os squamosum and

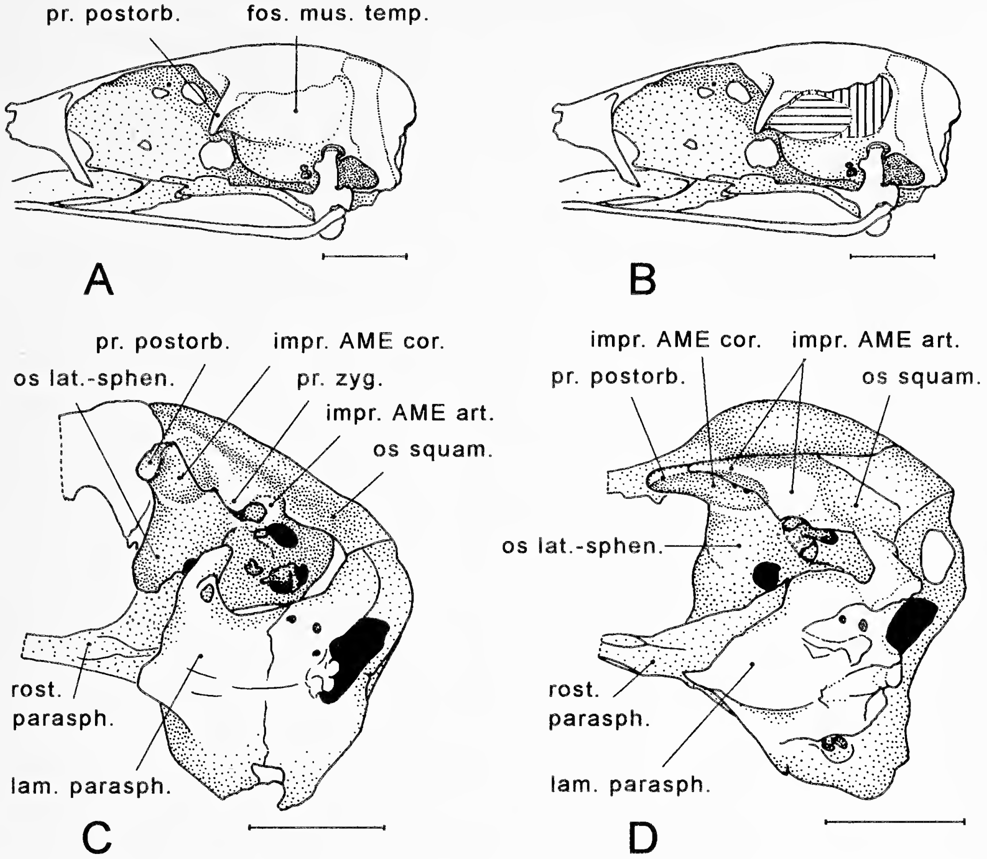

Fig. 9.—Facies lateralis cranii (A, B) and facies ventrolateralis cranii (C, D) of: (A, B) *Mergus merganser* (USNM 555255), adult, (Anseriformes: Anatidae), showing fossa musculares temporalis and (B) origins of AME coronoidea (horizontal hatching) and AME articularis (vertical hatching), inferred through dissection of USNM 505780; (C) *Meleagris gallopavo* (USNM 501018), juvenile (Galliformes: Meleagrididae); and (D) *Anas platyrhynchos* (BMNH 1986·48·1), juvenile (Anseriformes: Anatidae). Scale bar = 1 cm.

os laterosphenoidale, between the tip of the processus postorbitalis and impressio AME articularis (Fig. 9).

In most members of Anatidae, impressio AME coronoidea extends to the tip of processus postorbitalis as a ventrolaterally directed planum. Processus postorbitalis is variably reduced in size and more ventrally directed within Mergini, and exhibits a corresponding reduction in its involvement with impressio AME coronoidea. Only in *Lophodytes*, *Mergellus*, and *Mergus* (Mergini) is impressio AME coronoidea largely free from the processus postorbitalis and fully exposed in lateral view, where it merges imperceptibly with impressio AME articularis (Fig. 9). A less extreme but similar condition occurs in *Biziura* (Oxyurini). In these birds, crista zygomatica is much reduced in prominence. However, it is likely that AME coronoidea is obstructed largely or completely in lateral view by AME articularis in all Anseriformes.

Impressio AME Articularis

Galliformes.—Usually, this impressio is small or absent in gallinaceous birds (Fig. 9). The AME articularis originates extensively from the portions of aponeurosis zygomatica that lie both caudal and somewhat rostral to the processus postorbitalis, whether or not the aponeurosis is ossified (Fig. 8). Although AME articularis is enlarged, it does not expand dorsally on the regio temporalis as mentioned above for some other avian taxa.

Anseriformes.—The impressio AME articularis is small and located medially in Anhimidae and Anseranatidae, but the AME articularis expands rostrally along aponeurosis zygomatica as in Galliformes. Most Anatidae have a small- to medium-sized impressio AME articularis (Fig. 5, 7). When small, the fossa occupies the cranium between the caudal attachment of aponeurosis zygomatica and the meatus acusticus externus as in some Galliformes. Anseres resemble galliforms and anhimids in their relatively large AME articularis, which attaches rostrad along the caudal section of aponeurosis zygomatica to the processus postorbitalis. In addition, crista AME articularis gives rise to a superficial aponeurosis that extends rostrad, roughly parallel and dorsal to the linear origin of aponeurosis zygomatica. The narrow area between the lines of origin of these aponeuroses constitutes a rostral expansion of impressio AME articularis.

In some anatids (e.g., *Mergus merganser*), the impressio also expands dorsally and crista zygomatica is much reduced; thus, the fossa includes impressio AME coronoidea rostrally and impressio AME articularis caudally (Fig. 9). As there is no linea separating these adjacent muscle scars in *Mergus*, the single fossa is best referred to as fossa musculorum temporalium in this genus. Also, we could not confirm the finding of Goodman and Fisher (1962) that AME coronoidea (their AME medialis) occupies the entire fossa.

DISCUSSION

Homology of Processus Zygomaticus

Among the Galliformes, the processus zygomaticus is represented by an indistinct boss or crista. The processus is separated from the processus postorbitalis, and in many taxa the aponeurosis zygomatica is supported by the processus postorbitalis through ligamentum postorbito-zygomaticum (ossified or unossified). Anseriformes are characterized by the absence of a distinct processus zygomaticus, but the homologous locus may be marked by a tuberculum. However, waterfowl also are characterized by the extended origin of aponeurosis zygomatica along a linea or crista extending from impressio AME articularis rostrad toward or to the processus postorbitalis. Thus, in both the Galliformes and Anseriformes, processus zygomaticus (or its homologous locus) lies caudal to the processus postorbitalis.

This interpretation is contrary to the description by Dzerzhinsky (1982, 1995) of a processus "sphenotemporalis" in Anseriformes and its evolutionary derivation by fusion of the processus zygomaticus (or ossified aponeurosis zygomatica) with the processus postorbitalis. Our interpretation is influenced by the following facts pertaining to Anseriformes: (a) much of processus postorbitalis is formed exclusively from the os laterosphenoidale, a composition typical of many avian orders; (b) there is no indication of a processus zygomaticus (much less a long one) or an ossified aponeurosis zygomatica in skulls of juvenile, immature, or adult Anseres; and, (c) an ossified aponeurosis zygomatica in anhimids fuses with os squamosum mainly caudal to processus postorbitalis, and in some specimens passes medial or ventromedial to the apex of that processus. These distinctions, although subtle, permit a more precise definition of homologous characters.

Evolution of Unique Anseriform Morphology

We found little evidence favoring any single ontogenetic or evolutionary mechanism that would best explain the probable transformation to anseriform morphology from that of a common ancestor with galliforms. However, two such hypotheses could be modelled after morphological states represented among the galliform taxa we examined: (a) reduction and medial rotation of impressio AME coronoidea and development of an overhanging crista (Megapodiidae); (b) reconfiguration of the position or shape of the processus zygomaticus or ossified aponeurosis zygomatica (and/or processus postorbitalis) to constrict the impressio AME coronoidea (*Coturnix*). A third hypothesis—ossification of the aponeurotic surface of AME coronoidea, thereby closing the fossa musculorum temporalium—was not reflected in the morphology of any galliform examined.

Interpretation of Adductor Mandibulae Externus

Here we compare our interpretation of muscle homologies with those of authors who have studied not only Galliformes and Anseriformes, but also a variety of other orders. Terminology applied by each author to jaw muscles in taxa whose structure is non-controversial provided the key to understanding their concepts of muscle homologies in the more problematic Galliformes and Anseriformes.

In order to facilitate comparisons with the published works that disagree most markedly with our interpretation of the myology of anseriforms, we present a synonymy for the nomenclature applied to the AME by Lakjer (1926) and Starck and Barnikol (1954), based on taxa for which their interpretations of the muscles agree with those presented here (Table 1). We also show the interpretations of both authors concerning the AME in the Anatidae, using both their terminology and ours to highlight the differences in interpretation (Table 1). Lakjer (1926) did not distinguish between AME articularis externus and internus. In essence, Lakjer grouped our AME articularis externus, zygomaticus, and superficialis into AME superficialis, and he considered AME coronoidea to be absent. Starck and Barnikol (1954) synonymized our AME superficialis as part of AME zygomatica. They combined our AME articularis externus (rostral portion), AME zygomaticus, AME superficialis, and AME coronoidea into AME coronoidea. Their AME zygomaticus is our AME articularis externus (caudal portion). These studies postulate an expansion and diversification of AME superficialis (Lakjer, 1926) or AME coronoidea (Starck and Barnikol, 1954), whereas we hypothesize an expansion of AME articularis externus and a rostral displacement of AME zygomaticus and superficialis.

Dzerzhinsky (1982, 1995) identified muscle fibers that interconnect aponeuroses zygomatica and paracoronoidea externa as AME superficialis rather than AME articularis, and Weber (1996) regarded these same fibers as AME zygomatica (which subsumes AME superficialis). Since these fibers are already incorporated within a well-defined block of muscle tissue associated with aponeurosis paracoronoidea externa in chicks of several Anseres (Fig. 8), we think it more likely that the fibers in question represent AME articularis externus. Starck and Barnikol (1954:12) included comparable fibers with AME articularis (their Ap. 3 portion)

Table 2.—*Distribution of states of osteological characters associated with the AME complex in selected taxa of Galliformes and Anseriformes, based on the present study.*

Taxon	Processus zygomaticus	Crista zygomatica[a]	Fossa musculi temporales[b]	Impressio AME articularis[c]
Galliformes				
Megapodiidae	Small or absent	Absent	Partly medial and lateral (latter small)	Small or absent
Cracidae	Small or absent	Absent	Lateral (moderate)	Small or absent
Phasianidae	Small or absent	Absent	Lateral (moderate)	Small or absent
Anseriformes				
Anhimidae	Absent	Present	Entirely medial	Small, medial
Anseranatidae	Absent	Present	Entirely medial	Small, lateral
Anatidae	Absent	Present	Typically medial	Small, lateral

[a] From processus postorbitalis.

[b] Broadly equivalent to the "fossa temporalis" as traditionally defined (see text).

[c] Broadly equivalent to the "fossa subtemporalis" of some authors (see text).

in *Buteo buteo* (Accipitridae). Under our interpretation it follows that, in Galliformes and Anseriformes, the origins of AME superficialis and AME zygomatica are displaced to the portion of aponeurosis zygomatica rostral to the processus postorbitalis, and their insertions typically are restricted to the mandibula rostral to aponeurosis paracoronoidea externa.

Burton (1984) made comparisons between the AME of the Phoeniculidae (Coraciiformes) and Anseriformes with special reference to portions originating on the processus postorbitalis. He referred to these portions in both orders as the "postorbital lobe" and suggested that the lobes were homologous and plesiomorphous in the two orders. His "postorbital lobe" in Anseriformes equates to our AME superficialis and AME zygomatica. However, we found that AME zygomatica lies caudal to the "postorbital lobe" in *Phoeniculus*. Caput mediale of AME coronoidea has not been discussed previously in this paper because it is not present in the Galliformes and Anseriformes, but it occurs in Coraciiformes and other avian orders (Richards and Bock, 1973; Burton, 1984). The "postorbital lobe" of *Phoeniculus* may include elaborations of AME coronoidea medialis and AME superficialis.

Interpretations of Characters and Phylogenetic Implications

Alternative Views of Characters, States, and Ordering.—Although a phylogenetic analysis incorporating the anatomical information described herein is beyond the scope of this paper, the comparisons provide a framework for partitioning the Galliformes and Anseriformes into several broad taxonomic groups (Tables 2-3). Although most characters differ in the specific groupings suggested, most are hierarchically consistent with each other; i.e., one character suggests a nested subdivision of groups implied by another character (Table 3). Also, some characters are redundant; e.g., complementarity of fossa musculorum temporalium (Table 2) vs. origo AME coronoidea (Table 3).

Livezey (1997*a*) included one multistate, composite character (Appendix 1: character 8) that was intended to summarize the anatomical changes described herein (Table 3), one that emphasized the pattern of apparent changes in the cranial skeleton (notably orientation of processus postorbitalis and prominence of

Table 3.—*Distribution of states of myological and arthrological characters associated with the AME (m. adductor mandibulae externus) complex in selected taxa of Galliformes and Anseriformes, based on the present study.*

Order	Family	Ligamentum postorbito-mandibulare	Ligamentum postorbito-zygomaticum	Ossification aponeurosis zygomatica	Aponeurosis articularis	Origo AME superficialis	Origo AME zygomatica	Origo AME coronoidea	Origo AME articularis
Galliformes	Megapodiidae	Vertical	Absent	Variable	Strong	Rostral[a]	Rostral[a]	Lateral and medial	Rostrad to processus postorbitalis[b]
	Cracidae	Vertical	Present, ossified or unossified	Ossified	Strong	Rostral[a]	Rostral[a]	Lateral	Rostrad to processus postorbitalis[b]
	Phasianidae	Vertical	Present, ossified	Ossified	Strong	Rostral[a]	Rostral[a]	Lateral	Rostrad to processus postorbitalis[b]
Anseriformes	Anhimidae	Vertical	Absent	Ossified	Moderate	Rostral[a]	Rostral[a]	Medial	Rostrad to processus postorbitalis[b]
	Anseranatidae	Angled caudad	Absent	Unossified	Weak	Rostral[a]	Rostral[a]	Medial	Rostrad to processus postorbitalis[b]
	Anatidae	Angled caudad	Absent	Unossified	Weak	Rostral[a]	Rostral[a]	Medial	Rostrad to processus postorbitalis[b]

[a] I.e., origin at point parallel or rostral to apex of processus postorbitalis, a condition rare in other taxonomic groups of Aves.

[b] Rostral extension of origo AME articularis unknown in other taxonomic groups of Aves.

processus zygomaticus). Nomenclatural differences between this earlier character description and the present study aside, and in spite of the fact that the earlier character description was based primarily on assessments of prepared skulls, the four states delimited are consistent with the broad groupings substantiated by the present study (Tables 2-3). Furthermore, it should be noted that ordering of the previous coding scheme was not analytically influential, and the character had a consistency index of 1.0 whether or not the four states were treated *a priori* as ordered (Livezey, 1997*a*:420). Also, in the final phylogenetic hypotheses, the ordering implied by the sequence of states was preserved (Table 3), an ordering that confirmed the general primitive-derived sequence implied by the summary classification (Galliformes, Anhimidae, Anseranatidae, and Anatidae).

A majority of recent phylogenetic studies indicate that the basal polarities (primitive states) of these anatomical characters for the Galliformes and Anseriformes (Tables 2-3) are sought most reliably among the paleognathous birds (Cracraft, 1988; Livezey, 1997*a*; Groth and Barrowclough, 1999). Although detailed anatomical descriptions of these features among paleognaths are beyond the scope of the present study, several published works (Bock, 1963*b*; Elzanowski, 1987; Weber, 1996) provide a basis for some preliminary comparative comments. Presence of a strong processus zygomaticus in close proximity to the os quadratum is diagnostic for paleognaths, suggesting that the reduction of the processus and its disassociation from the os quadratum represent a synapomorphy of neognathous birds (including Galliformes and Anseriformes). Similarly, the well-defined AME articularis found in most neognaths is probably apomorphic relative to its absence or minimal development in paleognaths. The distinctive pattern of development of AME articularis described in this paper apparently is derived relative to its usual form in other neognaths; the pattern includes enlargement of AME articularis by expansion rostrally along aponeurosis zygomatica and along the mandibula, and rostral displacement of AME zygomatica and AME superficialis.

Given these provisional inferences of polarity, the details of interpretation of the anatomical states described (Table 3) have little or no impact on coding schemes. All of the alternative interpretations of the plausible evolutionary events that underlie these anatomical patterns considered here are consistent with the four-state coding scheme used by Livezey (1997*a*), and most would permit any of several alternative coding schemes (e.g., separate, binary characters treating changes in three to five of the osteological or myological features involved). Moreover, even the evolutionary interpretation proposed by Dzerzhinsky (1982)—including the disputed hypothesis of the "sphenotemporal process"—would be consistent with most or all of these alternative coding schemes, necessitating only a revision of the accompanying descriptions of character states. This "transparency" of evolutionary interpretation in the coding of this character complex is substantiated by the fact that an earlier draft of the description for this character by Livezey (1997*a*) was based in large part on the interpretation by Dzerzhinsky (1982), wherein the allocation of states among taxa was conserved.

Implications for Interordinal Relationships.—Data presented herein regarding the skeleton and musculature associated with the AME complex (Table 3) and provisional inferences of polarity based on the literature (Elzanowski, 1987; Dzerzhinsky, 1999) support (i.e., confirm without homoplasy) a sister relationship between the orders Galliformes and Anseriformes, as proposed in earlier anatomical assessments by Dzerzhinsky (1982, 1995) and Livezey (1997*a*). This proposal has been favored by a number of authorities for decades (e.g., Delacour, 1954;

Johnsgard, 1965), and is gaining support from recent morphological (Cracraft, 1988; Livezey, 1997*a*; Müller and Weber, 1998) and molecular analyses (Cracraft, 1981*a*; Cracraft and Mindell, 1989; Caspers et al., 1997; Groth and Barrowclough, 1999). Further insights into this interordinal group, and the morphological transformations which support this complex, may be gained through the continued study of several fossil taxa recently inferred to be allied with the Anseriformes—the Diatrymidae (Andors, 1992) and Dromornithidae (Murray and Megirian, 1998).

At least two cranial characters—absence of the ligamentum postorbito-zygomaticum, and medial displacement of impressio AME coronoidea—suggest that megapodes possess a morphotype intermediate to the condition typical of most Galliformes and that observed in modern Anseriformes. An "intermediate" condition of this complex in the Megapodiidae relative to other Galliformes is consistent with the majority view regarding it as the likely sister group of other Galliformes (review by Crowe, 1988). These conclusions can be tested by broader comparative studies within Aves (e.g., Livezey, 1997*a*), especially those emphasizing detailed comparisons of new character complexes and intensive sampling of Galliformes and Anseriformes.

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A NEW SPECIES OF *CARPOCRISTES* (MAMMALIA: PRIMATOMORPHA) FROM THE MIDDLE TIFFANIAN OF THE BISON BASIN, WYOMING, WITH NOTES ON CARPOLESTID PHYLOGENY

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ABSTRACT

A new species of Carpolestidae, *Carpocristes rosei*, is described from a middle Tiffanian locality in the Bison Basin, Fremont County, Wyoming. A phylogenetic analysis of all known carpolestid species identifies *C. rosei* as the most basal member of *Carpocristes*, a genus known from Tiffanian localities in North America and the Bumbanian Wutu Formation, Shandong Province, People's Republic of China. Available biostratigraphic and phylogenetic data suggest that *Carpocristes* originated in North America.

As reconstructed here on the basis of dental characters, phylogenetic relationships among carpolestids as a whole are highly compatible with the stratigraphic distributions of individual species. Nevertheless, stratigraphic disjunctions between inferred sister taxa imply ghost lineages that lasted roughly 5.6 Ma (for early members of the chronolestine clade), 2.3 Ma (for early members of the lineage culminating in *Elphidotarsius wightoni*), and 1.2 Ma (for early members of *Carpocristes*), respectively.

KEY WORDS: Paleocene, Carpolestidae, Phylogeny, Paleobiogeography

INTRODUCTION

The Carpolestidae are a family of plesiadapoid primatomorphs characterized by pronounced specializations of the posterior premolars (Rose, 1975). All carpolestid taxa other than *Chronolestes simul*, for which the monotypic subfamily Chronolestinae has been erected (Beard and Wang, 1995), possess a bladelike or "plagiaulacoid" P_4 that occluded with equally specialized, polycuspate P^{3-4} (Biknevicius, 1986). With some notable exceptions (Fox, 1984), these highly derived posterior premolars became progressively elaborate through time (Rose, 1975, 1977), and their morphology has formed the principal basis for reconstructing phylogenetic relationships within the group (Rose, 1975; Krause, 1978; Fox, 1984; Beard and Wang, 1995; Bloch and Gingerich, 1998).

Carpolestids are fairly common components of North American Paleocene mammal faunas, where they range in age from late Torrejonian (To3) to late Clarkforkian (Cf3) (Archibald et al., 1987). Recently, the first Asian carpolestids were described from the Wutu Formation in the Wutu Basin, Shandong Province, People's Republic of China (Beard and Wang, 1995). One of these Asian carpolestids, *Carpocristes oriens*, is morphologically very similar to North American *Carpocristes hobackensis* and *Carpocristes cygneus*, and all three of these species are thought to form a clade within Carpolestidae. This particular clade is interesting not only because of its widespread geographic distribution, but also because it appears to document a relatively rare example of the successful invasion of Asia by an endemic North American mammal (Beard and Wang, 1995; Beard, 1998).

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The purpose of this paper is to describe a new species of *Carpocristes* from the Bison Basin in south-central Wyoming. This new species, the oldest and most primitive yet known for the genus, further substantiates the North American origin of *Carpocristes*. It also suggests that carpolestids enjoyed their highest species richness during the middle Tiffanian, when at least three species—*Elphidotarsius wightoni*, *Carpodaptes hazelae*, and the new species of *Carpocristes* described below—are known.

Paleocene mammals from outcrops of the Fort Union Formation in the Bison Basin of south-central Wyoming were first reported by Gazin (1956). Additions and emendations to the Paleocene mammalian faunas of the Bison Basin have been made by McGrew and Patterson (1962), MacIntyre (1966), Van Valen (1966, 1978), Szalay (1973), Gingerich (1976, 1983), Sloan (1987), Gunnell (1989), and Thewissen (1990). Carpolestids have not previously been reported from the Bison Basin.

CM is the abbreviation used to designate specimens in the collections of the Section of Vertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. Measurements of tooth length (L) and width (W) follow those of Rose (1975:fig. 1).

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758
Mirorder Primatomorpha Beard, 1991
Superfamily Plesiadapoidea Trouessart, 1897
Family Carpolestidae Simpson, 1935
Subfamily Carpolestinae Simpson, 1935
Carpocristes Beard and Wang, 1995
Carpocristes rosei, **new species**
(Fig. 1)

Holotype.—CM 40567, left dentary fragment preserving the crowns of P_4-M_3 and the complete or partial alveoli for several anterior teeth; only known specimen (Fig. 1).

Type Locality.—Bison Basin Ridge locality, CM loc. 1035. Geographic and stratigraphic data for this locality, on file in the Section of Vertebrate Paleontology (CM), indicate that this is the same locality Gazin (1956) referred to as the Ledge locality. The mammalian fauna from the Bison Basin Ledge locality correlates with middle Tiffanian zone Ti3 (Archibald et al., 1987).

Known Distribution.—Middle Tiffanian (Ti3) of the Bison Basin, Fremont County, south-central Wyoming.

Diagnosis.—P_4 differs from that of other species of *Carpocristes* in being relatively taller and anteroposteriorly shorter, with larger ultimate apical cusp, only minor posterolingual excavation, and weaker crest uniting main shearing blade with talonid cusp. M_1 trigonid cusps less widely splayed than in other species of *Carpocristes*. P_4 further differs from that of *Carpocristes hobackensis*, *Carpodaptes,* and *Carpolestes* in being absolutely shorter anteroposteriorly. P_4 further differs from that of *Carpolestes*, *Carpocristes hobackensis*, and *Carpocristes oriens* in having fewer apical cusps. P_4 further differs from that of *Carpodaptes* in having ultimate apical cusp displaced posteroinferiorly.

Etymology.—For Kenneth D. Rose, whose monograph on the Carpolestidae (Rose, 1975) remains a standard reference for the group.

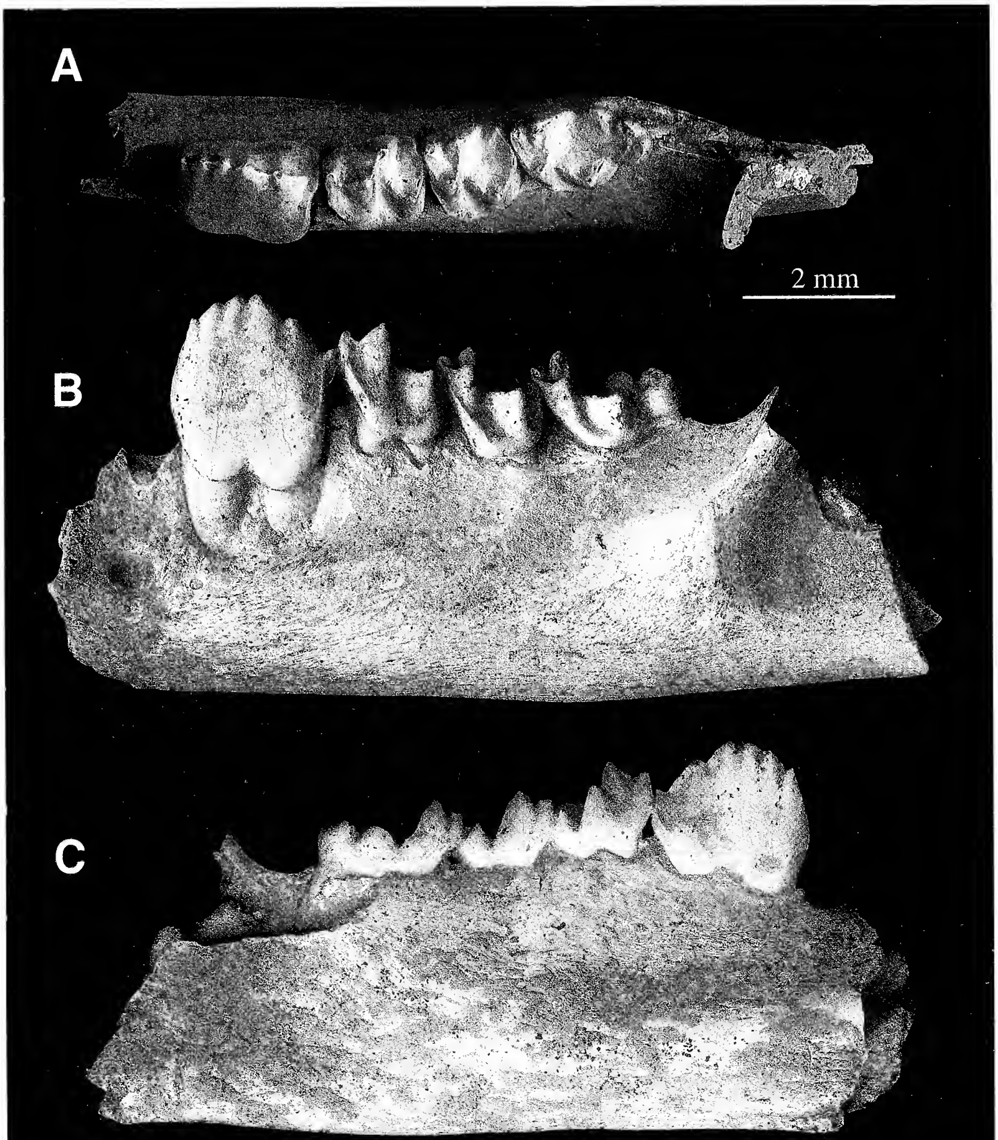

Fig. 1.—*Carpocristes rosei*, n. sp., holotype, CM 40567. Left dentary fragment preserving P_4-M_3 and whole or partial alveoli for anterior teeth in occlusal (A), buccal (B), and lingual (C) views. Note prominent region of alveolar bone resorption beneath P_4 in buccal view (B). Scale bar = 2 mm.

Description.—Anteriorly, the posterior part of the alveolus for I_1 is preserved in CM 40567. This relatively large alveolus is nearly horizontal in orientation, reflecting the procumbent disposition of I_1 in carpolestids. At least two small alveoli are present between the crown of P_4 and the alveolus for I_1, although this part of the dentary is damaged in the holotype. The more posterior of these two alveoli supported a diminutive, single-rooted P_3 by analogy with other carpolestid taxa in which the crown of this tooth is preserved (Rose, 1975; Beard and Wang, 1995). The more anterior alveolus, of which only the posterior part is preserved in CM 40567, must have housed another single-rooted tooth that was similar in size to P_3. The homology of the latter tooth locus is uncertain given the fragmentary

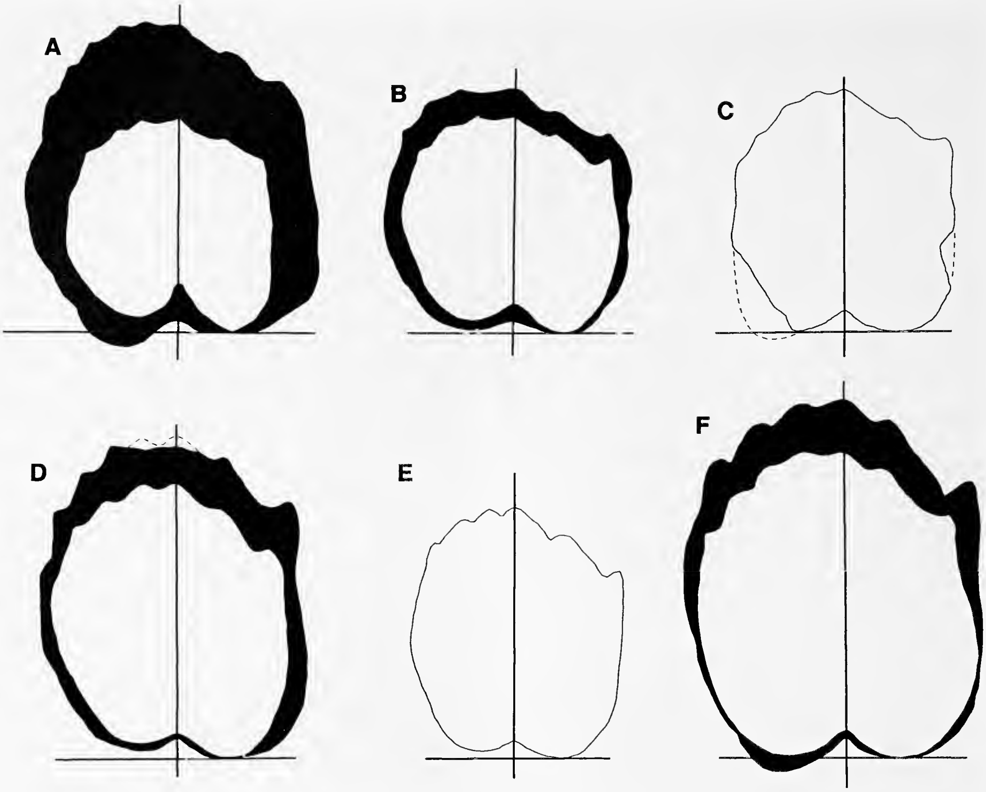

Fig. 2.—Camera lucida tracings of the labial profiles of P_4 among selected Carpolestinae (after Krause, 1978:fig. 7). Samples depicted are as follows: (A) *Carpocristes cygneus*, Roche Percée local fauna, *n* = 19; (B) *Carpocristes cygneus*, Swan Hills site 1, *n* = 4; (C) *Carpocristes hobackensis*, Dell Creek Quarry, *n* = 1; (D) *Carpocristes* sp., Police Point local fauna, *n* = 3; (E) *Carpocristes rosei*, Bison Basin Ridge locality, *n* = 1; (F) *Carpodaptes hazelae*, Scarritt Quarry and Cedar Point Quarry, *n* = 2.

nature of the only known specimen of *C. rosei*, but it must have been either C_1 or P_2. That which is preserved of the anterior part of the dentary in CM 40567 does not differ appreciably from comparable parts of the dentary in *Carpodaptes hazelae* and *Carpocristes cygneus*.

The most noteworthy feature on the labial aspect of the dentary is a prominent area of missing bone beneath the crown of P_4, which may have been due to pathology.

The labial profile of P_4 (L, 2.00 mm; W, 1.30 mm) closely resembles that of *Carpodaptes hazelae*, from which it differs primarily in being smaller and in the placement of the ultimate apical cusp (Fig. 2). P_4 in *Carpocristes rosei* is relatively taller and anteroposteriorly shorter than in other species of *Carpocristes*. Five apical cusps are present, which is fewer than occur on P_4 in *Carpocristes oriens* (*n* = 7; Beard and Wang, 1995), and at the low end of the range for *Carpocristes cygneus* (*n* = 5–7, mode = 6; Krause, 1978). In contrast to its more anterior position in *Carpodaptes*, in *Carpocristes rosei* the ultimate apical cusp is located almost equidistant between the talonid cusp and the penultimate apical cusp. This posteroinferior displacement of the ultimate apical cusp is a diagnostic apomorphy for *Carpocristes* (Beard and Wang, 1995:fig. 14). In *C. rosei* the ultimate apical cusp is large and cuspidate, in contrast to the condition in other species of *Carpocristes*, in which this cusp is smaller and less readily distinguished from the crest that unites the talonid cusp with the remainder of the P_4 blade. The latter crest itself is decidedly weaker in *C. rosei* than in other species of *Carpocristes*, which is a second reason that the ultimate apical cusp is so manifest in *C. rosei*. Lingually, vertical ribs are well developed beneath all of the apical cusps of P_4. The posterolingual part of the crown is only weakly excavated. As a result, the anterior apical cusps are located almost directly

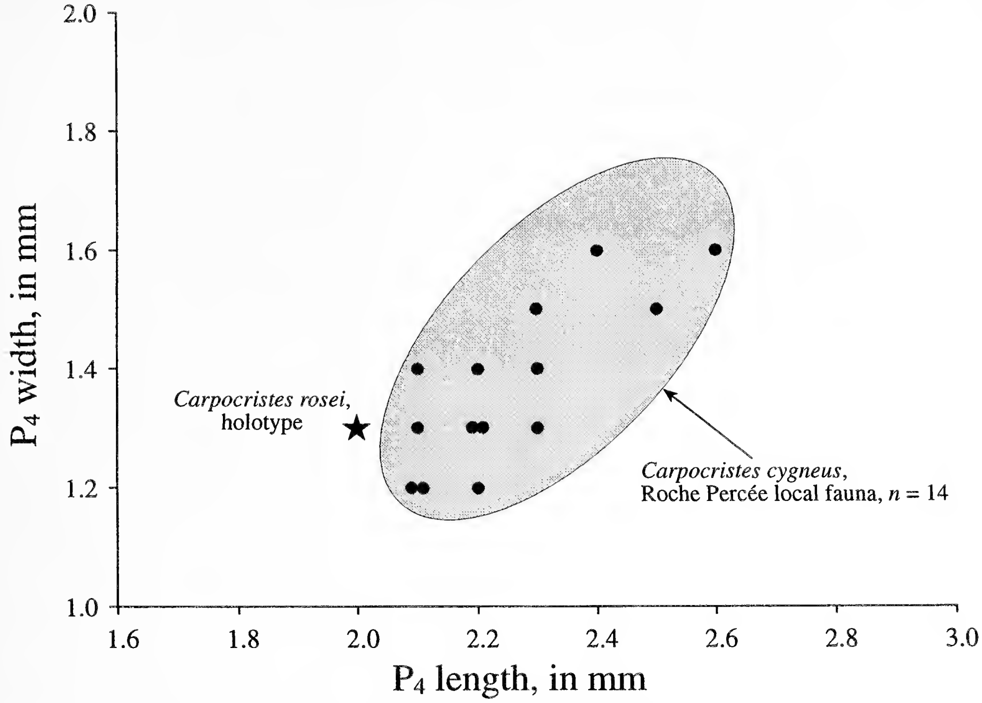

Fig. 3.—Bivariate plot of P_4 dimensions in the holotype of *Carpocristes rosei* (CM 40567) and a sample of *Carpocristes cygneus* from the Roche Percée local fauna of Saskatchewan [*C. cygneus* data from Krause (1978:table 2)].

anterior to the ultimate apical cusp, rather than being tilted or displaced lingually with respect to the ultimate apical cusp, as is the case in other species of *Carpocristes*.

The lower molars of *C. rosei* differ little from those of other species of *Carpocristes*, and need not be described in detail here. In *C. rosei* the paraconid and metaconid cusps on M_1 are less widely splayed than is the case in other species of *Carpocristes*. Unlike *C. hobackensis*, there is no development of a lingual cingulid on the trigonid of M_1 in *C. rosei*. In general, the lower molar cusps in all species of *Carpocristes* seem to be less inflated and bear better-developed crests than do their homologues in *Carpodaptes* and *Carpolestes*. Measurements of the lower molars in CM 40567 are as follows: M_1 L, 1.20 mm; M_1 W, 1.20 mm; M_2 L, 1.10 mm; M_2 W, 1.25 mm; M_3 L, 1.80 mm; M_3 W, 1.10 mm.

Discussion.—*Carpocristes rosei* is most easily confused with *Carpocristes cygneus*, which is closely related to the new form. However, extensive comparisons between the holotype of *C. rosei* and casts of specimens of *C. cygneus* from the Roche Percée local fauna of Saskatchewan described by Krause (1978) revealed consistent morphological differences, which are summarized in the diagnosis. P_4 in the holotype of *C. rosei* also falls outside the range of metric variation observed in the large sample of *C. cygneus* from Roche Percée (Fig. 3).

The most nearly complete and most reliably referred specimens of *C. cygneus* are derived from sites belonging to late Tiffanian zone Ti4. While these late Tiffanian specimens differ from the holotype of *C. rosei* in ways that support a species-level distinction, fossils from various middle Tiffanian (Ti3) sites that have previously been referred to *C. cygneus* appear to be more problematic. Some or even all of these specimens may ultimately prove to belong to *C. rosei* rather than to *C. cygneus.* For example, based on published descriptions and illustrations (Krishtalka, 1973:fig. 16; Krause, 1978:fig. 7), the carpolestid from the Police Point local fauna of southeastern Alberta is very similar to *C. rosei*, and these specimens may well document a northern range extension for this species (Fig. 2). Likewise, it is possible that middle Tiffanian specimens from localities along the Blindman River in central Alberta referred by Fox (1990) to *C. cygneus* pertain to *C. rosei* instead. However, the latter specimens have yet to be described or illustrated, so that their species-level attribution remains uncertain. Finally, specimens from the Williston Basin of western North Dakota referred by Holtzman (1978) to *C. cygneus* may instead belong to *C. rosei.*

CARPOLESTID PHYLOGENY AND THE PHYLOGENETIC POSITION OF *CARPOCRISTES ROSEI*

Introduction

The broad outlines of carpolestid phylogeny have been established for at least a quarter of a century, when Rose (1975) published his monograph on the group. Relationships among generic-level taxa of North American carpolestids have remained stable throughout this interval, although the affinities of two Asian genera have proven to be somewhat more controversial (Beard and Wang, 1995; Bloch and Gingerich, 1998). Despite this virtual consensus at the generic level, certain species-level relationships within the group have so far defied resolution. For example, there is little or no consensus regarding which of the four described species of *Elphidotarsius* is most closely related to the clade that includes *Carpodaptes*, *Carpocristes*, and *Carpolestes*, despite virtual unanimity regarding the paraphyly of *Elphidotarsius* (Rose, 1975; Krause, 1978; Fox, 1984). Similarly, the affinities of both *Carpolestes* and *Carpocristes* with respect to the phylogenetically more basal species traditionally included in *Carpodaptes* have yet to be resolved satisfactorily, although *Carpodaptes jepseni* is often cited as being closely related to *Carpolestes* (Rose, 1975; Bloch and Gingerich, 1998). Various workers have entertained the possibility that *Carpolestes* and some or all of the species now included in *Carpocristes* are more closely related to each other than either are to *Carpodaptes* (Dorr, 1952; Rose, 1975; Krause, 1978). However, this conclusion conflicts with the phylogeny published by Beard and Wang (1995:fig. 14), in which a relatively basal dichotomy between *Carpocristes* and *Carpolestes* was inferred, with both *Carpodaptes hazelae* and *Carpodaptes jepseni* being more closely allied to *Carpolestes* than to *Carpocristes.* A major obstacle to resolution of these lower-level relationships among carpolestids is our poor knowledge of the anatomy of many of the relevant taxa, which are often documented by unique or extremely fragmentary specimens.

Methods

In an attempt to clarify these details of carpolestid phylogeny, I extended the taxon-character matrix published by Beard and Wang (1995:appendices 1, 2) to include additional dental characters and all known carpolestid species (Appendices 1, 2). Multistate characters were treated as ordered in cases in which convincing evidence for a morphocline exists. For example, the number of apical cusps on P_4, which varies from two to eight among carpolestids, was treated as an ordered character on the assumption that the number of apical cusps on P_4 evolved consecutively rather than randomly. Likewise, certain other characters were treated as irreversible when, as in the case of the presence or absence of a particular tooth locus, evolutionary reversal seems highly implausible. All character state transformations were weighted equally. Details regarding character status are provided in Appendix 1. Trees were rooted by designating *Pronothodectes matthewi*, *Chronolestes simul*, and a hypothetical ancestor as outgroups to carpolestine taxa. Phylogenetic analysis of this enhanced dataset using PAUP 3.1.1 (Swofford, 1993) yielded nine most parsimonious trees, a strict consensus of which is illustrated in Figure 4.

Results

The topology of the strict consensus tree (Fig. 4) is fully consistent with that published by Beard and Wang (1995:fig. 14), although additional taxa are included here. As has long been assumed, *Elphidotarsius* emerges as a highly paraphyletic assemblage of species that successively approximates more derived carpolestids (Fig. 4, nodes 2-4). Both *E. shotgunensis* and *E. russelli* appear to be more closely related to the *Carpodaptes* + *Carpocristes* + *Carpolestes* clade than is either *E. florencae* or *E. wightoni* (Fig. 4, node 4). However, neither of the former species of *Elphidotarsius* is represented by relatively complete material, and their derived P_4 structure forms the only unambiguous character support presently available for the phylogenetic relationships reconstructed here. More nearly complete material of either or both of these species will be necessary to evaluate their affinities adequately. As originally proposed by Fox (1984), *E. wightoni* appears to be related more closely to the *Carpodaptes* + *Carpocristes* + *Carpolestes* clade than is *E. florencae* (Fig. 4, node 3).

Among more advanced carpolestids (Fig. 4, node 5), a fundamental dichotomy appears to define two basic clades. One of these clades is equivalent to the genus *Carpocristes* (Fig. 4, node 6), the most basal species of which is *Carpocristes rosei*. Relationships among more advanced species of *Carpocristes* are the same as those proposed by Beard and Wang (1995). That is, *Carpocristes cygneus* appears to be the sister group of a clade consisting of *Carpocristes hobackensis* and *Carpocristes oriens* (Fig. 4, nodes 7, 8). The sister group of *Carpocristes* appears to be a clade that includes both *Carpodaptes* and *Carpolestes*.

The phylogenetic position of *Carpodaptes hazelae*, inferred here to be the sister group of all other species of *Carpodaptes* and *Carpolestes* (Fig. 4, node 9), is the weakest node on the consensus tree. This node occurs in only 35% of bootstrapped trees, and is supported by a single character transformation (the loss of P_2, which occurred four times in parallel within Carpolestidae according to the character walk optimized here). Regardless of the affinities of *Carpodaptes hazelae*, and despite Beard and Wang's (1995) transfer of *C. cygneus* and *C. hobackensis* (both formerly included in *Carpodaptes*) to *Carpocristes*, *Carpodaptes* continues to emerge as a paraphyletic group of species that successively approximates *Carpolestes*. The type species of *Carpodaptes*, *C. aulacodon*, appears to be the sister group of a clade that includes *Carpodaptes jepseni* and *Carpolestes* (Fig. 4, nodes 10, 11). Relationships among species of *Carpolestes* agree with those recently proposed by Bloch and Gingerich (1998): *C. dubius* appears to be the sister group of a clade that consists of *C. nigridens* and *C. simpsoni* (Fig. 4, nodes 12, 13).

Discussion

Perhaps the most notable result from the phylogenetic analysis of carpolestids performed here is the cohesion of the *Carpocristes* clade with respect to other

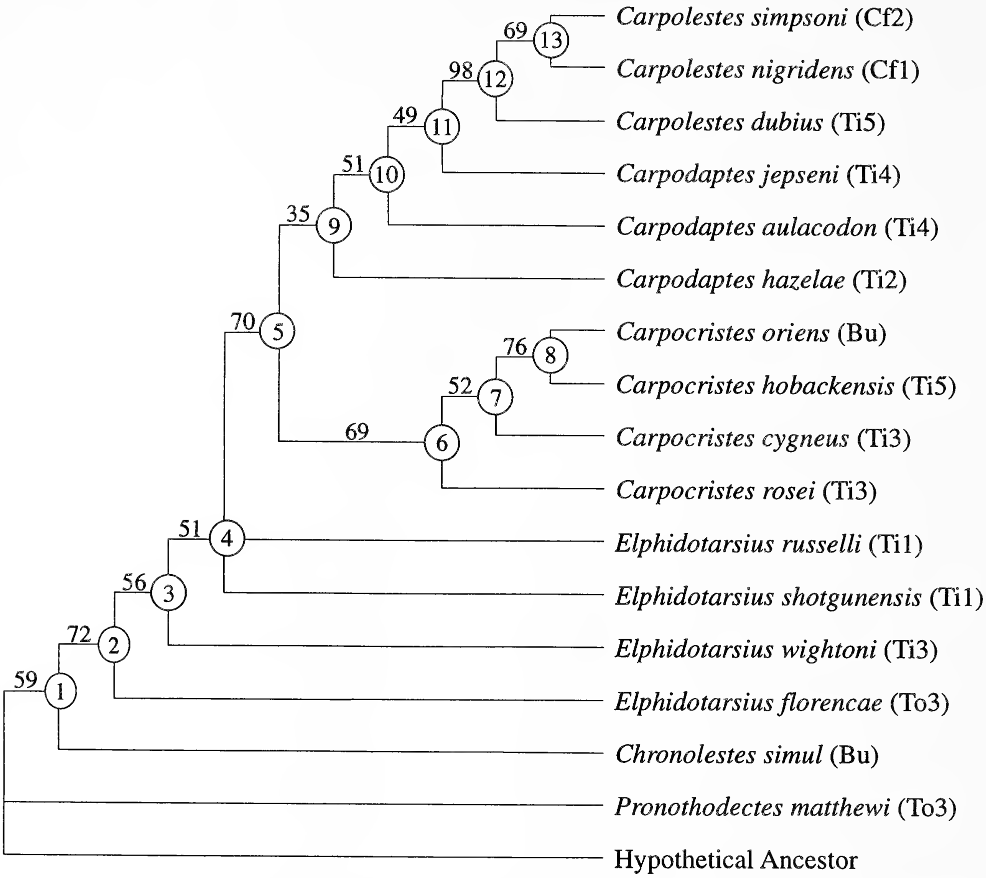

Fig. 4.—Strict consensus of nine most parsimonious trees recovered from branch-and-bound search in PAUP 3.1.1 (Swofford, 1993) of character-taxon matrix given in Appendix 2. For details regarding character status, see Appendix 1. Tree length = 75; consistency index (excluding uninformative characters) = 0.757. Numerical values above stems of clades indicate percent frequency with which those clades were supported in 100 bootstrapped trees. Earliest known stratigraphic occurrence of each species is given in parentheses. For details regarding stratigraphic occurrence and estimated antiquity of each species, see Appendix 3.

Using the ACCTRAN character-state optimization algorithm, synapomorphies supporting each node are as follows (see Appendix 1 for description of character states): Node 1 (Carpolestidae), Character 14 (0→1), Character 25 (0→1), Character 32 (0→1), Character 37 (0→1), Character 38 (0→1), Character 41 (0→1); Node 2 (Carpolestinae), Character 3 (0→1), Character 4 (0→1), Character 9 (0→1), Character 16 (0→1), Character 18 (0→1), Character 19 (0→1), Character 20 (0→1), Character 26 (0→1), Character 32 (1→3), Character 39 (0→1), Character 42 (0→1); Node 3, Character 5 (0→1), Character 6 (0→1), Character 11 (0→1), Character 12 (1→2), Character 40 (0→1); Node 4, Character 5 (1→2), Character 7 (1→2), Character 13 (1→2), Character 17 (0→1), Character 33 (0→1), Character 34 (0→1); Node 5, Character 22 (0→1), Character 24 (0→1), Character 32 (3→4); Node 6 (*Carpocristes*), Character 10 (0→1), Character 15 (0→1), Character 21 (0→1), Character 35 (0→1), Character 36 (0→1); Node 7, Character 32 (4→5); Node 8, Character 7 (2→3), Character 8 (0→1), Character 10 (1→2), Character 15 (1→2), Character 27 (0→1), Character 28 (0→1), Character 31 (0→1); Node 9, Character 23 (0→1); Node 10, Character 6 (1→2), Character 8 (0→1), Character 29 (0→1); Node 11, Character 32 (4→5); Node 12 (*Carpolestes*), Character 27 (0→1), Character 28 (0→1), Character 30 (0→1), Character 32 (5→7); Node 13, Character 8 (1→2).

advanced carpolestids. This supports the recognition of *Carpocristes* as a genus distinct from *Carpodaptes*, all species of which appear to share more recent common ancestry with *Carpolestes* than with *Carpocristes*. Given the phylogenetic relationships depicted in Figure 4, cladogenesis between *Carpocristes* and other carpolestids must have occurred sometime prior to the late early Tiffanian (Ti2). This inference is based on the earliest known occurrence of the *Carpodaptes* + *Carpolestes* clade, which is provided by *Carpodaptes hazelae* at Scarritt Quarry in the Crazy Mountains Basin of south-central Montana. All species of *Carpocristes* other than *C. oriens* are restricted to North America. Both phylogenetic and biostratigraphic data therefore imply that *Carpocristes* originated in North America prior to dispersing to Asia sometime during the late Paleocene (Beard and Wang, 1995; Beard, 1998).

In general, there is marked agreement between the tree topology depicted in Figure 4 and the stratigraphic ranges of carpolestid species. This can be quantified using Huelsenbeck's (1994) stratigraphic consistency index (SCI), which is the proportion of internal nodes on a cladogram that are consistent with the stratigraphic distributions of sister taxa divided by the total number of internal nodes. Of the 13 internal nodes in Figure 4, ten are consistent with the stratigraphic distributions of sister taxa, yielding an SCI of 0.769. Estimates of ghost lineage durations for the stratigraphically inconsistent nodes are based on correlation of Paleocene mammal-bearing strata from the Western Interior of North America with the Geomagnetic Polarity Time Scale (Butler et al., 1981, 1987; Berggren et al., 1995) and biostratigraphic correlations between North America and Asia proposed by Beard and Dawson (1999) (Appendix 3). The longest ghost lineage implied by the phylogeny depicted in Figure 4 and the stratigraphic distribution of carpolestid species is that between *Chronolestes* and Carpolestinae. The duration of this ghost lineage is equivalent to the difference between the earliest known occurrence of a carpolestine (provided by *Elphidotarsius florencae* in zone To3, estimated at 61.4 Ma) and the much younger occurrence of *Chronolestes* (Bumbanian, estimated at 55.8 Ma), which is roughly 5.6 Ma. A shorter ghost lineage of about 2.3 Ma duration separates the anachronistically young *Elphidotarsius wightoni* (zone Ti3, estimated at 58.3 Ma) from the earliest known occurrence of its sister taxon (zone Ti1, estimated at 60.6 Ma). In contrast, the duration of the ghost lineage implied by the earliest known occurrences of *Carpocristes* (Ti3, estimated at 58.3 Ma) and the *Carpodaptes* + *Carpolestes* clade (Ti2, estimated at 59.5 Ma) is only about 1.2 Ma.

Despite the stratigraphically dense succession of carpolestids known from Paleocene basins in western North America, significant episodes of their evolutionary history remain undocumented by the fossil record. The documentation of incompatibility between robust phylogenetic trees and the stratigraphic distributions of individual taxa is a useful endeavor because it highlights these elusive episodes of evolutionary history, thereby providing a guide to fertile areas of future research.

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APPENDIX 1

Character Descriptions, with Character Status in Italics

1. Laterocone or disto-apical cusp on I^1: absent (0); or present (1).

2. Mediocone on I^1: absent (0); or present (1).

3. Mesio-basal cusp on I^1: absent (0); or present (1).

4. Lingual crest on P^3: absent (0); or present (1).

5. Number of cusps on lingual crest of P^3: none (0); one (1); or two (2) (*ordered*).

6. Parastyle on P^3: absent (0); present (1); or present, with neomorphic cusp anterior to it (2) (*ordered*).

7. Number of buccal cusps posterior to paracone on P^3: none (0); one (1); two (2); or three (3) (*ordered*).

8. Parastylar lobe on P^3: does not project anteriorly with respect to lingual part of tooth (0); moderate anterior projection (1); or extreme anterior projection (2) (*ordered*).

9. Median crest on P^3: absent (0); or present (1).

10. Number of median crests on P^3: one (0); two (1); or three (2) (*ordered*).

11. Position of primary median crest on P^3: lingual, closely appressed to lingual crest (0); or labial, widely separated from lingual crest (1).

12. Parastyle on P^4: absent (0); present, single (1); or present, dual (2) (*ordered*).

13. Number of buccal cusps posterior to paracone on P^4: none (0); one (1); or two (2) (*ordered*).

14. Median crest on P^4: absent (0); or present (1).

15. Number of median crests on P^4: one (0); two (1); or three (2) (*ordered*).

16. Position of protocone on P^4: anterior (0); or central (1).

17. Number of lingual cusps on P^4: one (0); or three (1).

18. Crest running anterior to paracone on P^4: absent (0); or present (1).

19. Position of paraconule on P^4: anterior (0); or central (1).

20. Postparaconule crista on P^4: incomplete (0); or complete (1).

21. Size of upper and lower molars: larger than in *Carpocristes* spp. (0); or as in *Carpocristes* spp. (1).

22. I_3: present (0); or absent (1) (*irreversible*).

23. P_2: present (0); or absent (1) (*irreversible*).

24. P_3: double-rooted (0); or single-rooted (1) (*irreversible*).

25. Size of P_3: unreduced (0); or reduced or absent (1) (*irreversible*).

26. Plagiaulacoid P_4: absent (0); or present (1).

27. Vertical rib beneath ultimate apical cusp on lingual side of P_4: present (0); or absent (1).

28. Crest uniting penultimate apical cusp with talonid cusp on P_4: weak (0); or strong (1).

29. Vertical ribs beneath anterior apical cusps on lingual side of P_4: vertically oriented (0); or steeply inclined from base of tooth anteriorly to apical cusps posteriorly.

30. Position of P_4 talonid cusp: well below the level of M_1 trigonid (0); or elevated to near the level of M_1 trigonid (1).

31. Ultimate apical cusp on P_4: cuspate (0); or indistinct or absent, being incorporated within crest uniting main shearing blade of P_4 with talonid cusp (1).

32. Number of apical cusps on P_4: one (0); two (1); three (2); four (3); five (4); six (5); seven (6); or eight (7) (*ordered*).

33. Position of ultimate apical cusp (= metaconid) on P_4: slightly to moderately lingual to penultimate apical cusp (0); or directly posterior to it (1).

34. Position of apical cusps immediately preceding penultimate apical cusp (= protoconid) on P_4: slightly to moderately lingual to penultimate apical cusp (0); or directly anterior to it (1).

35. Position of ultimate apical cusp on P_4: near penultimate apical cusp (0); or more posterior in position, roughly equidistant between penultimate apical cusp and talonid cusp (1).

36. Posterolingual excavation on P_4: absent (0); or present (1).

37. Anteroposterior elongation of P_4: absent (0); or present (1).

38. Exodaenodonty on P_4: absent (0); or present (1).

39. Paraconid of M_1: not widely splayed relative to metaconid (0); or widely splayed (1).

40. Talonid notch on M_1: weak to absent (0); or strong (1).

41. Protoconid of M_1: same height as paraconid and metaconid (0); or taller than paraconid and metaconid (1).

42. Talonid of M_1: similar in anteroposterior length to that of M_2 (0); anteroposteriorly abbreviated (1).

APPENDIX 2

Taxon-Character Matrix Used in Parsimony Analysis

Hypothetical Ancestor	0000?	00?0?	?000?	00000	00000	0???0	?0???	00000	00
Pronothodectes matthewi	1100?	01?0?	?110?	00000	01000	0???0	?0???	00000	00
Chronolestes simul	0000?	00?0?	?0010	00000	01011	000?0	010?0	01100	10
Elphidotarsius florencae	???10	01?10	01110	10111	01001	10000	03000	01110	11
Elphidotarsius wightoni	???11	11010	12110	10111	011?1	10000	03000	01111	11
Elphidotarsius russelli	?????	?????	?????	?????	0????	10000	03110	011??	??
Elphidotarsius shotgunensis	?????	?????	?????	?????	000?1	10000	03110	01111	11
Carpodaptes hazelae	11112	12010	12210	11111	01111	10000	04110	01111	11
Carpodaptes aulacodon	?????	?????	?????	?????	0??11	10010	04110	01111	11
Carpodaptes jepseni	?????	?????	?????	?????	0????	10010	05110	01111	11
Carpolestes dubius	???12	22110	12210	11111	01111	11111	07110	01111	11
Carpolestes nigridens	10112	22210	12210	11111	01111	11111	07110	01111	11
Carpolestes simpsoni	10112	22210	12210	11111	011?1	11111	07110	01111	11
Carpocristes rosei	?????	?????	?????	?????	1???1	10000	04111	11111	11
Carpocristes cygneus	10112	12011	12211	11111	111?1	10000	05111	11111	11
Carpocristes hobackensis	?????	?????	?????	?????	11111	11100	15111	11111	11
Carpocristes oriens	???12	13112	12212	11111	110?1	11100	16111	11111	11

APPENDIX 3

Explanatory Notes for the Age Estimates Used Here for Carpolestids and Related Taxa, based on Biostratigraphy and Paleomagnetic Stratigraphy

Pronothodectes matthewi: Gidley Quarry, Crazy Mountains Basin, MT (To3). Assigned to upper part of Chron 27r, based on paleomagnetic data from Silberling Quarry, Crazy Mountains Basin and Rock Bench Quarry, Bighorn Basin (Butler et al., 1987). Absolute age estimated at 61.4 Ma (Berggren et al., 1995).

Chronolestes simul: Wutu Formation, Shandong Province, People's Republic of China (Bumbanian). Estimated to correlate with North American zone Cf2 based on biostratigraphy (Beard and Dawson, 1999). Assigned to lowest part of Chron 24r, based on paleomagnetic data from the Bighorn Basin (Butler et al., 1981). Absolute age estimated at 55.8 Ma (Berggren et al., 1995).

Elphidotarsius florencae: Gidley Quarry, Crazy Mountains Basin, MT; Rock Bench Quarry, Bighorn Basin, WY (To3). Assigned to upper part of Chron 27r, based on paleomagnetic data from Silberling Quarry, Crazy Mountains Basin and Rock Bench Quarry, Bighorn Basin (Butler et al., 1987). Absolute age estimated at 61.4 Ma (Berggren et al., 1995).

Elphidotarsius wightoni: University of Alberta localities DW-1 and DW-2, near Red Deer, Alberta (Ti3). Fossils possibly pertaining to this species were cited by Fox (1990:59) from Aaron's Locality (Ti1 or Ti2), but the stratigraphic range for the species is not extended here, pending formal description of the relevant specimens. Assigned to upper part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 58.3 Ma (Berggren et al., 1995).

Elphidotarsius shotgunensis: Keefer Hill local fauna (= Shotgun local fauna), Wind River Basin, WY (Ti1). Assigned to lower part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 60.6 Ma (Berggren et al., 1995).

Elphidotarsius russelli: Cochrane 2 locality, Porcupine Hills Formation, Alberta (Ti1). Assigned to lower part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 60.6 Ma (Berggren et al., 1995).

Carpocristes rosei: Ridge locality [= Ledge locality of Gazin (1956)], Bison Basin, WY (Ti3). Assigned to upper part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 58.3 Ma (Berggren et al., 1995).

Carpocristes cygneus: Swan Hills site 1, Alberta; Canyon Ski Quarry, Alberta; Roche Percée local fauna, Saskatchewan (Ti4). Several possible records from zone Ti3 (e.g., from University of Alberta locality DW-1 near Red Deer, Alberta; Police Point local fauna, Alberta) have been listed by Fox (1990). Additional specimens from the Judson and Brisbane localities in western North Dakota (Ti3) may also pertain to *C. cygneus*. Although the best samples of this species are known from Ti4 sites, the earliest known records of *C. cygneus* are provisionally considered to be Ti3. Assigned to upper part of Chron 26r, based on paleomagnetic data from the Crazy Mountains Basin and Bighorn Basin (Butler et al., 1981, 1987). Absolute age estimated at 58.3 Ma (Berggren et al., 1995).

Carpocristes hobackensis: Dell Creek Quarry, Hoback Basin, WY (Ti5). Assigned to middle part of Chron 25r based on paleomagnetic data from the Bighorn Basin, WY (Butler et al., 1981). Absolute age estimated at 57.0 Ma (Berggren et al., 1995).

Carpocristes oriens: Wutu Formation, Shandong Province, People's Republic of China (Bumbanian). Estimated to correlate with North American zone Cf2 based on biostratigraphy (Beard and Dawson, 1999). Assigned to lowest part of Chron 24r, based on paleomagnetic data from the Bighorn Basin (Butler et al., 1981). Absolute age estimated at 55.8 Ma (Berggren et al., 1995).

Carpodaptes hazelae: Scarritt Quarry, Crazy Mountains Basin, MT (Ti2); Cedar Point Quarry, Bighorn Basin, WY (Ti3); Hand Hills West locality, Alberta (Ti3); various localities in the Paskapoo Formation along the Blindman River near Red Deer, Alberta (Ti3); Joffre Bridge Roadcut, lower level, Alberta (Ti3). Earlier specimens that may pertain to this species are known from the Keefer Hill local fauna of the Wind River Basin, WY (Ti1) and from the Cochrane 2 site in Alberta (Ti1). However, pending fuller description of these specimens, the earliest reliable occurrence of *C. hazelae* is here regarded as Ti2. Assigned to the middle part of Chron 26r, based on paleomagnetic data from Scarritt Quarry, MT (Butler et al., 1987). Absolute age estimated at 59.5 Ma (Berggren et al., 1995).

Carpodaptes aulacodon: Mason Pocket locality, Animas Formation, San Juan Basin, CO (Ti4). Assigned to lower part of Chron 25r, based on paleomagnetic data from the local section (Butler et al., 1981). Absolute age estimated at 57.4 Ma (Berggren et al., 1995).

Carpodaptes jepseni: Divide Quarry, Bighorn Basin, WY (Ti4). Assigned to lower part of Chron 25r, based on paleomagnetic data from the Bighorn Basin (Butler et al., 1981). Absolute age estimated at 57.4 Ma (Berggren et al., 1995).

Carpolestes dubius: Princeton Quarry and nearby sites, Bighorn Basin, WY (Ti5). Assigned to middle part of Chron 25r based on paleomagnetic data from the Bighorn Basin, WY (Butler et al., 1981). Absolute age estimated at 57.0 Ma (Berggren et al., 1995).

Carpolestes nigridens: Bear Creek locality, northern Bighorn Basin, MT (Cf1); Big Multi Quarry, Washakie Basin, WY (Cf1). Assigned to early part of Chron 25n based on paleomagnetic data from the Bighorn Basin, WY (Butler et al., 1981). Absolute age estimated at 56.3 Ma (Berggren et al., 1995).

Carpolestes simpsoni: various localities in the northern Bighorn Basin, WY (Cf2-Cf3). Assigned to lowest part of Chron 24r, based on paleomagnetic data from the Bighorn Basin (Butler et al., 1981). Absolute age estimated at 55.8 Ma (Berggren et al., 1995).

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THE UPPER PALEOLITHIC BONE INDUSTRY OF KLITHI ROCK SHELTER, NORTHWEST GREECE

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ABSTRACT

Little has been published to date on the range of bone artifacts from the upper paleolithic of Greece, so even relatively small collections can yield significant information that assists in understanding the technology of the region in the Late Pleistocene. The Klithi rock shelter represents an important period (21,300–12,600 B.P.) just before the end of the Ice Age when paleolithic hunters moved into a previously uninhabitable area in order to hunt ibex and chamois. Their bone artifacts reveal that they conducted domestic activities in the rock shelter, wore ornaments, and obtained some objects outside the gorge through trade or travel. Manufacturing techniques were simple, but aspects of needle fabrication seem to indicate an indigenous process not reported in western Europe or the Near East.

KEY WORDS: bone artifacts, Greek archaeology, upper paleolithic

INTRODUCTION

The upper paleolithic site of Klithi is located about 40 km north of the city of Ioannina, the provincial capital of Epirus, in northwest Greece (Fig. 1). The site is situated in a rock shelter in the Voïdomatis gorge (Fig. 2) and contains deposits from 21,300–12,600 B.P. Excavated by a team of scientists headed by Geoffrey Bailey in 1983–1988, Klithi has yielded considerable information about the repeated use of the rock shelter over a span of 9,000 years.

The Klithi shelter (Fig. 3) is 25 m wide at the entrance, extends back into the rock 10 m, and has an overhanging ledge 40 m above its floor (Adam, 1989:224). Excavations revealed deposits of accumulated natural scree and rockfall from the shelter's ceiling, hearths and ash deposits, a lithic industry based heavily on flakes and backed bladelets, red ocher, faunal remains dominated by ibex and chamois, marine and terrestrial mollusk shells, and a small assemblage of bone artifacts.

The early prehistory of Epirus is poorly known, partly because of the rugged regional terrain and partly because of the limited investigation it has received until recently. Based on its position, northwest Greece might have served as a cultural conduit between the Near East and Europe during the paleolilthic, but instead the glaciated mountains of the region probably acted as a hurdle that impeded the flow of people and ideas during the Pleistocene.

THE ENVIRONMENT

Epirus is a region of great topographic and geographic variation. In the northeastern part of Epirus the Pindus Mountains reach heights over 2,500 m and form deep vertical river gorges. Albania, to the northwest, is also mountainous. On the southwest Epirus is bounded by the Ionian Sea and on the south by the Gulf of Arta and the low relief of Akarnania.

During the last glacial maximum between 20,000–16,000 b.p., Epirus probably

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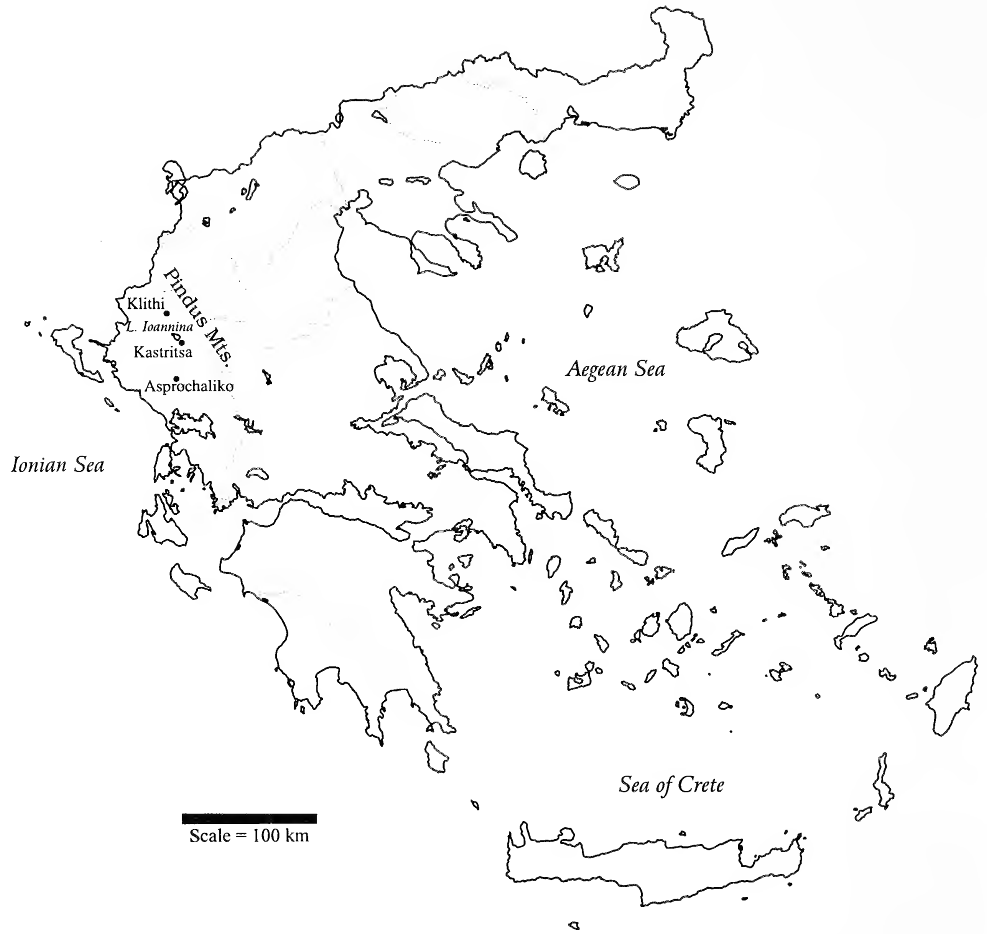

Fig. 1.—Map of Greece locating Klithi, Kastritsa, and Asprochaliko.

presented an inhospitable environment for human occupation (Bailey et al., 1990). Bailey et al. (1993) attribute the paucity of sites from this temporal range to low biomass, snow cover in winter, and a shortage of sources of water.

According to pollen studies (Bottema, 1974; Willis, 1989), the Late Würm of this area was cold and semi-arid. The vegetational regime was forest-steppe, consisting mainly of *Artemisia*-dominated grasslands associated with groves of oak and pine. Winters were probably 5–6° C colder than today and summers were arid and 2–3° C cooler than present (Prentice et al., 1992).

Today the site of Klithi is located about midway up a steep, vertical-sided gorge. At an elevation of 500 m, it is surrounded by Mount Gamila (elevation 2,500 m) and other peaks of the Pindus chain. Currently, the rock shelter is precipitously perched 30 m above the Voïdomatis River. The difficult access to the shelter at present is somewhat deceptive, however, because the valley has undergone significant changes in the last 10,000 years. At the time of occupation, the valley was partially filled with a river terrace referred to as the Aristi Unit up to just 12 m below the rock shelter (Bailey et al., 1990). The river was a few

Fig. 2.—Voïdomatis river gorge near Klithi rock shelter.

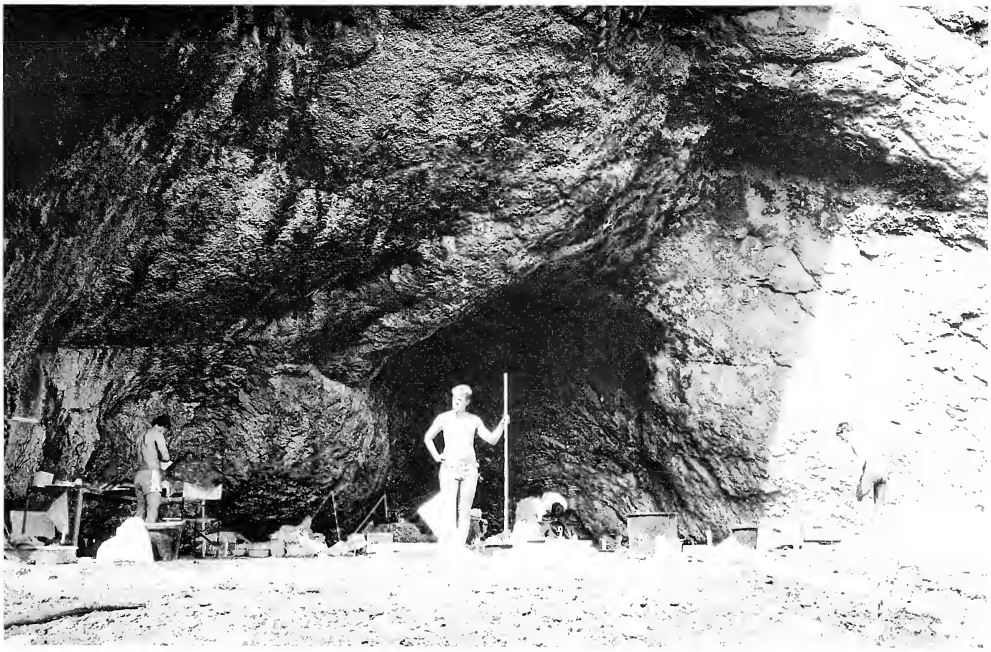

Fig. 3.—Klithi rock shelter.

meters below that and the contours of the valley would have been broadly U-shaped. The terrace's geologic constituents made it a suitable source for the small nodules of flint used by the occupants of Klithi for manufacturing stone tools (Adam, 1989:225; Bailey et al., 1990:148). Much of the terrace was gouged out in the Holocene to expose the greater depths of the gorge.

The broad river valley and rising mountains apparently provided an ideal environment for ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*), the dominant herbivores in the faunal assemblage at Klithi. With their gentler topography and lower elevations, other regions like the Ioannina Basin to the south and the coast to the west were home to red deer (*Cervus elaphus*).

PALEOLITHIC SITES IN THE REGION

In the 1960s, Eric Higgs (Dakaris et al., 1964; Higgs and Vita-Finzi 1966; Higgs et al., 1967) led several expeditions into northwest Greece searching for paleolithic sites. His surveys revealed three of particular interest: Asprochaliko, Kastritsa, and Klithi (Fig. 1). The oldest site in Epirus containing a dated stratigraphic sequence is Asprochaliko, an open-air occupation near the coast containing (from bottom to top): Typical Mousterian, Micro-Mousterian, and upper paleolithic deposits. The earliest upper paleolithic radiocarbon date is 26,100 ± 900 b.p. (uncalibrated) (Bailey et al., 1983:22). The lower levels of the upper paleolithic may represent Gravettian, moving up into Epi-Gravettian comparable to the Italian industry known from 20,000 b.p. on (Palma di Cesnola, 1976; Bailey et al., 1983:30). More recent dates of 17,200 ± 400 b.p. and 13,700 ± 260 b.p. for deposits on the talus slope appear unreliable because of mixing (Bailey et al., 1983:22).

Kastritsa is an upper paleolithic site located in a rock crevice near Lake Ioannina about 40 km south of Klithi. Kastritsa has a longer temporal span than Klithi, ranging from around 20,200 ± 480 b.p. (Bailey et al., 1983:29) to 12,400 ± 210 b.p. (Adam, 1989:252), but ends 2,000 years before the abandonment of Klithi. Based on its selection of stone tools, Kastritsa shows some affinity with the Epi-Gravettian industries of Italy after 20,000 b.p. (Bailey et al., 1983). Its location in the lowlands near the lake impacted strongly on the economy of its inhabitants and their raw materials for bone artifacts. Unlike Klithi, where the occupants survived primarily on ibex and chamois, the Kastritsa people were mainly red deer hunters. The bone artifact assemblage from Kastritsa is compared to and contrasted with Klithi's assemblage in this report.

THE BONE ARTIFACTS FROM KLITHI

The sample of bone artifacts (Table 1) analyzed from the 1983–1985 excavations at Klithi is small (n = 38 objects) in comparison to the abundance of unmodified faunal remains and the vast lithic assemblage. Despite this fact, the collection yields considerable information about the upper paleolithic bone technology in this locality and can be productively compared to the collections from neighboring regions, like the Ioannina Basin. The worked bones are mostly derived from cultural layers that date to between 17,400–12,600 B.P. (calibrated). Adam and Kotjabopoulou (1997) examined additional bone tools from later excavations, but no significant new information was uncovered.

The osseous artifacts contribute to the interpretation of the site by providing possible evidence for seasonal migration of hunters. The faunal material shows a

Table 1.—*Klithi Bone Artifacts.*

Type	Part	Number	Provenance	Spit	Layer	Taxon	Element
Awl	whole	B5805	P25 D 900	13	16	mammal	long bone
Awl	whole	B5608	P 24 C 900	14	16	mammal	long bone
Awl	whole	A46	W29 8 W1	—	17/18	mammal	long bone
Awl	whole	C5419	Q27 CD 903	13	18	mammal	long bone
Awl	base	B3208	Q210 900	16	14	mammal	long bone
Awl	shaft	A 23	W28/29 8 S	—	15–18	mammal	long bone
Awl	shaft, tip	B4810	Q24 C	15	16	mammal	long bone
Awl	shaft	C3023	BD 665	—	—	*Capra ibex/Rupicapra*	tibia
Awl	shaft	C7007	X29? C/A 901	—	—	large mammal	long bone
Awl	shaft	B2015	R22 D 605 (907)	16	15	mammal	long bone
Awl	tip	A56-3	W29 8 W	—	17/18	mammal	long bone
Awl	tip	A71	W31 W1	21		mammal	long bone
Awl	tip	B5805	P25 D 900	13	16	mammal	long bone
Awl	tip	C6026	P26 C	13	—	mammal	long bone
Awl	tip	B3005	Q22 A 901	15	15	mammal	long bone
Awl	tip	B2412	R20 B 903	16	15	mammal	long bone
Awl	whole	B5007	Q25 C 901	13	16	mammal	long bone
Awl	whole	C1014	S22 DD 901	16	13	mammal	long bone
Awl	whole	C6712	B/B	—	—	*Capra ibex/Rupicapra*	metatarsal
Awl	tip	C5410	Q27 DD 901	11	16	mammal	long bone
?Awl	shaft	C1014	wet sieve	—	—	mammal	long bone
Needle	base	C4618	R27 BC 901	13	16	mammal	long bone
Needle	base, shaft	A 53	W29 8S	—	—	mammal	long bone
Needle	whole	C6031	D C	—	—	mammal	long bone
Needle	tip	B4206	R25 A L2, 901	14	16	mammal	long bone
Needle	tip	C6214	P27 BC 903	12	18	mammal	long bone
Needle off-cut	whole	C5223	A/C 905	—	—	mammal	long bone
Needle off-cut	whole	B5208	Q26 D 903	13	16	mammal	long bone
Needle off-cut	whole	B5008	Q25 C #625 (900)	13	16	mammal	long bone
Notched bone	fragment	C6713	A D W27	—	—	*Capra ibex/Rupicapra*	metapodial
Notched bone	fragment	B3208	Q21 D 901	16	14	small mammal	long bone
Notched bone	fragment	A62	W29/30 8 S -1 W1	—	17/18	mammal	long bone
Notched bone	fragment	A39	W29 8 W1	—	15/16	mammal	long bone
pendant	whole	C6215	P27 AD 901	12	18	*Cervus elaphus*	canine
pendant	whole	C0416	D/A 902	—	—	*Cervus elaphus*	canine
pendant	whole	B2010	R22 D 901	15	15	*Cervus elaphus*	canine
pendant	whole	C1421	S20 BA	17	15	*Cervus elaphus*	canine
Worked antler	above tip	B3001	Q22 A 903	15	14	*Cervus elaphus*	antler tine

strong preference for hunting ibex and chamois in the gorge. Curated artifacts made from red deer canines and antler indicate that the Klithi people either hunted in other areas or, less likely, received trade items from outside the immediate vicinity of the rock shelter.

The excavations at Klithi were very meticulous. The site was excavated in quarter-meter square units, recording artifact depth by natural layers and 5 cm arbitrary levels. Soil was dry- and wet-sieved with fine mesh. Flotation samples were taken in some quads and one of these samples yielded the largest awl (Fig. 6). All artifacts were recorded three-dimensionally from the datum. Because of Greek antiquities laws, all bone artifacts had to be analyzed in Greece and therefore could not be removed for scanning electron microscopic analysis or further study.

Although both unworked and worked bones at Klithi were often severely comminuted by roof fall, trampling, and natural pedoturbation, the surfaces of most of the artifacts are relatively unmarred by taphonomic processes. The limestone rock shelter provided a nearly ideal environment for bone preservation because of its alkalinity. Three of the objects exhibit root-etching, one is pitted by roots or some other natural agent, and the surface of one is partially exfoliated. The fairly good state of preservation allows interpretations of manufacturing techniques and possible use to be made in many cases.

Burning of bone artifacts was quite common, with ten (26%) of the pieces showing evidence of direct exposure to heat. The best explanation for the burning of the worked bone is that the objects were discarded or lost in or near hearths. The rock shelter floor is strewn with accumulations of osseous material, some of which is incorporated in the hearths.

In general, the bone artifacts are in deposits consisting of a mixture of faunal material (food refuse) and lithic tools and debitage. These deposits do not clearly indicate functional work areas, such as manufacturing stations, and specific locations of bone tools do not, unfortunately, assist in extrapolating the functions of the objects or the materials upon which they were used.

Raw Materials.—Given the volume of the faunal assemblage, it is clear that raw material for the manufacture of bone implements and ornaments was plentiful. Although most of the artifacts were made on medium mammalian long bones that do not retain identifiable features, the cortical thickness and overall dimensions of the objects suggest that they were manufactured from the limb bones of ruminants within the size range of the predominant species, ibex and chamois. There was just one example each of the use of a long bone of a small mammal (fox-sized) and a large mammal (red deer-sized).

Antler, whether modified or not, is extremely rare in the rock shelter deposits. This is not surprising, given that the rocky terrain and mountain slopes that surround the site are better suited to ibex and chamois than to cervids. There is a sharp contrast between the use of a major resource like antler at Kastritsa, in the Ioannina basin and Klithi in the Voïdomatis gorge. Only a single antler tine (field number B3001) shows cultural modification at Klithi, whereas Kastritsa produced numerous pieces of worked antler. The shortage of antler as a raw material at Klithi appears to be the most important factor in the differences in tool types between the two areas.

Despite the rarity of antler and postcranial elements of red deer, their canines do occur in the site as pendants. The frequency of these isolated teeth at Klithi indicates a cultural preference which must have involved curation of a product obtained either during forays outside the immediate hunting territories or derived through trade with neighboring people.

Manufacturing Techniques.—The range of techniques employed in making bone artifacts at Klithi is somewhat limited. Fortuitous splinters of long bones, probably obtained when breaking bone for marrow extraction, were modified into artifacts by means of simple longitudinal scraping. The most efficient method of scraping bones to shave off excess material is to use the stout edge of a burin facet. Burins are in the Klithi lithic assemblage, although they are not extremely common (Adam, 1989:240). Other tools, including the edges of unretouched flakes and the dorsal ridges of flakes, can also be used, but are normally less effective.

Because most tools were made by scraping splinters of broken bone, manufacturing debitage is not common. The only debitage that has been observed in this collection consists of tabular offcuts produced when needles were finished (Fig. 4 A–C). After the needle shaft and point were shaped, the basal tab that was used to hold the needle blank during manufacture was removed by making an annular groove around the needle shaft where it intersected with the tab and then snapping the tab off at that point (see description under Needles and Needle Debitage heading). Evidence of the groove-and-snap technique was not documented among any other bone artifacts, although it may have been used rarely to cut out long awl blanks.

Sawing with a sharp stone blade was performed to make a series of short, transverse notches on large mammal bones, the function of which is unknown.

Perforations were made by two methods: gouging and drilling. Gouging, a technique observed only on perforated canine pendants, was done by repeatedly incising back and forth in one spot with a pointed tool, such as a piercer, graver, or tip of a burin, to form a short groove or trough. After a groove was made on one side, the object was turned over and a similar trough was made on the opposite surface until the bone was very thin at the center of the trough. A small hole could then be easily made by punching through the dividing wall with the same stone tool. The opening was then enlarged and smoothed by reaming it out with the piercer or by drilling.

Biconical drilling, sometimes using a very delicate drill, was employed in the manufacture of the eyes of needles. Biconical drilling involves the rotation of a stone drill until a pit is made through about half the thickness of the material. The object is then turned over and a similar pit is drilled in the opposite side in the same area until the two pits connect and a perforation is made through the material. The opening can then be enlarged by reaming. The profile of the perforation, as the term biconical implies, is hourglass-shaped in outline. This is because a stone drill is usually tapered, with the narrower part at the tip. Reaming opens up the center and reduces the conical slope of the perforation, however. The needles show that a flat surface was first prepared on the basal portion of the shaft so that the drill would not slide off the narrow, rounded surface. It is likely that a tiny pit was made with the tip of the drill by hand at first to "spot" the drill so that it did not slip when rotated.

Light grinding with an abrader, probably made of local granular stone, was performed on the basal end of one needle (field number C4618) to smooth its ragged surface after the tab was removed by the groove-and-snap technique.

The variety of manufacturing techniques expressed in the bone artifacts from Klithi is limited and most of the objects could have been made within a few

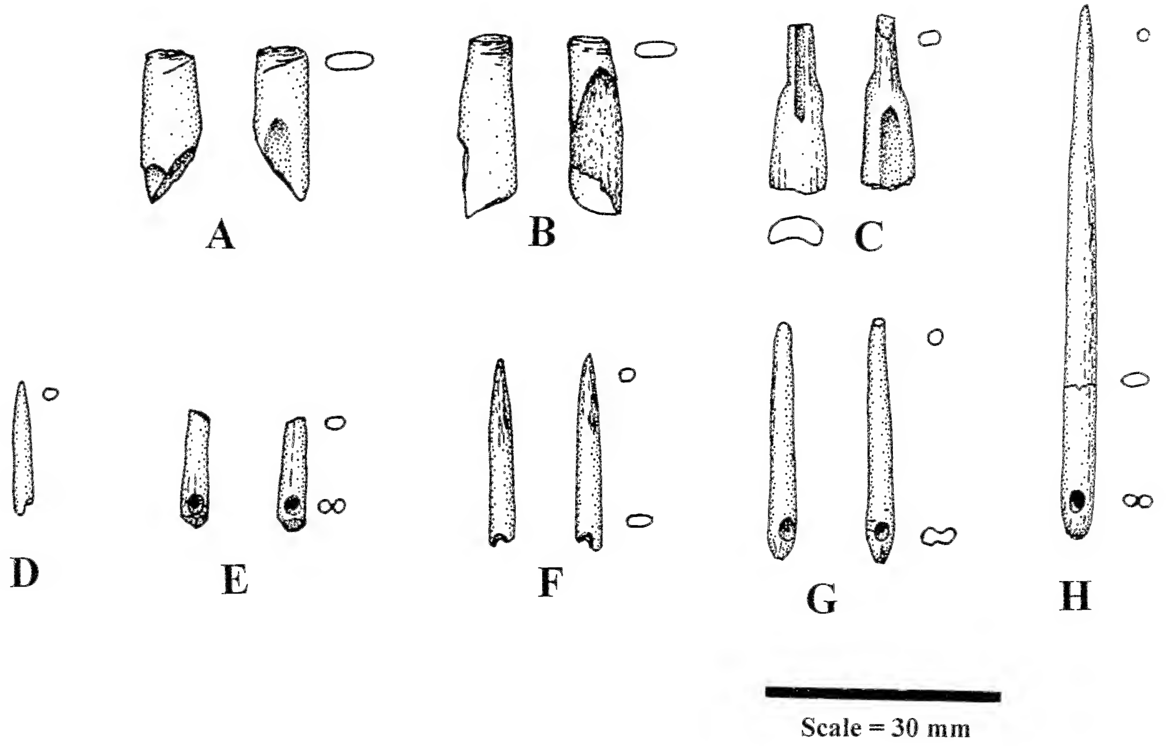

Fig. 4.—Needle off-cuts and needles (with cross-sections): A. needle off-cut (C5223), B. needle off-cut (B5208), C. unfinished needle with tab still attached (B5008), D. needle shaft and tip (B4206), E. needle base (C4618), F. needle (C6214), G. needle (A53), H. needle (C6031).

minutes. Only the needles demonstrate a considerable investment of time and labor. Further details of the step-by-step manufacturing processes are provided in the description of individual artifact types.

Awls.—The awls in this collection (Fig. 5) were made on fortuitous splinters by sharpening one end by means of longitudinal scraping with a stone tool such as a burin. This easy process leaves behind no by-products of manufacture, except other fragments indistinguishable from unutilized products of marrow extraction and very fine shavings, which are not likely to be recovered. Scraping traces extend up the edges of the shaft on only five of the awls (field numbers A46, B3208, C6712, C3023, and C5419). The others retain their unmodified fracture edges and the original outline of the splinter except at the tip.

One awl (Fig. 6) was shaped extensively, however. It was made on a metatarsal of a ruminant (ibex/chamois-sized) and retained a small portion of the proximal articular surface at the base. The narrow shaft was scraped longitudinally over its entire surface, giving it an oval cross section and straight, gradually tapering sides.

Artifacts made on splinters that are only modified slightly are generally asymmetric and irregular in shape. In the case of awls, it is mainly the tip, i.e., the functional part, which is limited by certain size and shape constraints and therefore receives the most attention during manufacture. Previous research (Olsen, 1984) has shown that the optimal awl tip for working hides or making normal-sized coiled baskets has a round to oval cross section and measures less than 4 mm in diameter (measured at a standard point 5 mm up from the end). For the seven awls from Klithi from which measurements could be taken, the average tip width is 2 mm and the average thickness is 1.8 mm (Table 2). None exceeds 2.5 mm in diameter. This means that these artifacts are too delicate to have been used as projectile points, but would have been quite suitable for piercing soft hides or for weaving fine coiled baskets. Seven of the awls exhibit use polish at the tip and partially up the shaft along the edges. Polish on bone tools has not proven to be reliably characteristic for particular contact materials.

Awls from Kastritsa were also made on splinters, but because red deer bones served as the common raw material, overall dimensions and cortical thicknesses are often much greater for the Kastritsa awls than for the small splinter awls made on ibex or chamois bones at Klithi.

Needles and Needle Debitage.—The needles from Klithi (Fig. 4) were made in a way that is significantly different from those common in other European and Near Eastern paleolithic to neolithic sites (Stordeur, 1977, Stordeur-Yedid, 1978). The more common method consisted of making two semi-parallel grooves in a long bone and then removing a carefully-shaped blank by means of the groove-and-snap technique (also known as the groove-and-splinter technique).

Needles at Klithi, however, were made from fortuitous splinters of slender outline obtained by shattering long bones (Fig. 7A). The method of manufacture involved scraping the splinter with longitudinal strokes down all sides with a burin or similar tool until it had the proper morphology (Fig. 7B). By retaining a broad tab at the base of a needle blank, the worker could grip the piece firmly while scraping down the narrow shaft with the edge of a burin facet. This was done so the needle could be shaped from base to tip without the fingers getting in the way. It also eliminated the difficulty of trying to hold a thin, delicate needle while scraping it with considerable pressure. When the needle shaft had been properly shaped so that its sides were straight and slightly tapered and its cross section was round to oval, the tab was removed from the base by sawing an

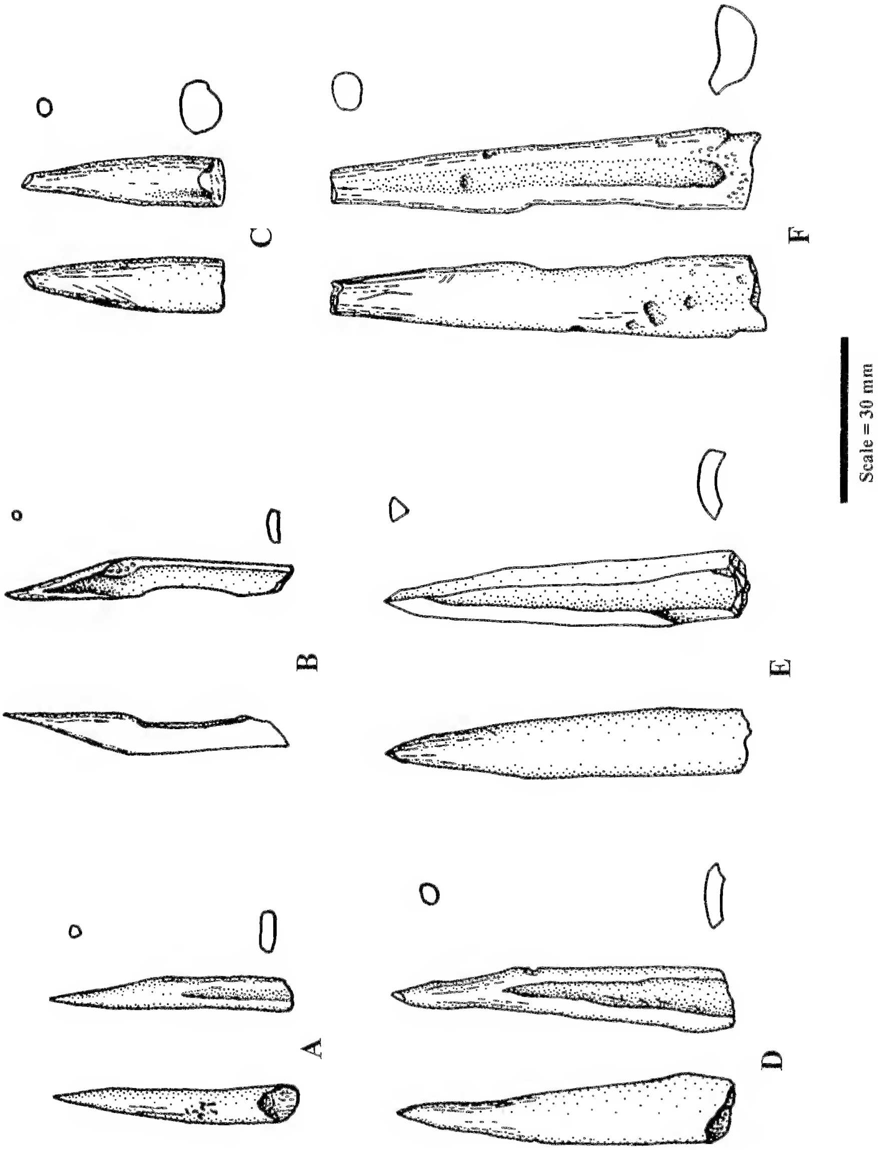

Fig. 5.—Awls: A. C1014, B. B5007, C. C7007, D. B5608, E. B4810, F. awl made on ibex/chamois tibia, C3023.

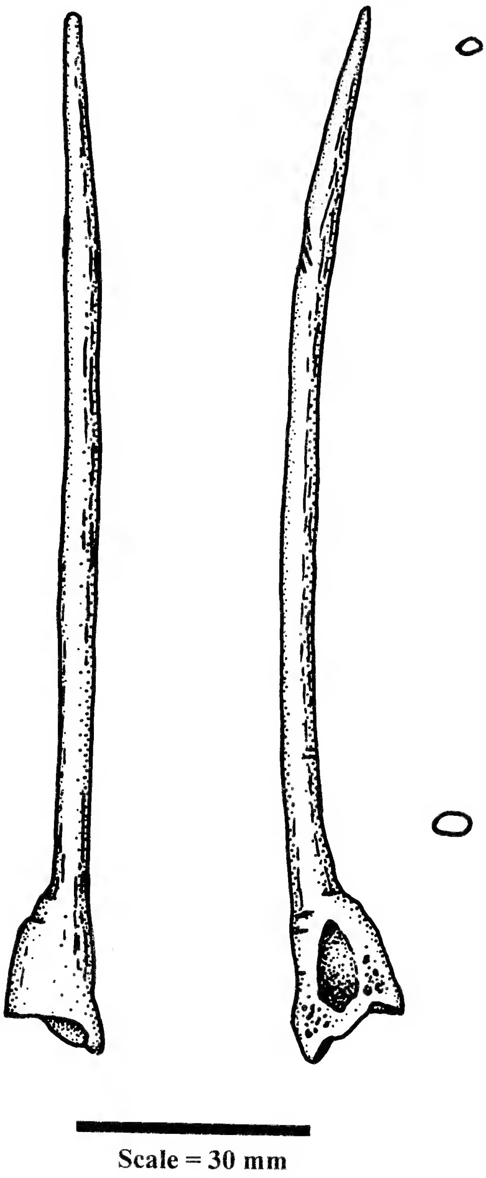

Fig. 6.—Two views of large awl made on an ibex/chamois metatarsal (C6712).

annular groove around the shaft and snapping it in two (Fig. 7C). This produced a tabular off-cut which retained the rough edges of the original splinter. Two of these off-cuts (Fig. 4A, B) were recovered, as well as the base of an unfinished needle with the tab still attached (Fig. 4C). Each tab exhibits traces of the termini of longitudinal scraping facets and annular incisions made by the groove-and-snap technique that frees the tab from the needle. The presence of manufacturing debitage and an unfinished piece indicates that needles were made on site at Klithi.

Table 2.—*Awl Tip Dimensions.*

Artifact #	Tip Width (mm)	Tip Thickness (mm)
A46	2.00	1.80
B3005	1.60	1.60
B5007	1.50	1.50
B5805	1.80	1.80
C1014	2.10	2.00
C6026	2.50	1.70
C6712	2.50	2.00
Mean	2.00	1.80

Evidence for the removal of a tab by the groove-and-snap technique is visible on the base of a needle from Kastritsa, as well.

As the manufacturing process continued, the base of the needle was abraded to smooth away the rough manufacturing traces left when the tab was removed. Direct evidence of abrading is visible on one needle base (Fig. 4E), but is not detectable on others because use polish has obliterated any possible trace of it.

Before the eye was made, two opposing surfaces near the base were scraped flat to ease spotting of the drill (Fig 7D). This is clearly demonstrated by the scraping facets on the bases of two needles (A53 and C4618) (Fig. 4G).

One unfinished (Fig. 4G) and three finished needles (Fig. 4E, F, H), retaining all or part of their eyes, show that these perforations were made by means of biconical drilling. Very fine holes were made by first drilling on one side of the base until the middle was reached and then turning the needle over and drilling on the opposite side until the perforations met (Fig. 7E). The unfinished needle

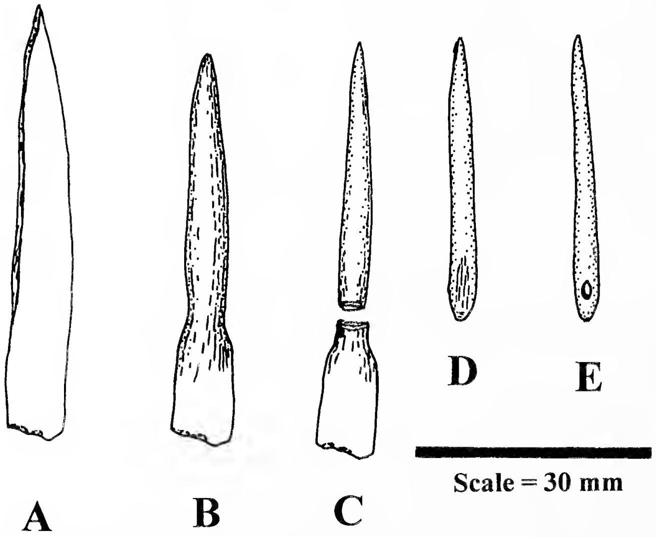

Fig. 7.—Needle manufacturing stages: A. an appropriately-shaped unmodified splinter is selected, B. the needle preform is shaped by longitudinal scraping, C. the tabular off-cut is removed by the groove-and-snap technique, D. the base is ground and the basal shaft is flattened to spot the drill where the eye will be made, E. the eye is made by biconical drilling.

Table 3.—*Needle Tip Dimensions.*

Artifact #	Tip Width (mm)	Tip Thickness (mm)
B4206	1.20	1.20
C6031	1.50	1.50
C6214	1.60	1.20
Mean	1.40	1.30

(Fig. 4G) was apparently abandoned because it was drilled too close to the edge from both sides and the two holes are misaligned.

One large needle (Fig. 4H) was recovered nearly intact. Its length is about 7 cm, basal width is 3.5 mm, and basal thickness is 1.2 mm. The tips of three needles are preserved and could also be measured (Table 3). The average tip width and thickness for needles is less than that of splinter awls.

Most of the needles show some use polish at the tip and along the shaft. One needle tip (field number C6214) has a polished shaft and overlying scraping facets at the end indicating that it was resharpened after use. Handling polish on the base of the unfinished needle (Fig. 4G) suggests that this tool was recycled into an awl when drilling of the eye failed.

Notched Bones.—An interesting, but perplexing group of artifacts from Klithi consists of four long-bone shaft fragments, each of which has one or more rows of short, transversely incised lines (Fig. 8D–G). In all of the examples, the surface of the bone was first prepared by longitudinal scraping to smooth it and remove rugosities. Transverse notches or grooves were then made by sawing with a sharp stone flake or blade. All the fragmentary pieces have from eight to ten notches preserved per row, but there is no way to determine how many notches a whole artifact would have had. One of the fragments (Fig. 8D), made on an ibex/chamois metapodial, has two parallel rows of incisions. Powdered red ocher was rubbed into the notches on two of the specimens (Fig. 8D–E). Three of the notched bones were charred brown to light gray (Fig. 8D–F).

Only one of these artifacts bears a polish on the notched surface (Fig. 8F). Because the notches are not worn in three of the objects and are filled with pigment in at least two, it is unlikely that they served as musical sounding rasps (Queen, 1978; Olsen, 1979; Lund, 1981). They may, instead, have been parts of ornaments (none are complete) or perhaps were tallies of some sort. The pigment could have been used for decorative purposes or simply to make the incisions on the clean white bone more visible.

Notched bones are found in the upper paleolithic of France beginning with the Chattelperonian and occur in the Near East at such sites as Mugharet el Kebara (Garrod, 1954:177), the terminal Aurignacian of ha-Yonim (Davis, 1974), the upper paleolithic of Ksar Akil (Tixier, 1974), and the Kebaran of Jiita (Copeland and Hours, 1977).

No notched bones were identified among the Kastritsa faunal material.

Red Deer Canine Pendants.—Four perforated red deer canines were found in the Klithi excavations (Fig. 8A–C). These were made by first gouging a shallow trough in the tooth root on both sides, followed by punching a small hole through the thinnest part of the wall between the grooves, and reaming or drilling the perforation from both sides to open it up to the desired diameter (2.7–4 mm).

Two of the teeth (Fig. 8B, C) show polish that indicates that a thong or cord passed through the hole and rubbed on the top of the perforation's rim as the

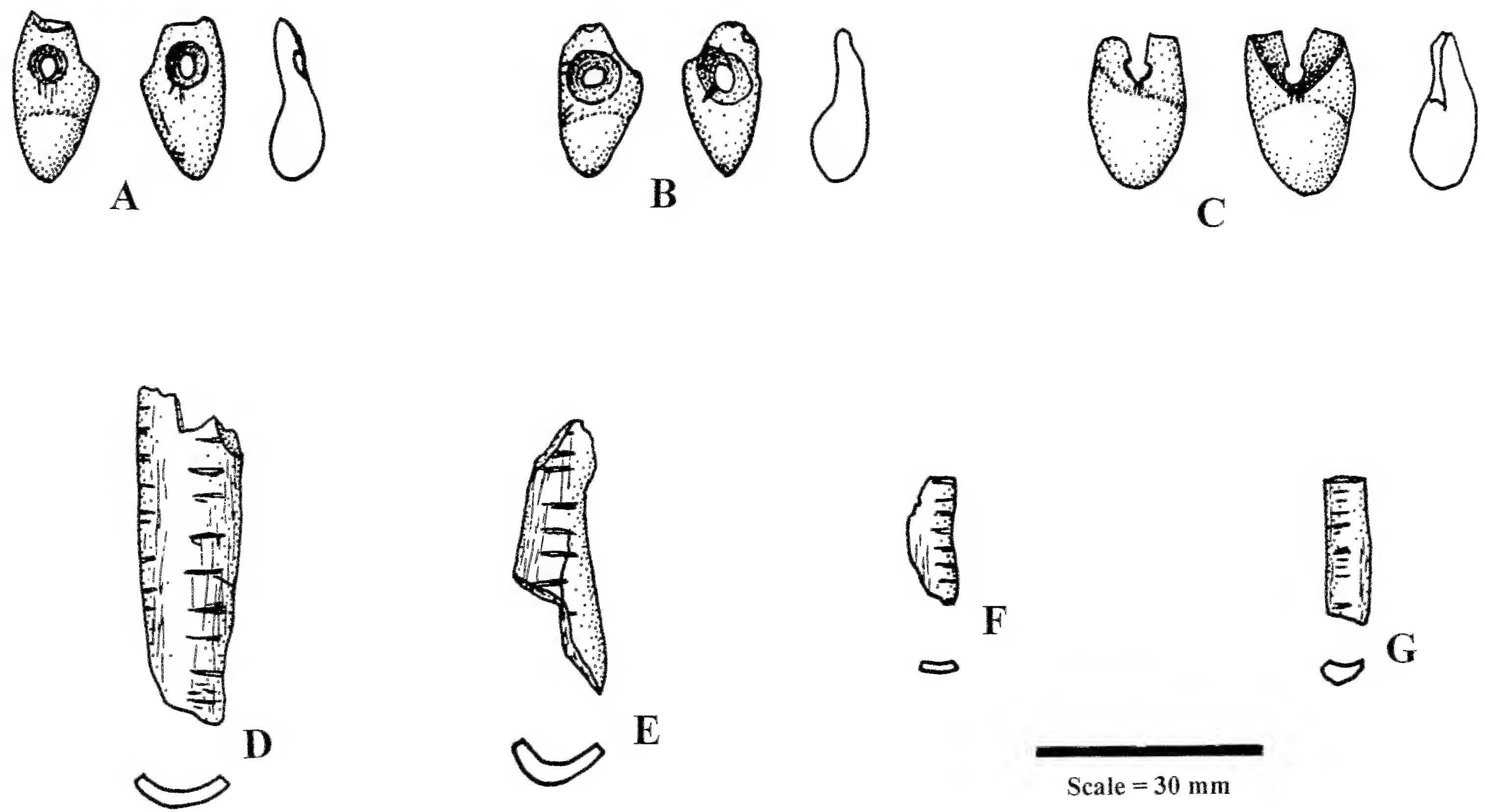

Fig. 8.—Red deer canine pendants (A–C) and notched bones (D–G): A. B2010, B. C1421, C. C6215, D. C6713, E. A62, F A39, G. 3208.

tooth hung downward. The teeth could have either been attached to a necklace or sewn to clothing or bags.

Deer canines were significant objects across Europe and the Near East in prehistoric times. Generally only occurring in male deer, they were apparently quite prized by a number of cultures. Kastritsa produced at least ten canine pendants and many more unmodified canines, but there red deer is the dominant animal in the faunal assemblage. At El Wad, in Israel, a Natufian headdress included bone beads carved to resemble deer canines—a kind of counterfeiting of a rare commodity (Garrod and Bate, 1937). Similar globular bone beads and genuine perforated canines have been found at ha-Yonim Cave (Bar Yosef and Tchernov, 1970).

At Klithi, it seems peculiar to find four of these objects because antler and deer bones are rare in the faunal assemblage. What this may suggest is that some of the occupants of Klithi ventured outside the gorge on hunting forays, as part of their seasonal round, perhaps downstream on the more open flood plain of the Voïdomatis where red deer would find a more suitable habitat. Otherwise, the canine pendants may represent trade objects from other cultures in neighboring regions. These pendants would have been "curated" simply by wearing them, perhaps for years before they finally broke or were dropped.

Worked Antler Tine.—Only one piece of worked antler appears in this collection. It consists of a tine fragment that has been scraped down to sharpen the tip. The most logical use of this artifact would be as a pressure flaker, but unfortunately the end that would have borne traces of use wear has been broken off.

CONCLUSIONS

It is useful to make comparisons between the Klithi bone artifacts and those from the nearby site of Kastritsa. The bone technology of the two sites is basically the same, with the modifications being made on splinters by scraping with a stone tool. Awls, needles, and perforated canines occur at Kastritsa and Klithi. In addition, however, Kastritsa yielded large quantities of bipointed antler projectile points and grooved ruminant incisors that could have been sewn on clothing or worn as pendants. Because many of the Kastritsa awls are made on red deer long bones and occasionally retain an articular condyle, they are significantly larger than the splinter awls from Klithi made from smaller chamois or ibex bones. The differences between the two bone assemblages reflect availability of specific raw materials (i.e., red deer incisors, antlers, and bones) at Kastritsa, rather than any real technological dissimilarities. No substitutes for antler points were made from ibex or chamois long bones at Klithi, perhaps because bone is less resilient and more susceptible to shattering on impact than antler (MacGregor and Curry, 1983; Arndt and Newcomer, 1986). The cortical thickness of ibex and chamois bones is also at the lower end of the range that is normally required to make a reliable, reusable projectile point. A small bone bipoint was found at Kastritsa, but this may have been a gorge or barb from a composite weapon used for fishing or hunting.

When the Kastritsa and Klithi lithic assemblages were compared (Adam, 1989: 250–251), there were numerous technological and typological differences, as well as similarities. Some of the variance can be attributed to the fact that most of the lithic material from Klithi consisted of small, brittle pieces of flint from the Voïdomatis river bed, while more variety in size and quality was available at Kastritsa. This difference in lithic raw material parallels the differences observed in the bone artifact assemblages, where antler was available at Kastritsa. Affinities are strong in both bone and stone assemblages. However, several stone tool types found at Kastritsa are missing in the Klithi assemblage, and there are some important details that differ in lithic production techniques (Adam, 1989; Bailey, 1997). These significant differences suggest that contemporaneous levels of the two sites represent two related cultures, rather than the same culture.

The collection from Klithi, although small, has already yielded information not only about bone artifact technology, but also regarding how adjustments are made to suit the availability of raw material and how some of the stone tools, such as burins, piercers, and drills, may have been employed. The presence of red deer canines and a fragment of worked antler suggests that some artifacts or raw material may have been brought in from hunting forays to other areas or through trade. Manufacturing debitage from needles indicates that these fine objects were made at Klithi.

Analysis of small collections of bone artifacts from upper paleolithic sites in this poorly known region is important in establishing the extent of contact between Greece and its neighbors at this time. Almost all manufacturing techniques for bone industries were established in the Near East and western Europe during the upper paleolithic, so learning how the industry was advancing in an intermediate location like Epirus can be quite instructive. This relatively isolated region shows only minimal use of the groove-and-snap technique compared to its neighbors, but also documents a rather innovative method of needle manufacture.

The worked bones at Klithi are derived from 3 m of cultural layers that date to between 21,300–12,600 B.P. (Gowlett et al., 1997). Tool types are consistent through time, as far as can be discerned from this small sample. However, most of the material in this collection comes from the upper five levels, dating to between about 17,400 and 12,600 B.P. This makes the assemblage comparable to the Epi-Gravettian in Italy. By the Gravettian, perforated red deer canines appear at the Grotta del Broion in the Berici Hills near Mossano, Italy (Broglio, 1995: 57). Notched awls and other bones have been reported in the Sauveterriano (9,500–8,200 B.P.), or middle Mesolithic, which follows the Epi-Gravettian, at Romagnano III, 10 km south of Trent, Italy (Broglio, 1995:104–108). In addition, Romagno III produced a number of tools made on red deer antler and bone, including axes and spatulas. During the French Magdalenian, c. 14,000–12,500 b.c., bone needles were made using the groove-and-splinter technique (Stordeur-Yedid, 1978).

Needles manufactured in the fashion documented at Klithi are not reported in either western Europe or the Near East. This technique appears to be an indigenous and isolated trait of the Klithi culture.

Splinter awls like those from Klithi occurred in western Europe and the Near East from the Aurignacian on, but these are nearly universal and are not useful cultural markers. Antler tine flakers are even more ancient and are also too ubiquitous to shed light on specific cultural identity. Notched bones were found in the Near East at upper paleolithic sites like Ksar Akil, Lebanon, (Tixier, 1974) and later. Perforated canines and counterfeit imitations appear somewhat later than Klithi in the Natufian at El Wad (Garrod and Bate, 1937) and ha-Yonim Cave (Bar Yosef and Tchernov, 1970), in Israel.

This analysis has demonstrated that even small collections of bone artifacts can contribute to the accumulated knowledge of prehistory. Bone artifacts are valuable indicators of both shared and unique technological innovations. Close inspection demonstrates that these artifacts reveal much about the methods and step-by-step processes involved in their manufacture. This, in turn, assists in assigning uses to implements made of stone or other materials. In some cases use wear can supplement overall morphology to indicate probable function (Olsen, 1984). Identifying the likely material on which bone artifacts were used contributes indirect evidence for the use of perishable materials, like worked hides or baskets. Because osseous artifacts may be curated far longer than unmodified bones, they can provide important information about the access a people may have had to species not well-represented as food refuse at a seasonal camp site like Klithi. Such was the case with the piece of antler and perforated canines of red deer. Finally, it is useful for the faunal analyst to understand how the prehistoric people were exploiting raw materials obtained from the animals that they hunted. These data supplement the evidence inferred from cutmarks on bones that indicate the taking of hides, tendons, meat, horns, antlers, hoofs, and other materials.

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REVIEW OF MIOCENE (HEMINGFORDIAN TO CLARENDONIAN) MYLAGAULID RODENTS (MAMMALIA) FROM NEBRASKA

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ABSTRACT

Mylagaulid rodents have been widely recognized in faunas from the Miocene of North America for over 125 years, but a thorough review of the family at the species level has not been done in nearly a century. A large sample of specimens is now available for study from throughout the Miocene section in Nebraska. This sample permits a reexamination of the systematics and phylogeny of this family. It also has allowed for the study of other unique attributes of this family such as sexual dimorphism.

Three subfamilies of mylagaulids are recognized: Mylagaulinae, Mesogaulinae, and Promylagaulinae. The Promylagaulinae are not considered within the scope of this study. The Mesogaulinae are limited to the nominal genus and restricted to the early Hemingfordian. Only two species of *Mesogaulus* are recognized, *M. ballensis* Riggs, and *M. paniensis* (Matthew); only the latter is known from Nebraska. The Mesogaulinae appear both temporally and morphologically ancestral to the later, more advanced mylagaulines.

The Mylagaulinae is comprised of six genera; *Mylagaulus* Cope, *Ceratogaulus* Matthew, *Hesperogaulus* Korth, *Umbogaulus* n. gen., *Pterogaulus* n. gen., and *Alphagaulus* n. gen. *Epigaulus* Gidley is considered a junior synonym of *Ceratogaulus*. All but *Hesperogaulus* are known from Nebraska. *Alphagaulus* is the most primitive and contains species from the late Hemingfordian and early Barstovian. Two species are present in the Nebraska record, *A. vetus* (Matthew) and a new species, *A. tedfordi*. Two other previously described species are referred to this genus, *A. pristinus* (Douglass), and *A. douglassi* (McKenna). The remaining four genera of mylagaulines from Nebraska represent distinct lineages, all of which begin in the Barstovian and continue into the Hemphillian except *Umbogaulus*, which ranges from the late Hemingfordian into the Barstovian only. Three new species are recognized among these genera: *Umbogaulus galushai*, *Ceratogaulus anecdotus*, and *Pterogaulus barbarellae*. *Mylagaulus monodon* Cope is referred to *Umbogaulus*, and *M. laevis* Matthew and *"M." cambridgensis* Korth are referred to *Pterogaulus*. Each of the recognized lineages increases in size through time except *Mylagaulus* and *Umbogaulus*, which decrease in size. It is evident that the presence of nasal horns is not a sexually dimorphic character but defines *Ceratogaulus* as a unique genus as other genera are defined by other forms of ornimentation of the nasal bones.

There is also a biogeographic limitation of these genera. *Ceratogaulus*, *Umbogaulus*, and *Pterogaulus* are restricted to the northern Great Plains; *Mylagaulus* is found only in Florida, northwestern Kansas, and possibly Nebraska. *Hesperogaulus* is present in Barstovian to Hemingfordian faunas from the Great Basin only.

KEY WORDS: Mylagaulidae, Miocene, Biostratigraphy, Phylogeny, Sexual dimorphism, Fossorial

INTRODUCTION

Cope (1878) first named *Mylagaulus sesquipedalis* from the Sappa Creek fauna of Kansas. This species was represented by P^4 (AMNH 8329, later to be named as the holotype) and an isolated incisor and P_4 (AMNH 8330). A few years later, Cope (1881*a*) named an additional species, *Mylagaulus monodon*, from the Barstovian Driftwood Creek fauna of Nebraska (see Voorhies [1990*a*] for age of fauna). The latter species was represented by a partial mandible with P_4 (AMNH

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8327). Later in the same year, Cope (1881*b*) included these unusual rodents in their own family, the Mylagaulidae. Riggs (1899) named a second genus of mylagaulid, *Mesogaulus*, based on a new species, *M. ballensis*, from the Hemingfordian North American Land Mammal Age of Montana.

The first cranial material of a mylagaulid to be described was from Colorado in beds that are now known to be Barstovian in age. Matthew (1901) originally identified this specimen (AMNH 9043) as *Mylagaulus monodon* but later named it as the holotype of a new species, *M. laevis* Matthew (1902). The year after the description of the first skull of *Mylagaulus*, Matthew presented a review of the family. In this review, he described the skull of a mylagaulid from the same horizon as that of the skull of *M. laevis* that had "a pair of large connate processes on the nasals . . . " (Matthew, 1902:291). Matthew named a new genus and species for this skull, *Ceratogaulus rhinocerus*. He suggested the possibility that the unique horn cores of this new skull were a male character of *Mylagaulus*. He rejected this idea in the end because there is no evidence of any marked sexual dimorphism in any other rodents, fossil or Recent (also see Matthew, 1924).

Since Matthew's (1902) review of the Mylagaulidae, five additional genera of mylagaulids have been named. Cranial material is known for four of them: *Promylagaulus* (McGrew, 1941), *Trilaccogaulus* (Nichols, 1976; Korth, 1992), *Epigaulus* (Gidley, 1907; Hibbard and Phillis, 1945), and *Hesperogaulus* (Shotwell, 1958; Korth, 1999*a*). In addition, the skulls of several species of *Mylagaulus* and *Mesogaulus* have been described (Matthew, 1924; McKenna, 1955; Shotwell, 1958; Fagan, 1960; Wilson, 1960; Wahlert, 1974; Galbreath, 1984; Munthe, 1988). Of the genera with known cranial material, only *Epigaulus* has the horn cores on the nasal bones as in *Ceratogaulus*.

It has been the practice in the past to refer isolated cheek teeth and mandibles of mylagaulids from Barstovian to Hemphillian times to a species of *Mylagaulus* if no cranial material is associated. The identification of either horned genus, *Ceratogaulus* or *Epigaulus*, is only done when cranial material with evidence of horns is known. Previously, no dental morphology was used to separate the horned species from the hornless species. In fact, the assignment of the hornless skulls to the genus *Mylagaulus* is completely arbitrary because the holotype of the type species of the genus is an isolated P^4. Hibbard and Phillis (1945) even suggested that the Clarendonian species from Kansas, *Epigaulus minor* (with known presence of horns) and *Mylagaulus sesquipedalis* (type species of the genus), may be synonyms because of their dental similarity and the lack of cranial material of the latter. This suggests that the type species of *Mylagaulus* might have had horn cores, eliminating the previously defined generic difference between *Mylagaulus* and the horned genera.

In Matthew's (1902) review, he also noted the fossorial adaptations of the postcranial skeleton of mylagaulids. All subsequent descriptions of postcranial material of mylagaulines have verified Matthew's observations (Gidley, 1907; Hibbard and Phillis, 1945; Fagan, 1960).

In the century since Matthew's (1902) review of the Mylagaulidae, numerous specimens have been collected from Miocene-aged horizons in Nebraska. The bulk of these were first collected by Ted Galusha and Morris Skinner of the Frick Laboratories in the 1930s through the 1970s. These collections are now housed at the American Museum of Natural History. More recently, beginning in the 1970s, extensive collections of Miocene mammals have been made by M. R. Voorhies and field parties from the University of Nebraska State Museum. These extensive collections contain numerous cranial, dental, and postcranial specimens that are the basis for this study.

The definition of the Promylagaulinae used below follows that of Rensberger (1980). Cranial features of promylagaulines are based on those described by McGrew (1941), Wahlert (1974), Nichols (1976), Munthe (1988), and Korth (1999*b*).

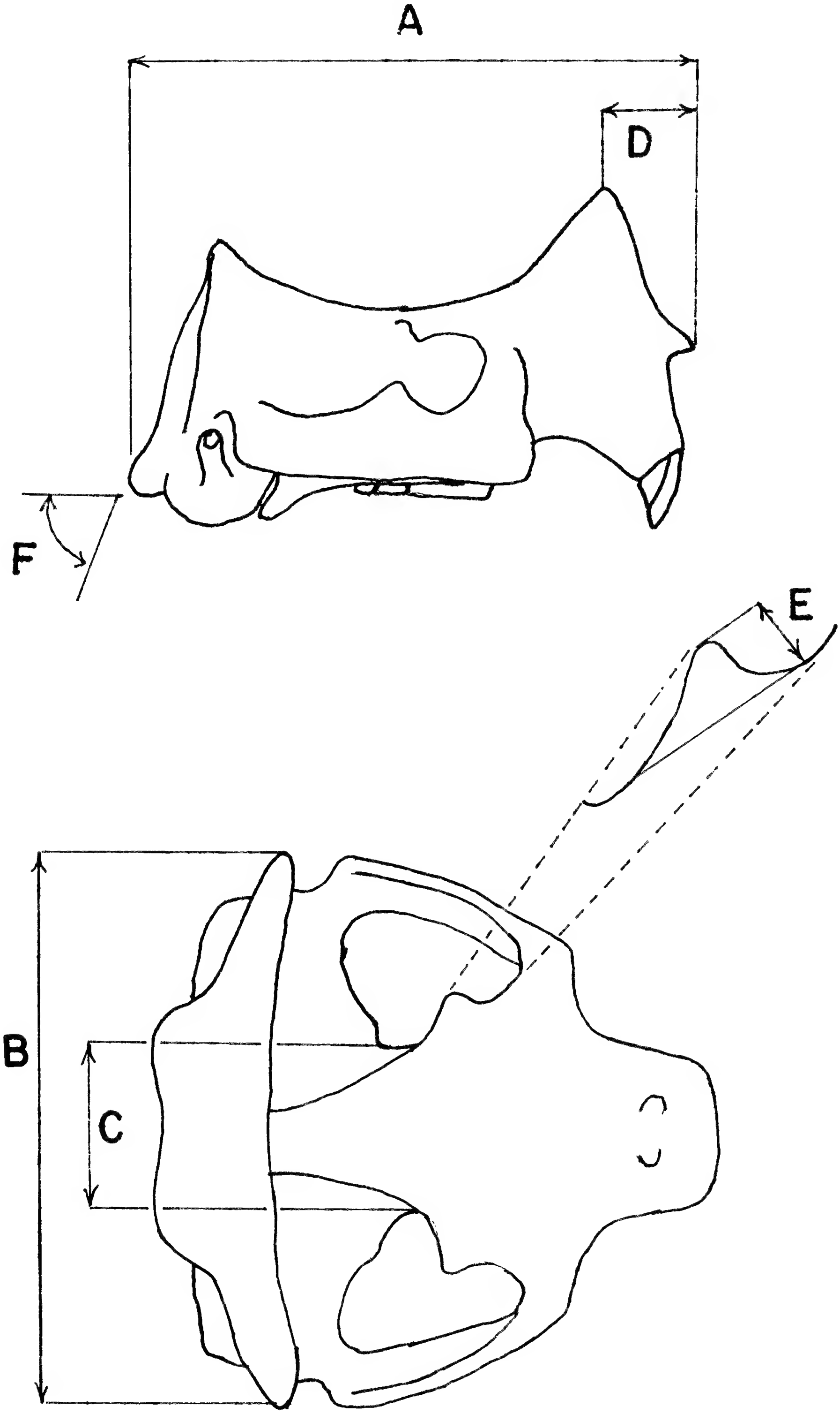
METHODS

Cranial Measurements and Indices.—The placement and orientation of skull measurements are presented in Figure 1. Horn placement index (NHI) is calculated by dividing the distance from the apex of the nasal horn to the anterior edge of the nasal by the total length of the skull. Postorbital process size index (POI) is calculated by dividing the length of the postorbital process on one side of the skull by the minimum width of the postorbital constriction. Cranial width index (W/L) is calculated by dividing the posterior width of the skull by the anteroposterior length of the skull. The angle of the occipital bone (OA) is measured with respect to the plane of the palate. Cranial indices for all mylagaulid species for which they are known are presented in Table 1.

Dental Measurements and Terminology.—Measurements of the premolars of mylagaulids used here represent the maximum width and length of the tooth. The occlusal length was used only in specimens in very late stages of wear where the occlusal measurements are the maximum. Abbreviations for dental dimensions appearing in tables are as follows: a-p, anteroposterior length; tr, transverse width.

The terminology for the fossettes (-ids) of mylagaulid premolars is difficult because different schemes have been proposed by virtually everyone who has worked on this family (Riggs, 1899; McGrew, 1941; Shotwell, 1958; Rensberger, 1979; Munthe, 1988; Korth, 1994). The difficulty with using any system of naming the fossettes is that the homologies of the fossettes are difficult to determine except in very primitive forms that have only a few fossettes that are traceable from the unworn surface of the tooth. Here, the fossettes of the cheek teeth will be referred to only by their position on the tooth (e.g. posterolingual, etc.). The only fossette that appears to be significant in terms of the evolutionary changes in mylagaulids is the anterocentral (or anterobuccal) fossette of P^4. This fossette is forked anteriorly and the separation of the branches of the forked end is a significant character that is used to define genera. In the following text this fossette will be referred to as the *parafossette*. Since the number of fossettes (-ids) on the premolars varies somewhat within a given sample of any one species, the mean number of fossettes, as well as the modal number, are used for comparisons between species and populations (Table 2). Any reference to cusps or styles on the premolars is taken from the terminology of Wood and Wilson (1936).

Reference to early, middle, or late stages of wear on the premolars will be used as defined by Korth (1999*a*); teeth that have been worn to a level within the first 20% of the presumed total height of the tooth are considered to be in early wear, and those in the presumed last 20% of the total crown height are considered to be in a late stage of wear. All others are considered to be in middle or moderate wear (central 60% of the crown height). Clearly, these are approximations. However, the pattern of premolars in early and late wear is distinct (see section on variation in Conclusions); lateral sides of the tooth tilt toward the center of the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B
C

Table 1.—*Cranial indices of mylagaulids.*

	W/L	POI	NHI	OA
Trilaccogaulus lemhiensis	0.46	0.27		110°
Galbreathia novellus	0.52	0.24		90°
Mesogaulus paniensis	0.82	0.32		90°
Alphagaulus vetus	0.77–0.83	0.26–0.36		60°–75°
Alphagaulus pristinus		0.31		79°
Alphagaulus tedfordi	1.22	0.25		90°
Umbogaulus galushai	0.87	0.35		75°
Umbogaulus monodon	0.87	0.35–0.36		75°
Ceratogaulus rhinocerus	0.95	0.19	0.19–0.21	70°
C. cf. *rhinocerus*	0.85–0.88	0.12–0.15	0.16–0.22	67°–68°
Ceratogaulus minor	0.93	0.12	0.29	62°
Ceratogaulus anecdotus	1.00	0.12	0.30	60°
Ceratogaulus hatcheri	0.95	0.11	0.38	63°
Pterogaulus laevis	0.90–1.04	0.39–0.41		68°–75°
Pterogaulus sp.	0.83–0.90	0.34–0.46		54°–60°
Pterogaulus barbarellae	0.85–1.03	0.40–0.57		52°–60°
Hesperogaulus gazini	0.97	0.31–0.35		55°–57°
Hesperogaulus wilsoni	0.80–0.87	0.22–0.25		50°

occlusal surface in early wear, and strongly away from the center of the tooth in late wear.

Abbreviations for Institutions.—AMNH, American Museum of Natural History, New York, New York; CM, Carengie Museum of Natural History, Pittsburgh, Pennsylvania; FAM, Frick Collections of the AMNH, New York, New York; FMNH, Field Museum of Natural History, Chicago, Illinois; UCMP, University of California Museum of Paleontology, Berkeley, California; UNSM, University of Nebraska State Museum, Lincoln, Nebraska; UOMNH, University of Oregon Museum of Natural History, Eugene, Oregon; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D. C.

BIOSTRATIGRAPHY

The biostratigraphy of the middle and later Tertiary of Nebraska used below generally follows that presented by Tedford et al. (1987) for the Hemingfordian through Clarendonian. However, there are two instances where this paper deviates from the latter work. First, Voorhies (1990*a*) argued convincingly that the Barstovian-Clarendonian boundary, based on the Nebraska stratigraphic section, should be at the base of the Burge Member of the Valentine Formation as was initially intended in the original definition of the Clarendonian (Wood et al., 1941). This differs from Tedford et al. (1987), who included the fauna of the Burge Member in the latest Barstovian (late-late Barstovian). In the following text, Voorhies' interpretation will be used and the Burge fauna will be included as the early Clarendonian (Fig. 2).

←

Fig. 1.—Cranial measurements of mylagaulids. A. Total length. B. Total posterior width. C. Width of postorbital constriction. D. Distance of apex of nasal horn from anterior end of nasal. E. Length of postorbital process. F. Angle of occipital. Cranial indices used in text: NL = D/A; POI = E/C; W/L = B/A.

Table 2.—*Number of fossettes (-ids) on premolars of mylagaulids.*

		$\bar{x}$	Mode	Range
Mesogaulus paniensis	P^4	5.0	5	5–5
	P_4	5.2	5	4–6
Mesogaulus ballensis	P^4	—	—	—
	P_4	4	—	—
Alphagaulus vetus	P^4	6.7	7	5–9
	P_4	5.9	5	5–9
Alphagaulus tedfordi	P^4	6	—	—
	P_4	6	—	—
Alphagaulus pristinus	P^4	6.0	6	6–6
	P_4	5.3	5	5–6
Alphagaulus douglassi	P^4	7	—	—
	P_4	—	—	—
Umbogaulus galushai	P^4	8.3	9	7–9
	P_4	8.4	8	7–11
Umbogaulus monodon	P^4	7.9	8	6–10
	P_4	7.3	7	5–9
Ceratogaulus rhinocerus	P^4	8.0	7	7–10
	P_4	8.2	7	8–10
Ceratogaulus cf. *rhinocerus*	P^4	6.7	6–7	6–8
	P_4	7.1	7	5–9
Ceratogaulus minor	P^4	6	—	—
	P_4	7	—	—
Ceratogaulus anecdotus	P^4	7.5	7	6–9
	P_4	7.4	7	6–10
Ceratogaulus hatcheri	P^4	8	—	—
	P_4	9	—	—
Pterogaulus laevis	P^4	6.5	6	5–9
	P_4	5.7	5	5–7
Pterogaulus sp.	P^4	7.2	8	5–10
	P_4	7.0	6	6–11
Pterogaulus barbarellae	P^4	7.8	8	6–10
	P_4	6.5	6	5–8
Pterogaulus cambridgensis	P^4	7.3	8	6–9
	P_4	7.0	7	6–8

Second, Tedford et al. (1987:fig. 3) figured the "Sand Canyon Beds" as biostratigraphically equivalent to the Olcott Formation. However, the former (based on the fauna from Observation Quarry in Dawes County, Nebraska) appears to be older than the fauna from the type area of the Olcott Formation in Sioux County, and is assumed here to represent an earlier deposit.

The Miocene biostratigraphy of Wyoming was not presented by Tedford et al. (1987), so the position and correlation of the Split Rock fauna (late Hemingfordian) is based on the interpretation presented in Munthe (1988:fig. 3).

Systematic Paleontology

Order Rodentia Bowdich, 1821
Family Mylagaulidae Cope, 1881
Subfamily Mesogaulinae, **new subfamily**

Definition.—Intermediate-sized mylagaulids; first molar lost with eruption of last permanent premolar; P^3 retained, but cheek teeth higher crowned than in promylagaulines; rudimentary roots present on premolars at advanced stage of

NALMA		STRATIGRAPHY	
Clarendonian	late	Ash Hollow Formation	Merritt Dam Member
	middle		Cap Rock Member
	early	Valentine Formation	Burge Member
Barstovian	late		Crookston Bridge Member
	middle		Cornell Dam Member
	early	Olcott Formation	
		"Sand Canyon Beds"	
Hemingfordian	late	Sheep Creek Formation	
	early	Running Water Formation	
		Marsland Formation	

Fig. 2.—Miocene stratigraphic sequence for the Nebraska section used in this paper. Width of units drawn equally, not intended to represent absolute duration (time) or thickness of section.

wear; P^4 retains outline of mesostyle and parastyle and P_4 retains outline of metastylid (lost in mylagaulines); upper incisor with smooth anterior enamel surface (grooved in mylagaulines); skull not as broad as in mylagaulines, but broader than in promylagaulines (W/L = 0.80); occipital not anteriorly tilted (OA = 90°); single sagittal crest on skull (doubled in mylagaulines); postcranial skeleton with fossorial adaptations.

Included Genus.—*Mesogaulus* Riggs, 1899.

Mesogaulus Riggs, 1899

Type Species.—*Mesogaulus ballensis* Riggs, 1899.

Included Species.—*Mesogaulus paniensis* (Matthew, 1902).

Range.—Hemingfordian of Montana, Colorado and Nebraska.

Diagnosis.—Only genus of the subfamily.

Discussion.—The last published classification of mylagaulids at the species level cited six species of *Mesogaulus* ranging from the Hemingfordian to Barstovian (Korth, 1994:109). However, only two of those species are considered here as species of this genus. *Mesogaulus pristinus* and *M. proximus* from the early Barstovian of Montana (Douglass, 1903) are shown to be synonyms and are referable to a new genus of primitive mylagauline (see below). *Mesogaulus novellus*, from the Hemingfordian of Wyoming and Nebraska (Matthew, 1924; Black and Wood, 1956; Munthe, 1988), was referred to a new genus of specialized promylagauline, *Galbreathia* (Korth, 1999*b*). Finally, *M. praecursor* from the Hemingfordian of Nebraska (Cook and Gregory, 1941) has been shown previously to be a junior synonym of *M. paniensis* (Wilson, 1960). All of the conclusions presented in the following discussions regarding *Mesogaulus* are based on the only two species of the genus recognized here, *M. ballensis* and *M. paniensis*.

In his first description of *Mesogaulus*, Riggs (1899) noted that the morphology of the genus was intermediate between *Mylagaulus* and an ancestral form. *Mesogaulus* has developed cranial, dental, and postcranial features that are clearly mylagauline-like, but are more primitive than any true mylagaulines. The skull, while being posteriorly broadened and generally more robust than that of promylagaulines (Wilson, 1960; Galbreath, 1984; Korth, 1999*b*), has not attained the degree of development of these features found in other mylagaulines. Similarly, the dentition is advanced over that of promylagaulines in hypsodonty and complexity of the occlusal surface, however, P^3 is still retained in adult individuals, a promylagauline feature. Features of the limb bones are similarly developed with the hypertrophy of the forelimb seen in later Tertiary mylagaulines (Galbreath, 1984; Korth 1999*b*).

Mesogaulus is a likely ancestor to later mylagaulines. Its age, early Hemingfordian, is also intermediate between promylagaulines and mylagaulines (see Korth, 1994 for age ranges of promylagaulines). The only exception is the late occurrence of the derived promylagauline *Galbreathia* (Korth, 1999*b*).

Mesogaulus paniensis (Matthew, 1902)
(Fig. 3A, B, 4)

Mylagaulus paniensis Matthew, 1902.
Mesogaulus paniensis (Matthew) Cook and Gregory, 1941.
Mesogaulus praecursor Cook and Gregory, 1941.

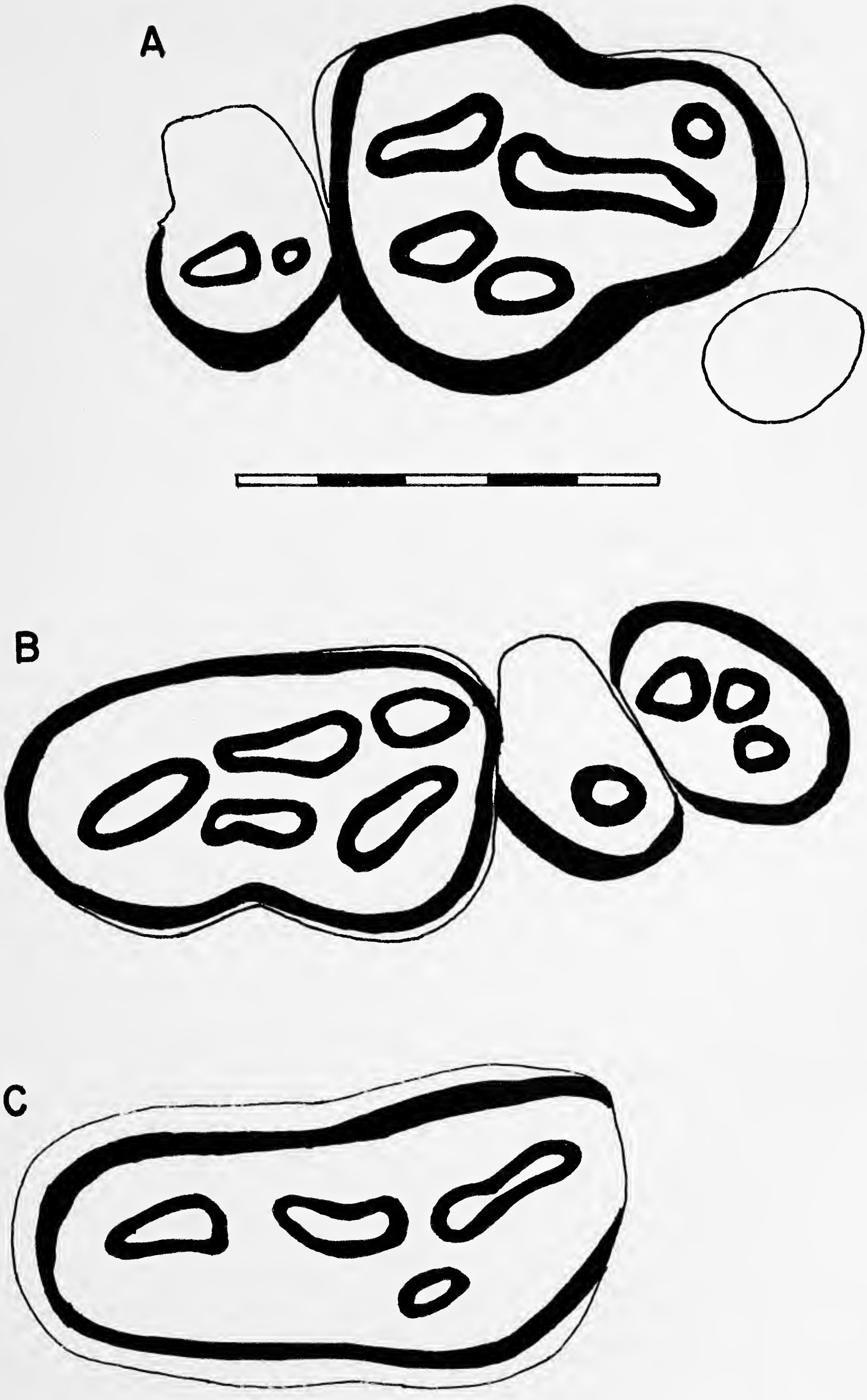
Type Specimen.—AMNH 9361, partial mandible with incisor and P_4 (Matthew, 1902:fig. 4).

Referred Specimens.—Additional topotypic specimens listed in Galbreath (1953:95) and Wilson (1960:51–53); referred specimens from Nebraska cited in Cook and Gregory (1941:551) as *Mesogaulus praecursor*; and FAM 65511, nearly complete skull with complete dentition, associated mandibles, and some postcranial bones.

Horizon and Locality.—Topotypic specimens from Quarry A, Martin Canyon beds, Logan County, Colorado; referred specimens from "four miles north of Agate" (Cook and Gregory, 1941:551), Marsland Formation, Sioux County, Nebraska; FAM 65511 from Runningwater Formation, Cottonwood Creek, Dawes County, Nebraska.

→

Fig. 3.—Dentitions of species of *Mesogaulus*. A, B. *Mesogaulus paniensis*, FAM 65511. A. P^3– P^4, M^2. B. P_4, M_2–M_3. C. Holotype of *M. ballensis*, FMNH P 25223, P_4.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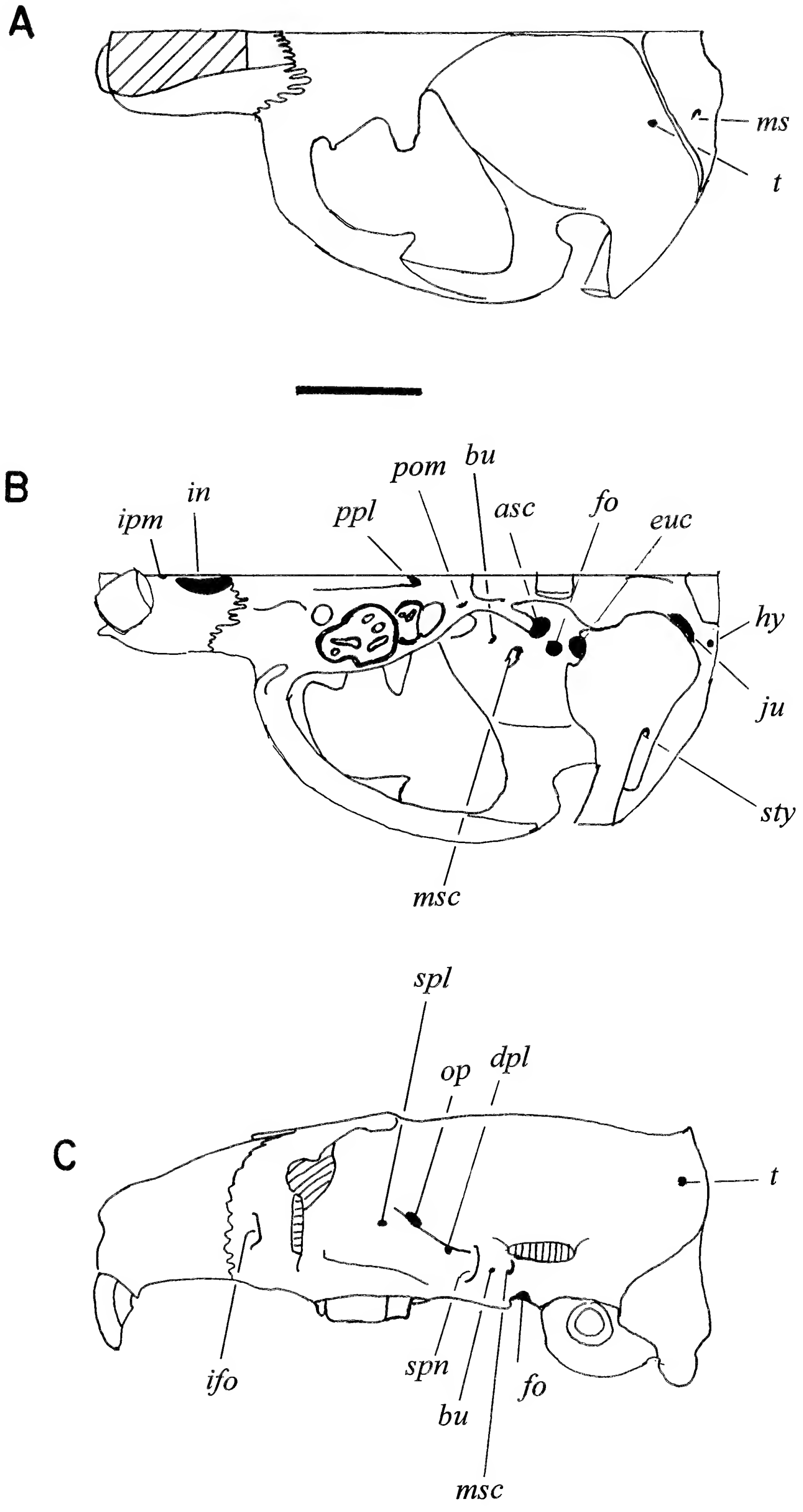
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Age.—Early Hemingfordian (early Miocene).

Emended Diagnosis.—Five or more fossettes (-ids) on P_4, more than in *M. ballensis*.

Description.—Galbreath (1953, 1984) and Wilson (1960) have fully described the dentition of *M. paniensis* along with some skull material and postcranial elements. A nearly complete skull with associated limb elements, FAM 65511, is clearly referable to *M. paniensis*. The skull is generally low, and posteriorly broadened as in mylagaulines, but has not attained the degree of posterior expansion seen in the latter (W/L = 0.82). The postorbital processes are intermediate in size (POI = 0.32) which appears to be primitive for the family. The angle of the occipital is 90°, again a primitive condition, and similar to promylagaulines. However, the positions of all cranial foramina are identical to those of later mylagaulines (Wahlert, 1974:fig. 13).

Dentally, the upper incisors of *M. paniensis* also lack the broad, shallow groove along their medial border that is present in all mylagaulines, and a P^3 is retained in all adult individuals of *M. paniensis* (this tooth is lost in all mylagaulines). The humeri of FAM 65511 are proportioned as in later mylagaulines and are clearly broader than in promylagaulines (Table 3).

Discussion.—In virtually all features of the skull, dentition, and postcranial skeleton, *M. paniensis* is intermediate between promylagaulines and later, more derived mylagaulines. Cook and Gregory (1941) believed that additional specimens of *Mesogaulus* from Nebraska represented a new species, *M. praecursor*, but Wilson (1960) demonstrated that this latter species was a junior synonym of *M. paniensis*. Although Matthew (1902) argued against synonymy, it is possible that the type species of the genus, *M. ballensis* Riggs (1899), is synonymous with the much better represented *M. paniensis* because the former is known only from the holotype, FMNH P 25223, which contains heavily worn cheek teeth (Fig. 3C). This argument cannot be settled until additional topotypic material of *M. ballensis* is recovered and described.

Subfamily Mylagaulinae Cope, 1881*b*

Definition.—Large mylagaulids; P^3 absent; last premolar greatly enlarged (more than twice the size of molars); at least first molars lost with eruption of permanent premolars; no evidence of roots on premolars; upper incisor with broad, shallow groove along medial border of anterior surface of enamel; posterior width of skull nearly equal to anteroposterior length of skull (W/L = 0.77–1.04); occipital tilted anteriordorsally (OA ≤ 75°) except in most primitive species; sagittal crest doubled (=parasagittal crests); primitively, small boss of rugose bone present dorsally on anterior end of nasal bones; fossorial adaptations of postcranial skeleton greatly enhanced (ratio of distal width to length of humerus greater than 0.43).

Included Genera.—*Mylagaulus* Cope, 1878; *Ceratogaulus* Matthew, 1902; *Hesperogaulus* Korth, 1999*a*; *Pterogaulus* n. gen.; *Umbogaulus* n. gen.; and *Alphagaulus* n. gen.

←

Fig. 4.—Skull of *Mesogaulus paniensis*, FAM 65511. A. Dorsal view. B. Ventral view. C. Left lateral view (zygoma removed). Abbreviations for cranial foramina: asc, alisphenoid canal; bu, buccinator; dpl, dorsal palatine; euc, eustachian canal; fo, foramen ovale; hy, hyoid; ifo, infraorbital; in, incisive; ipm, interpremaxillary; ju, jugular; ms, mastoid; msc, masticatory; op, optic; pom, posterior maxillary; ppl, posterior palatine; spl, sphenopalatine; spn, sphenoidal fissure; sty, stylomastoid; t, temporalis. Diagonal lines indicate broken areas. Bar scale = 1 cm.

Table 3.—*Humeral index (distal width/length) of species of mylagaulids.*

Galbreathia novellus	0.38
Mesogaulus paniensis	0.43
Alphagaulus tedfordi	0.43
Umbogaulus galushai	0.43
Ceratogaulus rhinocerus	0.42–0.45
Ceratogaulus minor	0.45
Ceratogaulus hatcheri	0.44
Pterogaulus laevis	0.43–0.44
Pterogaulus sp.	0.45

Alphagaulus, **new genus**

Type Species.—Mylagaulus vetus, Matthew, 1924.

Referred Species.—Alphagaulus pristinus (Douglass, 1903), *A. douglassi* (McKenna, 1955), and *A. tedfordi* n. sp.

Range.—Late Hemingfordian of Wyoming and Nebraska; early Barstovian of Nebraska and Montana.

Diagnosis.—Range in size from the smallest to intermediate-sized mylagaulines; skull not as wide posteriorly as other mylagaulines (W/L = 0.77–0.83); low bosses of rugose bone at anterior end of nasals; postorbital process intermediate in size (POI = 0.25–0.35); premolars simpler than other mylagaulines—fewer fossettes (minimum of five fossettids on P_4); P^4 parafossette remains forked until very late wear stage.

Discussion.—In morphology of the skull and dentition, as well as temporal occurrence (late Hemingfordian to early Barstovian), *Alphagaulus* is transitional between *Mesogaulus* and more advanced mylagaulines. In overall size and the morphology of the parafossette on P^4, the species of *Alphagaulus* appear to be divisible into two groups. Both *A. vetus* (Matthew, 1924) and *A. pristinus* (Douglass, 1903) are more gracile, and the buccal branch of the parafossette on P^4 separates from the rest of the fossette in very late stages of wear. *Alphagaulus douglassi* and the new species described below have much more robust skulls than the former species and the lingual branch of the parafossette on P^4 separates first at an earlier stage of wear. These differences suggest possible ancestral relationships to specific later, more derived mylagaulines.

In addition to the two species of this genus recognized from Nebraska, two previously described species are referred here to *Alphagaulus* as well. Douglass (1903) based the species *Mylagaulus? pristinus* on a single mandible with a newly erupted P_4 (CM 742). However, he sectioned the premolar at the level of its maximum dimensions, providing a view of the premolar at an advanced stage of wear for comparison with other species (Fig. 6E). *Alphagaulus pristinus* differs from all other species of the genus in being smaller in size. In the same article, Douglass (1903) described an additional species, *Mylagaulus proximus*, from the same horizon as *A. pristinus*. It was also based on a single specimen, CM 843, a mandible with dP_4-M_3 with an erupting P_4. This specimen is nearly identical to the holotype of *A. pristinus* in size and morphology (Douglass, 1903:189–190, fig. 27). Therefore, *M. proximus* is believed to be a junior synonym of *A. pristinus*.

Alphagaulus pristinus most closely approaches *A. vetus* in size and morphology. Now that a sufficient number of specimens of both of these species is known

Table 4.—*Measurements of premolars of* Alphagaulus vetus *from different areas. Topotypic material is from Sheep Creek Formation of Nebraska. *Split Rock data from Munthe (1988:table 2), no ranges were given. Statistical abbreviations:* n, *number of specimens;* $\bar{x}$, *mean; OR, size range;* s, *standard deviation;* cv, *coefficient of variation.*

		n	$\bar{x}$	OR	*s*	*cv*
Late Hemingfordian (Split Rock, Wyoming)*						
P^4	a–p	3	7.4	—	0.4	4.8
	tr	3	5.7	—	0.3	5.1
P_4	a–p	4	8.2	—	1.1	13.4
	tr	4	4.3	—	0.3	6.7
Late Hemingfordian (Sheep Creek Formation, Nebraska)						
P^4	a–p	4	7.8	7.5–8.0	0.2	2.6
	tr	5	5.2	5.0–5.6	0.2	4.3
P_4	a–p	12	8.1	7.3–9.3	0.7	8.2
	tr	12	4.6	4.1–5.2	0.3	7.3
Early Barstovian (Observation Quarry, Nebraska)						
P^4	a–p	15	8.0	7.3–9.0	0.5	6.6
	tr	15	4.7	4.7–6.1	0.4	7.8
P_4	a–p	31	8.4	6.9–9.3	0.6	7.6
	tr	31	4.4	3.3–5.6	0.5	12.0

(Table 4; Sutton and Korth, 1995:table 3); it is evident that *A. pristinus* is indeed smaller than representative samples of *A. vetus*.

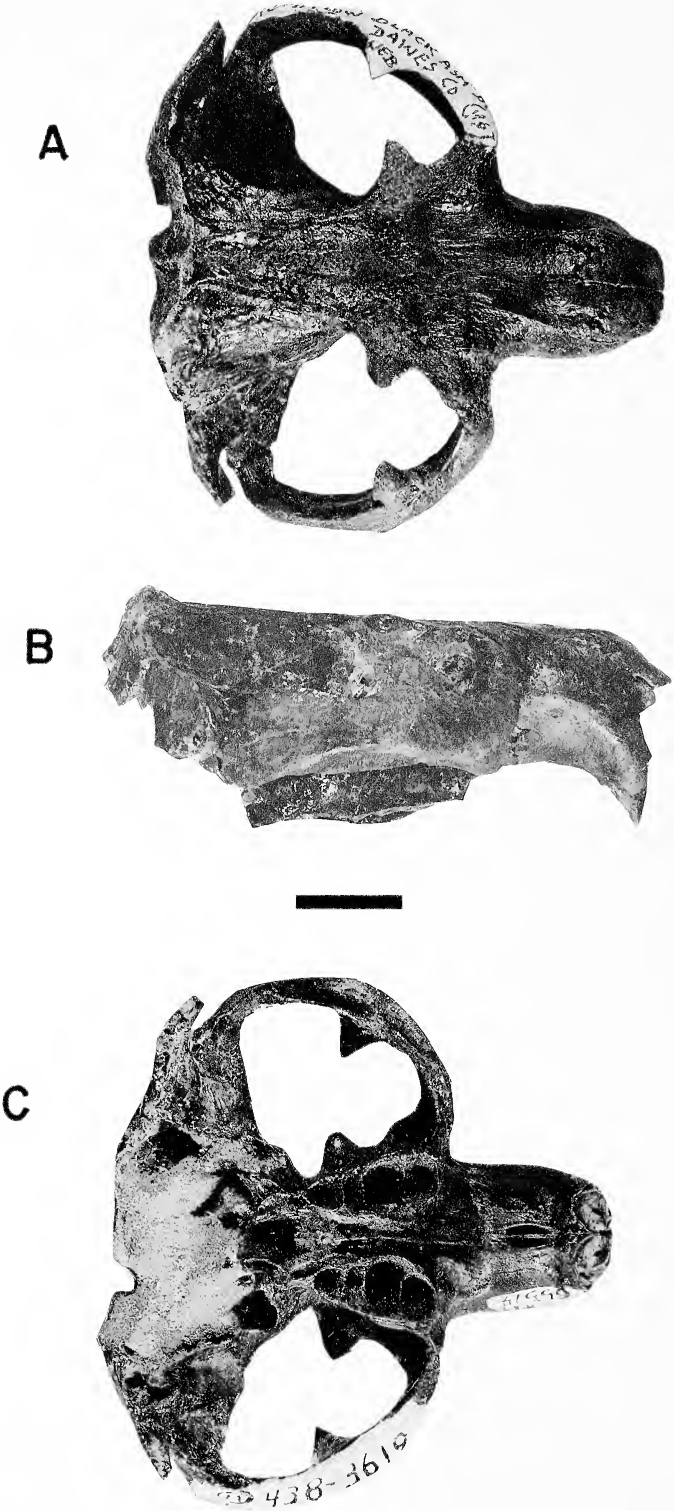
A partial skull from the Barstovian of Montana, AMNH 21307, is assigned to *A. pristinus* based on size and occurrence. It is smaller than skulls of *A. vetus* (width of occipital slightly more than half that of skulls of *A. vetus*), but the angle of the occipital (OA = 79°) and relative size of the postorbital processes (POI = 0.31) are very similar to these measurements in skulls of the type species. The sagittal crest is also doubled as in skulls of *A. vetus*.

Alphagaulus pristinus is restricted to the early Barstovian of Montana. Although Black (1961) and Sutton and Korth (1995) referred specimens from this area to other species (*Mesogaulus paniensis* and *Mylagaulus vetus*, respectively) they are all clearly referable to *A. pristinus*.

Alphgaulus douglassi is represented by a single specimen, UCMP 44694, a partial skull with cheek teeth (McKenna, 1955:fig. 1). This species is also referable to *Alphagaulus*. The major difference between *A. douglassi* and the other species is in the separation of the lingual fork of the parafossette on P^4 (buccal fork separates in *A. vetus* and *A. pristinus*). This separation apparently occurs at an earlier stage of wear than in *A. vetus*. McKenna (1955) noted that the skull of *A. douglassi* had longer parietals than other known species of mylagaulids. This clearly indicates that the angle of the occipital is nearly vertical, as in *A. vetus*, although the posterior end of the skull is missing on the only known specimen of *A. douglassi*. In more derived mylagaulines, the parietals are shortened by the anterior tilting of the occiptal bone. The skull of *A. douglassi* is very robust and has a single, broad sagittal crest, unlike that of *A. vetus* and all known mylagaulines that have a doubled sagittal crest.

Alphagaulus vetus (Matthew, 1924)
(Fig. 5, 6A–D; Table 4)

Mylagaulus vetus Matthew, 1924.
Mesogaulus vetus (Matthew) Cook and Gregory, 1941.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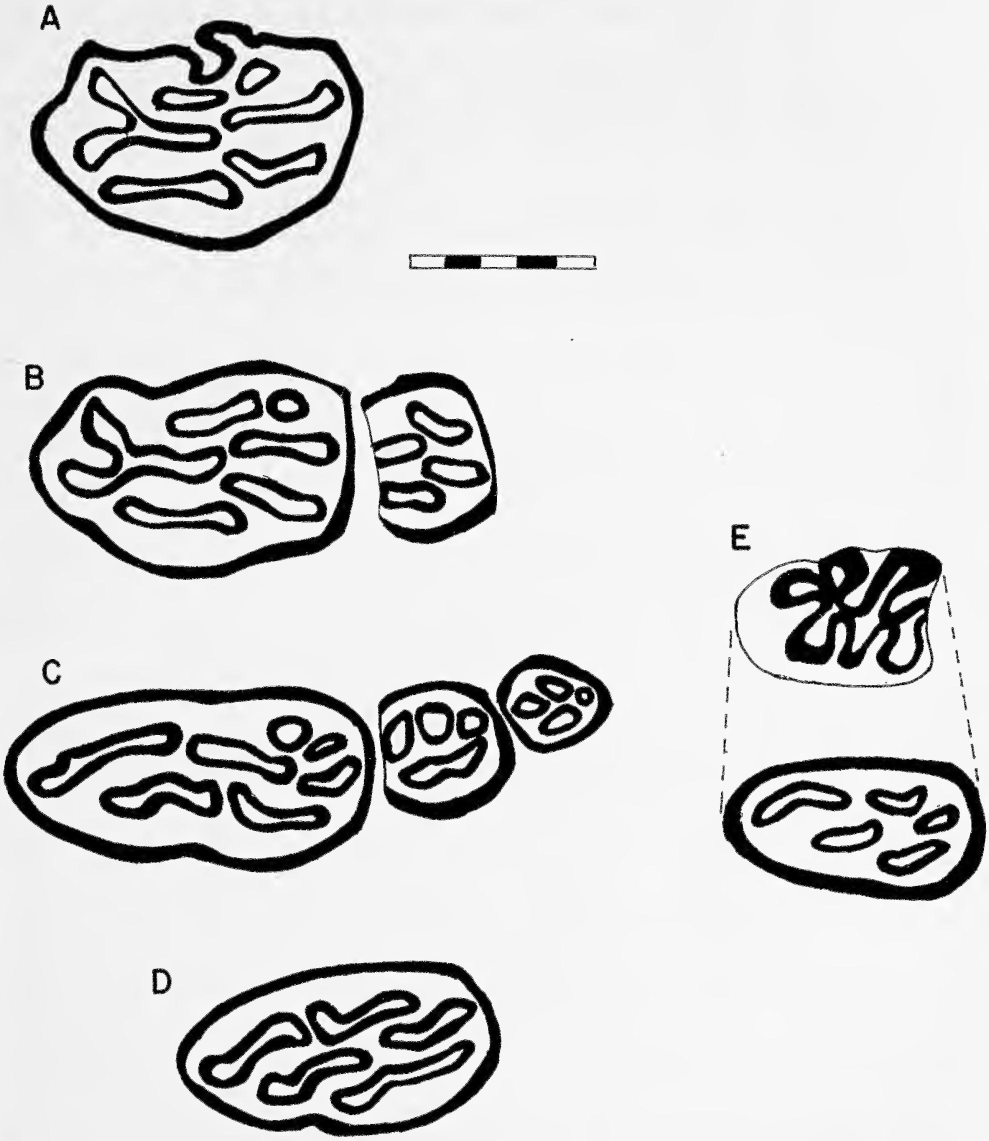

Fig. 6.—Dentition of *Alphagaulus vetus* and *A. pristinus*. A–D. *Alphagaulus vetus* from early Barstovian Observation Quarry, Nebraska. A. FAM 65547, left P^4. B, C. FAM 65536. B. left P^4, M^2. C. left P$_4$, M$_2$–M$_3$. D. FAM 65542, left P$_4$. E. *Alphagaulus pristinus*, holotype, CM 742, little-worn occlusal surface (above) and surface of cross section at midheight of tooth (below). Bar scale = 5 mm.

←

Fig. 5.—Skull of *Alphagaulus vetus*, FAM 65514. A. Dorsal view. B. Lateral view. C. Ventral view. Bar scale = 1 cm.

Type Specimen.—AMNH 18905, right mandible with incisor and P_4, M_2 (Sutton and Korth, 1995:fig. 3H).

Referred Specimens.—Topotypic specimens: AMNH 20504, 20507, 90734; FAM 65515, 65517–65520, 65523, 65526, 65527. From Observation Quarry: FAM 65532, 65534–65536, 65538–65551, 65556, 65558, 65559, 65561. Also see Munthe (1988:24) for list of referred specimens from Split Rock fauna.

Horizon and Locality.—Holotype and some referred specimens from the late Hemingfordian Thompson Quarry, Sheep Creek Formation of Sioux County, Nebraska; other referred specimens from the late Hemingfordian Split Rock local fauna of Wyoming and the earliest Barstovian Observation Quarry, Dawes County, Nebraska.

Age.—Late Hemingfordian to early Barstovian (late-early to early-middle Miocene).

Emended Diagnosis.—Larger than *A. pristinus*; skull not as deep (dorsoventrally) or robust as in *A. douglassi* and *A. tedfordi*; in late stages of wear buccal branch of parafossette of P^4 separates from the remainder of the fossette (lingual branch separates in *A. douglassi*).

Description.—The proportions of the skull of *A. vetus* are intermediate between that of *Mesogaulus* and later mylagaulines. In general, the skull is low and broad as in all mylagaulines (W/L = 0.77–0.83; similar to that of *Mesogaulus*) but is not as posteriorly expanded as other mylagaulines (W/L ≥ 0.88). Similarly, the angle of the occipital (OA) ranges from 60° to 75°, much less than in *Mesogaulus* (OA = 90°) but not as low as in advanced mylagaulines where the angle is as low as 50° (Table 1). The postorbital process is intermediate in size (POI = 0.26–0.36), similar to that of *Mesogaulus*.

A small bump is present on the nasal bones at their anterior end. It is variable in size but is present on specimens that preserve the nasals from the late Hemingfordian and early Barstovian as well. All other features of the skull and mandible are similar to those described by Munthe (1988) for the species, and by Wahlert (1974) for the family.

The number of fossettes on the upper premolar varies from five to nine. The majority of specimens (80%) have six or seven ($\bar{x}$ = 6.7, mode = 7). The largest fossette is the parafossette, which remains forked until very late stages of wear. Of the over 20 specimens examined, only two showed the separation of the buccal branch of the parafossette. Both of these specimens were in very late stages of wear. The remainder of the fossettes on P^4 follow a basic pattern: two on the anterior half of the tooth (one buccal and one lingual to the parafossette); and three on the posterior half of the tooth, roughly aligned with the three on the anterior half of the tooth. The seventh fossette is usually a small, circular one along the buccal edge of the tooth near its center. Heavily worn specimens often eliminate one or more of these fossettes, reducing their number. Specimens with more than seven fossettes appear to be the result of one of the larger fossettes dividing into two or more smaller fossettes.

The lower premolar also consists of anteroposteriorly elongated fossettids, typical of mylagaulines. The number of fossettids ranges from nine to five ($\bar{x}$ = 5.9, mode = 5). As with the upper premolars, the number of fossettids generally is reduced with age. Those specimens with more than five or six fossettids are usually younger individuals. The specimens that are at a moderate stage of wear usually have only five or six. Again, as with the upper premolars, additional fossettids on P_4 are produced by the splitting of one or more of the larger fossettids into two. There is a general pattern in the location of the five main fossettids: three along the lingual edge of the tooth, and two along the buccal side of the tooth.

Discussion.—*Alphagaulus vetus* is the best represented species of the genus. It is also one of the best represented species of mylagaulines. There is virtually no difference in the size ranges and morphology of the samples of *A. vetus* from the late Hemingfordian of Wyoming and Nebraska and the early Barstovian of Nebraska (Table 4). The size of the boss at the anterior end of the nasals varies somewhat, but is always present on specimens that preserve the nasals. *Alphagaulus vetus* is slightly larger than *A. pristinus*. In a very late stage of wear of P^4, the buccal branch of the parafossette separates from the rest of the fossette, unlike *A. douglassi*. This only occurs in very few specimens, all of which are of senile individuals.

Alphagaulus vetus is morphologically intermediate between *Mesogaulus* and later, more advanced mylagaulines in the construction of the skull. The skull of *A. vetus* is broader and has a lower angle of the occipital than *Mesogaulus*, but is not as broad as in other mylagaulines and has a steeper occipital angle. The dentition is also intermediate, having a greater number of fossettes (-ids) on the premolars than *Mesogaulus* but fewer than other mylagaulines.

Alphagaulus tedfordi, **new species**
(Fig. 7, 8, 9B, C)

Type and Only Specimen.—FAM 65711, nearly complete skeleton.

Dental Measurements of Holotype.—P^4, a-p 7.50 mm, tr 5.70 mm; P_4, a-p 6.74 mm, tr 5.40 mm.

Horizon and Locality.—Hot Springs drainage system (below level of Observation Quarry), NE ¼, SE ¼, section 4, T31N, R47W, Dawes County, Nebraska.

Age.—Latest Hemingfordian or earliest Barstovian.

Diagnosis.—Slightly larger than *A. douglassi*; skull robust with vertically oriented occipital (OA = 90°); lingual fork of parafossette on P^4 separates first (as in *A. douglassi*); P^4 retains outline of mesostyle, not becoming completely oval as in other species.

Etymology.—Patronym for R. H. Tedford.

Description.—The postcranial skeleton is similar to that of other mylagaulines with robust limbs, especially the forearms and manus. The ratio of distal width to length of the humerus is within the range that of other mylagaulids (Table 3). The skull is also robust and retains a number of features of *Mesogaulus*. The angle of the occipital is 90°, as in *Mesogaulus* and the promylagaulines (Table 1) and the postorbital process is primitively intermediate in size (POI = 0.25). However, there are a number of features of the skull that make this specimen clearly a mylagauline. The skull is wider posteriorly than in *Mesogaulus* and most other mylagaulines (W/L = 1.22) and there are bosses of rugose bone on the anterior ends of the nasals. These bosses are larger than those of *A. vetus*, but considerably smaller than those of *Umbogaulus* (described below). There appears to be no difference between the arrangement of sutures or foramina on the skull of *A. tedfordi* and of other mylagaulines. The auditory bullae have the characteristic elongated external meatus of all mylagaulids.

The upper premolar of the type specimen is in a moderate stage of wear and has six fossettes; four elongated fossettes (two on the anterior half, two on the posterior half), and a minute buccocentral fossette. The lingual branch of the parafossette has separated to form the minute seventh fossette. This arrangement of the major fossettes is very similar to that of *Mesogaulus* and advanced promylagaulines. The separation of the lingual branch of the parafossette is characteristic of *A. douglassi* (Fig. 9A) and all species of *Ceratogaulus* and *Mylagaulus*. The occlusal outline of P^4 retains the outline of the mesostyle, a character of *Mesogaulus* and promylagaulines.

The lower premolar has six fossettids, reminiscent of the premolars of *A. vetus*, but is much more robust than the latter. Both the upper and lower premolars are wider relative to length than in *A. vetus*.

Discussion.—*Alphagaulus tedfordi* retains a number of primitive *Mesogaulus*-like characters of the skull and dentition. The angle of the occiptial is vertical and the postorbital processes are intermediate in size, as in *Mesogaulus*. Similarly, the outline of the mesostyle is preserved on P^4, another primitive character for mylagaulines. However, the posterior widening of the skull of *A. tedfordi* is much greater than that of *Mesogaulus* and promylagaulines, and the presence of bumps on the nasal bones is also a mylagauline trait.

Alphagaulus tedfordi more closely resembles *A. douglassi* than the other species of the genus. Both *A. tedfordi* and *A. douglassi* are more robust than *A. vetus* and *A. pristinus*, and the lingual branch of the parafossette on P^4 separates at an

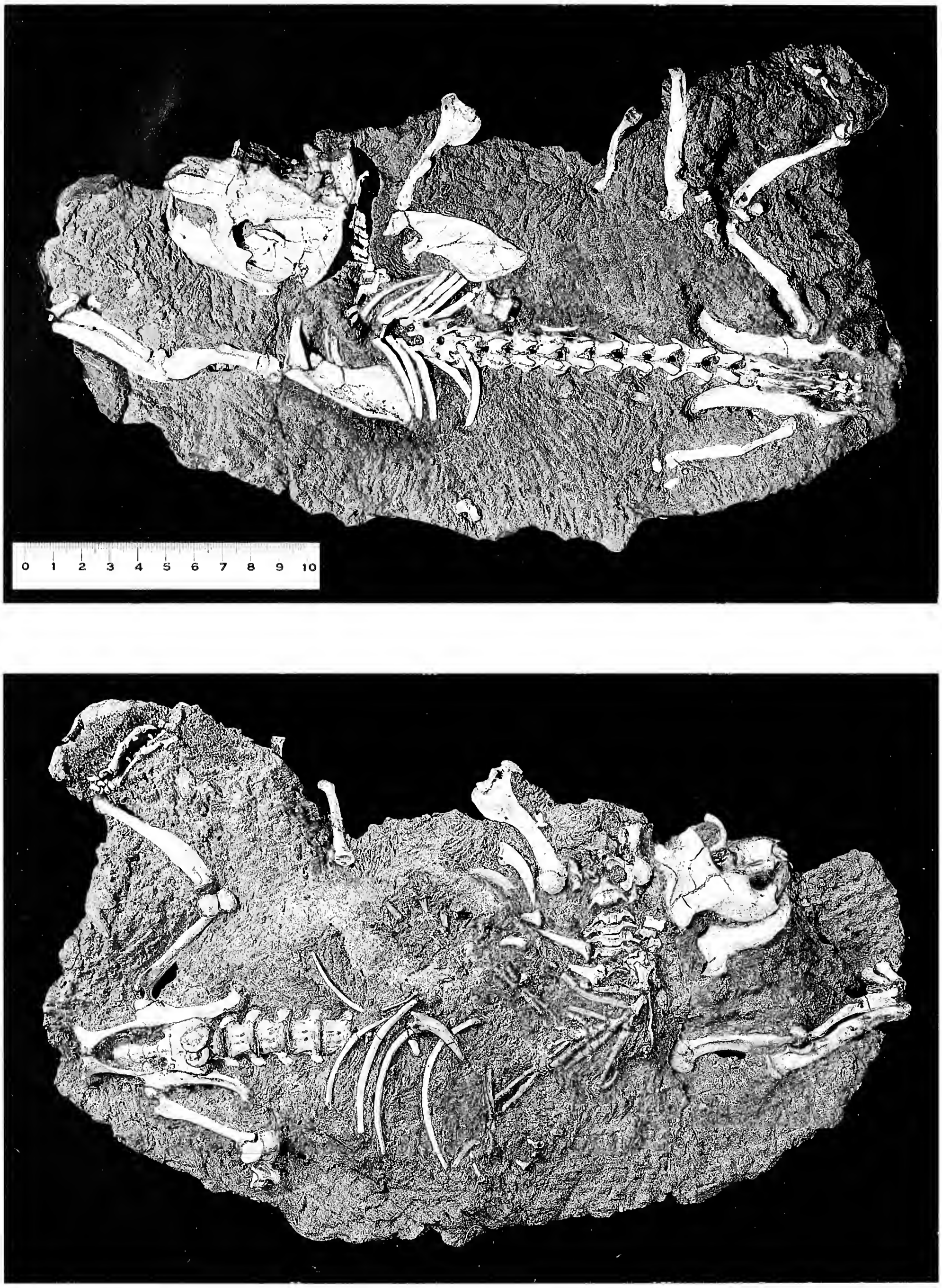

Fig. 7.—Photograph of skeleton of *A. tedfordi*, holotype, FAM 65711. Dorsal view above, ventral view below. Scale is in cm.

Fig. 8.—Stereo photograph (dorsal view) of skull of *A. tedfordi*, holotype, FAM 65711. Scale = 1 cm.

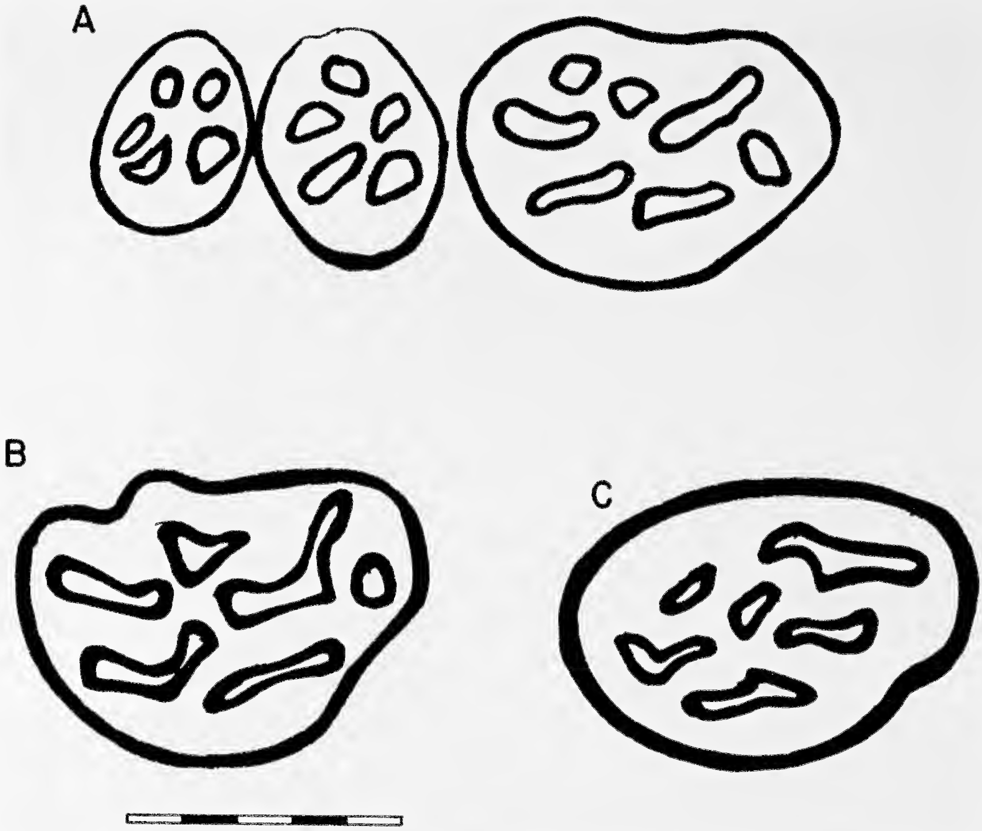

Fig. 9.—Dentitions of the holotypes of *Alphagaulus douglassi* and *A. tedfordi*. A. *Alphagaulus douglassi*, UCMP 44694, P^4, M^2–M^3. B, C. *Alphagaulus tedfordi*, FAM 65711. B. Right P^4. C Right P_4. Bar scale = 5 mm.

earlier stage of wear. *A. tedfordi* can be distinguished from *A. douglassi* by its slightly larger size and the retention of the outline of a mesostyle on P^4.

The more robust skull and separation of the lingual rather than the buccal fork of the parafossette on P^4 in *A. tedfordi* and *A. douglassi* suggest primitive positions of these species with respect to later species of *Ceratogaulus* that share these same characters. The small bosses on the nasals can also be considered primitive to the nasal horns of *Ceratogaulus*. The nasal bosses on a new genus, *Umbogaulus* (described below), are much larger than those of *A. tedfordi* and the premolars have many more fossettes (-ids) than the latter, distinguishing it from *Umbogaulus*.

Umbogaulus, **new genus**

Type Species.—*Umbogaulus galushai* n. sp.

Referred Species.—*Umbogaulus monodon* (Cope, 1881*a*).

Range.—Late (and possibly early) Barstovian of Nebraska.

Diagnosis.—Larger than species of *Ceratogaulus*; large bosses on anterior end of nasals; premolars circular to oval in occlusal outline with multiple minute fossettes (-ids), more complex than *Ceratogaulus*; branches of parafossette of P^4 remain attached until very late stages of wear; anterocentral fossettid of P_4 usually anteriorly forked or widened.

Etymology.—Greek, *umbos*, knob or boss; and *gaulos*, bucket.

Discussion.—*Umbogaulus* differs from *Ceratogaulus* in the presence of large bosses at the anterior end of the nasals rather than paired conical "horns." Dentally, *Umbogaulus* has a greater number of fossettes complexity on the premolars than even the most advanced Hemphillian species of mylagaulines. The greatest difference in the premolars of advanced species of *Ceratogaulus* and *Umbogaulus* is that the premolars of *Ceratogaulus* are relatively longer compared to width than are those of *Umbogaulus*, and all the fossettes (-ids) are narrow, nearly straight, and anteroposteriorly oriented. In *Umbogaulus* the fossettes are often rounder and the teeth are relatively much wider (P^4 nearly round in occlusal outline).

Umbogaulus galushai, **new species**
(Fig. 10, 11A; Table 5)

Type Specimen.—FAM 65576, left P_4.

Referred Specimens.—FAM 65571–65575, 65590–65592, isolated premolars; FAM 65577–65582, edentulous mandibles; FAM 65566, 65567, partial skulls; FAM 65586, two humeri.

Horizon and Locality.—Observation Quarry, "Sand Canyon beds," Dawes County, Nebraska.

Age.—Earliest Barstovian (middle Miocene).

Diagnosis.—Largest species of the genus; greater number of fossettes (-ids) on the premolars (P^4: $\bar{x} = 8.3$, mode 9; P_4: $\bar{x} = 8.4$, mode 8).

Etymology.—Patronym for T. Galusha.

Description.—The two skull fragments of this species preserve only the anterior half of the skull. Both show enlarged bony bosses at the end of the nasals, and are generally heavily built. The premaxillaries are laterally splayed at their dorsal extent to accommodate the enlargement of the anterior end of the nasals and development of the nasal bosses. The centers of these bosses are more anterior than the centers of the horn cores in even the most primitive species of *Ceratogaulus*. Due to breakage, little else can be determined about the skulls.

The premolars are generally larger than in other mylagaulids and are proportionally wider than in species of *Ceratogaulus* (ratio of width to length of P^4 approximately equals 0.75). The upper premolars (represented by only four specimens) are nearly circular in occlusal outline. The number of fossettes ranges from 7 to 9 with 9 as the modal number. The anterior branches of the parafossette do not separate on any of the available specimens, suggesting that any separation will occur in only very late stages of wear. There are several small, circular to oval fossettes along the buccal margin of the tooth posterior to the parafossette. The lingual fossettes are elongated.

The lower premolars are less circular in outline, being distinctly longer than wide but still relatively wider than in other mylagaulines. The number of fossettes ranges from 7 to 11 ($\bar{x} = 8.4$, mode = 8), more than in most other mylagaulines except the most advanced Hemphillian species of *Hesperogaulus* (Shotwell, 1958; Korth, 1999*a*). The fossettids are arranged anteroposteriorly in three rows—lingual, central, and buccal. The buccal row usually consists of only two elongated fossettids and the central row of three. The greatest variability occurs in the lingual row of fossettids. The number of fossettids in this row can range from two to as many as five. The size and shape of the fossettids in the lingual row are clearly dependent on the number. If the fossettids are small and circular, there can be many of them, if elongated, there are fewer fossettids. On approximately 50% of the specimens of P_4, the anterocentral fossettid is anteriorly forked or widened. In some cases a minute fossettid is in the place of one of the branches of the fork.

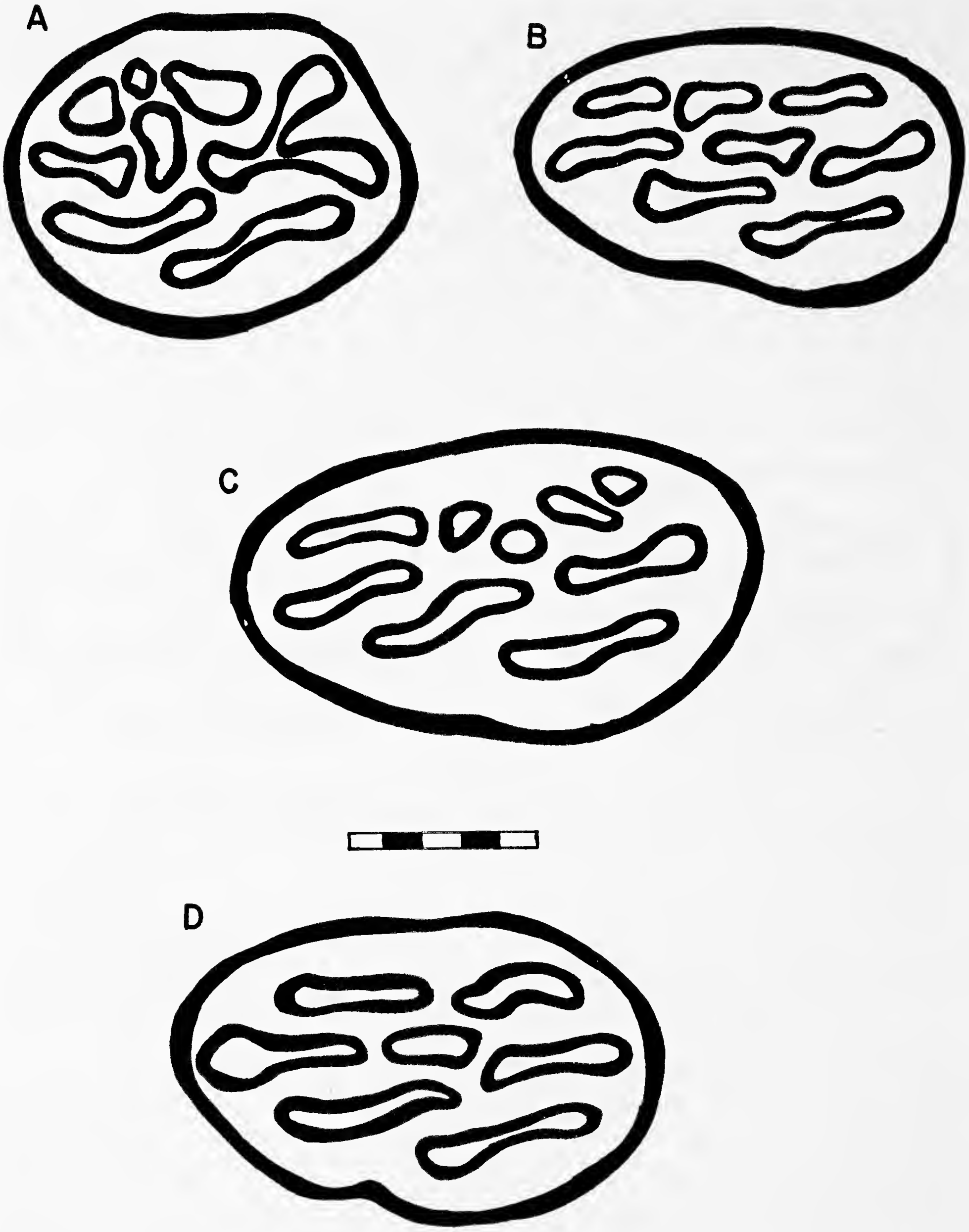

Fig. 10.—Premolars of *Umbogaulus galushai*. A. FAM 65568, right P^4. B. FAM 65574, left P_4. C. FAM 65575, left P_4. D. FAM 65576, holotype, left P_4. Bar scale = 5 mm.

Discussion.—Although the morphology of the nasal bosses and their position on the skull of *Umbogaulus galushai* appear to be primitive relative to species of *Ceratogaulus*, the size and complexity of the cheek teeth exceed that of any species of the latter, so it is unlikely that *U. galushai* is the ancestor to any species of *Ceratogaulus* even though the temporal occurrence (earliest Barstovian) is appropriate for an ancestor of *Ceratogaulus.*

Among all species of mylagaulids, *Umbogaulus galushai* most closely resembles the holotype of "*Mylagaulus*" *mondon* (AMNH 8327). The latter is slightly smaller than *U. galushai* with fewer fossettids on P_4. "*M.*" *monodon* cannot be referred to the same species as *U. galushai,* but is referable to the same genus.

Umbogaulus monodon (Cope, 1881*a*)
(Fig. 11B, 12; Table 5)

Mylagaulus monodon Cope, 1881*a*.

Type Specimen.—AMNH 8327, partial mandible with incisor and P_4.

Referred Specimens.—AMNH 13866, 13868, 13869,17215, 18899, 21466, 22044, 22045, 81071, 81074, 81077, 81080, 81081, 81084, 81085, 81592, 95047, 95054, 95056, 95057; FAM 65713–65716, 65785, 65944, isolated premolars; FAM 65695, mandible with cheek teeth; FAM 65016, 65712, 65784, partial skulls.

Horizon and Locality.—Holotype from Ogallala Group, Driftwood Creek (Hazard Homestead quarry), Hitchcock County, Nebraska; all referred specimens from various localities in the Olcott Formation, Sioux County, Nebraska.

Age.—Early and late Barstovian.

Diagnosis.—Slightly smaller than *U. galushai*; fewer fossettes on the premolars (P^4: $\bar{x} = 7.9$, mode 8; P_4: $\bar{x} = 7.3$, mode 7).

Description.—The nearly complete skull of this species lacks only the nasal bones. It is evident that it is a robust skull, similar to that of *U. galushai* and is posteriorly widened (W/L = 0.87). The only evidence for the formation of large bosses on the anterior end of the nasals is the splaying of the premaxillaries along the naso-premaxillary suture. This morphology is present in the skulls of *U. galushai* that preserve the nasals. The postorbital processes are intermediate in size, probably reflecting the primitive conditon in mylagaulids (POI = 0.35). The occipital is slightly tilted anteriorly (OA = 75°) but not as much as in most other advanced mylagaulines. In all other features, the skull of *U. monodon* is like the cranial material of all other mylagaulines.

The premolars, as in the type species of the genus, are larger and relatively wider than in other mylagaulines. The parafossette of P^4 remains forked until late stages of wear, when either of the branches may be separate. The number of fossettes varies from six in a very young individual to as many as ten. Both the mean and modal number of fossettes are fewer than in *U. galushai* ($\bar{x} = 7.9$, mode 8).

The lower premolars are very similar to those of the type species, differing only in being slightly smaller (Table 5) and having slightly fewer fossettids ($\bar{x} = 7.3$, mode = 7). The anterocentral fossettid of P_4 is also forked or widened as in *U. galushai.* This occurs in approximately 65% of the specimens, a higher percent than in *U. galushai.*

Discussion.—*Mylagaulus monodon* was the second species of the genus described by Cope (1881*a*). It was from the Republican River beds, Hitchcock County, Nebraska. This species was based on a single mandible with an incisor and P_4 (AMNH 8327). The locality from which this specimen was collected has been determined to be late Barstovian in age (Fiorillo, 1988; Voorhies, 1990*a*).

Nearly all specimens of large mylagaulids from the Barstovian to the Hemphillian that have not been associated with cranial material, as well as some hornless skulls, have been referred to *Mylagaulus monodon* (Wilson, 1937*a*, 1937*b*; McGrew, 1941; Gregory, 1942; Webb, 1969; Baskin, 1979; Korth, 1998). In spite of this universal use of the species name, the holotype of *M. monodon* does not appear to match any of this referred material. Even though more collections have been made at the type locality of this species (Fiorillo, 1988), no topotypic material has been found to define better the species itself. The holotype

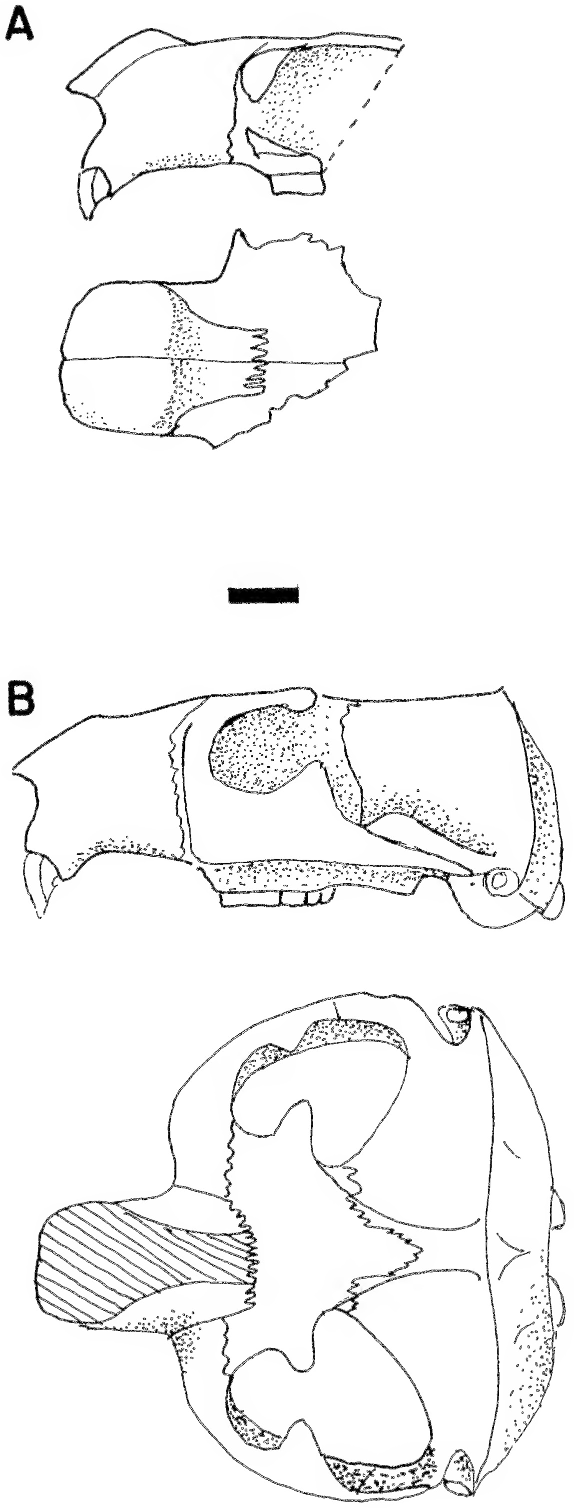
A
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Table 5.—*Measurements of premolars of* Umbogaulus. *Statistical abbreviations as in Table 4.*

		n	x̄	OR	*s*	*cv*
Umbogaulus galushai						
P^4	a–p	4	10.88	10.20–12.00	0.68	6.28
	tr	4	7.21	6.40–7.65	0.48	6.73
P_4	a–p	21	12.02	10.30–13.25	0.79	6.56
	tr	22	6.53	5.50–7.55	0.58	8.81
Umbogaulus sp., cf. *U. monodon*						
P^4	a–p	28	10.24	8.50–12.30	0.97	9.40
	tr	27	6.26	5.50–7.60	0.46	7.28
P_4	a–p	32	11.05	4.50–13.15	1.00	9.06
	tr	32	5.54	4.75–7.10	0.55	9.84

of *M. monodon* differs from the species of *Mylagaulus*, which are characterized by having smaller, more simplified lower premolars (fewer fossettids). The type premolar of *M. monodon* is much larger with more fossettids. It is clear that "*M.*" *monodon* cannot be referred to *Mylagaulus*.

All of the referred specimens of *Umbogaulus monodon* listed above are from the early Barstovian Olcott Formation. There is no morphological difference between this sample and the holotype of the species, but there is a distinct age difference between the holotype (late Barstovian) and the referred material (early Barstovian).

Among known species of mylagaulids, the lower premolars of *Umbogaulus galushai* most closely resemble the type specimen of *M. monodon*, therefore the latter is referred to *Umbogaulus*. The lower premolars of *U. galushai* are distinct from those of *U. monodon* in being slightly larger and having more fossettids.

Mylagaulus Cope, 1878

Type Species.—*Mylagaulus sesquipedalis* Cope, 1878.

Included Species.—*Mylagaulus kinseyi* Webb, 1966, and *M. elassos* Baskin, 1980.

Range.—Possibly late Barstovian of Kansas and Nebraska; Clarendonian and Hemphillian of Florida.

Emended Diagnosis.—P^4 with posterobuccal fossette C-shaped (open posterobuccally) and parafossette with lingual branch separated first in early wear (as in *Ceratogaulus*); P^4 oval in occlusal outline (no indication of stylar cusps); P_4 simpler, with fewer fossettids (six) than other advanced mylagaulines.

Discussion.—Baskin (1980) demonstrated that the two species of *Mylagaulus* from the Clarendonian and Hemphillian of Florida, *M. kinseyi* and *M. elassos*, belonged to a lineage that reduced size through time. The only species of *Mylagualus* from the Great Plains with smaller size was the type species, *M. sesquipedalis*. The separation of the lingual branch of the parafossette of P^4, generally smaller size, reduced complexity (fewer fossettes [-ids] on the premolars), and

←

Fig. 11.—Skulls of *Umbogaulus*. In both A and B top is left lateral view, bottom is dorsal view. A. *Umbogaulus galushai*, FAM 65566. B. *Umbogaulus monodon*, FAM 65016. Nasals missing on B. Bar scale = 1 cm.

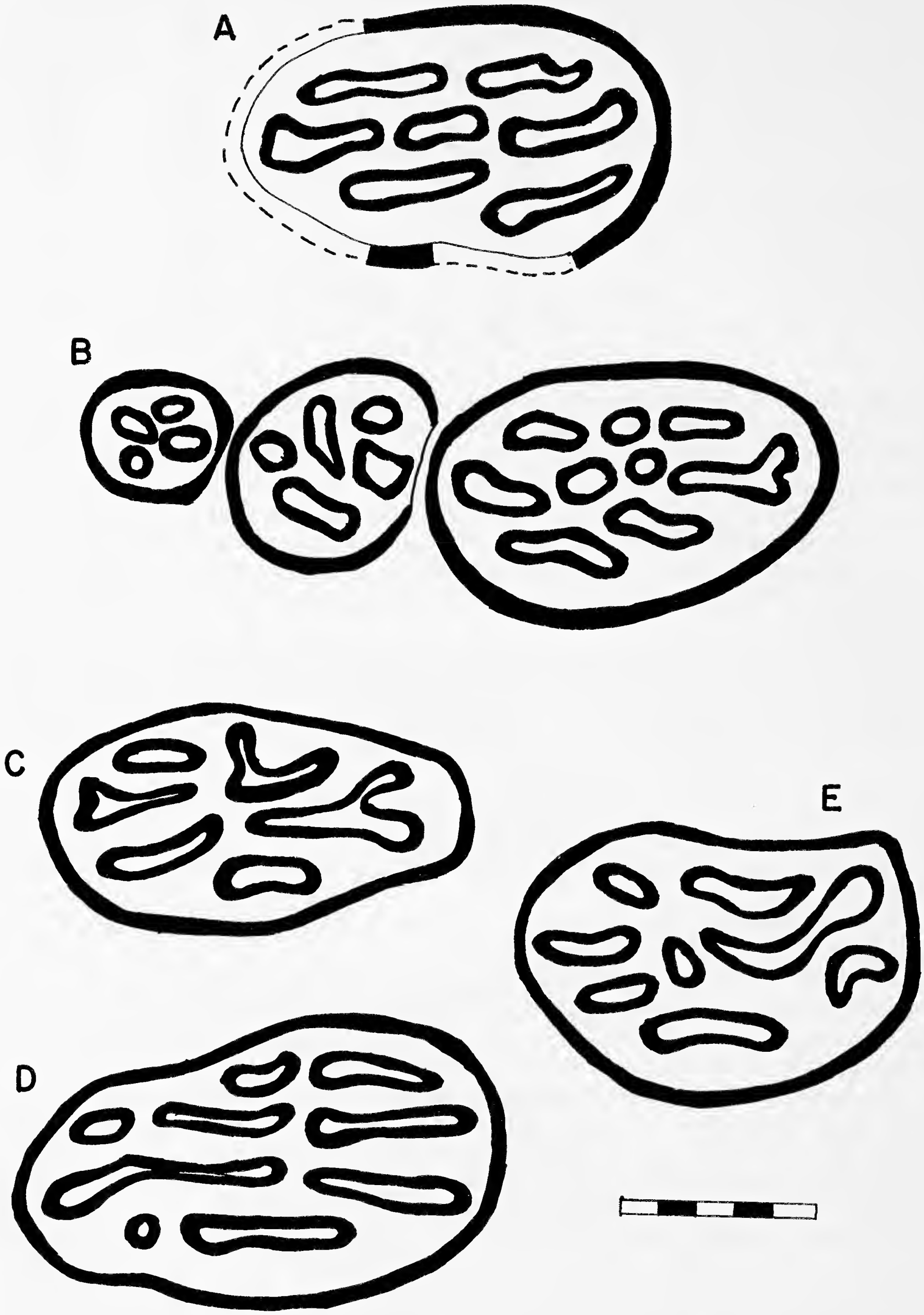

Fig. 12.—Premolars of *Umbogaulus monodon*. A. AMNH 8327, holotype, left P_4. B. FAM 65695, right P_4, M_2–M_3. C. FAM 95057, right P^4. D. AMNH 22044F, right P^4. E. FAM 95052, left P^4. Bar scale = 5 mm.

the C-shaped posterobuccal fossette on P^4 are features that are shared by *M. sesquipedalis* and the Florida species, making these three species a distinctive genus.

The only significant difference between *M. sesquipedalis* and the Florida species is its larger size. The temporal occurrence of *M. sesquipedalis*, possibly latest Barstovian (see discussion below), fits well into the sequence of species of *Mylagaulus* from larger to smaller through time. Being the earliest species, *M. sesquipedalis* is the largest species, *Mylagaulus elassos* from the Clarendonian is slightly smaller, and *M. kinseyi* from the late Hemphillian is the smallest species (see Baskin, 1980:fig. 1).

Mylagaulus sesquipedalis Cope, 1878
(Fig. 13)

Type Specimen.—AMNH 8329, left P^4.

Possible Referred Specimen.—AMNH 8330, left P_4.

Horizon and Locality.—Holotype from Ogallala Group, Sappa Creek, Rawlins County, Kansas. Referred specimen from the "Republican River Beds," Driftwood Creek, Hitchcock County, Nebraska.

Age.—?Late Barstovian.

Emended Diagnosis.—Largest species of the genus.

Discussion.—Cope (1878) erected *Mylagaulus sesquipedalis* based on an isolated upper premolar. The age of the fauna from Sappa Creek, from which the holotype of *M. sesquipedalis* came, is uncertain but has been referred to by previous authors as Clarendonian (Hibbard and Phillis, 1945:552; Baskin, 1980). However, it appears that the Sappa Creek fauna may be older than previously thought. The AMNH specimens from the Sappa Creek fauna include those collected by Cope's field parties in the late 1870s, and a few specimens collected by George Sternberg for the Frick Collections in the early 1930s. Besides the holotype of *Mylagaulus sesquipedalis*, the collected fauna consists of five mammalian taxa: a horse, *Protohippus medius*; a rhino, *Teleoceras fossiger*; a peccary, *Prosthennops servus*; a mastodont, *Tetralophodon campester*; and a merycodont artiodactyl, *Ramoceros kansanus*. *Protohippus medius*, *Prosthennops servus*, and *Tetralophodon compester* are represented by the holotypes of each of these species. The holotype of *P. medius* (AMNH 8360) is the skull of a senile individual where the teeth are completely worn, eliminating nearly all of the occlusal pattern. This species of *Protohippus* has not been recognized by any later workers (notably Osborn, 1918; and Stirton, 1940). The specimen has facial fossae consistent with those of *Protohippus*, and a size equivalent to that of *P. perditus* (R. L. Evander, personal communication) which is limited to the late Barstovian of Nebraska (Voorhies, 1990*a*). The merycodont similarly limits the age of the fauna because *Ramoceras* does not extend any later than the late Barstovian in the Nebraska section (Voorhies, 1990*a*). However, the peccary is very large and is similar to Hemphillian species. There is clearly a mixing of faunas in the Sappa Creek fauna. The mastodont is an advanced species which suggests a younger, possibly Hemphillian age. The rhino is known elsewhere to be late Clarendonian or early Hemphillian in age. Clearly, further collecting in the type area of Sappa Creek is necessary to verify the age of the fauna.

Matthew (1902) reported on a second specimen of *M. sesquipedalis*, AMNH 8330, that included a lower premolar, an incisor, and a metacarpal. He stated that

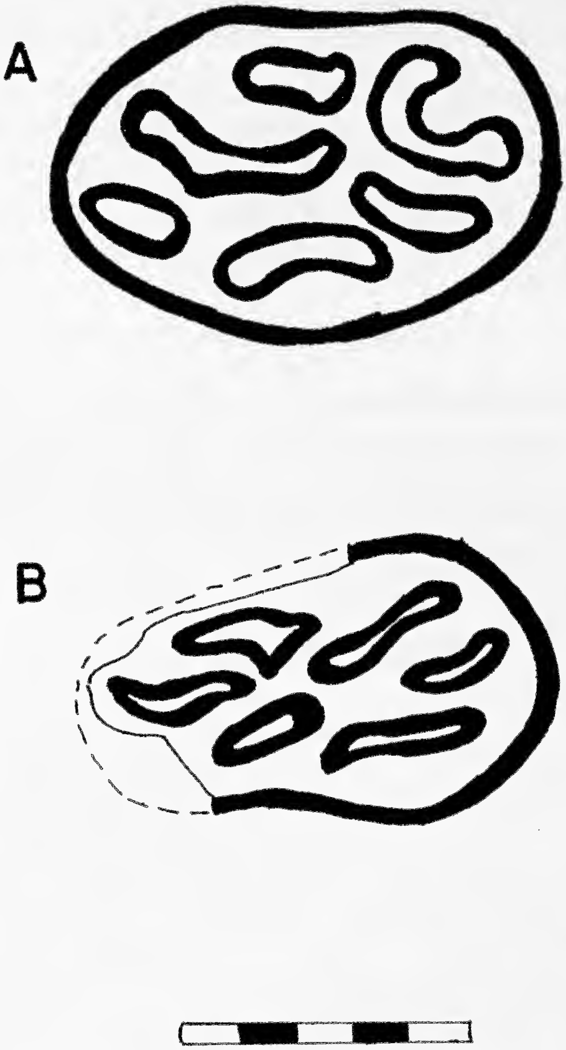

Fig. 13.—Dentition of *Mylagaulus sesquipedalis*. A. holotype, AMNH 8329, right P^4. B. paratype, AMNH 8330, left P$_4$. Bar scale = 5 mm.

the referred specimen was from the same locality as the holotype of *M. monodon*, Driftwood Creek, which is late Barstovian in age (Fiorillo, 1988; Voorhies, 1990*a*). At present, only the holotype and referred premolar are in the AMNH collections. The isolated incisor and metacarpal of the referred specimen cannot be located. While the reference of the referred P$_4$ to *M. sesquipedalis* may be questionable, it is morphologically consistent with the remainder of the species referred to the genus, *M. kinseyi* and *M. elassos*. This specimen was previously figured by Cope and Matthew (1915:pl. CXIXc, fig. 10), but was mistakenly labelled as the holotype. The occurrence of the referred specimen from a late Barstovian indicates that the species occurred at this time.

Both Hibbard and Phillis (1945) and Korth (1998) discussed the possibility of the synonymy of the Clarendonian species *Epigaulus minor* and *M. sesquipedalis*, noting that no conclusion could be drawn simply because of the lack of comparative material. The upper premolars of *E. minor* are slightly larger than the holotype of *M. sesquipedalis* and they are also wider relative to length. The morphology of the parafossette on P^4 is the same on both species, but the morphology of the posterobuccal fossette on specimens of *E. minor* is not the rounded C-shape that is diagnostic of *M. sesquipedalis*. If, however, these species do prove to be synonymous in the future, *Mylagaulus* would have priority, making the presence of horns on the nasals a generic character for *Mylagaulus*.

Ceratogaulus Matthew, 1902

Type Species.—*Ceratogaulus rhinocerus* Matthew, 1902.

Diagnosis.—Large mylagaulines; horns present on nasal bones; postorbital processes progressively reduced (POI $\leq$ 0.20); slope of occipital in Hemphillian species not as low as in other genera (OA = 60°–63°); occipital crest forms straight, transverse line (not deflected anteriorly as in other genera); upper premolars relatively wide (width to length ratio $\geq$ 0.68); lingual branch of parafossette separates first on P^4; anterolingual fossette attaches to lingual branch of parafossette on P^4 with wear; anterocentral fossettid of P_4 V-shaped in early wear.

Included Species.—*Ceratogaulus hatcheri* (Gidley, 1907), *C. minor* (Hibbard and Phillis, 1945), and *C. anecdotus*, n. sp.

Range.—Early Barstovian to Hemphillian (middle to late Miocene) of the northern Great Plains.

Discussion.—*Ceratogaulus* differs from all other mylagaulids in the possession of horns (or horn cores) on the nasal bones. The progressive changes in the genus through time are the more posterior placement of the nasal horns and reduction of the postorbital processes (Fig. 14). The nasal horns not only are placed progressively more posteriorly on the skull, but the horns also have narrower bases and are generally taller. In the late Barstovian *C. rhinocerus*, the horns are pointed but have a very wide base, giving them a pyramid-like profile. In the Clarendonian specimens of the former, the nasals are slightly more posterior (NHI = 0.16–0.22). In the Hemphillian *C. hatcheri*, the horns have narrow bases, are circular in cross section, and are nearly dorsal to the orbits (NHI $\geq$ 0.28). Similary, the postorbital processes are reduced through time: in *C. rhinocerus* they are moderately large (POI = 0.18–0.26), probably near the primitive condition; in *Ceratogaulus* sp., cf. *Ceratogaulus rhinocerus* in the early Clarendonian, the processes are smaller (POI = 0.12–0.15); and, ultimately, in Hemphillian species the postorbital processes are nearly absent (POI = 0.11).

Gidley (1907) named *Epigaulus* for a species, *E. hatcheri*, from the Hemphillian of Kansas, noting that it differed from the type of *Ceratogaulus rhinocerus* (only known species of the genus at that time) from the Barstovian in the more posterior position of the nasal horns, more enlarged premolars, and presence of cement around the premolars. All of these characters are now known to represent gradational changes in the known species of *Ceratogaulus* from throughout the entire time of occurrence of the genus (Table 1). There is no evidence indicating that *Epigaulus* exists as a genus separate from *Ceratogaulus*, but more likely represents the most derived species.

Ceratogaulus is geographically restricted to the northern Great Plains from Kansas to Saskatchewan. Species of *Ceratogaulus* are frequently found in faunas

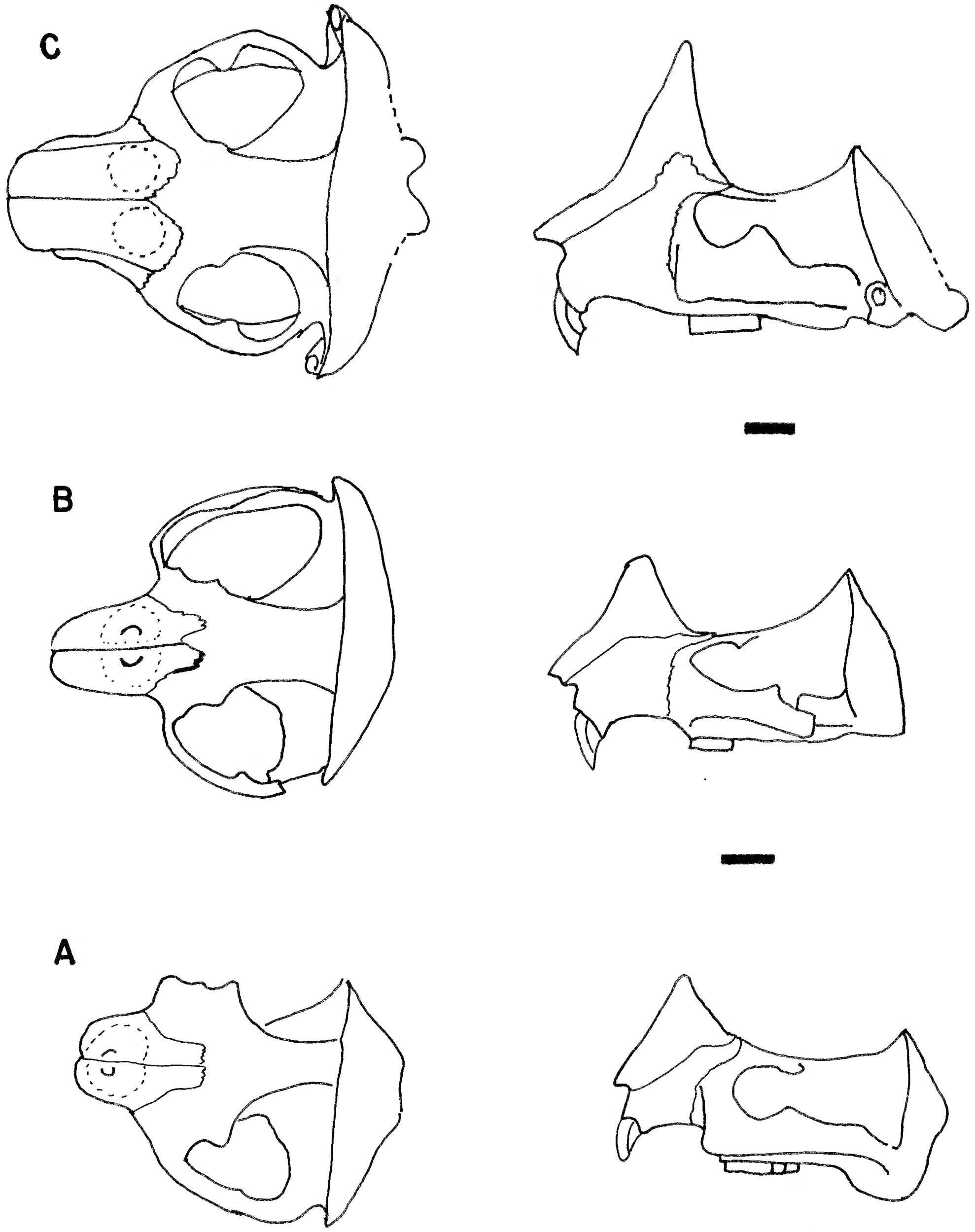

Fig. 14.—Outlines of skulls of *Ceratogaulus* showing progressive changes through time (position of nasal horns and reduction of postorbital process). Dorsal view on left, left lateral view on right. A. Barstovian *C. rhinocerus*, AMNH 9456 (holotype). B. Early Clarendonian *C.* sp., cf. *C. rhinocerus*, FAM 65385. C. Hemphillian *C. hatcheri* (holotype) USNM 5485. Bar scale = 1 cm.

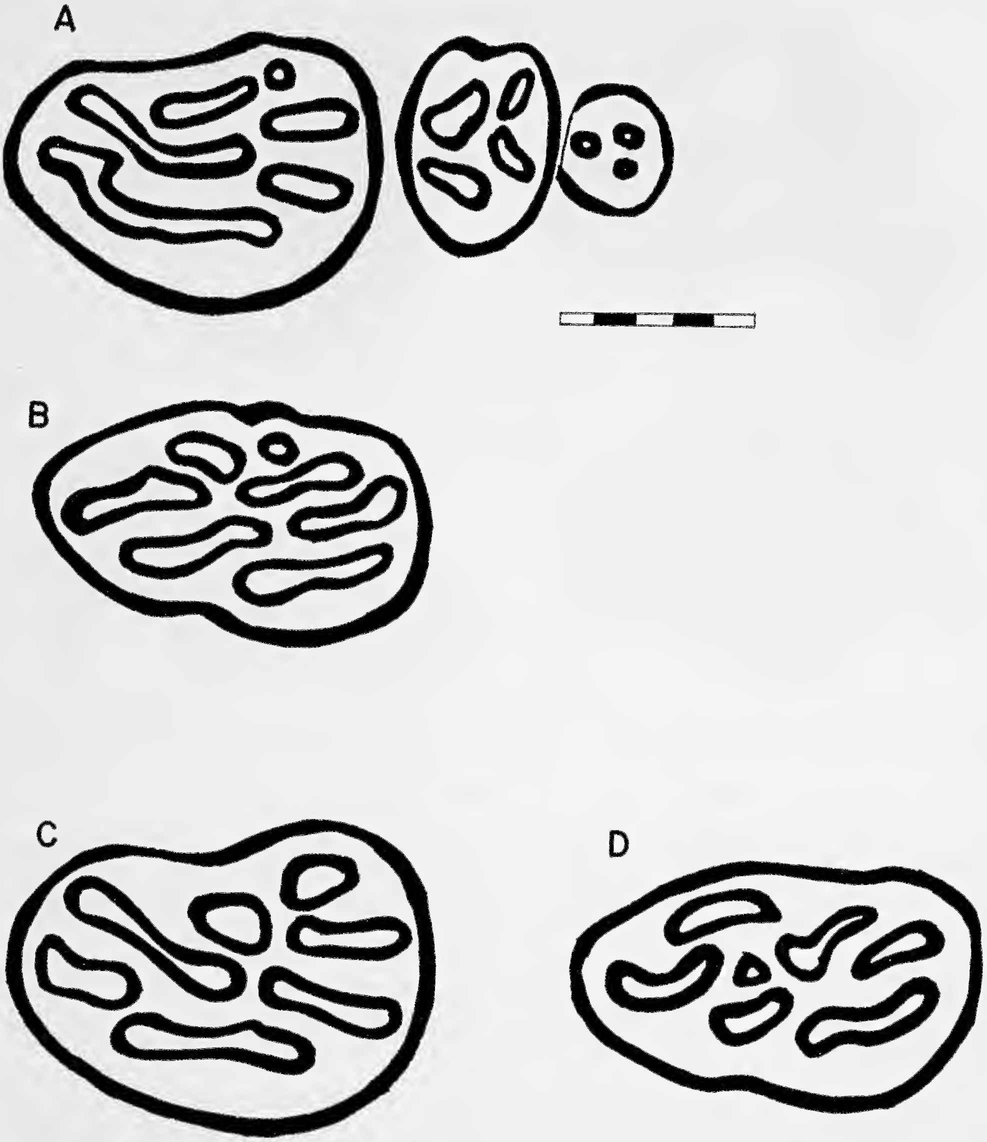

Fig. 15.—Premolars of *Ceratogaulus rhinocerus*. A, B. AMNH 9456 (holotype), Barstovian. A. Left P^4, M^2–M^3. B. Left P_4. C, D. *Ceratogaulus* sp., cf. *C. rhinocerus*, early Clarendonian (Burge). C. FAM 65385, left P^4. D. FAM 65408, left P_4. Bar scale = 5 mm.

that also contain species of a hornless genus of mylagauline described below (see discussion of *Pterogaulus*).

Ceratogaulus rhinocerus Matthew, 1902
(Fig. 14C, 15A, B; Table 6)

Type Specimen.—AMNH 9456, nearly complete skull with associated lower jaw (Matthew, 1902:fig. 1).

Table 6.—*Measurements of premolars of* Ceratogaulus. *Statistical abbreviations as in Table 4.*

		n	$\bar{x}$	OR	*s*	*cv*
Ceratogaulus rhinocerus						
Late Barstovian (Crookston Bridge Member)						
P^4	a–p	3	9.82	9.78–9.88	—	—
	tr	3	6.91	6.57–7.10	—	—
P_4	a–p	4	11.04	10.25–12.35	—	—
	tr	4	6.45	6.10–6.61	—	—
Late Barstovian (Devil's Gulch Member)						
P^4	a–p	3	9.50	8.30–11.60	—	—
	tr	3	6.70	5.70–8.40	—	—
P_4	a–p	1	9.20	—	—	—
	tr	2	5.75	5.70–5.80	—	—
Ceratogaulus sp., cf. *C. rhinocerus*						
Early Clarendonian (Burge Member)						
P^4	a–p	15	9.16	8.35–9.80	0.53	5.79
	tr	16	6.21	5.40–7.00	0.56	8.99
P_4	a–p	20	10.23	8.70–11.45	0.79	7.73
	tr	21	5.43	4.90–6.15	0.38	7.00
Ceratogaulus anecdotus						
Late Clarendonian (Merritt Dam Member)						
P^4	a–p	3	10.16	9.10–12.20	—	—
	tr	3	6.86	6.20–7.90	—	—
P_4	a–p	3	12.66	10.00–14.70	—	—
	tr	4	5.55	5.05–6.70	—	—

Referred Specimens.—AMNH 18899; UNSM 122005, 122007, 122010, 122009.

Horizon and Locality.—Holotype from Pawnee Creek beds, Logan County, Colorado; AMNH 18899, from Olcott Formation, Sioux County, Nebraska; UNSM specimens from Crookston Bridge Quarry, Crookston Bridge Member, Valentine Formation, Cherry County, Nebraska.

Age.—Early to late Barstovian (middle Micoene).

Emended Diagnosis.—Horns on nasals positioned more anteriorly than in other species (NHI = 0.19–0.21), and not as tall; postorbital processes small, triangular flanges (POI = 0.19), larger than in other species.

Decription.—Matthew (1902) fully described and figured the skull of *Ceratogaulus rhinocerus*. The upper premolar has from five to ten fossettes ($\bar{x}$ = 7.4; mode = 7). While the mean number of fossettes on P^4 is slightly higher than other species of the genus, the modal number is identical for all species of *Ceratogaulus* (Table 2). The parafossette is the longest of the fossettes and its lingual branch separates from the rest of the fossette in early stages of wear. A single lingual fossette runs most of the length of the tooth, occasionally uniting anteriorly with the lingual branch of the parafossette once it has separated. The remainder of the fossettes on P^4 are smaller and directed anteroposteriorly. Frequently, there is one minute, circular fossette present along the buccal edge of the tooth just posterior to the center of the tooth. P^4 is not perfectly oval in occlusal outline. There is always a slight concavity along the buccal edge of the tooth (created by a vestige of the mesostyle) with its deepest curvature near the middle of the tooth.

The lower premolar has seven to ten fossettids ($\bar{x}$ = 7.7; mode = 7). There are three elongated fossettids along the lingual side and three along the buccal side of the tooth with one or more small, circular accessory fossettids randomly positioned. The elongated fossettids are all oriented obliquely (posterolingual to anterobuccal). The most anterior fossettid is V-shaped in early stages of wear with the apex of the V pointed posteriorly. After a moderate amount of wear, the lingual arm of the V separates from the rest of the fossettid, and ultimately disappears with additional wear.

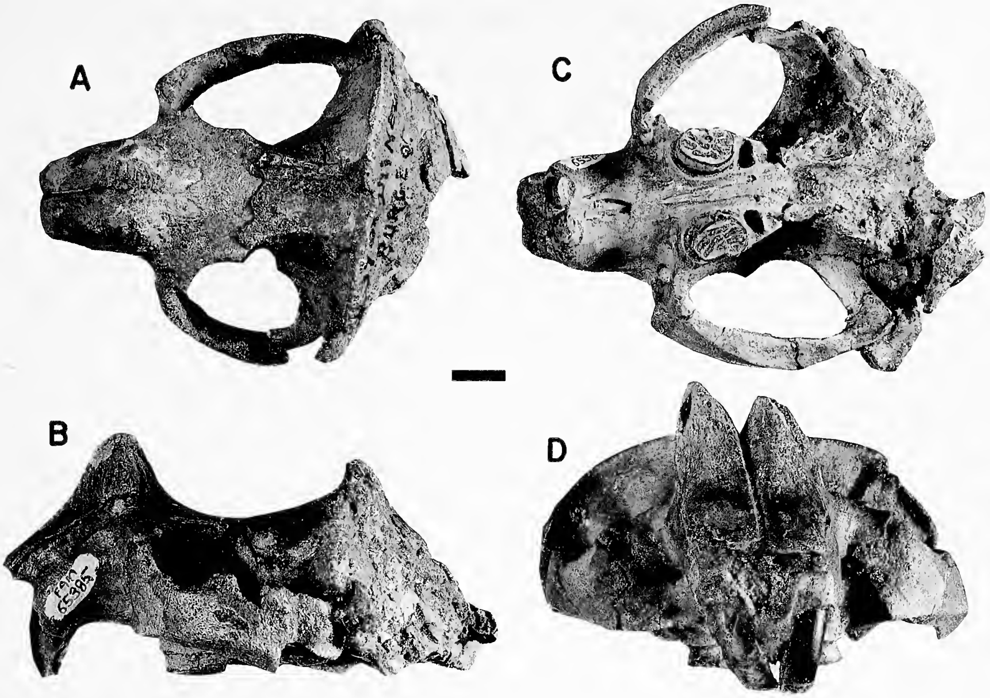

Fig. 16.—Skull of *Ceratogaulus* sp., cf. *C. rhinocerus*, FAM 65385, from Burge Quarry (early Clarendonian). A. Dorsal view. B. Left lateral view. C. Ventral view. D. Anterior view. Bar scale = 1 cm.

Discussion.—Specimens of *C. rhinocerus* show a consistent morphology of the skull and dentition throughout the entire range of the species. The dentition is especially conservative in terms of morphological change. There is little or no change in the size or morphology of the premolars from the early Barstovian to the early Clarendonian.

Ceratogaulus rhinocerus differs from the late Clarendonian and Hemphillian species of *Ceratogaulus* mainly in the morphology of the premolars. The upper premolars of *Ceratogaulus* are relatively wide compared to their length (length to width ratio of ≥ 0.71). P^4 of *C. rhinocerus* is not entirely oval in outline, maintaining a slight concavity on the buccal margin between the mesostyle and parastyle. Later species of *Ceratogaulus* have much narrower premolars (P^4 length to width ratio ≤ 0.65), cement appears around the premolars at an earlier stage of wear, and the premolars are oval in outline, lacking the slight buccal concavity present on P^4 of *C. rhinocerus.*

Ceratogaulus sp., cf. *C. rhinocerus*
(Fig. 14B, 15C, D, 16; Table 6)

Referred Specimens.—FAM 65012, 65013, 65370, 65371, 65373, 65374, 65375, 65377, 65385, 65388, 65398, 65399, 65403, 65404, 65406, 65408, 65412, 65413, 65418, 65420, 65422, 65476, 65489, 65833; UNSM 122006.

Horizon and Locality.—All specimens from various quarries (Burge, Midway, White Face, Lucht, June, Gordon Creek) in the Burge Member, Valentine Formation, northcentral Nebraska (see Skinner and Johnson, 1984, for location of quarries).

Age.—Early Clarendonian.

Discussion.—Dentally, it is virtually impossible to distinguish the Burge specimens of *Ceratogaulus rhinocerus* from those from lower in the Valentine Formation. However, the cranial material is somewhat different. The Burge specimens, referred here to *Ceratogaulus* sp., cf. *C. rhinocerus*, have more posteriorly placed horns and more reduced postorbital processes (Table 1). The skulls are also slightly larger. The slightly larger skull size is not reflected in the dimensions of the dentition (Table 6) or the complexity of the premolars (Table 2). The horns on the specimens from the Burge have narrower bases and are more nearly circular in cross section than those from the late Barstovian.

It would be impractical to name a new species for the Burge specimens at this time because the majority of the specimens recovered are dentitions which cannot be separated from the Barstovian specimens morphologically. The Burge skulls are clearly more advanced in having more posteriorly placed horns and smaller postorbital processes (Fig. 14, 16).

Ceratogaulus anecdotus, **new species**

(Fig. 17; Table 6)

Epigaulus minor Hibbard and Phillis; Korth, 1997 (in part).
Mylagaulus sp., cf. *M. monodon* Cope; Korth, 1997 (in part).

Type Specimen.—FAM 65800, fragmentary skull with both upper premolars and some postcranial fragments.

Referred Specimens.—FAM 65466, partial skull; FAM 65456, 65464 isolated P^4s; FAM 65456, associated upper and lower premolars; FAM 65430, 65468, 65481, 65497; UNSM 101813, mandible with P_4, M_2–M_3.

Horizon and Locality.—Holotype and some referred specimens from Pratt Quarry (UNSM locality Bw-123), Merritt Dam Member, Ash Hollow Formation, Brown County, Nebraska; other referred specimens from various localities in the Merritt Dam Member; FAM 65466 from "Prospect 28-18," Cap Rock Member, Ash Hollow Formation, Brown County, Nebraska.

Age.—Middle to late Clarendonian (early late Miocene).

Diagnosis.—Smaller than *C. hatcheri*, larger than other species of the genus; premolars more elongated than in *Ceratogaulus rhinocerus*, but less than in *C. hatcheri* (width to length ratio of $P^4 = 0.64$–0.66); fewer fossettes (-ids) on premolars than in *C. hatcheri*; P^4 oval in occlusal outline; cement surounds premolars in an earlier stage of wear than in *C. rhinocerus*; postorbital process subequal to that of *C. hatcheri* and smaller than in *C. rhinocerus* (POI = 0.12); nasal horn less posterior than *C. hatcheri*, more posterior than in *C. rhinocerus* (NHI = 0.30).

Etymology.—Greek, *anekdotos*, unpublished or secret.

Description.—The nearly complete skull of a juvenile individual of *C. anecdotus*, FAM 65466, is badly broken but most of the morphology of the skull is recognizable. A nearly complete skull in the UNSM collections (field number 2-26-5-15) is being studied elsewhere, but allows for a determination

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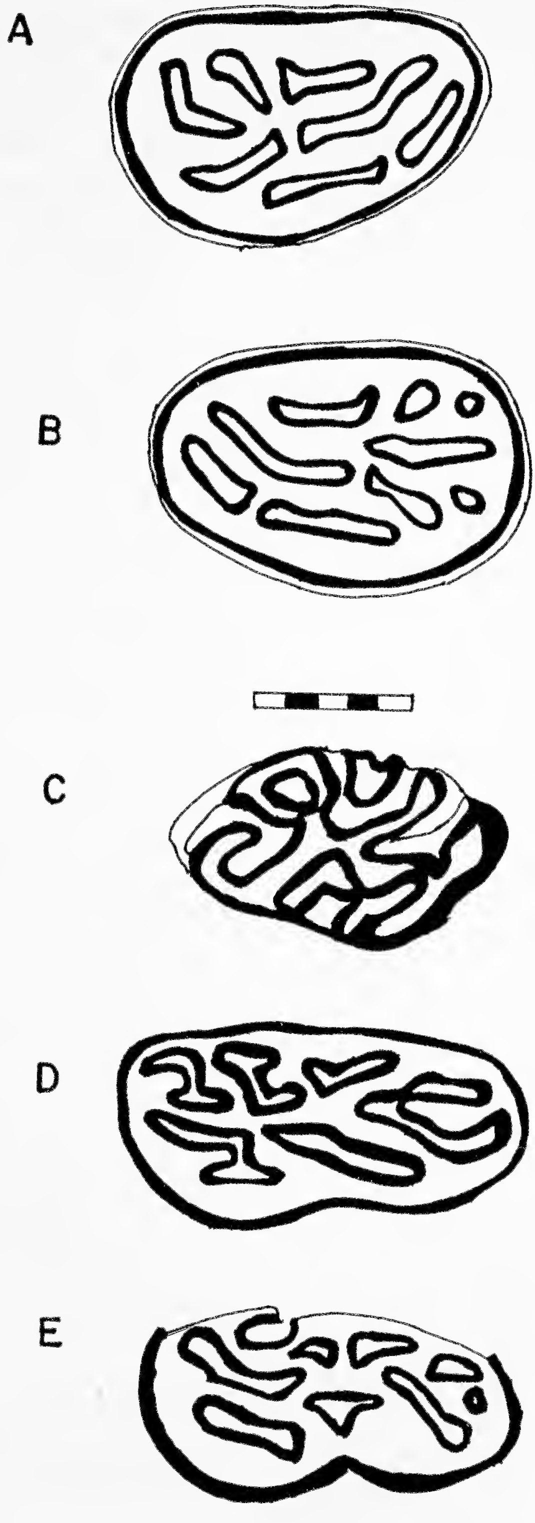
Fig. 17.—Dentition of *Ceratogaulus anecdotus*. A, B. Holotype, FAM 65800. A. Right P^4. B. Left P^4. C. FAM 65484, right P_4. D. UNSM 101813, right P_4. E. FAM 65497, right P_4. Bar scale = 5 mm.


A
B
C
D
E

of the position of the nasal horn (NHI = 0.30) and the angle of the occipital (OA = 60°). The holotype also contains fragments of the skull including a complete nasal bone that preserves the horn. The horn is roughly circular in cross section and is posteriorly positioned. Its position is slightly more anterior than in *C.hatcheri* but more posterior than in any skull of *Ceratogaulus rhinocerus* (Table 1). The postorbital processes are more reduced than in any other species of *Ceratogaulus* except *C. hatcheri*. The premolars are larger than those of *C. rhinocerus*, but smaller than those of *C. hatcheri*. The number of fossettes on P^4 ranges from 6 to 9, similar to that of *C. rhinocerus* (Table 2). P^4 is narrower than in *C. rhinocerus* and *C. minor* (width to length ratio = 0.65). One specimen of P^4 (FAM 65465) has little wear and appears a little wider, within the range of *C. rhinocerus*. The arrangement of the fossettes of P^4 is similar to those of *C. minor* and *C. rhinocerus*, differing only in having several minute fossettes on the posterior half of the tooth. The two P^4s of the holotype are only moderately worn and already are completely surrounded by cement. This appears to occur much earlier in *C. anecdotus* than in *C. rhinocerus*.

The lower premolars of *C. anecdotus* differ from those of *C. rhinocerus* in the same way as do the upper premolars. The range of the number of fossettids is 6 to 10, again similar to the range in *C. rhinocerus*. The only other differences between P_4 of *C. anecdotus* and those of *C. rhinocerus* are larger size and earlier appearance of cement around the tooth.

Discussion.—*Ceratogaulus anecdotus* is more advanced than *C. rhinocerus* based on the morphology of the horn (more posterior, circular cross section), proportions of the premolar, reduction of the postorbital process, larger size, and earlier occurrence of cement around the cheek teeth. It differs from *C. hatcheri* in having a more anteriorly placed horn, smaller size, and fewer fossettes (-ids) on the premolars.

Korth (1997) originally referred the holotype of *C. anecdotus* to *Epigaulus minor*. However, this specimen differs from *C. minor* not only in the cranial features cited above, but also in its larger size and narrower upper premolars. Similarly, a specimen figured by Korth (1997:fig. 1B) as *Mylagaulus* sp., cf. *M. monodon*, UNSM 101813, is clearly referable to *C. anecdotus* with the characteristic V-shaped anterior fossettid on P_4.

Pterogaulus, **new genus**

Type Species.—Mylagaulus laevis Matthew, 1902.

Referred Species.—*P. cambridgensis* (Korth, 2000), *P. barbarellae* n. sp., and *Pterogaulus* sp.

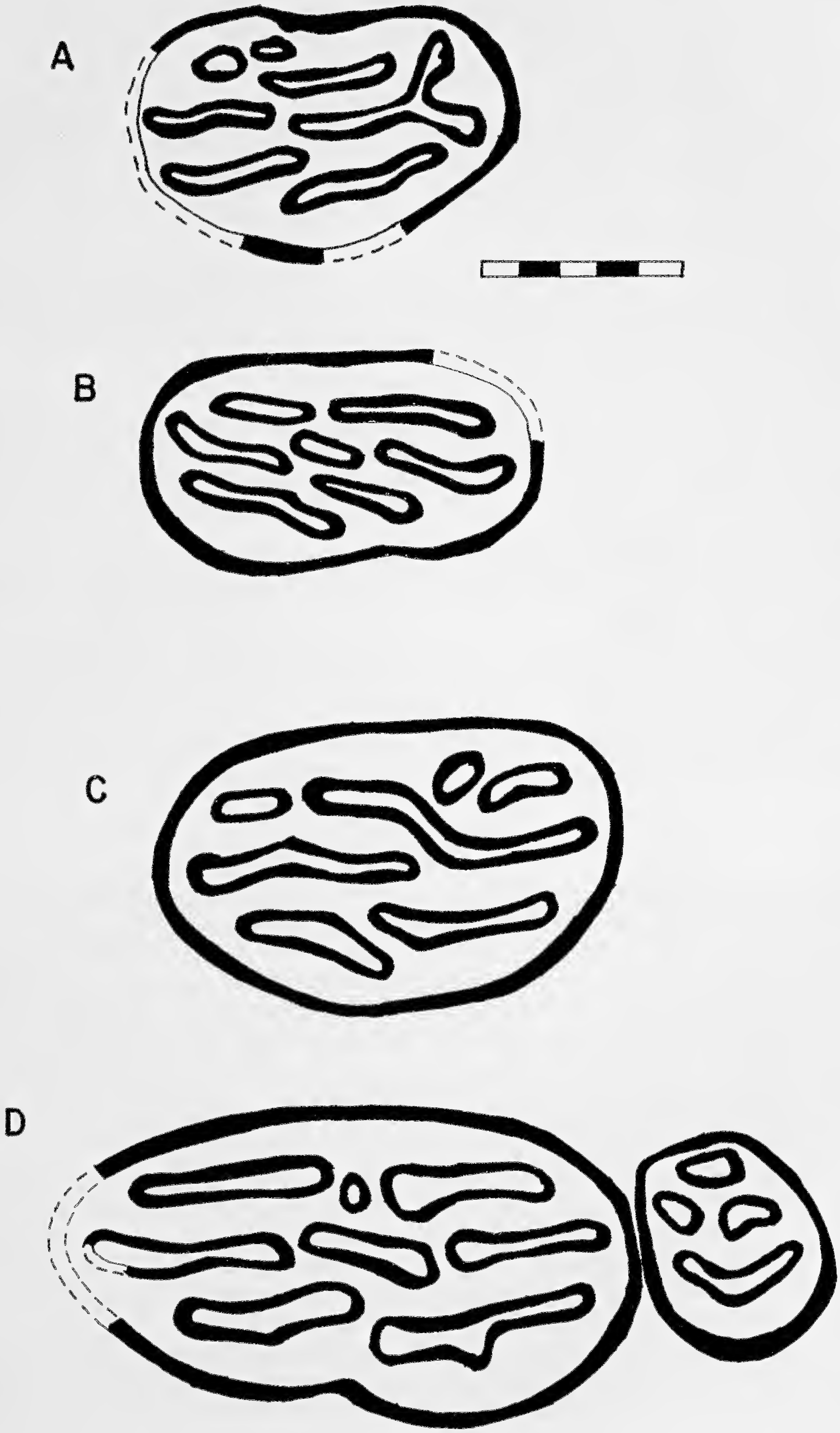
Range.—Barstovian to Hemphillian of northern Great Plains.

Etymology.—Greek, *pteron*, wing; and *gaulos*, bucket.

Diagnosis.—Intermediate to large mylagaulines; horns or bosses lacking on nasals; frontals with enlarged, wing-like postorbital processes (POI = 0.39–0.57); angle of occipital in advanced species generally lower than in other genera (OA < 60°) but not as low as in *Hesperogaulus*; occlusal pattern of premolars with anteroposteriorly oriented linear fossettes(-ids); in advanced species, first and second molars lost with eruption of permanent premolars; buccal branch of parafossette on P^4 separates from remainder of fossette first; premolars more anteroposteriorly elongated than in *Ceratogaulus* (P^4 width to length ratio ≤ 0.68).

→

Fig. 18.—Premolars of *Pterogaulus laevis* and *P. barbarellae*. A, B. *Pterogaulus laevis*, AMNH 9043, holotype. A. Right P^4. B. Right P_4. C, D. *Pterogaulus barbarellae*. C. FAM 65491, holotype, left P^4. D. FAM 65493, left P_4, M_2. Bar scale = 5 mm.


A
B
C
D

Pterogaulus laevis (Matthew, 1902)
(Fig. 18A, B, 19A; Table 7)

Mylagaulus monodon (in part) Matthew, 1901.
Mylagaulus laevis Matthew, 1902.

Type Specimen.—AMNH 9043, anterior half of skull with associated mandible and pelvis (Matthew, 1901:figs. 3, 4, 5, 6).

Referred Specimens.—KU 9807, 9808, 9969; and specimens from Sioux County, Nebraska cited in Matthew (1924:78).

Horizon and Locality.—Holotype and KU specimens from Pawnee Creek Formation of northeastern Colorado (Matthew, 1924), referred specimens from Olcott Formation, Sioux County, Nebraska (Matthew, 1924; Skinner et al., 1977).

Age.—Barstovian (middle Miocene).

Emended Diagnosis.—Smallest species of the genus; postorbital process smaller than in other species (POI = 0.39–0.41); angle of occipital greater than in late Barstovian and Clarendonian species (OA = 68°–75°); parafossette of P^4 more persistent than in other species (buccal branch separates very late in wear); fewer number of fossettes (-ids) on premolars than in later species (P^4: $\bar{x} = 6.5$, mode = 6; P_4: $\bar{x} = 5.7$, mode = 5).

Discussion.—Matthew (1901, 1902, 1924) fully described and figured the skull and dentition of *Pterogaulus laevis*. The skeleton was fully described by Fagan (1960).

This species is both temporally older and morphologically more primitive than later species of this genus. Its early Barstovian occurrence predates that of all other species. In its smaller size and morphology of the skull (angle of occipital, size of postorbital processes) and dentition (fewer fossettes, separation of parafossette fork later in wear), it is clearly more primitive than the later species.

Pterogaulus sp.
(Table 7)

Discussion.—Several authors have previously identified specimens of this species from the Barstovian of Nebraska and Saskatchewan as *Mylagaulus* cf. *M. laevis* (Storer, 1975; Voorhies, 1990*b*; Evander, 1999). The cranial and dental features of this species are clearly intermediate between those of the early Barstovian *Pterogaulus laevis* and the late Clarendonian species described below. This previously described material, and additional material more recently recovered by UNSM clearly represents a new species. However, the description and naming of this species will not be presented here; it is part of a larger faunal study currently underway by workers at UNSM.

The stratigraphic range of *Pterogaulus* sp. is similar to that of *Ceratogaulus rhinocerus*, but extends from the middle Barstovian to the middle Clarendonian, slightly later than the last occurrence of *C. rhinocerus* (early Clarendonian). There appears to be no discernible difference in morphology or size between specimens from the lowest level (Norden Bridge Quarry) and those from the highest level (Cap Rock Member), unlike specimens of *C. rhinocerus*, which show advancements in the skull in the early Clarendonian specimens.

While *Pterogaulus* sp. and *C. rhinocerus* are contemporaneous for most of their known records, they rarely occur at the same quarry. For example, at the Norden Bridge Quarry, West Valentine Quarry, and Stewart Quarry (see Voorhies, 1990*a*,

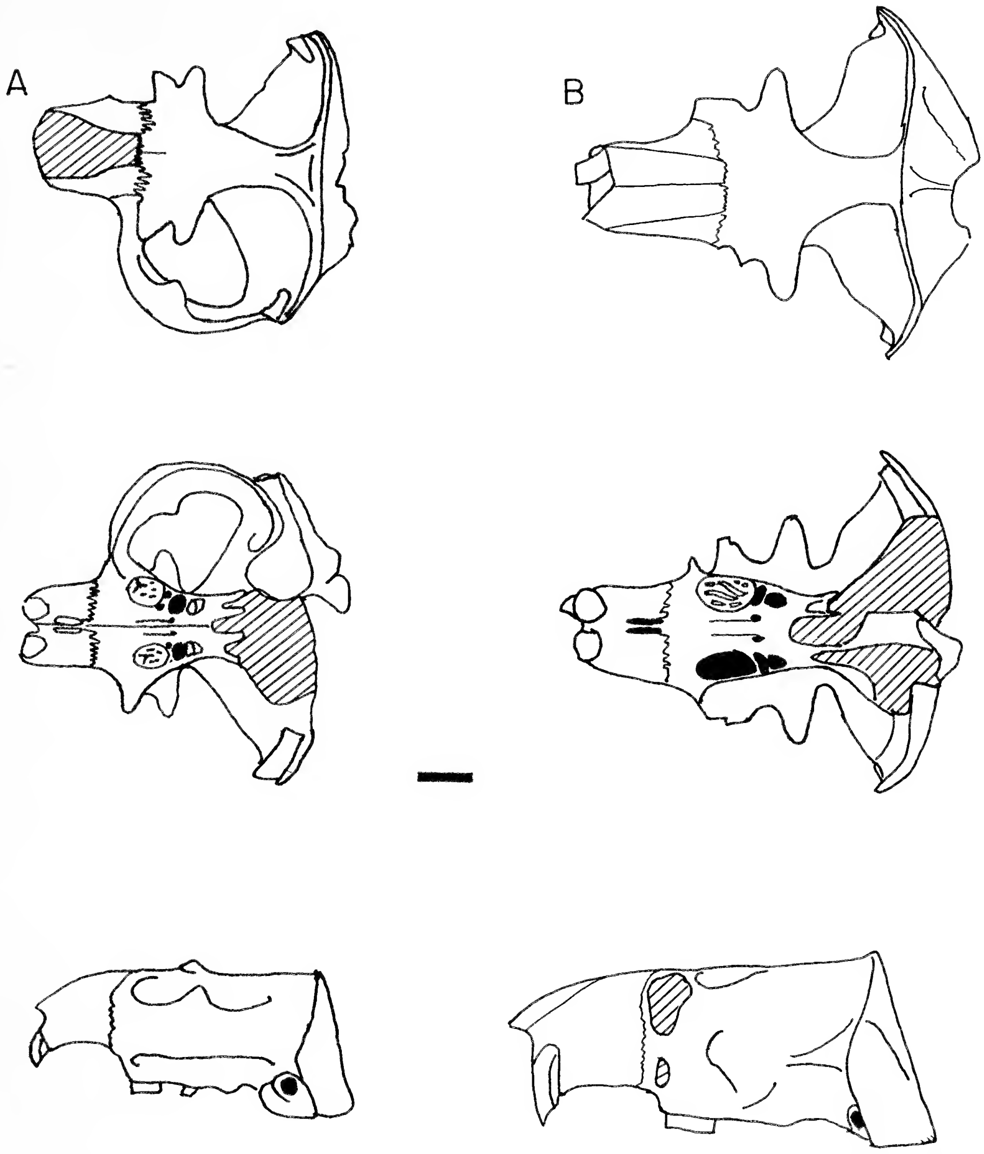


Fig. 19.—Skulls of *Pterogaulus*, dorsal view (top), ventral view (center), and left lateral view (bottom). A. *Pterogaulus laevis*, AMNH 17576. B. *Pterogaulus barbarellae* holotype, FAM 65491. Scale = 1 cm.

and Voorhies and Timperley, 1997, for location of quarries), where *Pterogaulus* sp. is abundant, there are no specimens of *Ceratogaulus*. In other quarries from the same horizon in the Valentine Formation, such as the Cornell Dam Quarry, only specimens of *C. rhinocerus* have been recovered. This suggests that these species were mutually exclusive in terms of geography, possibly competing for resources with one another.

Table 7.—*Measurements of premolars of* Pterogaulus. *Measurements from middle Barstovian sample of* Pterogaulus *sp. from Voorhies (1990*b*:A84). Statistical abbreviations as in Table 4.*

		n	x̄	OR	*s*	*cv*
Pterogaulus laevis						
P^4	a–p	15	7.87	7.00–9.00	0.58	7.4
	tr	15	4.97	4.35–5.45	0.30	6.0
P_4	a–p	11	8.18	7.40–9.30	0.51	6.2
	tr	11	4.12	3.60–5.00	0.34	8.3
Pterogaulus sp. (middle Barstovian)						
P^4	a–p	8	9.0	8.3–10.0	—	—
	tr	8	5.5	4.8–6.5	—	—
P_4	a–p	9	9.4	8.7–10.2	—	—
	tr	9	5.0	4.5–5.5	—	—
Pterogaulus sp. (Clarendonian)						
P^4	a–p	9	8.9	7.6–10.2	0.8	8.9
	tr	9	5.8	5.4–6.4	0.3	5.2
P_4	a–p	2	9.8	8.5–11.2	—	—
	tr	2	5.0	4.75–5.2	—	—
Pterogaulus barbarellae						
P^4	a–p	19	10.48	8.80–12.50	1.20	11.48
	tr	18	6.27	5.55–7.50	0.62	9.91
P_4	a–p	18	11.40	9.45–13.30	1.19	10.41
	tr	18	5.43	4.85–6.85	0.51	9.36

Pterogaulus barbarellae, **new species**
(Fig. 18C, D, 19B; Table 7)

Mylagaulus ? Gregory, 1942.
Mylagaulus cf. *monodon* Webb, 1969 (in part).
Mylagaulus cf. *M. mondon* Voohries, 1990*a*.
Mylagaulus sp., cf. *M. mondon* Korth, 1997 (in part).
Mylagaulus monodon Cope, Korth, 1998 (in part).

Type Specimen.—FAM 65491, skull with P^4.

Referred Specimens.—FAM 65008, 65435, 65436, 65439–65443, 65446, 65448, 65454, 65465, 65475, 65491–65496, 65498, 65499, 65787, 65788, 65791, 65797.

Horizon and Locality.—Holotype from Xmas Quarry, Xmas and Kat Channels, Ash Hollow Formation, Cherry County, Nebraska; referred specimens from various late Clarendonian localities in Merritt Dam Member, Ash Hollow Formation, Nebraska.

Age.—Late Clarendonian (early-late Miocene).

Diagnosis.—Larger than *P. vetus* and *Pterogaulus* sp.; postorbital processes larger than in any other species (POI = 0.40–0.57); angle of occipital less than in other species (OA = 52°); fossettes(-ids) on premolars more elongated and anteroposteriorly aligned than in other species but similar in number (P^4: $\bar{x} = 7.8$, mode = 8; P_4: $\bar{x} = 6.5$, mode = 6); first two molars lost with eruption of permanent premolar.

Etymology.—Patronym for Barbara Lamb.

Description.—The skull of *Pterogaulus barbarellae* is more advanced than that of *Pterogaulus* sp. in having larger postorbital processes and having a lower angle of the occipital (Table 1). It is also clearly larger in size (Table 7). All other features of the skull appear to be the same as in all other species of the genus, with no indication of a horn or boss on the nasals.

The premolars of *P. barbarellae* are larger than in other species in proportion to the rest of the dentition. It appears that with the eruption of the permanent premolar, the first two molars are shed instead of just M^1 or M_1. P^4 has a nearly equal number of fossettes to P^4 of *Pterogaulus* sp. with a similar range (6 to 10) but a slightly greater mean number (7.8 rather than 7.2 for *Pterogaulus* sp.). The buccal fork of the parafossette is separated from the rest of the fossette on nearly all specimens. The only specimens that retain this connection are those of very young individuals with little or no wear on the teeth.

On P_4, the number of fossettids is not greater than in *Pterogaulus* sp. but they are relatively longer and more directly anteroposteriorly oriented, forming an almost linear pattern on the occlusal surface. The length of most of the main fossettids is approximately half the total length of the tooth.

Discussion.—Pterogaulus barbarellae is larger and more derived than either of the older species of the genus. It clearly follows the trends in morphology of the skull (larger postorbital processes, lower angle of occipital) and dentition (larger premolars, more elongated fossettes) that are recognizable in earlier species. Another species of this genus, *P. cambridgensis*, is present in the Hemphillian of Nebraska (Korth, 2000). The latter also follows these same morphoclines for the skull and dentition.

Ceratogaulus anecdotus is contemporaneous with *P. barbarellae*, similar to the case of *C. rhinocerus* and *Pterogaulus* sp. in the Barstovian and early Clarendonian. However, the occurrence of the late Clarendonian species does not appear to be mutually exclusive as is the case with the Barstovian species. In at least two localities (Beaman Creek, Pratt Quarry) specimens of both *C. anecdotus* and *P. barbarellae* are present. However, the fossil quarries in the late Clarendonian "Xmas and Kat Channels" (Skinner and Johnson, 1984) have produced only specimens of *Pterogaulus*. There are no specimens of *Ceratogaulus* in the AMNH Frick Collections from these quarries, although they were extensively collected.

CONCLUSIONS

Variation in Premolars within Species.—Black and Wood (1956) made a detailed study of the progressive changes in the number and shape of fossettes on the cheek teeth of the Hemingfordian "*Mesogaulus*" *novellus*. Shotwell (1958) sectioned the premolars of a number of specimens of later Tertiary mylagaulids to demonstrate ontogenetic changes in the species he discussed. Korth (1997) also discussed ontogenetic changes in premolars from the late Clarendonian specimens that he referred to *Mesogaulus monodon* (referred here to *Pterogaulus barbarellae*). The pattern of change in the occlusal morphology of premolars of mylagaulines in an individual, and the range of variation in a population, appear to be fairly consistent throughout the family.

The number of fossettes in a single premolar of any species varies throughout the life of the individual. In unworn specimens of premolars that are just reaching the level of occlusion, the number of fossettes is the fewest. At this time the major fossettes are often joined at their ends, forming a number of star-like fossettes with many branches. As the tooth reaches an intermediate stage of wear, the major fossettes separate from one another, and the highest number of fossettes is attained. In most senile individuals with heavily worn premolars, the number is near the maximum, with only a few of the smallest fossettes, which are shallower, being lost. At this time the proportions of the tooth are such that the tooth is much narrower than at any other time, and the fossettes(-ids) are generally more anteroposteriorly aligned and closely packed together.

Because the premolar tapers toward its base, once the tooth has worn past its maximum dimensions it becomes surrounded by a layer of cement. In *Mesogaulus* and primitive mylagaulines, this occurs in very late stages of wear. In the more advanced species, where the premolar is proportionally much larger, cement is present at the occlusal surface at an earlier stage of wear.

The parafossette of P^4 also shows some changes through the life of an individual. Originally, the parafossette maintains its two anterior branches. In more primitive species, these remain attached to the remainder of the fossette until very late stages of wear. When there is a preferred pattern of separation of the anterior forks of the parafossette, as in *Pterogaulus* or *Ceratogaulus*, this separation occurs at progressively earlier stages of wear (Fig. 20). Ultimately, in most specimens that are at extremely late stages of wear, both forks are separated from the main part of the parafossette and are minute, circular fossettes.

The greatest source of variation in the number of fossettes(-ids) on the premolars of a single sample of a mylagaulid species is the division of one of the major (longer) fossettes into two or more smaller fossettes. It is not uncommon to have specimens that have divided even two of these major fossettes into more, smaller fossettes. In looking at the range of variation in number of fossettes in a single sample, it appears that the calculation of the mean and modal number of fossettes is very useful. In some genera, such as *Umbogaulus*, there is a distinct progressive change over time in the number of fossettes among its species. The minimum number of fossettes also appears to be consistent within a single species. If the maximum number of fossettes is dependent on the division of the "major" fossettes, the minimum number will be little changed within a single sample.

Variation in Premolars among Species.—There is a general trend in mylagaulids, from the early, more primitive species to the latest, most specialized species: the number of fossettes(-ids) on the premolars increases. However, within any single genus, the number appears to increase by "steps" rather than in the form of a gradual change. The best example of a gradual change in the number of fossettes is in *Umbogaulus* where the later species, *U. monodon*, has fewer fossettes on the premolars than the earlier *U. galushai*. This difference is in the mean number of fossettes rather than in the range, maximum, or even minimum number. The lineage with the best evidence for a gradual increase in the number of fossettes is the one represented by species previously referred to *Mylagaulus* cf. *laevis* or *M.* cf. *monodon* from the Great Basin (Shotwell, 1958:table 2), later assigned to *Hesperogaulus* (Korth, 1999*a*). The range and mean number of fossettes in this lineage clearly increases from the early Barstovian sample (*H. gazini*) through the Hemphillian sample (*H. wilsoni*).

Within most genera, the change in the fossettes is morphological, or the change in the number of fossettes occurs in steps. For example, within the species of *Pterogaulus*, the range and mean number of fossettes on the premolars change very little from the early Barstovian *P. laevis* to the middle Hemphillian *P. cambridgensis* (Table 2), but the relative size of the fossettes does change. In the early species, the fossettes are elongated, but are no longer than about one-fourth the total length of the premolar. In *P. barbarellae* and *P. cambridgensis*, the fossettes are at least half the length of the tooth.

Evolutionary Changes in Mylagaulidae.—Even in the earliest known skulls of promylagaulines (McGrew, 1941; Nichols, 1976) many of the derived characters of mylagaulids are present: posteriorly broadened cranium with well-developed occipital crests; elongated external auditory meatus; fusion of cranial sutures early in life; enlarged last premolar; and increased hypsodonty of the cheek teeth. However, the degree of development of these features becomes much greater in the

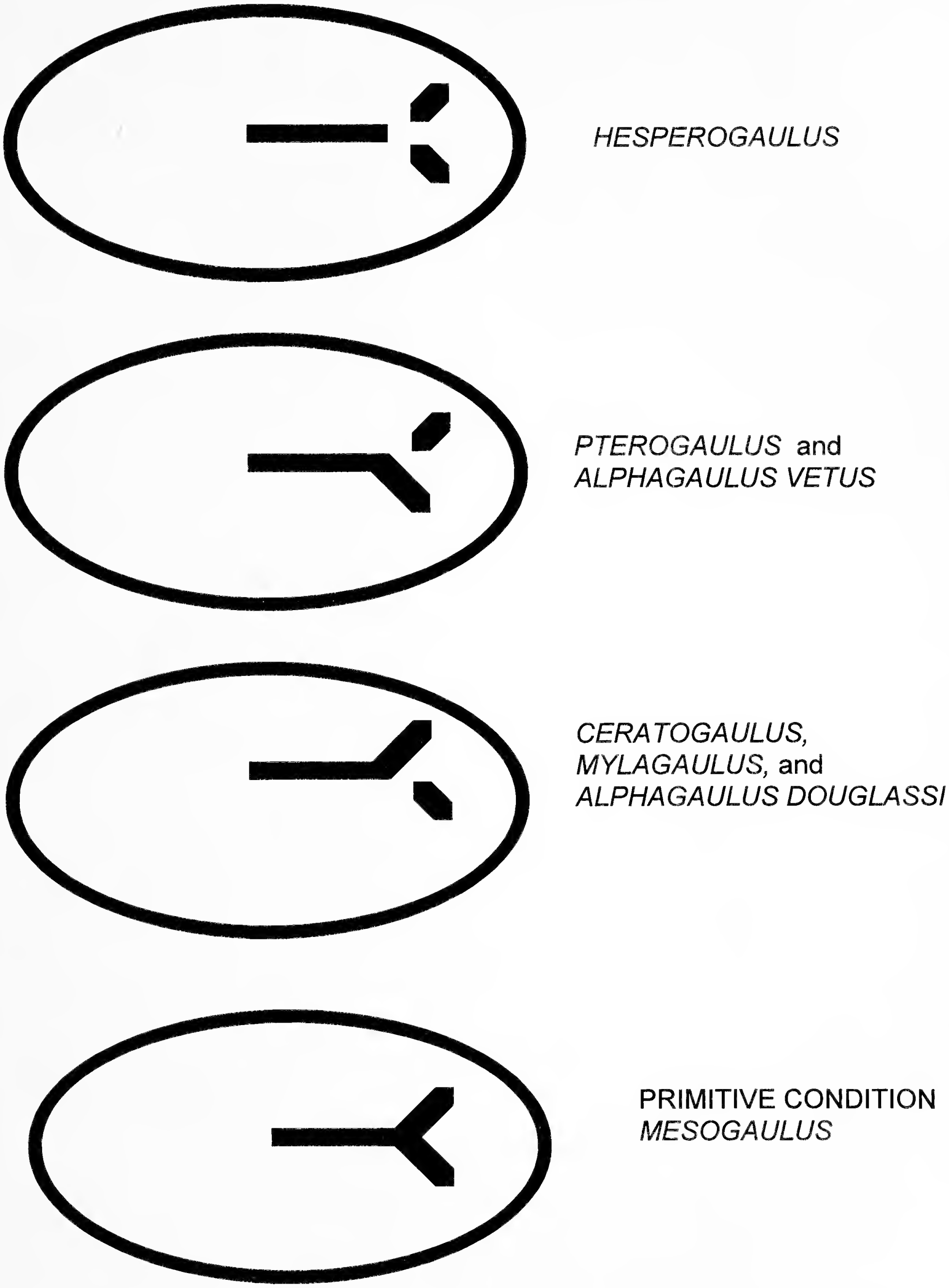


Fig. 20.—Schematic diagrams of right P^4 showing the development of the parafossette in different mylagaulids.

mylagaulines, where the cheek teeth attain nearly complete hypsodonty, anterior molars are lost with eruption of the enlarged permanent premolar, and the posterior width of the skull is nearly equal to its total anteroposterior length. *Mesogaulus* is clearly intermediate between the promylagauline condition and that of the mylagaulines. Even in the broadening of the bones of the forearm, promylagaulines appear less derived (Table 3; Korth, 1999*b*).

As in many families of mammals, there appears to be a disinct increase in size through time, with only a few exceptions. Promylagaulines are generally small species, while the majority of mylagaulines are among the largest rodents of their time. In most genera, such as *Hesperogaulus*, *Pterogaulus*, and *Ceratogaulus*, the later species are larger than the earlier species (Korth, 1999*a*; Tables 6, 7). The exception is *Mylagaulus*, which appears to decrease in size through time (Baskin, 1980).

The morphology of the cheek teeth follows a similar pattern in most genera. The mylagaulines have many more fossettes on the premolars than do promylagaulines, along with increased hypsodonty and relative size of the premolar compared to the molars. The number or relative size of the fossettes(-ids) on the premolars changes differently within different genera (see above discussion). As the relative size of the premolars increases, the number of molars lost with the eruption of the permanent tooth also increases. In promylagaulines (with the exception of *Galbreathia novellus* [Korth, 1999*b*]), P^3 and all the molars are retained in adult individuals. In *Mesogaulus*, P^3 is retained but the first molar is lost. In all mylagaulines, at least the first molars are lost with the eruption of the premolars. In advanced (Hemphillian) species of *Pterogaulus* and *Hesperogaulus*, the first two molars are shed.

Several changes have occurred in cranial morphology among mylagaulines as well. The skull of all mylagaulines has the same overall shape. The skull is posteriorly broadened with well-developed occipital crests, the cranium is relatively low, the rostrum is short, and the zygoma is robust and broad. Primitively, there are small swellings near the anterior end of the nasals. In all mylagaulids, the cranial sutures over most of the skull completely fuse early in life and are not traceable on adult individuals. The greatest changes in cranial morphology involve the modifications of the nasal bones, relative development of the postorbital processes, and the angle of the occipital. In *Alphagaulus*, the most primitive of the mylagaulines, the angle of the occipital ranges from 90°–60°, the postorbital processes are intermediate in size (POI = 0.25–0.36), and small bosses are present on the nasals. Within each lineage (genus) the changes in these features are unique to each genus.

In the short-lived lineage of *Umbogaulus*, the only modification is in the size of the bosses on the nasals. In *Umbogaulus* the bosses become very large and retain a spherical shape. The angle of the occipital and relative size of the postorbital processes remain as in *Alphagaulus*. In *Pterogaulus* the postorbital processes become greatly enlarged (POI = 0.34–0.57), the nasals are dorsally smooth (small swellings lost), and the range of the angle of the occipital is lower (OA = 52°–75°). The skull of *Ceratogaulus* develops paired horns (or horn cores) on the nasals, and the postorbital processes are greatly reduced (POI = 0.11–0.19). Within *Ceratogaulus*, the nasal horns develop progressively more posteriorly in a temporal series of species. The angle of the occipital is not as low as in *Pterogaulus* (OA = 60°–70°), but the shape of the occipital crest is modified. The primitive shape of the occipital crests for *Mesogaulus* and mylagaulines in dorsal view is that it is normal to the long axis of the skull at its center, and as it descends laterally, there is a distinct anterior flexure or bend in the crest at a point approximately one-half the distance from the center of the skull to its lateral border. However, in *Ceratogaulus*, the occipital crest is a straight line in dorsal view. The anterior bend has been lost.

The skull of *Hesperogaulus* has been modified by greatly reducing the angle of the occipital (POI = 50°) and broadening and flattening the nasals anteriorly (Korth, 1999*a*). The occipital crests on skulls of Barstovian *Hesperogaulus* are similar to those of other genera with anterior bends. However, in the Hemphillian species, the flexion is lost and the crest forms a straight line as in *Ceratogaulus*. This feature is clearly attained separately in *Hesperogaulus* and *Ceratogaulus*. It is achieved in the former as part of the decrease in the occipital angle, which pushes the anterior margin of the occipital farther anterior.

Phylogeny of the Mylagaulinae.—It is impossible at this time to determine whether any of the known Arikareean promylagaulines is directly ancestral to the later mylagaulines. It is evident that the latest of the promylagaulines (late Hemingfordian-early Barstovian) are more derived than *Mesogaulus* and are clearly not the ancestors of any mylagaulines (Korth, 1999*b*). Rensberger (1979) suggested that none of the species of promylagaulines that he studied were ancestral to later mylagaulines. However, it is likely that some unspecialized promylagauline in the late Arikareean or early Hemingfordian was morphologically transitional between the promylagaulines and *Mesogaulus*.

In the proportions of the skull and skeleton and in dental adaptations (enlargement of premolars, loss of molars), *Mesogaulus* is distinctly transitional between promylagaulines and mylagaulines. Not only are the cranial proportions intermediate between the latter two subfamilies, but the dentition is also similar to that of mylagaulines and advanced over promylagaulines in some characters (loss of molars), but similar to promylagaulines and more primitive than mylagaulines in others (retention of P^3). There is nothing in the morphology of *Mesogaulus* that would exclude it from the ancestry of all mylagaulines (Fig. 21).

Within the Mylagaulinae, *Alphagaulus* is the earliest (late Hemingfordian-early Barstovian) and most primitive genus. This is evidenced by the proportions of the skull, presence of a small boss on the nasals, and angle of the occipital (Table 1), as well as the relatively fewer number of fossettes(-ids) on the premolars (Table 2). At least two of the later lineages (genera) of mylagaulines can be derived from species of *Alphagaulus*. Both *A. vetus* and *A. pristinus* have relatively gracile skulls and separate the buccal fork of the parafossette on P^4 with wear. These characters can be traced to species of *Pterogaulus* and even possibly species of *Hesperogaulus* (Korth, 1999*a*). *Alphagaulus douglassi* and *A. tedfordi* have more robust skulls, a larger nasal boss, and separate the lingual fork of the parafossette on P^4; characters found in *Ceratogaulus* and *Mylagaulus*. Besides *Alphagaulus*, five genera appear in the Barstovian. The earliest is *Umbogaulus*, which is restricted to the Barstovian. This genus is generally primitive cranially, but develops a much larger boss on the nasals than do species of *Alphagaulus*. Dentally, this genus is far advanced over the other genera of the Barstovian in the much greater number of fossettes on the premolars. *Umbogaulus* is short-lived, restricted temporally to the Barstovian, and clearly not ancestral to any other. The only character that might relate *Umbogaulus* with any other genus is the enlarged bosses on the nasals, which are more similar to the nasal horns of

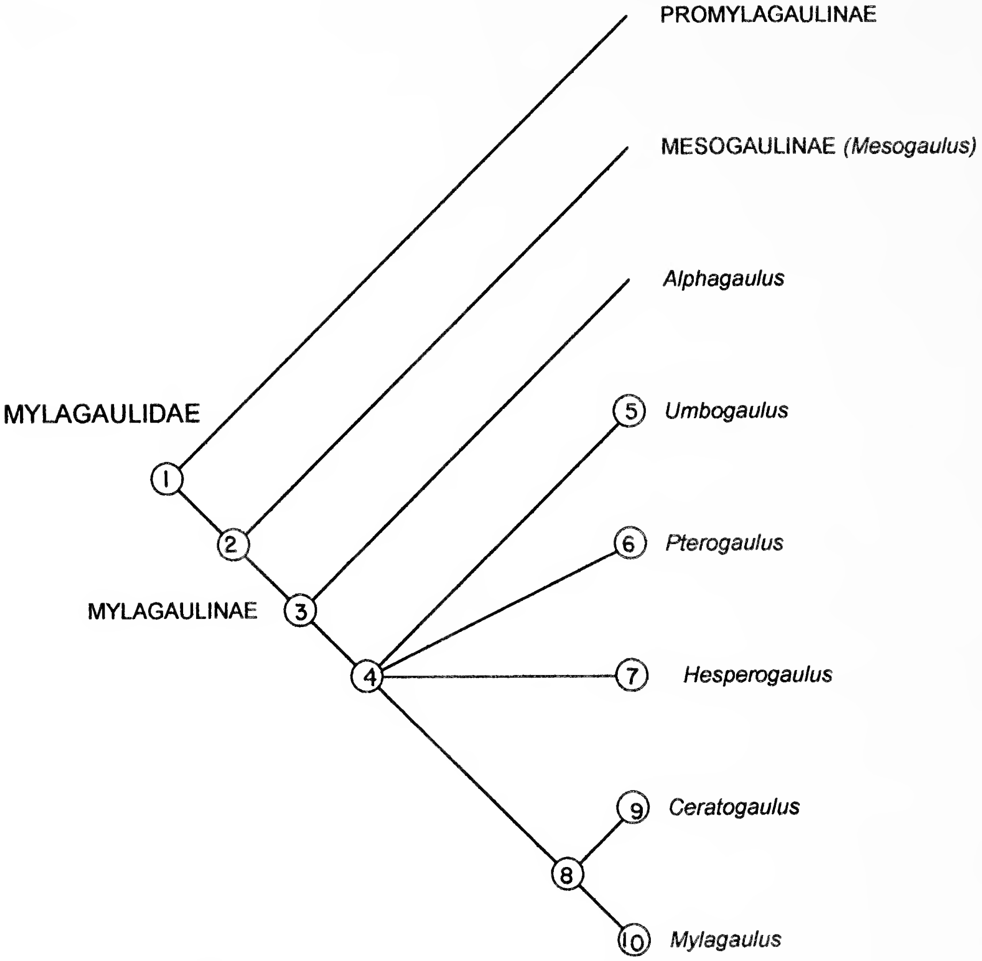


Fig. 21.—Cladogram of relationships of mylagaulids. Explanation of nodes: **1.** Mylagaulidae: protrogomorphous zygomasseteric structure; uniserial microstructure of incisor enamel; incisors broadened; low, broad, robust skull with heavy occipital crest and shortened rostrum; postorbital process present on frontals; cranial sutures completely fuse relatively early; auditory bulla with elongated external meatus; postcranial skeleton fossorially adapted; last premolars largest cheek teeth; cheek teeth lophate, occlusal pattern reduced to isolated enamel "lakes" (cusps reduced); cheek teeth progressively hypsodont. **2.** Larger size; posterior width of skull subequal to anteroposterior length; postcranial skeleton fossorially adapted (humeral index ≥ 0.40); first molars lost with eruption of permanent premolars; premolars at least twice the size of molars. **3.** Mylagaulinae: P^3 lost; broad, shallow groove on upper incisor; greater number of fossettes(-ids) on premolars (minimum number and six for P^4, five for P_4); premolars completely hypsodont (roots lacking); small paired bosses on anterodorsal end of nasal bones; double sagittal crest. **4.** Largest mylagaulids; premolars nearly oval in occlusal outline (loss of outline of stylar cusps); occipital anteriorly tilted (OA ≤ 90°). **5.** *Umbogaulus*, nasal bosses greatly enlarged; number of fossettes(-ids) on premolars increased ($\bar{x}$ = 8–9); upper premolars wider relative to length than other mylagaulines. **6.** *Pterogaulus*, postorbital processes greatly enlarged (POI = 0.35–0.54); bosses on nasals lost; buccal fork of parafossette of P^4 separates first; premolars narrower relative to length than in other mylagaulids. **7.** *Hesperogaulus*, angle of occipital lower than other mylagaulids (OA = 50–57°); bosses on nasal bones low and anteriorly broadened and squared-off; either of the anterior branches of forked parafossette of P^4 may separate first. **8.** lingual fork of parafossette on P^4 separates first; premolars wider relative to length than in *Pterogaulus*. **9.** *Ceratogaulus*, horns (horn cores) on nasal bones; postorbital process progressively reduced

Ceratogaulus than to the condition in any other genus. Again, the premolars of *Umbogaulus* are too complex to have been ancestral to *Ceratogaulus*.

A second lineage of mylagauline is represented by *Pterogaulus*. This genus is restricted to the northern Great Plains and is characterized by the loss of nasal bosses and enlargement of the postorbital process. It ranges from the Barstovian to the medial Hemphillian. Dentally, it can be distinguished by the separation of the buccal fork of the parafossette on P^4, which occurs at a progressively earlier wear stage in later species. This lineage shows through time an increase in skull size and proportional size of the premolar, increased size of the postorbital process, and increased length of the fossettes on the premolars.

Ceratogaulus is restricted temporally and geographically to the same time span as *Pterogaulus*, and they are often found in the same faunal horizons. It, too, shows a distinct increase in size over time along with the more posterior postition of the nasal horns and reduction of the postorbital process (Table 1).

A fifth genus, *Hesperogaulus*, from the Great Basin, originates in the Barstovian and exists until the Hemphillian, and exhibits an increase in size as well as complexity of the premolars (Korth, 1999*a*).

Biogeography of the Mylagaulinae.—Promylagaulines appear in the fossil record during the Arikareean and are limitied geographically to the northern Great Plains and Rocky Mountains (McGrew, 1941; Nichols, 1976; Rensberger, 1979, 1980; Korth, 1992). In the early Hemingfordian, species of *Mesogaulus* appear in approximately the same area (Riggs, 1899; Galbreath, 1953; Wilson, 1960). By the late Hemingfordian, the first mylagaulines appear alongside advanced promylagaulines, again limited to the northern Great Plains and Rocky Mountains. During the Barstovian the remainder of the genera of mylagaulines appear. Three of these genera (*Umbogaulus*, *Pterogaulus*, and *Ceratogaulus*) are limited geographically to the northern Great Plains. However, another distinctive lineage, *Hesperogaulus*, appears in the northern Great Basin (Shotwell, 1958; Korth, 1999*a*). The more primitive mylagaulines (*Alphagaulus* and *Umbogaulus*), along with the specialized promylagaulines (Korth, 1999*b*), do not survive the end of the age. The Clarendonian and Hemphillian occurrences of the four surviving genera show a distinct geographic isolation that began in the Barstovian. *Hesperogaulus* continues into the Hemphillian in Nevada and Oregon (Shotwell, 1958; Korth, 1999*a*). Clarendonian and Hemphillian species of *Mylagaulus* are known only from Florida (Webb, 1966; Baskin, 1980), even though this lineage probably originated in the Great Plains alongside two other genera, *Ceratogaulus* and *Pterogaulus* in the Barstovian or Clarendonian. The latter two genera are completely restricted to the northern Great Plains throughout their fossil records.

The geographic distribution of the species of mylagaulids (Fig. 22) suggests a number of conclusions. First, the origin and early radiation of the family was within the northern Great Plains and Rocky Mountains. Then, with the rapid diversification of mylagauline genera beginning in the Barstovian, there is a geographic dispersal of these genera with one lineage migrating to the Great Basin

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(POI = 0.24–0.11); occipital crest more robust than in other mylagaulines and forms straight transverse crest (no anterior bend on either side as in other mylagaulines); anterocentral fossettid on P_4 V-shaped in early wear (apex pointed posteriorly), lingual branch separates in early wear. **10.** *Mylagaulus*: posterobuccal fossette on P^4 C-shaped; reduction in size and complexity of premolars.

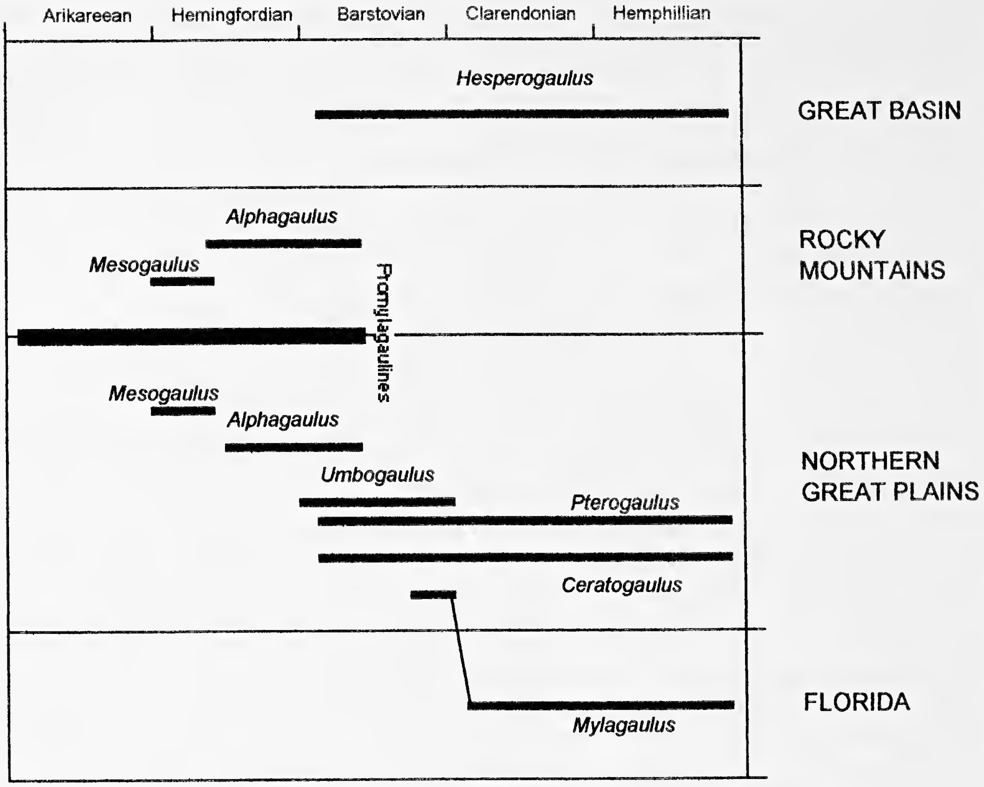

Fig. 22.—Biostratigraphic and geographic occurrence of mylagaulids.

(*Hesperogaulus*) and another to Florida (*Mylagaulus*). Only two lineages remain in the Great Plains until the end of the Hemphillian.

Among the specimens of the AMNH Frick collections are a number of mylagaulids from the Barstovian of New Mexico and the Hemphillian of Texas. These specimens were not included in this study; however, the New Mexico material may represent yet another morphologically and geographically distinct lineage. This lineage cannot be directly related to the Texas material from the Hemphillian at this time, but may prove to be related taxa.

Sexual Dimorphism.—In his initial description of *Ceratogaulus rhinocerus*, Matthew (1902) suggested that the horns on the nasals of this species were possibly a sexually dimorphic character, and that the skull of "*Mylagaulus*" *laevis*, from the same horizon which lacked horns, was the skull of a female individual. He rejected this idea (Matthew, 1902, 1924) mainly because there was no known example in rodents, Recent or fossil, that had this scale of dimorphism. It is now evident, with the discovery and description of numerous mylagaulid skulls, that the horns on the skulls of species of *Ceratogaulus* are a distinctive generic character and not a sexual one due to the fact that other cranial characters (size of postorbital processes) and dental characters (morphology of parafossette on P^4 and anterocentral fossettid on P_4) clearly separate the horned mylagaulids (*Ceratogaulus*) from the hornless mylagaulids (*Pterogaulus*) of the Great Plains.

However, in one lineage of mylagaulines there may be sexual dimorphism. In the species of mylagaulids from the Great Basin, cited by Shotwell (1958) that were later referred to *Hesperogaulus* (Korth, 1999*a*), there appears to be a difference in the relative robustness of the skulls of individuals with no evidence of a difference in dental dimensions or morphology. Skulls of *H. gazini* from the Barstovian and *H. wilsoni* from the Hemphillian of Oregon (Korth, 1999*a*) are divisible into larger and smaller sizes, suggesting a dimorphic condition. In no other species is there even a suggestion of sexual dimorphism. However, this disparity in size of skulls in *Hesperogaulus* may be due to the lack of an adequate sample for comparison.

Problematical Species.—There are examples of specimens or species of mylagaulids that are not clearly assignable to known genera or lineages of mylagaulids. These include *Mylagaulodon* and a pair of unusual specimens from the Clarendonian of Oregon.

Mylagaulodon angulatus was first named by Sinclair (1903) from the Hemingfordian of Oregon, and was believed to represent a transitional form between meniscomyine aplodontids and mylagaulids. Matthew (1924) argued that the premolars of the holotype of *M. angulatus* (UCMP 1652) were deciduous teeth and that the specimen was a juvenile of *Mylagaulus*. Despite Matthew's suggestion, later authors continued to consider *Mylagaulodon* as the basal mylagaulid (McGrew,1941).

Subsequent identifications of specimens of *M. angulatus* from the Great Plains (McGrew, 1941; Skwara, 1988) appear to be specimens of other mylagaulids (Korth, 1992:91). Korth (1992) suggested that *M. angulatus* represented an advanced meniscomyine aplodontid rather than a mylagaulid, later questionably including *M. angulatus* in the Meniscomyinae (Korth, 1994). Whether the type of *Mylagaulodon* is an advanced meniscomyine or a juvenile mylagaulid cannot be determined at this time. However, it does appear that it does not represent a species transitional between the mylagaulids and an aplodontid ancestor as had been previously suggested.

Shotwell (1958:fig 13) identified two isolated P^4s from the Clarendonian of Juntura Basin as *Epigaulus minor* (UOMNH F6165, F6166). Later, he (Shotwell and Russell, 1963) suggested that these two premolars were from the same individual. These two specimens are unique among all described mylagaulids. The fossettes are unusually branched and there is a deep reentrant valley along the buccal side of the tooth that is reminiscent of the mesoflexus of the upper cheek teeth of beavers. These specimens clearly belong to a mylagaulid, but do not fit into any genus recognized at the present time. These specimens should be considered as belonging to an indeterminate mylagaulid.

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APPENDIX 1

Cranial measurements of mylagaulid specimens examined in this study (see Figure 1 for orientation of measurements). Abbreviations for cranial measurements: L, length; PW, maximum posterior width; POC, minimum postorbital constriction; POP, length of postorbital process; OA, angle of the occipital with the plane of the palate; NL, horizontal distance of the apex of the nasal horn from the anterior end of the nasals (*Ceratogaulus* only). All measurements in mm. Asterisk indicates approximate measurement.

Specimen	L	PW	POC	POP	OA	NL	Horizon
Mesogaulus paniensis							
FAM 65511	48.05	39.5	11.05	4.05	90°	—	Marsland Fm., NE
Alphagaulus vetus							
AMNH 18903	—	51.2	14.1	4.3	—	—	Sheep Creek Fm., NE
AMNH 20507	58.7	51.6	15.4	4.9	75°	—	Sheep Creek Fm., NE
FAM 65515	62.5	50.1	14.6	—	60°	—	Sheep Creek Fm., NE
FAM 65532	62*	51.5	15.8	5.8	70°	—	Observation Quarry, NE
FAM 65533	—	—	16.2	4.1	—	—	Observation Quarry, NE
Alphagaulus pristinus							
AMNH 21307	—	22.65	11.20	3.50	79°	—	"Deep River Beds," MT
Alphagaulus tedfordi							
FAM 65711	64.7	78.8	14.60	3.60	90°	—	?Hemingfordian, NE
Umbogaulus monodon							
FAM 65016	79.3	69.35	20.00	7.10	75°	—	Olcott Fm., NE
Ceratogaulus rhinocerus							
AMNH 9456	66.7	70.6	17.50	4.55	70°	9.85	Pawnee Creek, CO
FAM 65815	—	—	23.75	4.20	—	—	Crookston Bridge Mb., NE
FAM 65014	—	—	—	—	—	19*	Devil's Gulch Mb., NE
FAM 65015	—	57.4	—	—	—	—	Devil's Gulch Mb., NE
FAM 65802	—	66.8	—	—	—	—	Devil's Gulch Mb., NE
FAM 65012	70.7	60.3	16.60	2.05	—	12*	Burge Mb., NE
FAM 65013	—	67.8	—	—	68°	—	Burge Mb., NE
FAM 65385	79.35	70.0	17.40	2.15	67°	17.40	Burge Mb., NE
FAM 65833	—	70.4	17.00	2.50	—	—	Burge Mb., NE
FAM 65489	76.2	60.7	18.00	2.40	—	18.30	Burge Mb., NE
Ceratogaulus anecdotus							
FAM 65466	63.0	63.0	17.25	2.12	—	17.5	Cap Rock Mb., NE
Pterogaulus laevis							
AMNH 17576	58.0	56.0	12.45	5.40	—	—	Olcott Fm., NE
FAM 65471	63.6	52.4	12.00	5.85	—	—	Olcott Fm., NE
Pterogaulus sp.							
FAM 65008	67.35	56.2	19.30	6.60	57°	—	Burge Mb., NE
FAM 65009	—	54.5	15.80	5.95	54°	—	Burge Mb., NE
FAM 65010	—	55.0	17.60	6.15	55°	—	Burge Mb., NE
FAM 65470	66.5	59.8	19.00	7.90	48°	—	Cap Rock Mb., NE
Pterogaulus barbarellae							
FAM 65435	67.9	61.6	17.40	8.90	—	—	Merritt Dam Mb., NE
FAM 65436	—	—	16.70	9.50	—	—	Merritt Dam Mb., NE
FAM 65491	72.9	63.3	18.60	9.30	52°	—	Merritt Dam Mb., NE
FAM 65499	69.2	73.0	19.90	9.05	52°	—	Merritt Dam Mb., NE

APPENDIX 2

Classification of Mylagaulidae included in this paper

Family Mylagaulidae Cope, 1881
  Subfamily Mesogaulinae, n. subfam.
    Mesogaulus Riggs, 1899
      Mesogaulus ballensis Riggs, 1899
      Mesogaulus paniensis (Matthew, 1902)
  Subfamily Mylagaulinae Cope, 1881
    Alphagaulus, n. gen.
      Alphagaulus vetus (Matthew, 1924)
      Alphagaulus pristinus (Douglass, 1903)
      Alphagaulus douglassi (McKenna, 1955)
      Alphagaulus tedfordi, n. sp.
    Umbogaulus, n. gen.
      Umbogaulus galushai, n. sp.
      Umbogaulus monodon (Cope, 1881)
    Mylagaulus Cope, 1878
      Mylagaulus sesquipedalis Cope, 1878
      Mylagaulus kinseyi Webb, 1966
      Mylagaulus elassos Baskin, 1980
    Ceratogaulus Matthew, 1902
      Ceratogaulus rhinocerus Matthew, 1902
      Ceratogaulus hatcheri Gidley, 1907
      Ceratogaulus minor (Hibbard and Phillis, 1945)
      Ceratogaulus anecdotus, n. sp.
    Pterogaulus, n. gen.
      Pterogaulus laevis (Matthew, 1924)
      Pterogaulus cambridgensis (Korth, 2000)
      Pterogaulus sp.
      Pterogaulus barbarellae, n. sp.

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