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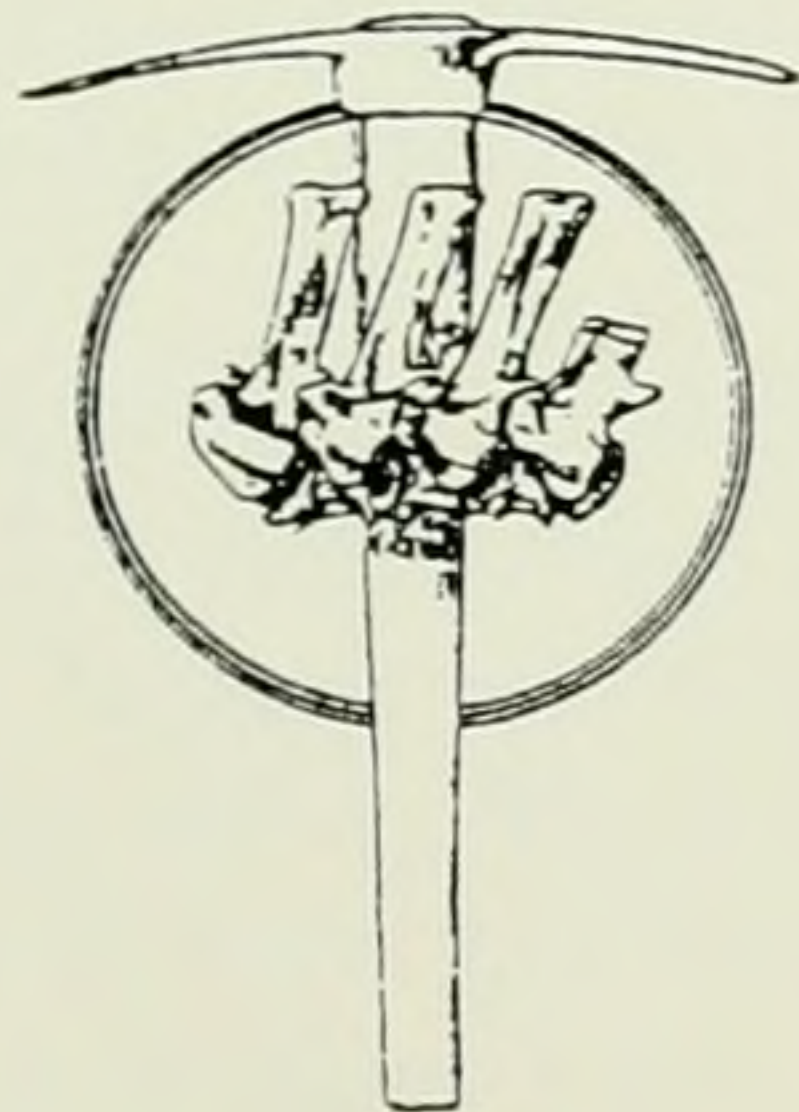
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CONTRIBUTIONS IN

MARINE MAMMAL PALEONTOLOGY

HONORING

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Contents

The Early Miocene Littoral Ursoid Carnivoran *Kolponomos*: Systematics and Mode of Life

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ABSTRACT.—Species of the large extinct early Miocene carnivoran *Kolponomos* Stirton, 1960, are known from a few fossils found in marine rocks along the northeastern margin of the Pacific Ocean in Oregon and Washington, U.S.A. These animals are notable for their massive skulls with markedly deflected rostra and broad, crushing cheek teeth like those of a sea otter. Originally based on an incompletely preserved snout from the marine lower Miocene Clallam Formation at Clallam Bay, Clallam County, Washington, and questionably assigned by Stirton to the Procyonidae, the taxon has until recently remained enigmatic and not certainly assigned to any particular carnivoran family. Additional specimens from the type locality, including a nearly complete cranium with some teeth, provide new data on the cranial morphology of the species. Another specimen, consisting of a nearly complete cranium, mandible with dentition, and some postcranial bones, from the lower Miocene Nye Mudstone on the Oregon Coast, represents a new species, *Kolponomos newportensis*.

The new material demonstrates that *Kolponomos* is an ursoid most closely related to members of the paraphyletic family Amphicynodontidae. Similar phylogenetic roots have been postulated for the pinnipeds as a whole, and cladistic analysis implies a sister-taxon relationship of *Kolponomos* with the Pinnipedimorpha. The few postcranial bones available demonstrate that *Kolponomos* was amphibious but not a strong swimmer.

Kolponomos was probably littoral in distribution, all specimens having been discovered in nearshore marine rocks. The crushing cheek teeth would have been suited to a diet of hard-shelled marine invertebrates. The anteriorly directed eyes and narrow snout indicate that *Kolponomos* could view objects directly in front of its head, of benefit to an animal that would selectively eat epifaunal marine invertebrates. The elongated upper canine and third incisor teeth clustered in thickened bone at the anterior end of the down-turned snout and the posteriorly retracted nasal opening are adaptations that would allow the animal to pry organisms from rocks while keeping its nostrils away from the substrate. Large paroccipital and mastoid processes indicate strong neck muscles that could provide powerful downward movements of the head. These features indicate that *Kolponomos* probably fed on marine invertebrates living on rocky substrates, prying them off with the incisors and canines, crushing their shells, and extracting the soft parts, as do sea otters.

Kolponomos represents an unique aquatic adaptation for marine carnivorans, whose mode of living and ecological niche are approached only by modern sea otters.

INTRODUCTION

The early Miocene carnivoran genus *Kolponomos* Stirton, 1960, is known from a few fossils found in marine rocks along the northeastern margin of the Pacific Ocean in Oregon and Washington. *Kolponomos* was originally based on an incompletely preserved snout from the marine lower Miocene Clallam Formation at Clallam Bay, Clallam County, Washington. The relationships and morphology of the type species of the genus, *K. clallamensis* Stirton, 1960, have remained problematic, and for many years the animal was not assigned with certainty to any particular carnivoran family. Stirton (1960) questionably assigned it to the Procyonidae, and was followed by Piveteau (1961), Romer (1966), and Thenius (1969). Carroll (1988) classified the taxon as Carnivora, *incertae sedis*, and Ray (in Barnes et al. 1985:43) regarded it as an enaliarctine pinniped.

Additional specimens, including a nearly complete cranium with some teeth, have now been collected from the Clallam Formation near the type locality of *Kolponomos clallamensis* at Clallam Bay. These provide additional data on the cranial morphology of the type species. Barnes et al. (1985) announced the discovery of a nearly complete cranium and mandible with some postcranial bones of *Kolponomos* from the lower Miocene Nye Mudstone on the Oregon coast. This specimen represents a new species of *Kolponomos*. The purpose of this study is to describe and illustrate

all known specimens of *Kolponomos*, to redescribe and rediagnose *K. clallamensis*, to describe a new species from Oregon, to comment on the relationships and taxonomy of the genus, and to discuss implications for its functional morphology and behavior.

METHODS AND MATERIALS

All specimens were in hard concretionary sandstone matrix. Those from Washington were prepared by use of pneumatic chisels and formic acid; those from Oregon were prepared by mechanical and air abrasive methods.

Geologic ages cited herein are modified according to the revised radiometric scale of Dalrymple (1979) and the correlations proposed by Armentrout et al. (1983). The acronyms for institutions are as follows: AMNH, American Museum of Natural History, New York, New York; BM(NH), British Museum (Natural History), London, England; LACM, Natural History Museum of Los Angeles County, Los Angeles, California; UCMP, University of California Museum of Paleontology, Berkeley, California; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Casts of the crania have been placed in AMNH, USNM, UCMP, LACM, and the University of Nebraska State Museum. Measurements, in millimeters, of the crania, dentitions, and mandible of the

species of *Kolponomos* have been provided in Tables 1 and 2. Cranial restorations of *Kolponomos clallamensis* are based on all available specimens.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Infraorder Arctoidea Flower, 1869

Parvorder Ursida Tedford, 1976

Superfamily Ursoidea (Gray), 1825

Family Amphicynodontidae (Simpson), 1945

Included genera.—This paraphyletic family includes *Amphicynodon* Filhol, 1882, *Pachycynodon* Schlosser, 1887 (including *Paracynodon* Schlosser, 1899), *Allocyon* Merriam, 1930, and *Kolponomos* Stirton, 1960.

Kolponomos Stirton, 1960

Kolponomos Stirton, 1960:346.
Kolponomus Carroll, 1988:635, 672.

Emended diagnosis of genus.—Stirton's diagnosis was based solely on the holotype of *K. clallamensis* and amounted to a description of that specimen. New material allows a refinement of that diagnosis. The characters noted are all derived with respect to other Carnivora: I^3 with large root; I_1 vestigial or missing; cheek teeth with strongly inflated principal cusps; P^{1-3} and P_{1-3} with anterior and posterior cingular cusps, P_4 also with prominent posterolingual cingular cusp; P^4 molariform with large protocone; M^1 with large conules, lingual cingulum only between principal cusps; M^2 markedly smaller than and lying posterolingual to M^1 with posterolingually placed metaconule; M_1 quadrate in occlusal outline; M_2 triangular with reduced talonid; M_3 absent.

Facial region of skull markedly flexed downward relative to basicranial plane; muzzle deep; nasal retracted to above P^1 or P^2, its sutural contact with frontal wide, slightly wider anteriorly than posteriorly; long process of premaxilla nearly meeting corresponding processes from frontal along nasal suture; palate highly vaulted anteriorly; infraorbital foramen greatly enlarged and opening into shallow fossa in maxilla; infraorbital canal very short; orbit facing forward and relatively small; zygomatic arch widely flaring with strong postorbital process and variably developed masseteric process; postorbital process of frontal lacking; lacrimal foramen small, variably present; sphenopalatine foramen large and closely associated with posterior palatine foramen; optic foramen small, nearly same size as ethmoid foramen; anterior process of alisphenoid forming strut bracing palate against braincase; mastoid process hypertrophied into long column extending laterally and ventrally; posterior carotid foramen well anterior to posterior lacerate foramen; foramina for venous occipital sinus in foramen magnum; lambdoidal crest strongly extended posteriorly on either side of midline.

Type species.—By original designation, *Kolponomos clallamensis* Stirton, 1960.

Included species.—*Kolponomos clallamensis* Stirton, 1960, late Early Miocene, Washington; *Kolponomos newportensis*, new species, Early Miocene, Oregon.

Kolponomos clallamensis Stirton, 1960

Figures 1–7, 13–14

Kolponomos clallamensis Stirton, 1960:347, figs. 1–4.

Diagnosis of species.—A species of *Kolponomos* differing from *K. newportensis*, new species, by the following derived features: cranium with anterior part of palate more highly vaulted; infraorbital foramen larger, approximately twice the diameter, opening into prominent fossa; large masseteric process on ventral surface of zygomatic arch at jugal/maxillary suture; maxilla rather than jugal forming anterior rim of orbit; paroccipital process larger, oriented vertically rather than posteroventrally; basioccipital narrower, especially posteriorly between posterior lacerate foramina; narrow, prominent vertical crest on occiput dorsal to foramen magnum lacking; zygomatic arch more strongly arched dorsally. In addition, *K. clallamensis* is distinguished by the following primitive features: rostrum narrower, with anterolateral margin of snout around canine and I^3 not flaring laterally, nearly vertical; hamular process of pterygoid straighter, smaller, not extending so far ventrally; mastoid process shorter, straighter, and oriented vertically rather than being twisted and projecting anteroventrally beneath the external auditory meatus; intercondylar notch present and deep.

Holotype.—UCMP 50056, anterior part of cranium with roots of left I^3 and both M^1's, collected in 1957 by Mrs. Betty Willison.

Type locality.—UCMP V5761, 250 yards east of Slip Point lighthouse near section line, NW 1/4 NE 1/4, Sec. 21, T. 32N, R. 12W, and LACM 5933, Slip Point, Clallam Bay, Clallam County, Washington.

Referred specimens.—LACM 131148, from the type locality, a nearly complete cranium with parts of the left I^2 and I^3 and right and left P^2 and M^1, collected by Albin Zukofsky, II, February 1988; LACM 123547, from Merrick's Bay, Clallam Co., Washington, a fragment of tooth (M_2?) collected by William Buchanan, May 1983.

Formation and age.—Extensive marine sedimentary deposits are exposed on the north side of the Olympic Peninsula in Washington. The lower Miocene Clallam Formation and underlying Eocene and Oligocene deposits are exposed in wave-cut cliffs and terraces and in man-made excavations for more than 70 miles (112 km) along the south shore of the Strait of Juan de Fuca. The stratigraphy and invertebrate paleontology of this thick sedimentary sequence are well known (e.g., Addicott 1976a,b,c; Armentrout et al. 1983; Feldman et al. 1991; Rau 1964; Snavely 1983; Snavely et al. 1980; Tabor and Cady 1978), but only a very few fossil vertebrates have been recorded [Stirton 1960 (carnivore); Olson 1980 (bird); Domning et al. 1986, and Ray et al. 1994, this volume (desmostylian); Barnes 1987, 1989 (whale)]. Specimens of *Kolponomos clallamensis* are from the Clallam Formation, deposited during the Pillarian Molluscan Stage (Addicott 1976a; Moore and Addicott 1987) of the early Miocene. A measured section at Slip Point (Addicott 1976b: fig. 4) shows that the rocks exposed there belong to the lower part of the Clallam Formation. The lower part of the Pillarian Molluscan Stage containing *K. clallamensis* includes an interval of time correlative with the late Arikareean North American Mammal Age.

Skull.—The nearly complete referred skull (LACM 131148) has parts of the left I^2 and I^3 and both P^2's and M^1's, but is missing the right zygoma and the anterolateral margin of the right premaxilla and maxilla, much of the ascending ramus of the right maxilla, the right nasal, the dorsal surface of the interorbital region, the sagittal crest, much of the roof of the braincase on the right side, and the lambdoidal crest (Figs. 1–4). Structures of the right orbit are fully exposed.

The skull of *Kolponomos clallamensis* is roughly triangular in dorsal aspect, with a broad occipital region and a narrow snout (Figs. 5–7). The dorsal profile is arched, and the zygomatic arches are prominent. At its anterior extremity, the rostrum is thick and ventrally deflected. In anterior view, the narial opening is elongated dorsoventrally and tapered ventrally. A considerable thickness of the premaxillae anterior to the narial opening separates the incisors from the anterior margin of the naris. There is a rather prominent vertically oriented premaxillary protuberance. On either side of it, the anterior surface of the premaxilla slopes abruptly anteroventrally. On either side in this area, the distal part of the root for I^3 forms a bulge in the premaxilla. Otherwise, the bone surface in this area is depressed. The vertical premaxillary eminence extends posterodorsally and is continuous with the relatively narrow and sharp margins of the naris. Immediately anterior to the naris, the bone surface is rugose and punctured by many small foramina.

The maxilla–premaxilla suture is fused and obliterated anteriorly on both the holotype and the referred cranium, but on both specimens the sutures bounding the premaxilla lateral to the naris and the nasal bone are discernable. The ascending process of the premaxilla extends posteriorly to about mid-length on the nasal. It does not meet the anterior process of the frontal as in living bears but stops approximately 2 to 3 mm from the frontal. Along the lateral margin of the naris, the premaxilla forms a nearly vertical lateral surface. It is almost horizontal adjacent to the nasal bone, however. The lateral surface of the snout is dorsoventrally high and flat. Between the canine and the zygomatic arch it is concave.

There is a nasolabialis fossa on the dorsal part of the ascending ramus of the maxilla immediately anterior to the orbital margin. This fossa is broad and shallow, and is bordered anterodorsally by a slight protuberance, dorsally by a faint horizontal ridge, and posteriorly by the orbital margin, which has a vertically elongated antorbital process. The infraorbital foramen has a large anterior opening, 18 to 21 mm high by 10 to 11 mm wide. The foramen opens into a broad fossa, strongly emarginated ventrally, and extending anteriorly nearly to the P^2.

The nasal bones are elongated, nearly parallel-sided, with rounded posterior borders. Where they join posteriorly they are not separated by the frontals. They slope anteroventrally and are nearly flat transversely. On the holotype they are approximately 74 mm long; on the referred cranium, although incomplete, the left nasal is 69 mm long as preserved. The nasals are narrowest just anterior to their mid-length and are wider both anteriorly and posteriorly. Their anterior margin is thick and slightly up-turned, especially near the sagittal line. They expand laterally at the anterior margin.

The posterior part of the nasals is at the highest part of the cranium, which has a smooth, domelike profile. The low supraorbital ridges of the frontals extend posterodorsomedially from just lateral to the posterior ends of the nasals. Posteriorly the interorbital constriction tapers uniformly toward the braincase, to its narrowest point in the intertemporal region. The top surface of the interorbital region on the referred cranium is weathered away, but on the holotype cranium a low crest extends posteromedially from each supraorbital process toward the sagittal plane. These crests lap anteriorly onto the frontals, and where they merge posteriorly on the midline they form a slight V-shaped sulcus. Posteriorly from this point there is a low, broad sagittal ridge on the holotype, but the cranium is missing posterior to the intertemporal region. The mid-sagittal region posterior to this area is broken on the referred cranium also.

The braincase is elongated and tapers anteriorly toward the interorbital constriction. Its dorsal surface slopes laterally toward the temporal fossa and flares posterodorsolaterally to the nuchal crest, which is, however, almost entirely lost on the referred cranium. The surface of the bone is slightly undulating but not strongly rugose or pitted. The frontal–parietal suture ascends the anterolateral wall of the braincase from the back of the orbital region, approaches the midline, then bends posteriorly over the dorsal surface of the braincase to extend posteromedially toward the midline. The squamosal fossa, forming the floor of the temporal fossa over the squamosal, is broad and shallow, does not slope anteriorly, and extends posteriorly into a broad sulcus in the lateral part of the nuchal crest.

The occipital shield is in the shape of a broad isosceles triangle, with the apical part broken away. A broad median crest extends dorsally from the foramen magnum toward the nuchal crest. This crest is flanked by a pair of broad fossae. In turn, each fossa is flanked laterally by a broad eminence, preserved on the left side and in part on the right of the referred cranium, that extends dorsolaterally to merge with the posterior side of the nuchal crest. From this point, the nuchal crest becomes narrower ventrolaterally and curls posteriorly in the area posterior to the temporal fossa. Dorsal to each condyle is a prominent transversely oriented fossa that is continuous with a large fossa lying dorsal to the paroccipital process and below the nuchal crest. The paroccipital process curves posteroventrally almost as far ventrally as do the occipital condyles. It has a vertical posterior swelling that extends dorsally into the lateral fossa. The foramen magnum is wide and compressed dorsoventrally. Its dorsal margin is a broad arch, only slightly peaked medially.

The occipital condyles are relatively small, canted dorsolaterally, with sharp edges around the lateral and ventral margins of the articular facets. The medial side of each is slightly excavated and has a small condyloid foramen. The condyles are separated ventrally by a broad U-shaped intercondylar notch. Their articular surfaces are not continuous ventrally but separated by a fossa that is a continuation of the intercondylar notch and aligned anteroposteriorly with the median ridge on the basioccipital. The condyles are positioned relatively ventrally in relationship to the basicranium. At the anterior margin of each condyle, immediately posterior to the hypoglossal foramen, is a recess in the margin of the articular surface.

The orbit is of rather small diameter, measuring approximately 33 mm transversely in the referred cranium. At the anterior margin of the orbit, immediately ventral to the antorbital process, is a small (3 mm diameter) lacrimal foramen. The anterior part of the orbit has a convex medial wall that protrudes into the orbit in the area posterior to the infraorbital foramen. Immediately posterior to this area is a large (9 mm diameter), round sphenopalatine foramen that is immediately dorsal to and very close to the slightly smaller (6 mm) orbital aperture of the posterior palatine foramen. The tract for the optic nerve is elongated and relatively deep, leading posteroventrally from the ethmoidal to the optic foramen and into the orbital fissure; these foramina are approximately equal in size. The anterior lacerate foramen (orbital fissure) and foramen rotundum lie in a large fossa as in pinnipeds, although a partition of bone separates them. As in other caniform carnivorans, the anterior aperture of the alisphenoid canal opens into the ventral wall of the anterior lacerate foramen and does not have a separate opening into the orbit.

The zygomatic arch is stout and curves uniformly outward from the orbit. The zygomatic process of the squamosal increases only slightly in thickness posteriorly, and the posterior extremity of the jugal diminishes equally in diameter as it extends posteriorly. The zygomatic arch is not straight in its middle but curves both laterally and dorsally. At its anterior end, it is massive, forming thick dorsal and ventral margins around the infraorbital foramen. The ventral root of the zygomatic arch is very stout and descends vertically to form a buttress dorsal to the M^1. This buttress forms a vertical component to the anterior end of the zygomatic arch that continues dorsally through the dorsal margin of the infraorbital foramen.
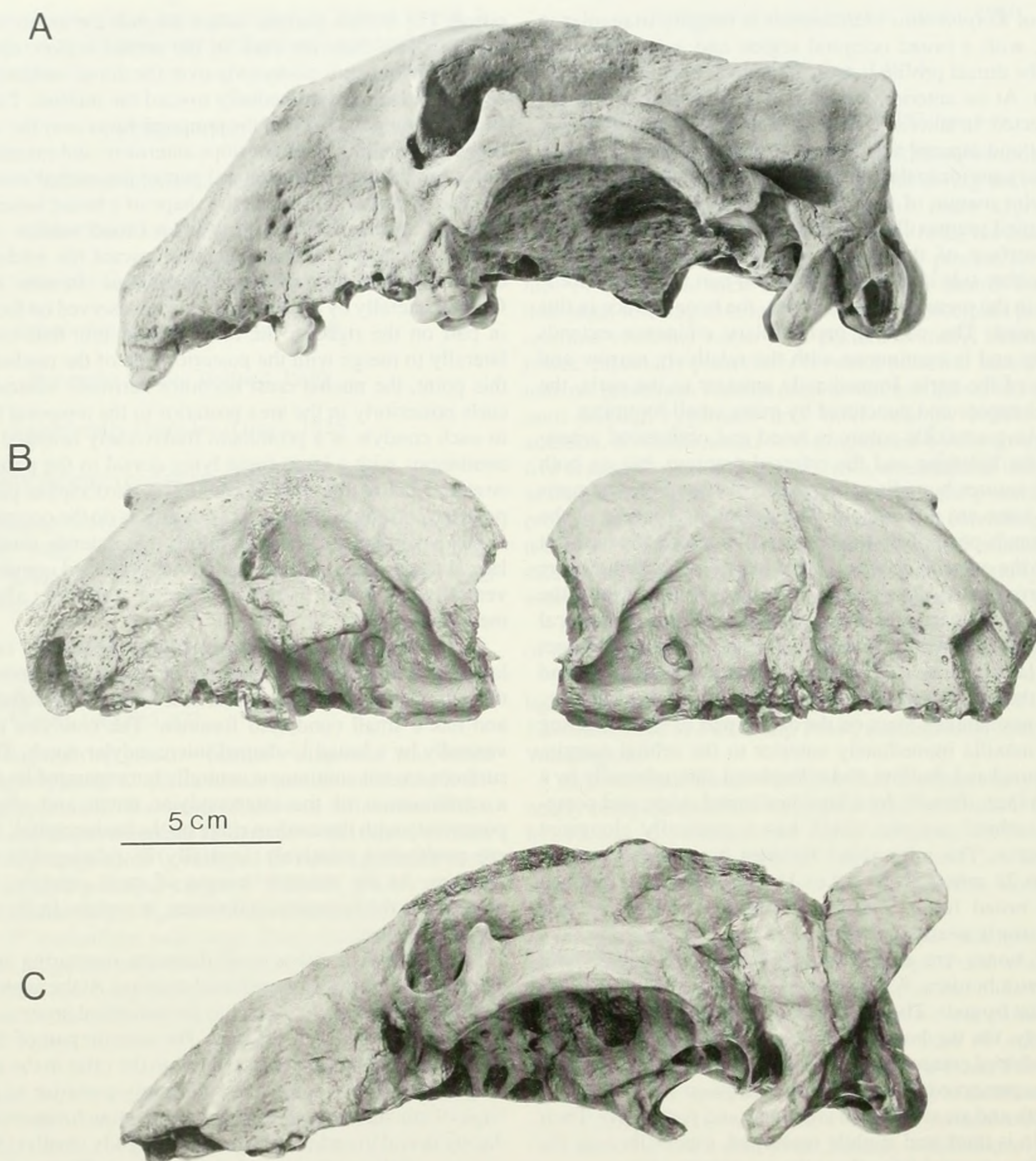
Figure 1. Lateral views of the crania of species of *Kolponomos*. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148, left side; B, *K. clallamensis*, holotype, UCMP 50056, left and right sides; C, *K. newportensis* n. sp., holotype, USNM 215070, right side reversed to left for comparison. All specimens to same scale.

From this point, the zygomatic arch flares posterolaterally to form the lateral margin of the orbit. The jugal bone extends anteromedially over the maxilla, forming a partially mortised joint. The jugal does not form the anterior rim of the orbit. Ventral to the orbit, the maxilla flares where it meets the jugal, and together they form a prominent masseteric process. This process projects ventrolaterally, and a crest extends posteriorly from it along the ventrolateral border of the jugal. The postorbital process of the jugal is stout, broad anteroposteriorly, and its apex is located anteriorly. The anterior extremity of the zygomatic process of the squamosal abuts the posterior side of the postorbital process and is dorsoventrally expanded and slightly up-turned. From this point the zygomatic process curves uniformly posteroventrally to the glenoid

fossa. At the glenoid fossa, the zygomatic process curves medially to form the dorsal surface of the glenoid fossa.

The glenoid fossa is elongated transversely, narrow anteroposteriorly, and has a smoothly curved articular surface. In contrast to that of typical Ursinae, the glenoid fossa is situated in a plane dorsal to the basioccipital plane. In ursines, the glenoid fossa is ventral to the plane of the basioccipital. As is typical of the Ursidae, the postglenoid process is well developed medially, projecting anteroventrally to the glenoid fossa, and diminishes laterally. The postglenoid process is thin anteroposteriorly and does not form an anteroposteriorly thickened buttress as in the Ursinae. There is a low preglenoid process laterally.

On the dorsal surface of the zygomatic process of the squamosal,
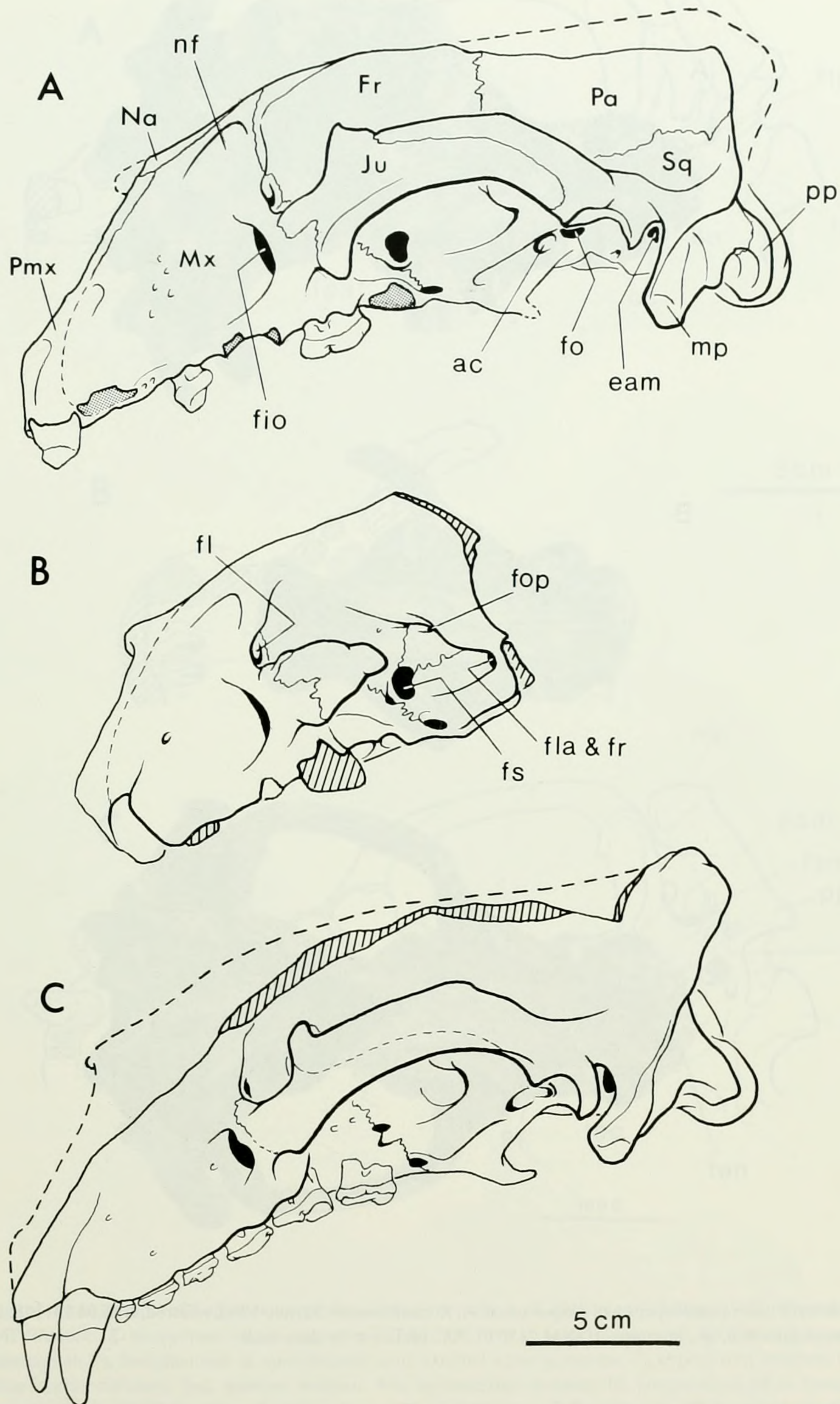
Figure 2. Outline drawings of restored crania of *Kolponomos* species viewed from the left and oriented so that the basicranial plane is horizontal. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype; UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070 with tooth row restored. All drawings to same scale. Symbols for anatomical features: ac, alisphenoid canal (posterior aperture); eam, external acoustic meatus; fio, infraorbital foramen; fl, lacrimal foramen; fla, anterior lacerate foramen; fo, foramen ovale; fop, optic foramen; Fr, frontal; fr, foramen rotundum; fs, sphenopalatine foramen; Ju, jugal; mp, mastoid process; Mx, maxilla; Na, nasal; nf, nasolabialis fossa; Pa, parietal; Pmx, premaxilla; pp, paroccipital (= jugular) process; Sq, squamosal.

Figure 3. Ventral views of the crania of species of *Kolponomos*. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070. All specimens to same scale.

where the zygomatic arch meets the squamosal fossa, there is a prominent tuberosity. This tuberosity also is at the anterolateral edge of the shelf dorsal to the external auditory meatus. This shelf slopes posteroventrally and expands dorsoventrally as it merges with the base of the mastoid process.

The palate is elongated and concave both anteroposteriorly and transversely. On either side of the midline the palate is subplanar, essentially flat transversely and gently arched anteroposteriorly, from the incisive foramina to the palatal notch. Anteriorly and laterally the palate descends abruptly to the inner margin of the dental arcade. The anterior end of the palate is deflected ventrally,

so that the alveolar margins of the canines and incisors are positioned more ventrally than those of the cheek teeth.

The septum separating the incisive foramina is continuous posteriorly with a slight raised ridge extending more than 30 mm posteriorly along the midline suture of the palate. These foramina are large and reniform. On either side of the palate, at the posterolateral corner just medial to the M^2 alveoli, are the posterior palatine foramina, closely associated with the maxillo–palatine suture. These foramina are variable in size and number. All are large on the holotype. On the referred cranium, the anterior foramina are both of intermediate size, while the posterior foramina are of different
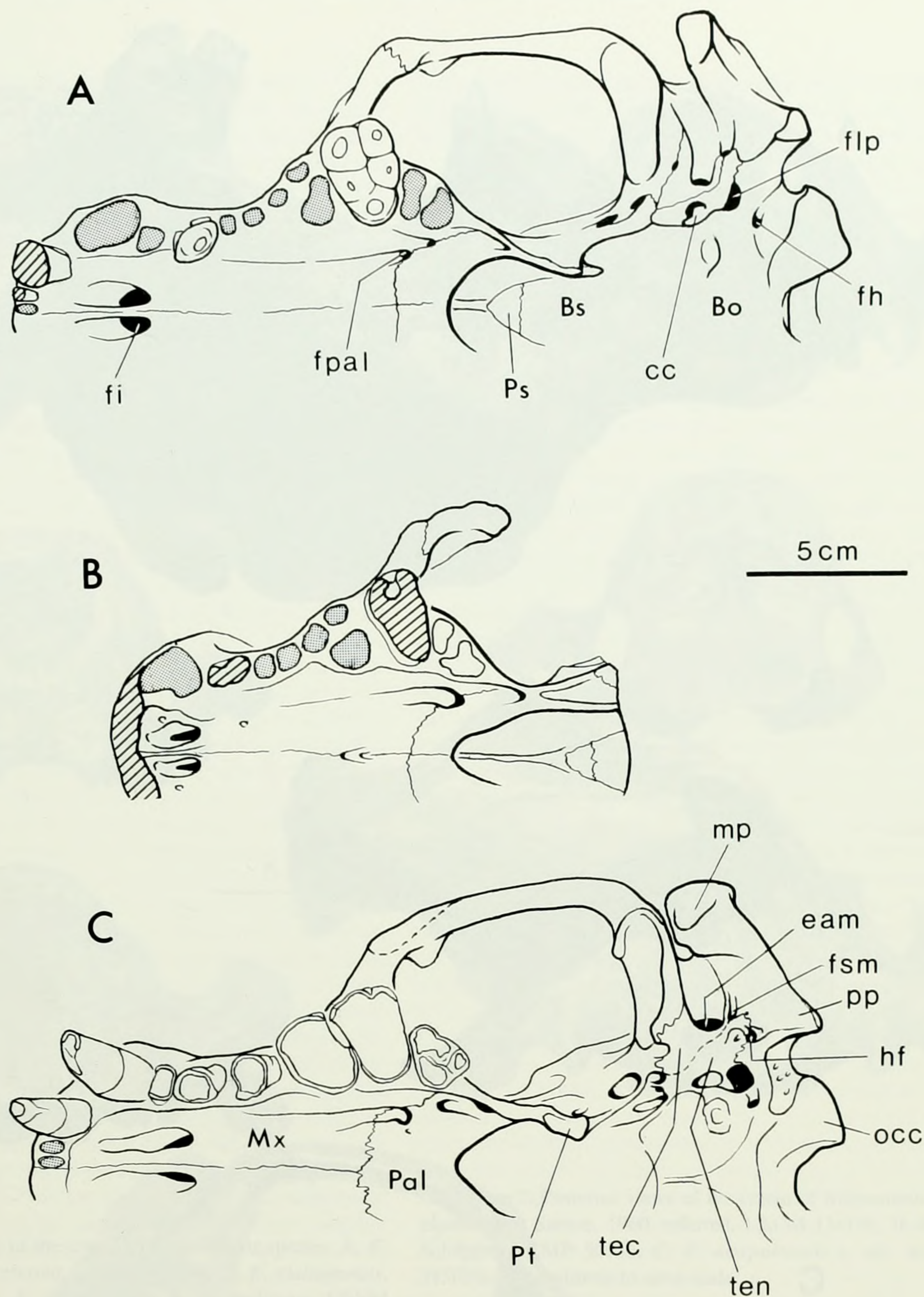
Figure 4. Outline drawings of restored crania of *Kolponomos* species, viewed ventrally. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070, with tooth row restored. All drawings to same scale. Symbols for anatomical features: Bo, basioccipital; Bs, basisphenoid; cc, carotid canal; eam, external acoustic meatus; fh, hypoglossal foramen; fi, incisive foramen (= palatine fissure); flp, posterior lacerate foramen; fpal, palatine foramen; fsm, stylomastoid foramen; hf, tympanohyal pit (= hyoid fossa); mp, mastoid process; Mx, maxilla; occ, occipital condyle; Pal, palatine; pp, paroccipital (= jugular) process; Ps, presphenoid; Pt, pterygoid; tec, ectotympanic; ten, entotympanic.

sizes, intermediate on the left and small on the right. On both crania the anterior foramen is continuous with a prominent antero-posteriorly elongated sulcus that extends anteriorly to a point where it disappears medial to the P³. Posterior to the palatine foramina and the M² the posterolateral palatal margin is formed by a narrow vertically oriented crest pierced by a foramen. This crest is continuous posteriorly with the sharply keeled ventral border of the ptery-goid hamulus. On the referred cranium, the hamulus is very thin transversely and concave laterally, as is typical of the Ursinae, but is bent sharply ventrally. The narrow posterior process of the ptery-goid hamulus extends posteriorly. The main part of the pterygoid–palatine strut ascends posteriorly, to join the basicranium around the posterior aperture of the alisphenoid canal. The lateral surface of the strut is rounded and convex and continues onto the ventrolat-
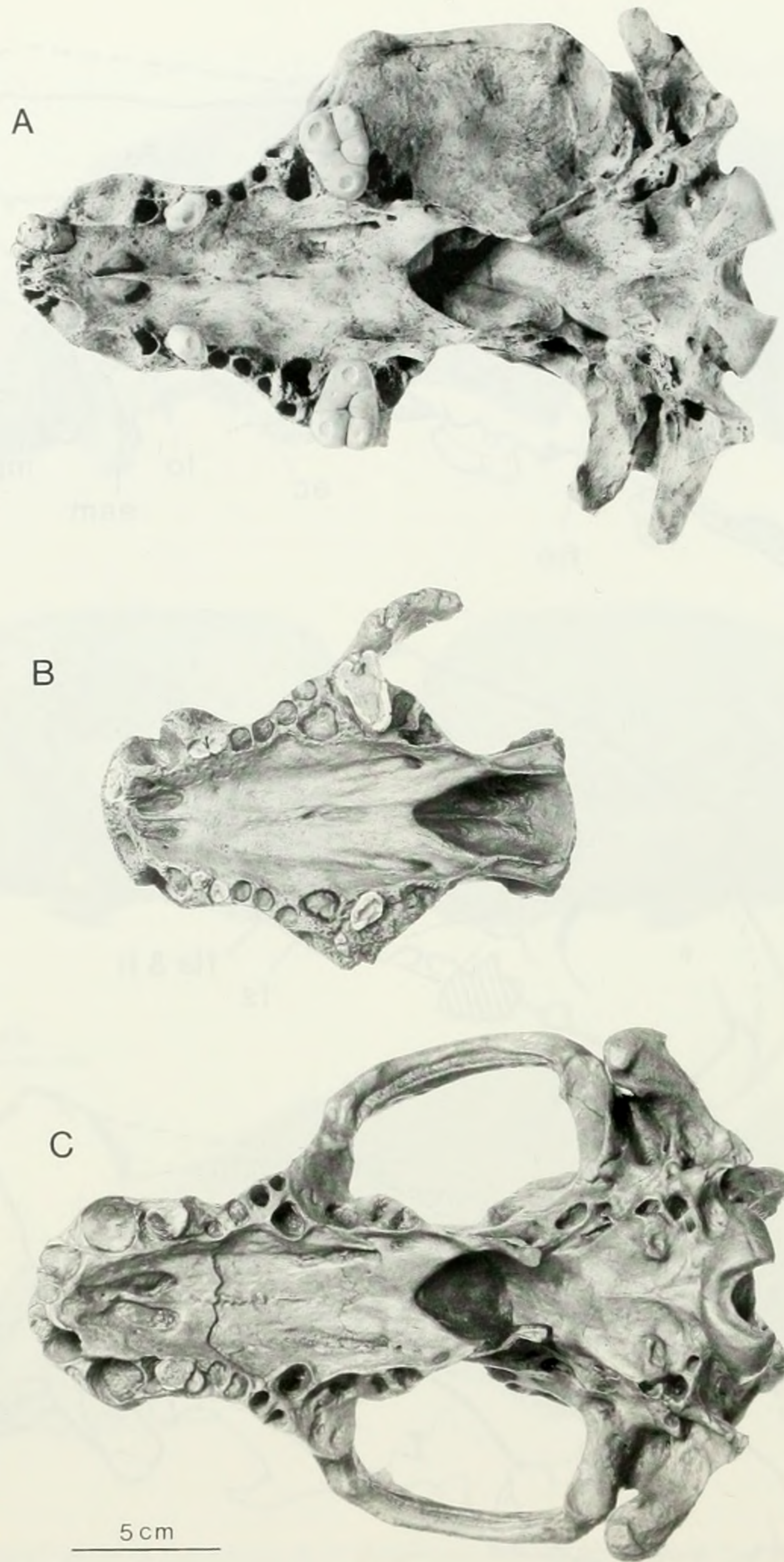
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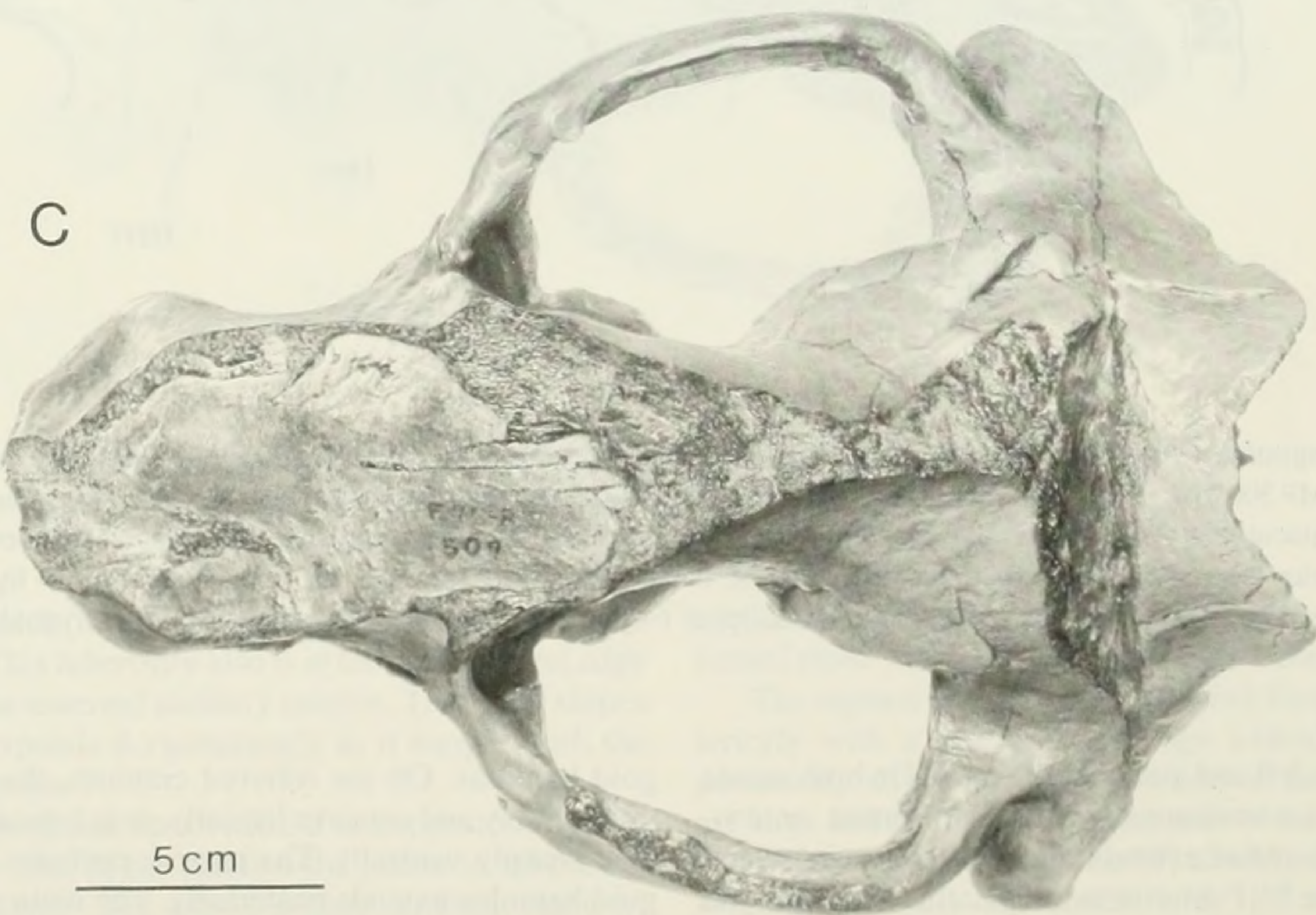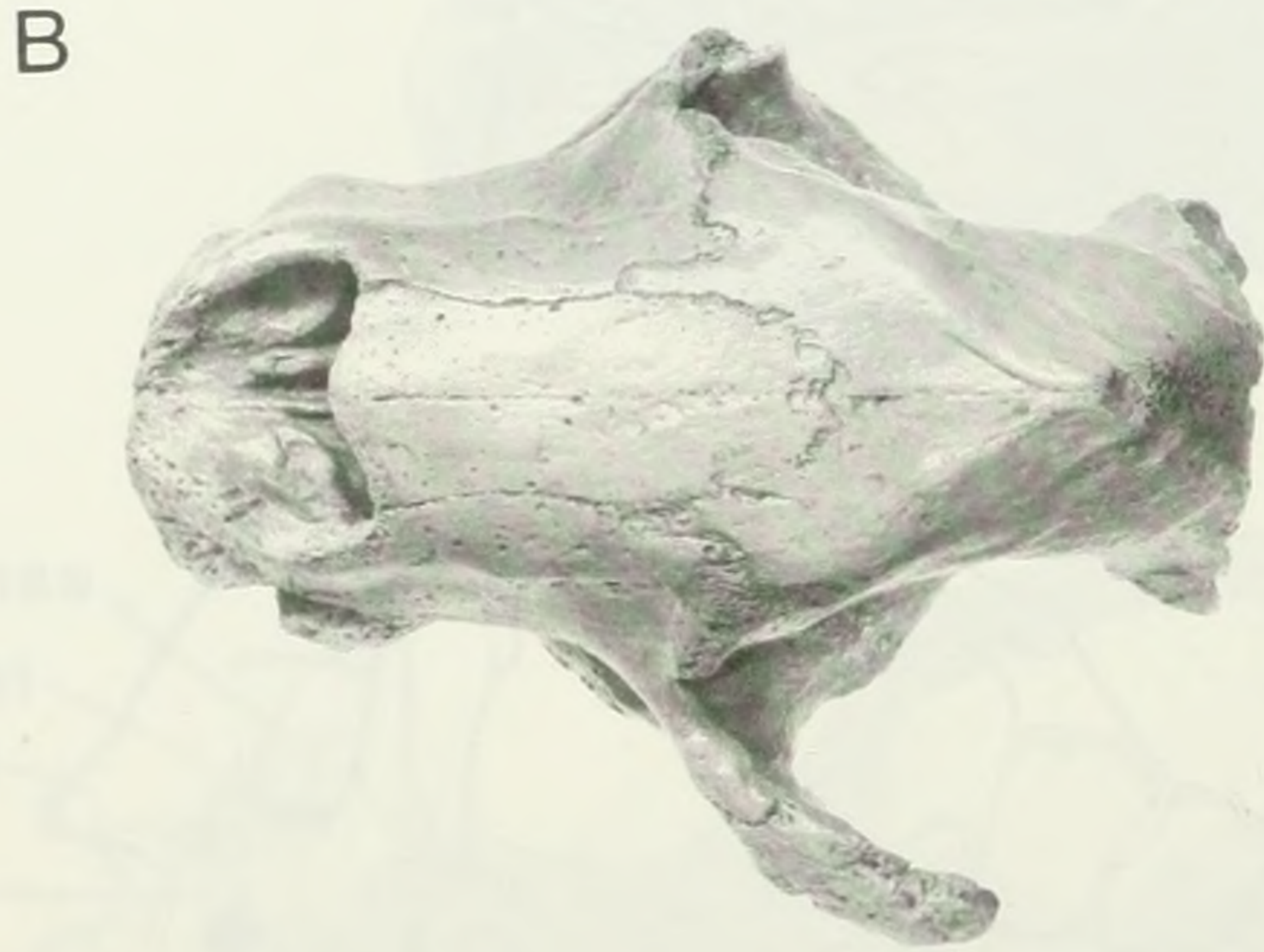
Figure 6. Anterior views of the crania of *Kolponomos* species. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070. All specimens to same scale.
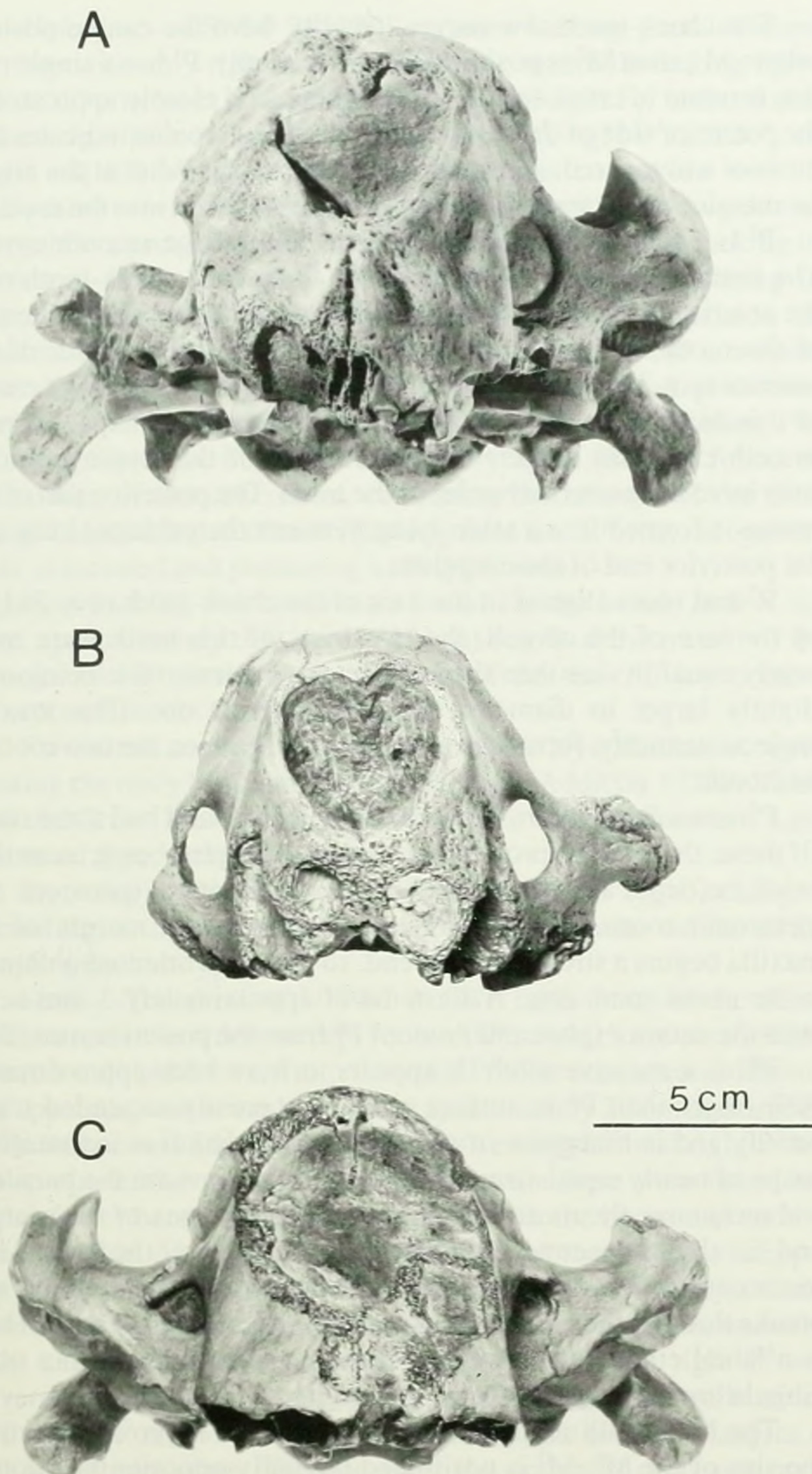

Figure 7. Posterior views of the crania of *Kolponomos* species. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070. All specimens to same scale.

eral surface of the braincase wall. From the pterygoid hamulus, a fine ridge extends posteriorly along the medial side of the posterior aperture of the alisphenoid canal and the foramen ovale and continues into the auditory tube of the bulla.

The internal narial opening is highly arched and wide. The palatal notch is broadly rounded in the referred specimen, has a slightly acute apex in the holotype, and extends anteriorly almost to a point between the centers of the M²'s. On either side of the internal narial opening, the palatine–pterygoid struts sweep medially to form a sharp, underhanging border. The roof of the internal narial opening ascends anteriorly and in its anterior part has a medial keel formed by the vomer and presphenoid. The presphenoid–basisphenoid suture is transversely oriented and is not

coossified. The basisphenoid is nearly flat where it forms the roof of the internal naris between the pterygoid hamulae. It expands posteriorly and at its lateral edge, dorsal to the pterygoid hamulus, bears a groove that extends posterolaterally into the median lacerate foramen. The median lacerate foramen is elongated anteroposteriorly and is situated at the anteromedial corner of the bulla.

The basioccipital–basisphenoid suture is fused, and its precise location is not visible. The basioccipital has a median crest that widens posteriorly and spreads toward each condyle. On either side are a curved fossa and a rugosity that mark the insertion of the rectus capitis ventralis muscles. Posterolateral to the fossa, between the condyle and the bulla, is the hypoglossal foramen, which is transversely oval and approximately 3 mm in diameter.

The tympanic bulla is small and has a rugose ventral surface. It is fused laterally to the squamosal and the base of the mastoid
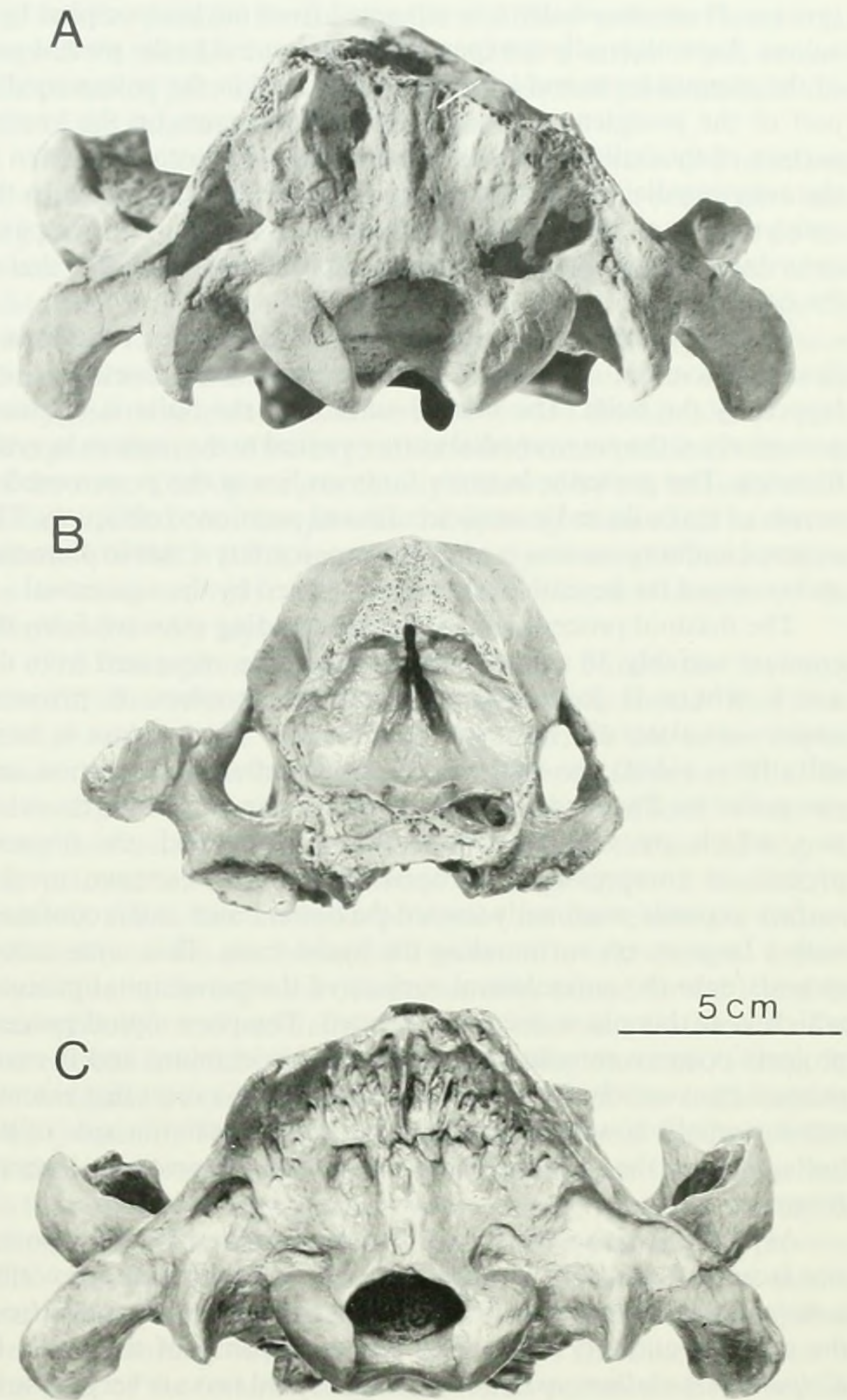
Figure 5. Dorsal views of the crania of *Kolponomos* species. A, *K. clallamensis* Stirton, 1960, referred, LACM 131148; B, *K. clallamensis*, holotype, UCMP 50056; C, *K. newportensis* n. sp., holotype, USNM 215070. All specimens to same scale.

process. Posteromedially it is separated from the basioccipital by a sulcus. Anterolaterally it expands posteroventral to the medial part of the glenoid fossa and is broadly appressed to the posteromedial part of the postglenoid process. An oblique crest on the ventral surface of the bulla that extends from the stylomastoid foramen to the anteromedial margin appears to mark the junction between the entotympanic and the ectotympanic. If this is true, the entotympanic contribution to the tympanic bulla is approximately equal to that of the ectotympanic.

There appears to be a small postglenoid foramen located in a fissure where the medial part of the postglenoid process is overlapped by the bulla. The ventral surface of the bulla is retracted posteriorly at the anteromedial corner ventral to the median lacerate foramen. The posterior lacerate foramen lies at the posteromedial corner of the bulla and is semicircular and positioned obliquely. The external auditory meatus is round, approximately 4 mm in diameter, and recessed far beneath a wide shelf formed by the squamosal.

The mastoid process is very long, extending outward from the cranium variably 38 and 44 mm on either side, measured from the notch where it joins the paroccipital process. It projects anteroventrolaterally from the basicranium. The process is basically three-sided; one flattened surface medial, one anterior, and one posterior. The medial surface is concave in contrast to the other two, which are slightly convex. At its distal end, the mastoid process is compressed anteroposteriorly. The concave medial surface expands proximally toward the basicranium and is confluent with a large recess surrounding the hyoid fossa. This same recess extends onto the anterolateral surface of the paroccipital process, which is at this place deeply excavated. The paroccipital process projects posteroventrolaterally from the basicranium and is compressed transversely. Its anteroventral margin is a crest that extends anteromedially toward the bulla, reaching the posterior side of the bulla between the stylomastoid foramen and the posterior lacerate foramen.

As in the Ursinae, the hyoid fossa is separated from the posterior lacerate foramen by a ridge of bone. The hyoid fossa sits within a deep recess. In ursines, the hyoid fossa is widely separated from the external auditory meatus by a wide expanse of the bulla. In *Kolponomos clallamensis*, however, the hyoid fossa is very close to the external auditory meatus. Also, in *K. clallamensis* the stylomastoid foramen lies midway between the hyoid fossa and the external auditory meatus, whereas in the Ursinae the stylomastoid foramen is widely separated from the external acoustic meatus and is within the recess that houses the hyoid fossa.

Dentition.—The upper dentition consists of I$^{1-3}$, canine, P$^{1-4}$, and M$^{1-2}$. The actual teeth present in the referred cranium are the roots of the left I$^{2-3}$ and the complete left and right P^2's and M^1's. On the left side, all alveolar margins are preserved, and it is that side that forms the basis for the following description.

The incisors and canines are clustered, without significant diastemata, in the thickened and downturned anterior end of the snout. The incisors are aligned transversely anterior to the canines. I^1 and I^2 are small and have transversely compressed roots. I^1 is smaller than I^2, and both teeth are implanted essentially vertically in the palate. The I^3's are much larger, being approximately four times the diameter of I^2 at the alveolar rim. Unlike the medial incisors, the I^3's are procumbent and deeply rooted in the premaxilla between the canine and the incisive foramen. The left I^3 measures 18.2 mm anteroposteriorly and 12.4 mm transversely at the alveolar rim. A diastema of 4 mm separates the alveolus for the left I^3 from that of the upper canine. The canine alveolus is oval and measures 20 mm anteroposteriorly and 17 mm transversely at the alveolar rim. The bulge in the lateral side of the rostrum indicates that the root for the canine is extremely long and extends nearly as far into the rostrum as the lateral edge of the nasal bone. The root is procumbent.

The cheek-tooth row curves laterally from the canine posteriorly to M^1, then M^2 is positioned more medially. P^1 has a single root that is round in cross-section, procumbent, and closely appressed to the posterior side of the canine alveolus. The alveolus indicates that the root was tapered, approximately 7 mm in diameter at the alveolar margin, and extended for approximately 15 mm into the maxilla.

P^2 is a robust tooth, with two roots and a large smooth crown. The tooth is oriented obliquely to the axis of the cheek-tooth row, the anterior root medial to the axis. The posterior root is on the axis of the tooth row and is approximately twice the diameter of the anterior root. The tooth tilts medially into the oral cavity. The crown of this tooth has a flat apical wear facet on the principal cusp. A smooth cingulum borders the lingual side of the crown from the anterior to the posterior border of the tooth. The posterior part of the crown is formed into a talon lying between the principal cusp and the posterior end of the cingulum.

P^3 had roots aligned in the axis of the cheek-tooth row. Judged by the size of the alveoli, the two roots of this tooth were more nearly equal in size than those of P^2, the posterior one being only slightly larger in diameter than the anterior one. The maxilla projects ventrally, forming a crest of bone between the two roots of this tooth.

P^4 was a large tooth, nearly as large as M^1, and had three roots. Of these, the medial (protocone) root is the largest, being more than twice the depth and diameter of either of the lateral (paracone and metacone) roots. Between P^3 and P^4, the lateral margin of the maxilla begins a strong lateral bend, so that P^4 is oriented obliquely to the cheek-tooth row. A diastema of approximately 3 mm separates the anterior (paracone) root of P^4 from the posterior root of P^3.

M^1 is a massive tooth. It appears to have been approximately 30% larger than P^4 in surface area. It is greatly expanded transversely and is triangular in occlusal view. It has five mammiform cusps of nearly equal sizes. The lateral two cusps are the paracone and metacone; the most medial cusp forms the apex of the triangle and is the protocone; intermediate cusps are the para- and metaconules. The surface of each M^1 shows extensive wear that breaks through the enamel to expose the inner dentinal core. There is a labial cingulum between the para- and metacones, but other cingula are lacking.

The M^2 alveoli indicate that this tooth was approximately half the size of the M^1. M^2 is positioned lingually opposite the talon of M^1. Like both P^4 and M^1, M^2 had three roots. Of these, the anterolateral (paracone) root was broadly joined with the medial (protocone) root to form a transversely oriented bilobate root. The posterior root is the metacone root and is rotated so that it is actually the most medial root of the tooth.

Kolponomos newportensis, new species

Figures 1-12

Kolponomos clallamensis Stirton, 1960. Barnes et al., 1985:43, figs. 9a, b.

Diagnosis.—A species of *Kolponomos* differing from *K. clallamensis* in the following derived cranial features: broad muzzle flaring laterally above canines and incisors; mastoid process twisted clockwise, extending forward beneath external auditory meatus as far as postglenoid process; intercondylar notch lacking so that the articular surfaces of the occipital condyles are continuous ventrally. In addition, *K. newportensis* is distinguished from *K. clallamensis* by the following primitive features: infraorbital foramen smaller and lacking marked excavation of maxilla anterior to it; prominent masseteric process of maxilla lacking and masseteric process on jugal reduced; jugal forming anterior rim of orbit; paroccipital process smaller and less downwardly pointing; paroccipital process lacking hyoid fossa.

Holotype.—USNM 215070, cranium lacking parts of dorsal surface with only right and left P^2 *in situ*; mandible lacking tips of coronoid processes and lacking incisors and right P_1; isolated associated right I^3 and C, right P^1, left P^1, left P^3, right P^4, left M^1, and right and left M^2. Recovered from the same concretion were the axis, third cervical vertebra, a broken proximal lumbar vertebra, a sternebra, a proximal part of an anterior rib, a thyrohyal lacking the proximal end, a complete ?ceratohyal, a metapodial lacking the distal end and half of the proximal end, a median phalanx, and unidentifiable bone fragments. The original half of the concretion containing the occipital part of the skull and most postcranial elements was collected by Douglas R. Emlong, October 1969 (Emlong field no. 603). On 26 January 1976 Emlong found the remainder of the concretion, containing the balance of the skull, mandible, and isolated teeth (Emlong field no. E76-B), recognizing it as associated and pertaining to *Kolponomos*.

Type locality.—A concretion found on the beach at low tide line, approximately 300 yards (274 m) south of the mouth of Big Creek and 100 yards (91 m) seaward of the sea cliff just north of Newport, Lincoln County, Oregon.

Formation and age.—Lower part of the Nye Mudstone, representing the early Pillarian Molluscan Stage (Addicott 1976a; Moore and Addicott 1987), correlative with the Late Arikareean Land Mammal Age, early Miocene.

Etymology.—Named for the town near the type locality to record the occurrence of the type species in a manner similar to that for the genoholotype.

Skull.—The skull of USNM 215070 lacks most of the dorsal surface and is toothless except for both P^2's, which are crushed into their alveoli and forward into those for P^1. The concretion enclosing the specimen was subspherical and aproximately 27 cm in diameter. Prior to its consolidation, all upper teeth except left and right P^2 had fallen out. In the course of gross preparation these were found in a tight cluster beneath the palate and between the horizontal rami of the mandible. Also prior to consolidation, the mandible had slipped out of articulation and moved forward and upward forcibly, coming to rest in a symmetrical undershot false occlusal position, undoubtedly causing the anterior displacement of left and right P^2 and severely crushing and comminuting the thin alveolar walls of left and right M^2 and M^1 and, to a lesser extent, the alveolar margins of the upper premolars. The apices of the coronoid processes were removed by abrasion of the smooth surface of the concretion as was much of the dorsal surface of the skull. The tightly appressed mandible was painstakingly separated from the skull and the tightly clustered isolated teeth were extracted by Gladwyn B. Sullivan in 1976 in the course of gross preparation of the specimen. This specimen represents an old individual as judged by its heavily worn teeth and advanced cranial fusion. Despite the latter, it is possible to make out many sutures, particularly in the orbital region.

A striking major feature of the skull, in common with all remains of the genus, is the flexure of the facial part of the skull relative to the basicranial plane (Fig. 2). Measured as the angle between the palate and basisphenoid, the flexure is approximately 155° in USNM 215070. The widely flaring zygomatic arches, the forward-oriented orbits, and the great hypertrophy of the mastoid processes are also distinctive features of the remarkable skulls of *Kolponomos*.

In USNM 215070 the muzzle is nearly as broad at the carnassial as the palate. The large anteroposteriorly elongated incisive foramina lie in the trough of the strongly arched palate with distinct grooves extending anteriorly from them nearly to the incisor alveoli. The interforamen septum forms a low S-curve anteriorly. Posteriorly the vaulted palate has strong anteroposteriorly oriented depressions along either side of the flattened medial part of the palate, becoming progressively deeper posteriorly and leading into

the anterior palatine foramina at the maxillary–palatine suture adjacent to the anterior root of M^2. Behind that a series of pits extends the posterior palatine groove to a foramen that penetrates the thin rim of the palatine portion of the palate.

The pterygoid hamuli are arcuate in palatal view and terminate in dorsoventrally flattened processes. Sutures with bones surrounding the pterygoid are too coossified for the precise outline of this element to be determined. The anterior or pterygoid process of the alisphenoid is defined by its suture with the palatine; with the palatine it forms a strong strut bracing the back of the palate against the braincase. Ventral to this strut a depression for the origin of the pterygoid muscle extends downward toward the hamular process. The posterior end of the large alisphenoid canal penetrates the base of the strut. This opening is closely followed by the foramen ovale, which lies in a common pit with the opening of the canal on the left side of USNM 215070, but on the right a groove joins these orifices as in most arctoids. The dorsal and posterior sutures of the alisphenoid with adjacent bones are closed.

The basisphenoid and basioccipital bones are strongly coossified and the sutures between them are eliminated. They form a trapezoidal figure with its base lying across the rectus capitis insertions just anterior to the posterior lacerate foramina. Thus the basioccipital is broadest across the rectus insertions where the winglike lateral processes of this bone overlap the medial edge of the petrosal and presumably floor the large tract for the inferior petrosal sinus. The knoblike processes for the rectus are situated bilaterally at the posterolateral corners of ovoid shallow depressions for muscle insertion that presumably extend forward onto the basisphenoid and medially to a low crest at the midline. The exoccipital is solidly fused with surrounding elements, except for its irregular contact with the posterior end of the bulla (caudal entotympanic). This bone contains the hypoglossal foramen, which is situated posteromedial to the posterior lacerate foramen as well as the posterior rim of the latter opening. Presumably the exoccipital also forms the medial wall and spine of the paroccipital process. The occipital condyles protrude slightly posterior to the nuchal crest. There is no intercondylar notch as the condyles are conjoined ventrally, uniting their articular surfaces. A shelflike extension of the floor of the foramen magnum extends posteromedially beyond these articular surfaces. Inside the foramen magnum the paired posterior openings of the hypoglossal foramina can be seen on its floor. An additional pair of foramina lying on the lateral wall of the foramen magnum at the level of the dorsal part of the condyles presumably accommodated venous drainage for sinuses within the occiput.

The auditory region is very small and nestled deeply within the ventrally projecting elements surrounding it, particularly the greatly hypertrophied mastoid process. The bulla is uninflated and extensively coossified with surrounding elements; nevertheless, most of its outline as well as its composition can be determined from bilaterally symmetrical suture traces and rugose coossification tracts. These observations indicate that the ectotympanic lacks an ossified meatal tube; its anterior limb spreads over the posteromedial surface of the postglenoid, forming the posterior wall of the slitlike postglenoid foramen. Anteromedially the ectotympanic overlaps the entotympanic and coossifies laterally with the alisphenoid behind the foramen ovale. A styloid process of the ectotympanic lies beneath the opening for the eustachian tube. The posterior limb of the ectotympanic is fused to the base of the mastoid process. Behind this union, the stylomastoid foramen emerges from the mastoid. The facial canal is thus separated from the large pit for the tympanohyal that opens above a prominent hyoid process of the entotympanic at the posterolateral corner of the bulla. There is no large hyoid fossa excavated into the anterior wall of the paroccipital process as in *K. clallamensis*.

The entotympanic is irregularly exposed along the medial edge of the bulla because of variable overlap of the ectotympanic; posteriorly the caudal element is sutured to a process from the exoccipital and posterolaterally to a process from the mastoid. There is a large posterior opening of the carotid canal well anterior to the posterior lacerate foramen. This opening is formed medially by the basioccipital wing and laterally by the entotympanic, but anteriorly the arterial tube is nearly completely surrounded by the entotympanic. The anterior carotid foramen lies medial to the styloid process of the ectotympanic and opens into a groove in the basisphenoid anterior to the median lacerate foramen. From this groove the artery must loop posteriorly to enter the median lacerate foramen and/or the presumed channel in the basioccipital that accommodates the inferior petrosal sinus.

The large mastoid process takes the form of an anteroposteriorly flattened column bending outward and downward from its base and curving forward at its tip to pass nearly under the postglenoid process (Fig. 7C). Its components are totally coossified, but the nuchal crest extends along the lateral surface of the process, thus marking the position of the mastoid–squamosal suture and indicating that the process is composed about equally of the two elements. The process terminates in a raised ovoid area that lies within the suture. This element may represent the secondary ossification center (epiphysis) frequently observed at the tip of the mastoid process in adult ursids. A ridge arises from the posteroproximal surface of the mastoid process and passes upward and posteriorly to join the paroccipital process. The paroccipital process curves posteroventrally and terminates in a sharp point.

The supraoccipital bones are solidly coossified with surrounding elements. They are concave and highly rugose beneath the nuchal crest; a thin ridge is present sagittally. At their lateral extremities a shallow pit is present dorsal to the base of the paroccipital processes. The lateral processes of the nuchal crest extend behind the inion and beyond the occipital condyles; consequently, the crest has a broad inflection at the midline. The parietal and squamosal bones are coossified, but their junction is probably marked by the bilaterally symmetrical collapse of the braincase wall under lithostatic load. Breakage dorsally has removed most of the sagittal crest of the parietal, but the remaining evidence indicates the presence of at least a low crest. The squamosal apparently makes a significant contribution to the anterior part of the mastoid process. Its glenoid fossa forms a cylindrical articulation nearly at right angles to the basicranial axis. Prominent recurved postglenoid processes are present, deepest medially, and the anterolateral part of the articular surface is bordered by a low preglenoid process. Most of the squamosal–jugal suture is visible; the squamosal contribution to the zygomatic arch seems to taper out at the base of the jugal postorbital process.

The anterior ends of the frontals have been removed by erosion, exposing a natural section of the narial cavity. Frontal–parietal sutures are coossified and not traceable, but they may have crossed the midline at about the point where the parasagittal crests appear to diverge anteriorly. The frontal sinuses seem to have extended backward over the braincase to about this point. Beneath these sinuses the braincase is sharply constricted anteriorly, probably indicating the greatly constricted form of the olfactory lobes of the brain as shown by the holotype of *K. clallamensis*.

Sutures in the orbital wall can be partially seen and the relative position of foramina and bones can be determined. In general the arrangement is like that described by Stirton for the holotype of the genotypic species. There is a large common opening for the anterior orifice of the alisphenoid canal, the foramen rotundum, and the anterior lacerate foramen as in pinnipeds. Anterodorsal to this opening the slitlike small optic foramen opens into a short groove. Dorsal to the

TABLE 1. Measurements (in mm) of crania of *Kolponomos clallamensis* and *K. newportensis*, new species.

	Kolponomos newportensis	Kolponomos clallamensis	
	USNM 215070	UCMP 50056[a]	LACM 131148[b]
Total (condylobasal) length	253.1	—	258.4
Postpalatal length (palatal notch to basion)	107.3	—	107.0
Basion to anterior edge of zygomatic root	155.2	—	153.7
Length C alveolus to M^2 alveolus	114.2	ca. 108	117.7
Width of rostrum across canines	75.2	—	(71)
Width of skull across alveoli of M^1	ca. 110	ca. 98	119.6
Width of skull at infraorbital foramen	78.3	75.2	74.3
Width of skull across antorbital process	74.9	80.9	(82)
Width of greatest intertemporal constriction	46.2	46.8	45.4
Width of braincase, anterior edge of glenoid fossa	72.3	—	82.3
Zygomatic width	179.5	—	(178)
Auditory width	137.0	—	141.2
Mastoid width	182.0	—	183.7
Paroccipital width	116.5	—	123.0
Greatest width of occipital condyle	61.5	—	74.0
Greatest width, anterior nares	—	37.0	38.5
Greatest height, anterior nares	—	36.3	—
Greatest width of foramen magnum	26.8	—	33.3
Greatest height of foramen magnum	18.3	—	15.0
Transverse diameter of infraorbital foramen	11.1	11.6	13.0
Height of infraorbital foramen	11.3	20.0	21.6

[a]For additional measurements see Stirton (1960:355).
[b]Bilateral measurements of the referred cranium of *K. clallamensis* are made on the left side. Parentheses indicate estimated measurements made by doubling a half width.

TABLE 2. Measurements of cheek teeth and mandible of *Kolponomos*. Where available, measurements of the left side entered first.

	K. newportensis (USNM 215070)	K. clallamensis (LACM 131148)
Upper teeth (length × width)		
I^3	12.8 × 10.7	—
C	15.4 × 13.9	—
P^1	7.3 × 11.5	—
P^2	16.2 × —	15.7 × 10.3
	17.2 × 12.5	
P^3	ca. 16 × 12	—
P^4	18.5 × 25.5	—
M^1	22.3 × 28.9	21.9 × 31.4
M^2	16.8 × 16.4	—
	17.8 × 17.1	
Lower teeth (length × width)		
C	17.2 × 13.1	—
	16.5 × 13.5	
P_1	— × ca. 9	—
	7.6 × 9.9	
P_2	13.7 × 10.8	—
	14.0 × 10.5	
P_3	16.1 × 11.2	—
	16.2 × 11.1	
P_4	18.0 × 14.0	—
	18.7 × 13.6	
M_1 length	27.3; 27.5	—
M_1 width trigonid	24.0; 24.5	—
M_1 width talonid	— ; 22.7	—
M_2	21.5 × 22.3	—
	21.3 × —	
Mandible		
Length of horizontal ramus, condyle to tip of rostrum	201.5	—
Length of base of coronoid process	55.5; 55.7	—
Depth of mandible beneath P_2	59.5; 59.8	—
Depth of mandible beneath anterior part of M_1	43.8; 44.2	—
Depth of mandible beneath posterior part of M_2	40.0; 42.2	—
Width of mandible at P_3	18.8; 20.5	—
Width of mandible at M_2	21.8; 24.2	—
Length of symphysis	53.5	—

optic foramen lies the equal-sized ethmoid foramen. The orbitosphenoid bone containing these foramina seems to pass anterodorsally along the orbital wall to a greater extent than in *K. clallamensis*. Ventral to these foramina, the sphenopalatine and posterior palatine foramina are closely associated, the former on the orbitosphenoid–palatine suture and the latter penetrating the adjacent palatine bone. The sphenopalatine foramen is about twice the size of the posterior palatine foramen; neither is as large as its counterpart in *K. clallamensis*. Indistinct sutures suggest that the palatine is attenuated between the frontal and maxilla and fails to reach the anterior end of the orbital fossa. There is a very small lacrimal foramen but no trace of the limits of the corresponding lacrimal bone.

The jugal forms the ventral part of the orbit and appears to extend nearly to the lacrimal foramen (in contrast to *K. clallamensis*). With the maxilla it forms the roof of the short infraorbital canal. There is a strong postorbital process and a low, elongated, rugose masseteric process formed by the jugal.

The dorsal part of the maxilla is eroded away so that only the lateral and palatal parts of this bone are preserved. The oval infraorbital canal penetrates the zygomatic process of the maxilla. This canal is large (see Table 1) and short (11.0 mm left), as is

characteristic of *Kolponomos* and pinnipeds. It opens onto the face into a shallow depression (infraorbital fossa) that is more extensively developed in *K. clallamensis*. There appears to have been a shallow fossa for the levator labii marked by a dorsal preorbital fossa as in *K. clallamensis*. The suture with the premaxilla is thoroughly coossified. The rostrum anterior to the canines is laterally expanded and bears low rises over the roots of the canine and I^3.

A natural oblique section through the narial cavity exposes the dorsal part of this region from the level of the canines to just behind the orbits, showing that the ethmoturbinals are placed laterally and are excluded from the narial opening as in other arctoids. The dorsal frontal sinus is also evident and must extend backward close to the frontoparietal suture.

Upper dentition.—Most of the upper cheek teeth of USNM 215070 (Fig. 8), with the exception of the *in situ* P^2's, were found grouped together in the matrix between the rami of the associated mandible. When prepared and fitted into their respective alveoli the following teeth were recovered: right I^3, C, right P^1, left P^1, left P^3, right P^4, left M^1, and right and left M^2. All except I^3 and C are highly worn and so furnish little information about their crowns' morphology.

The alveoli for I^{1-2} indicate that these teeth were much smaller than I^3. I^3 is procumbent and has a long cylindrical root and a relatively short crown with a recurved tip. There is no cingulum or carina. A facet for the lower canine is present, worn through the enamel at the posterolateral base of the crown. The tip has been fractured and a transverse groove has been cut across the anterior face of the crown, both probably representing damage during use of this tooth as a lever. The upper canine is broken across the root so that only about half the total length of the tooth remains. It is also procumbent; its crown is an attenuated cone, slightly recurved at the tip, and has no cingulum or carina. A wear facet for the lower canine extends from the tip to within 2 mm of the base of the crown. The tip is also worn apically, and a short transverse groove cuts the anterior face near the tip.

The P^1 is closely appressed to the canine. Its crown is oriented transverse to the axis of the tooth row. The crown has an ovoid outline and a posterior cingulum. Heavy wear has truncated the apex to a medially sloping wear surface cut to the crown's base. Its single root is anteroposteriorly flattened and bends posteriorly to accommodate the roots of C and P^2. The P^2 has two roots; its crown is an elongated oval in occlusal outline with cingular shelves anterior and posterior to the stout principal cusp. Wear has formed a medially truncated surface across the principal cusp that has cut nearly to the crown's base. P^3 is only slightly larger than P^2 and two-rooted, the more anterior root passing inside the posterior root of P^2 so that the tooth has an orientation oblique to the tooth row. The crown is ovoid in occlusal outline; wear has removed the principal cusp and anterior cingulum, but the posterior cingular shelf remains. This cingulum bears a low cuspule laterally and is bounded medially by a well-developed facet of interdental wear.

P^4 bears three roots, the lateral pair about the size of those of the anterior premolars, although the most posterior is slightly smaller than the anterior. A large medial root is nearly symmetrically placed with the lateral roots, but the whole tooth has an oblique orientation to align with the anterior surface of M^1, thus removing the embrasure pit found in most carnivores where carnassial shear is important. At the advanced stage of wear shown by the P^4 only an encircling band of thin enamel remains. The enamel is broken on the posterior side by abrasion between P^4 and the adjacent M^1. A remnant of the metastyle remains on the posterolateral part of the crown marked by a notch that may represent the base of the carnassial notch. Dentine-filled pulp cavities on the gently concave worn crown indicate the presence of a principal external cusp or coalesced cusps forming an anteroposteriorly elongated structure and large internal cusp ("protocone") supported by the strong internal
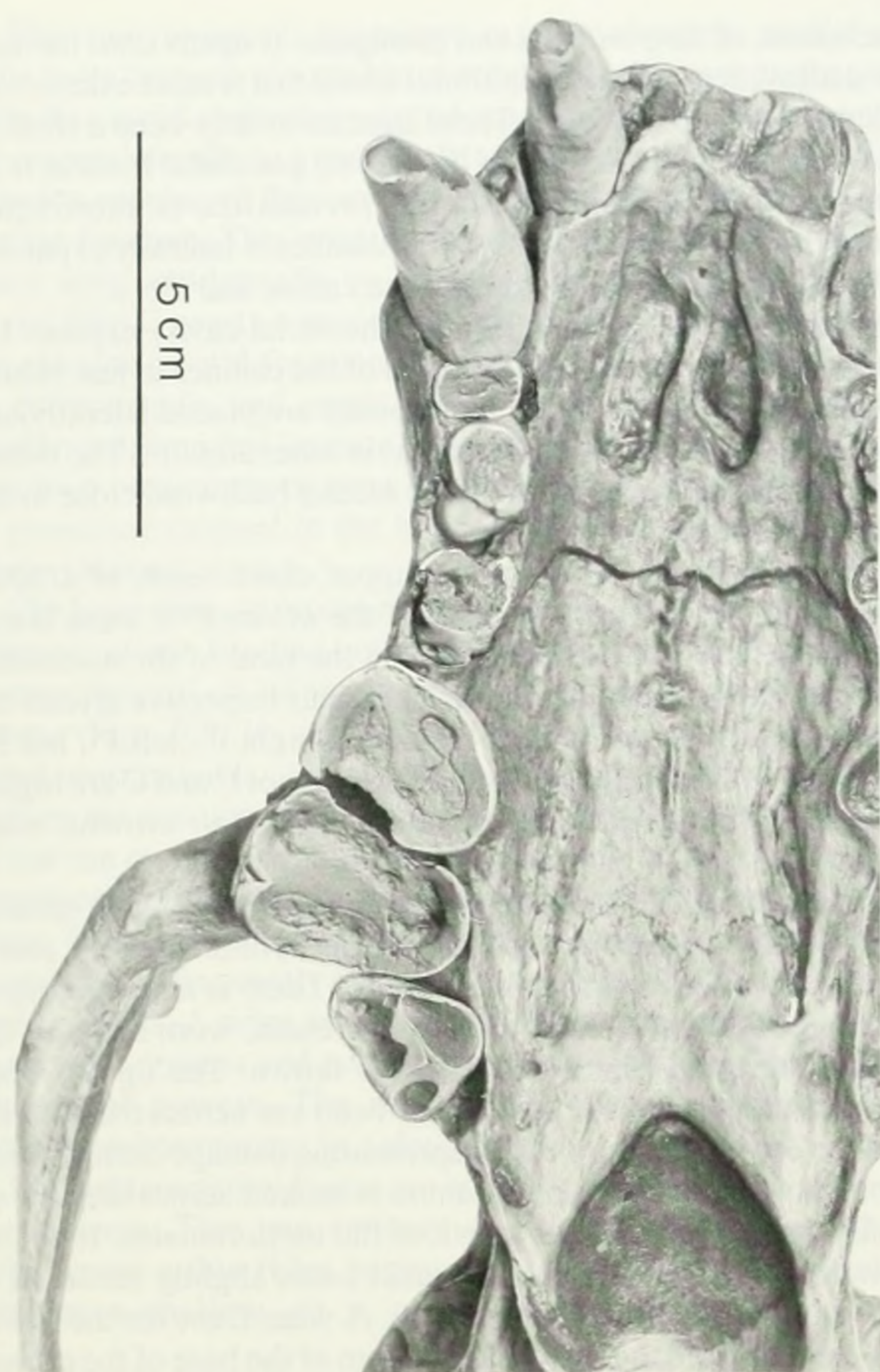
5 cm

A

5 cm

B

Figure 8. Upper cheek teeth of holotype of *Kolponomos newportensis* n. sp., USNM 215070. Right side with left P^2, P^3, and M$^{1-2}$ reversed to restore the complete cheek-tooth series.

Figure 9. Mandible of *Kolponomos newportensis* n. sp., holotype, USNM 215070. A, occlusal view; B, left side. At same scale as figures of crania.

root. Anterolateral to the latter a filled pulp cavity indicates the presence of another smaller cusp linked to the "protocone," probably indicating that the anterior cingulum bore a cusp analogous to the paraconule of tribosphenic molars. Thus the upper carnassial of USNM 215070 has been molarized, its sectorial nature changed to function with the molars as part of the masticatory battery.

The first upper molar has three roots. The labial roots supporting the paracone and metacone are anteroposteriorly compressed structures; the lingual root supporting the protocone is a short faceted cone. Filled pulp cavities indicate a pattern of cusps similar to the M^1 of *K. clallamensis*. A short section of the labial cingulum bridges the indentation between the paracone and metacone and, as in *K. clallamensis*, indicates that the paracone was larger than the metacone. Thin enamel rims the concave wear surface of this tooth, broken only at the junction with P^4. The M^2 is triangular in form and least worn on the left side. It is positioned lingually opposite the M^1 talon, in contrast to a labial position opposite the trigon as in most carnivorans. It bears two short stout roots; the anterior is anteroposteriorly flattened, the posterior triangular. The worn crown shows four inflated cusps that have coalesced, separated only by thin grooves similar to the condition in the less worn M^1 of *K. clallamensis*. These are interpreted as follows: the most labial is the paracone with the closely allied metacone immediately posterolingual to it; the large protocone occupies the anterolingual border,
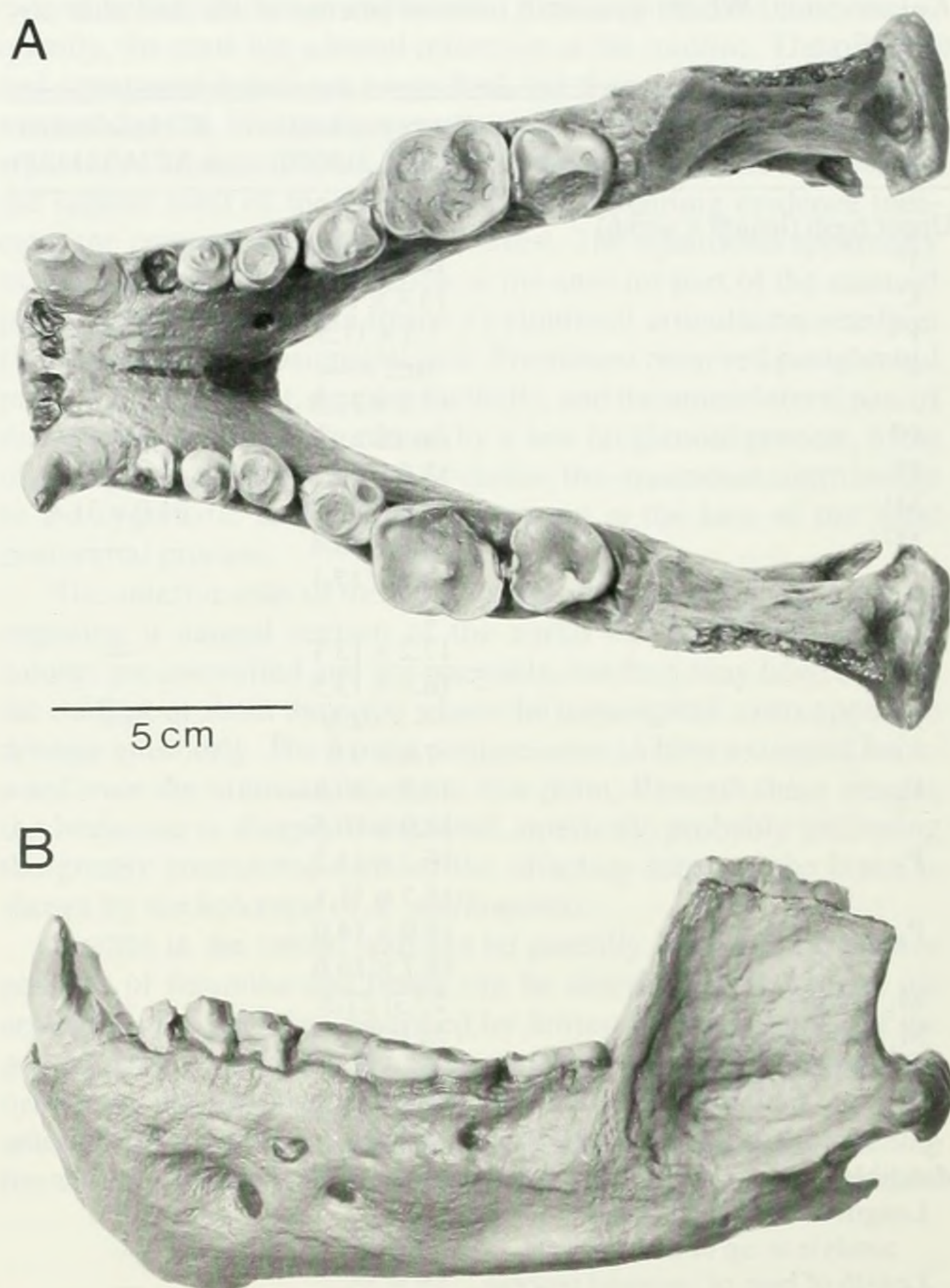
the labial projection of its wear facet representing the paraconule; the cusp at the posterolingual corner of the tooth is the metaconule. The enamel covering of these cusps is remarkably thin, as revealed by apical wear. An interdental wear facet with M^1 occurs on the anterior face of the tooth.

Mandible.—The nearly complete mandible of 215070 lacks only the tips of both coronoid processes (Figs. 9, 10). The rami are thoroughly ankylosed at the symphysis; the junction is raised externally, creating a symphyseal boss ventrally. The horizontal ramus is deepest at this boss and shallowest posteriorly. Anteroventrally paired foramina lie on either side of the symphyseal suture about at mid-depth. Laterally there are three mental foramina; the largest is the most ventral, lying beneath P$_3$ at the posterior end of a shallow depression. A second foramen lies anterodorsal to the first and beneath P$_2$ on the right side or posteriorly beneath the anterior root of P$_4$ on the left side. The third and most posterior foramen lies at mid-depth of the horizontal ramus beneath the posterior root of P$_4$. The rami are markedly rugose beneath the molars; the right side shows bone resorption around the protoconid root of M$_1$, and on the left side there is a pit in the lateral surface adjacent to the hypoconid root of the same tooth. The masseteric fossa has a deep anteroposteriorly elongated pit in its deepest recess. The masseteric crest does

A

B

Figure 11. Cervical vertebrae of holotype of *Kolponomos newportensis* n. sp., USNM 215070. A, axis, anterior and left lateral views, lateral view reversed from right side; B, third cervical, anterior and left lateral views.
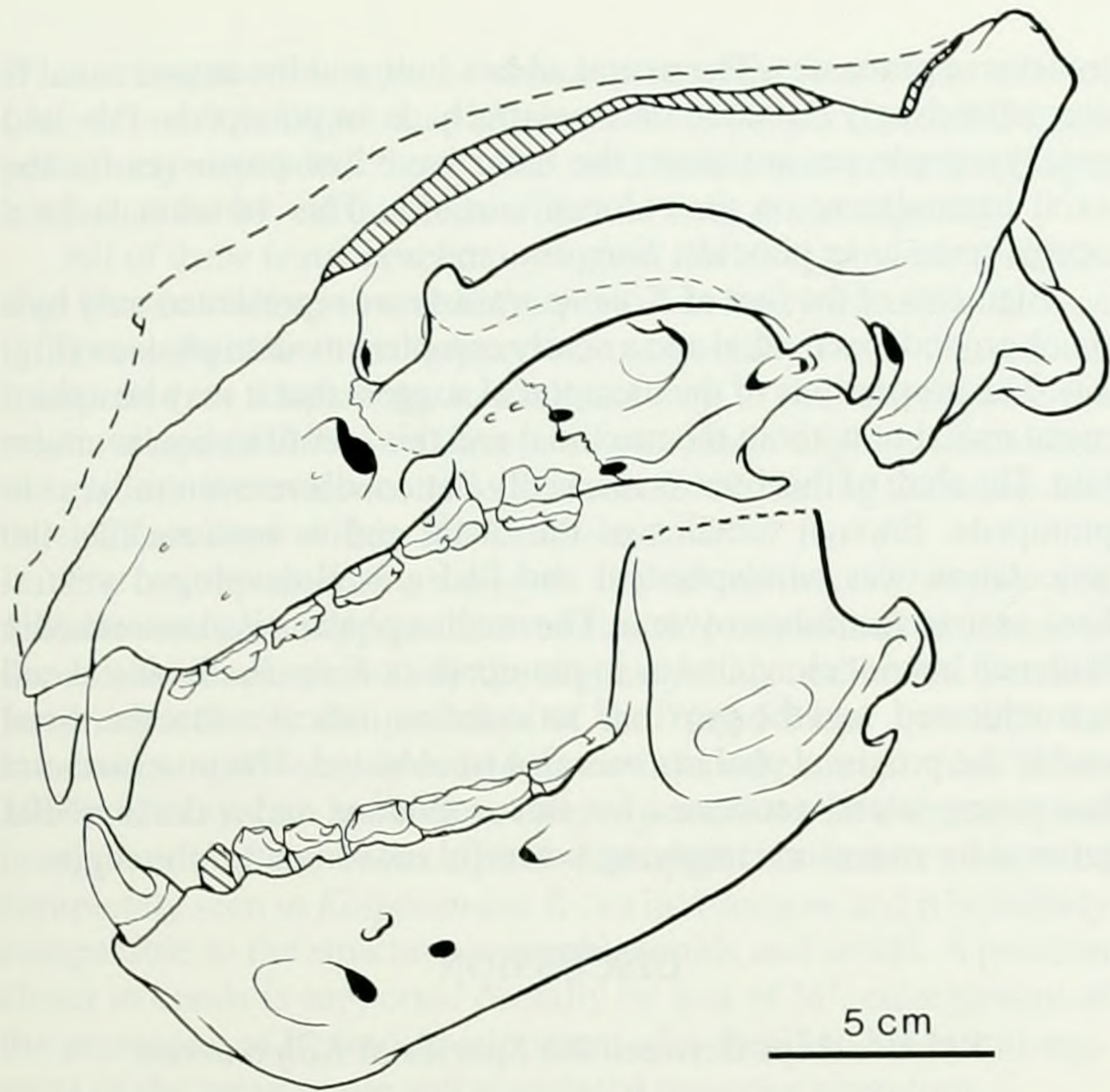

5 cm

Figure 10. Outline drawing of the holotype of *Kolponomos newportensis* n. sp., USNM 215070, viewed from the left. Upper dentition restored from isolated teeth found with the type.

not extend to the anterior end of the fossa but arises just above the base of the angular process and passes to the articular condyle. In harmony with the form of the glenoid fossa, the articular condyle is cylindrical, pointed laterally, and deepest medially; a pit for insertion of the external pterygoid muscle occurs at the anteromedial base of the condyle. The angular process is relatively small and markedly inflected medially. Its dorsal surface has a pit and ridge, and the medial surface is rugose, all for insertion of parts of the internal pterygoid muscle. There is a large mandibular foramen that lies below the level of the tooth row and the condyle and just above the level of the dorsal surface of the angular process, about midway along the base of the ascending ramus.

Lower dentition.—The central incisors seem to have been lost in life in USNM 215070 but it is not certain that I_1 was in fact present. The position of this tooth is occupied by spongy bone. The alveolus for the right I_2 is filled with spongy bone but the alveolus for the left I_2 is discernable. The roots of both I_3's are present. The canine has a long root and short crown. It is fully preserved only on the left side; the right canine appears to have had its apex broken away in life; the broken surface is polished and a secondary wear facet was established on the medial side of the broken tip. Occlusion with the upper canine has worn the tip and posterolateral side of each lower canine.

The premolar row diverges slightly posteriorly along an axis that lies wholly inside the axis of the molar row. The left P_1 is badly broken; the right P_1 was recovered from the surrounding matrix. Like its counterpart in the maxilla, the P_1 is anteroposteriorly compressed to fit between the base of the canine and the overhanging anterior margin of P_2. Its crown is heavily worn apically on a posteriorly slanting surface. There is a posterior cingulum pitted by breakage. The P_2 and P_3 are similar in form; the P_3 is larger. The apically worn crowns show a robust principal cusp and anterior and posterior cingular cusps connected by a lingual cingulum. There is no labial cingulum. The P_4 departs from this form in that a strong posterolingual cusp is also present; the anterior cingular cusp and
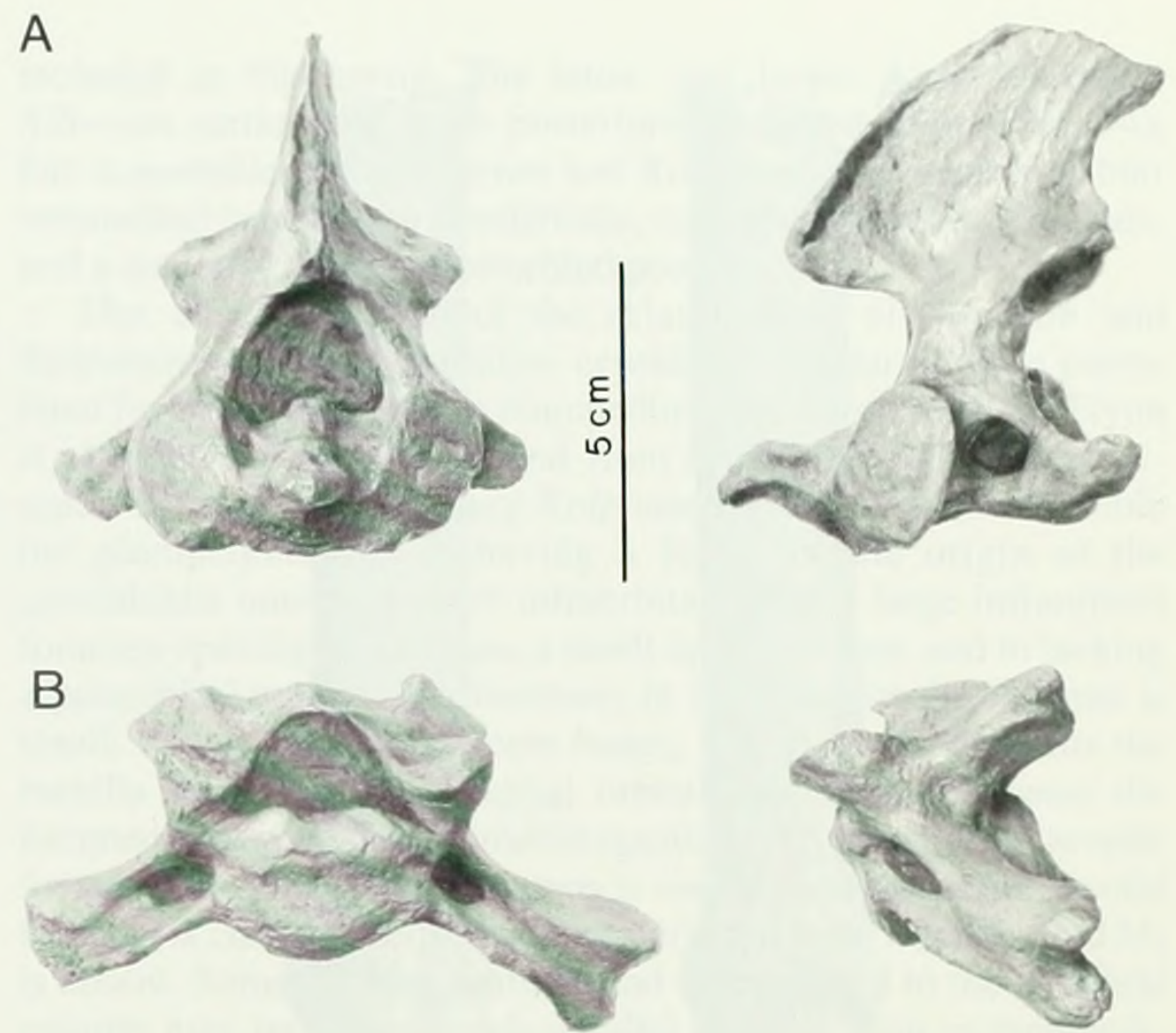
posterolabial cingular shelf combine to give this tooth a molariform appearance.

The M_1 is offset laterally so that only the anterolingual face of its paraconid overhangs the posterolabial cingulum of P_4; its crown is only a little longer than wide and worn nearly flat. On the left side the entoconid region is worn away, but on the right the crown is complete with its encircling thin enamel. A remnant of the enamel in the right talonid basin is preserved at this advanced stage of wear. Filled pulp cavities indicate the full tribosphenic complement of cusps; the protoconid, metaconid, and hypoconid were subequal in size, the paraconid and entoconid smaller. There are indentations internally at the carnassial notch and externally between the talonid and trigonid. There is no trace of a cingulum.

M_2 is wider than long, triangular in occlusal outline, and widest across the trigonid. Wear has removed the anterolingual corner of the right M_2 but not the left, which has lost marginal enamel along the anterior part of the tooth. Filled pulp cavities indicate the presence of three trigonid cusps and the hypoconid, which is represented by encircling enamel on the right and has not worn into the pulp cavity on the left. The pulp cavities seem best interpreted in comparison with the trigonid of M_1: a large protoconid on the anterolabial corner, a small paraconid directly lingual to it, and a large metaconid on the median lingual margin. Pulp cavities of the latter two cusps are connected. There is no M_3.

Postcranial skeleton.—An axis and third cervical vertebra are available and all structures are preserved on one side or the other of these bones. The axis (Fig. 11) has a short centrum and high neural spine as in pinnipeds and lutrine mustelids. The general form of the bone most resembles that seen in phocids or *Enhydra*, although the neural spine is larger overall than in the latter. The odontoid process points anterodorsally as in terrestrial carnivores and in contrast to most pinnipeds, and there is a shallow groove on its dorsal surface for the transverse ligament of the atlas, a feature usually missing in pinnipeds. A broad ridge continues the odontoid process into the spinal canal. The atlantoaxial articulations are joined beneath the odontoid process as in ursids, not separated by a notch as in pinnipeds. The centrum (less the odontoid process) is wider than long. Its

Figure 12. Metapodial and phalanx of holotype of *Kolponomos newportensis* n. sp., USNM 215070. A, metapodial, dorsal and ventral (right) views; B, phalanx, dorsal and ventral (right) views.

posterior articulation is dorsoventrally flattened. A marked ventral keel leads from the joined atlantoaxial articulation to the posterior articular epiphysis where there is a thickening of the keel into a low process. *Enhydra* and phocids show a similar structure. The robust transverse process sweeps in an arc backward beyond the centrum, as in pinnipeds. The vertebrarterial canal pierces the base of the transverse process. It is of large caliber as in pinnipeds and lutrine mustelids. The neural arch has a narrow base corresponding to the short centrum. The postzygapophyses project as flanges laterally; their articulations slant upward posteriorly and laterally. The high bladelike neural spine hooks posteriorly beyond the neural arch of the third cervical when in articulation. It is strongly inclined anteriorly, ending in a process for the rectus capitis that lies above the base of the odontoid. The neural spine is thin, wider only at the rectus capitis origin. Its form most approximates that of phocids rather than that of otariids or ursids, in which the spine is more robust and has a marked posterior process. The postzygapophyses lack dorsal processes for insertion of the axial muscles, but the base of the arch beneath the overhanging neural spine is excavated for the more medial elements of this muscle system.

The centrum of the third cervical vertebra is about as long as wide, and flattened dorsoventrally (Fig. 11) and keeled with a posterior enlargement, as in pinnipeds. The prominent transverse processes sweep posterolaterally and terminate in twin processes. They seem to lack an anterior spine as in phocids and in contrast to other carnivores. Large vertebrarterial canals pierce the bases of the

transverse processes. The neural arch is low, and the neural canal is correspondingly flattened dorsoventrally, as in pinnipeds. Pre- and postzygapophyses are stout; the latter have low processes for the axial musculature on their dorsal surfaces. This vertebra lacks a neural spine as in phocids, *Enhydra*, and ursids.

Elements of the foot of *K. newportensis* are represented only by a much eroded metapodial and a nearly complete median phalanx (Fig. 12). The proportions of the metapodial suggest that it may be a third metatarsal, but without the proximal end this identification is uncertain. The shaft of this bone is markedly flattened dorsoventrally, as in pinnipeds. Enough remains of the distal end to indicate that the articulation was hemispherical and had a well-developed ventral keel, as in terrestrial carnivores. The median phalanx is also markedly flattened but not elongated as in pinnipeds or *Enhydra*. Its distal end is trochleated, and the proximal articulation indicates that the distal end of the proximal phalanx was also trochleated. The proximal end has strong lateral processes for flexor tendons and a dorsomedial process for extensors, implying powerful movement of the digits.

DISCUSSION

Relationships Between the Species of *Kolponomos*

Although we have only one nearly complete cranium of each species, the characters cited in the diagnoses are similar to those that distinguish other nominal species of arctoid carnivores. Moreover, the two specimens of *K. clallamensis* are similar in important particulars that separate them from the specimen here described as *K. newportensis*, lessening the possibility that the differences between the specimens from Washington and Oregon are due to sexual dimorphism or individual variation. Nor is there evidence that the individuals differ in ways usually associated with sexual dimorphism in arctoid carnivores (gross size, size of canines, and development of muscular processes of the skull).

In some ways the cranium of *Kolponomos newportensis* seems the more primitive of the two, having some characters more like those seen in other arctoids. It has a less highly arched palate, a shorter paroccipital process, a smaller hyoid fossa, and a smaller infraorbital foramen. Also, the jugal rims the anteroventral part of the orbit. Some of its other diagnostic characters, however, such as the broad snout, lack of an intercondylar notch, and the more extremely developed mastoid process, are derived relative to *K. clallamensis* and other arctoids. *K. clallamensis* appears to have had a more specialized feeding mode, a more modified rostrum, and greater innervation to the fleshy lips.

Relationships of *Kolponomos* Among the Arctoid Carnivora

In 1960 Stirton compared *Kolponomos clallamensis* extensively with *Allocyon loganensis* Merriam, 1930, from the mid-Arikareean (Oligocene) John Day Formation at Logan Butte, Crook County, Oregon, and concluded that *A. loganensis* was "the carnivore most closely related to *Kolponomos*." Among the 29 features that he delineated, the following similarities seem most informative cladistically: presence of a nasolabialis fossa dorsoanterior to the orbit, short infraorbital canal and large infraorbital foramen with infraorbital fossa, and lack of a postorbital process. With the additional material of *Kolponomos* now available the following can be added: the basioccipital is wide posteriorly, the mastoid process is hypertrophied, and there is a depression anterior to the median lacerate foramen for the first loop of the internal carotid. The latter feature is correlated in *Allocyon* with a deeply excavated lateral margin of the basioccipital for reception of the carotid artery and inferior petrosal sinus, typical of ursids and amphicyonids.

Allocyon (Figs. 13, 14) and *Kolponomos* are similar in the following dental features that appear to represent synapomorphies:

P^4 is triangular in outline with a protocone nearly the size of (*Allodesmus*) or larger than (*Kolponomos*) the paracone; M^2 has a posteriorly expanded "heel" (the metaconule and posterior cingulum), and the M_1 talonid is as wide and long as the trigonid.

All of these features seem to support the close phyletic relationship between *Allocyon* and *Kolponomos*. In many features *Allocyon* is more primitive than *Kolponomos*, especially those that can be interpreted as adaptations to molluscivory in the latter. Since the relationships of *Allocyon* have not been made explicit heretofore, we explore the evidence here as a means of placing *Allocyon* and thus *Kolponomos* within the Carnivora.

The synapomorphies listed above uniting *Allocyon* and *Kolponomos* also support their relationship with basal members of the arctoid clade, especially the amphicyonids and ursids. Particularly important is the presence of the "ursid loop" in which the internal carotid artery is nested in the inferior petrosal sinus (Hunt 1977). This system has a clear bony signature in the deep marginal invagination of the basioccipital. Although this feature cannot be completely seen in *Kolponomos*, it can in *Allocyon*, and it is entirely comparable to the structure in amphicyonids and ursids. A position closer to ursids is supported dentally by loss of M^3, enlargement of the protocone of P^4, and development of a "heel" in M^2 by enlargement of the metaconule and associated posterior cingulum.

Within the Ursidae significant autapomorphies unite the subfamilies Hemicyoninae and Ursinae and exclude *Allocyon* and *Kolponomos*, whose relationships lie near or within the most basal ursoid group, usually referred to as the Amphicynodontinae (Simpson 1945). *Amphicynodon* and *Pachycynodon* are the most completely known taxa (Cirot and de Bonis 1992; Cirot 1992)

included in this group. The latter, and larger, form resembles *Allocyon* particularly in its posteriorly extended palate (Fig. 14), but it resembles both *Allocyon* and *Kolponomos* in having a short infraorbital canal, fossa nasolabialis, enlarged infraorbital foramen, and a similarly reduced postorbital process.

Our conclusions about the relationships of *Allocyon* and *Kolponomos* with the primitive ursoids are similar to those postulated for the most primitive pinnipedimorph, *Enaliarctos*, by Flynn et al. (1988), Berta (1991), and Hunt and Barnes (1994, this volume). In cranial morphology *Kolponomos* and *Allocyon* resemble the pinnipedimorphs in having a fossa for the origin of the nasolabialis muscle, a short infraorbital canal, a large infraorbital foramen opening into a fossa, a small optic foramen, and in lacking a postorbital process. Furthermore, in *Kolponomos* the lacrimal is small, fusing early to adjacent bones, and in *K. clallamensis* the maxilla forms the anterodorsal orbital rim. In *Kolponomos* the foramen rotundum has a common opening with the anterior lacerate foramen, the postglenoid foramen is vestigial, the posterior carotid foramen is clearly anterior to the posterior lacerate foramen, and M_3 is absent. Some of these features and others noted in the vertebral column may represent trends parallel to those seen in pinnipeds, especially with respect to aquatic adaptation (e.g., emphasis on the internal jugular drainage of the cranium and thus loss of the postglenoid exit), but the sum total suggests that *Allocyon* and *Kolponomos* represent early offshoots of the same stock that yielded enaliarctine pinnipedimorphs and that both have their roots in the earliest differentiation within the Superfamily Ursoidea.

A more explicit hypothesis of the relationships of *Kolponomos* to other ursoids and pinnipedimorphs can be made by using the

TABLE 3. Distribution of cranial and dental features discussed in the text (0, primitive state; 1, derived state).

Derived state	AMP	MUS	URS	AMC	PAC	ALL	KOL	ENA
1. Basioccipital excavated laterally	1	0	1	1	1	1	1	1
2. Shallow suprameatal fossa	0	1	1	1	?	0	0	0
3. M^3 absent	0	1	1	1	1	1	1	1
4. Basioccipital wide posteriorly	0	0	1	1	1	1	1	1
5. P^4 large protocone	0	0	1	1	1	1	1	1
6. M^2 with "heel"	0	0	1	1	1	1	1	1
7. M^{1-2} loss parastyle	0	0	1	1	1	1	1	0
8. M^{1-2} loss paraconule	0	0	1	1	1	?	0	0
9. M^1 lingual metaconule	0	0	1	0	1	?	0	0
10. M_2 reduced paraconid	0	0	1	1	1	?	0	?
11. M_2 size metaconid = protoconid	0	0	1	1	1	?	1	?
12. Infraorbital canal short	0	0	0	1	1	1	1	1
13. Infraorbital foramen large	0	0	0	1	1	1	1	1
14. P_4 short metastyle	0	0	0	1	1	1	1	1
15. Palate posteriorly extended	0	0	0	0	1	1	0	1
16. M_1 talonid as wide as trigonid	0	0	0	0	1	1	1	0
17. M_1 metaconid large	0	0	0	0	1	1	1	0
18. Nasolabialis fossa present	0	0	0	0	0	1	1	1
19. Infraorbital fossa present	0	0	0	0	0	1	1	1
20. Mastoid process large	0	0	0	0	0	1	1	0
21. Postorbital process absent	0	0	0	0	0	1	1	1
22. Alisphenoid "strut" present	0	0	0	0	0	0	1	1
23. Postglenoid foramen vestigial	0	0	0	0	0	0	1	1
24. M^2 lingual to M^1	0	0	0	0	0	0	1	1
25. Anterior lacerate foramen and foramen rotundum in common fossa	0	0	0	0	0	0	1	1
26. M_3 absent	0	1	0	0	0	0	1	1

[a]AMP, Amphicyonidae; MUS, Mustelida; URS, Ursinae and Hemicyoninae; AMC, *Amphicynodon*; PAC, *Pachycynodon*; ALL, *Allocyon*; KOL, *Kolponomos*; ENA, *Enaliarctos*.
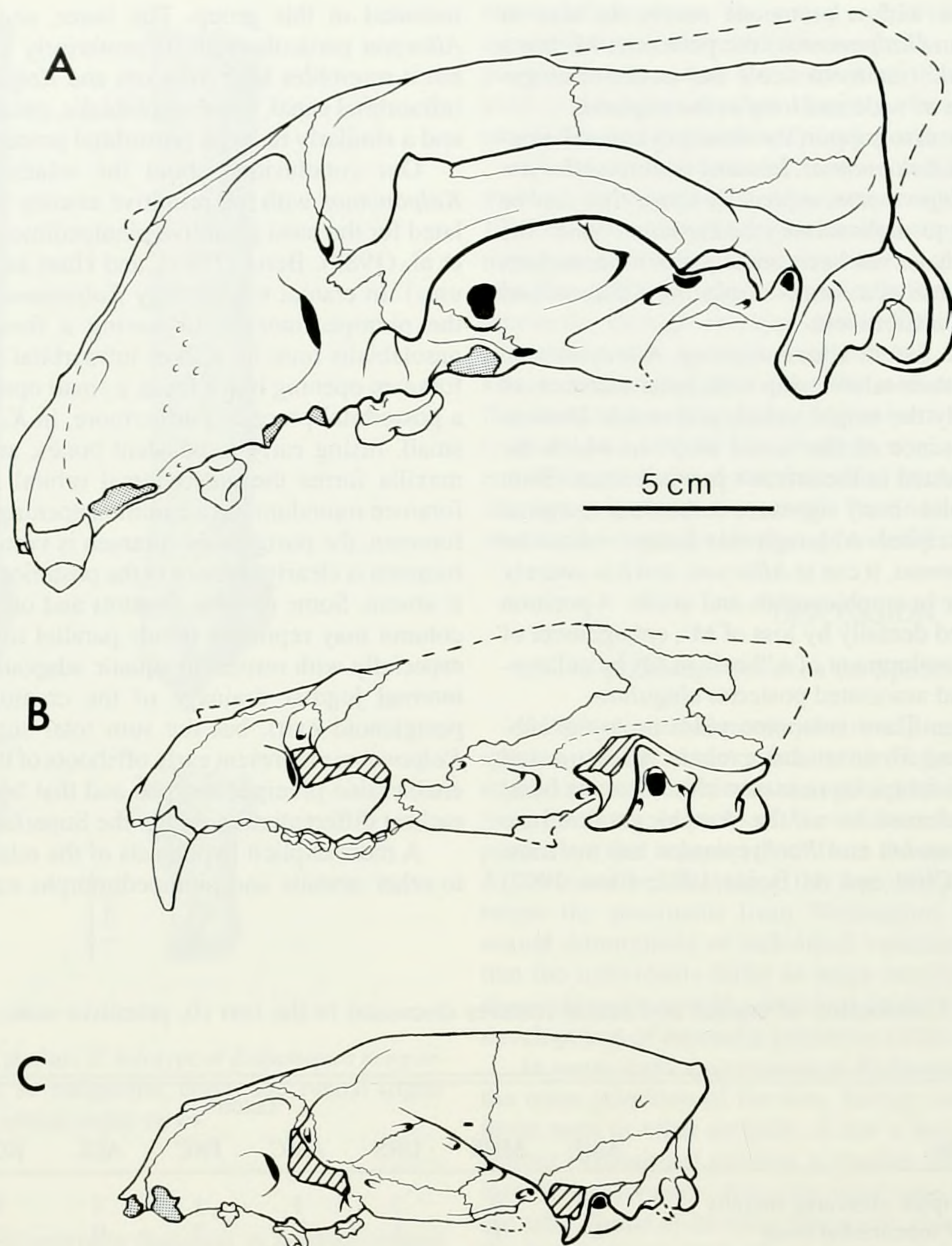
Figure 13. Comparative outline drawings of left side of crania. A, *Kolponomos clallamensis* Stirton, 1960, referred, LACM 131148; B, *Allocyon loganensis* Merriam, 1930, holotype, UCMP 24106, from Merriam (1930: fig. 1); C, *Pachycynodon boriei* (Filhol, 1877), holotype, from Filhol (1877: fig. 59).

sister taxon, the Mustelida (Procyonidae + Mustelidae), and a basal arctoid group, the Amphicyonidae, as outgroups. For this purpose we scored 26 of the binary characters discussed above among eight taxa (Table 3). The taxa are the Amphicyonidae (represented by *Daphoenodon*), Mustelida (represented by the archaic forms *Mustelictis*, *Amphictis*, and *Plesictis*; Schmidt-Kittler 1981), Ursidae (including the hemicyonine *Cephalogale* and the ursine *Ursus*), *Amphicynodon* (mostly *A. typicus*, BM(NH) M7491), *Pachycynodon boriei* (Filhol 1877:pl. 58–60, as *Cynodictis gryei*; Cirot 1992), *Allocyon* (Merriam 1930, UCMP 24106), *Kolponomos* (both species), and *Enaliarctos* (mostly *E. mealsi*, but also data from other species described by Berta 1991). The branch-and-bound algorithm of PAUP (2.4.1) found a single most parsimonious tree (Fig. 15) with a branch length of 36, a consistency index of 0.72, and a retention index of 0.73. Further explanation of the characters used as synapomorphies are as follows:

1. *Basioccipital deeply excavated laterally.*—As Hunt (1977) has shown in living ursids, the large inferior petrosal sinus containing the intracranial loop of the internal carotid artery lies in a deep excavation in the lateral margin of the basioccipital that extends to the posterior lacerate foramen. A morphologically identical structure occurs in the amphicyonids (including the daphoenines), implying a similar vascular pathway and a synapomorphy for the Arctoidea. Amphicynodontids and pinnipedimorphs (*Enaliarctos*; Hunt and Barnes 1994, this volume) retain this feature. Derived pinnipeds and members of the Mustelida lack it.

2. *Shallow suprameatal fossa present.*—All arctoids above the Amphicyonidae show a suprameatal fossa that may be later transformed into a deep pit in the squamosal dorsal to the external auditory meatus or may exist as shallow structures floored by the auditory tube and obliterated in ontogeny by fusion with the meatus (Schmidt-Kittler 1981). A small shallow fossa excavated dorso-
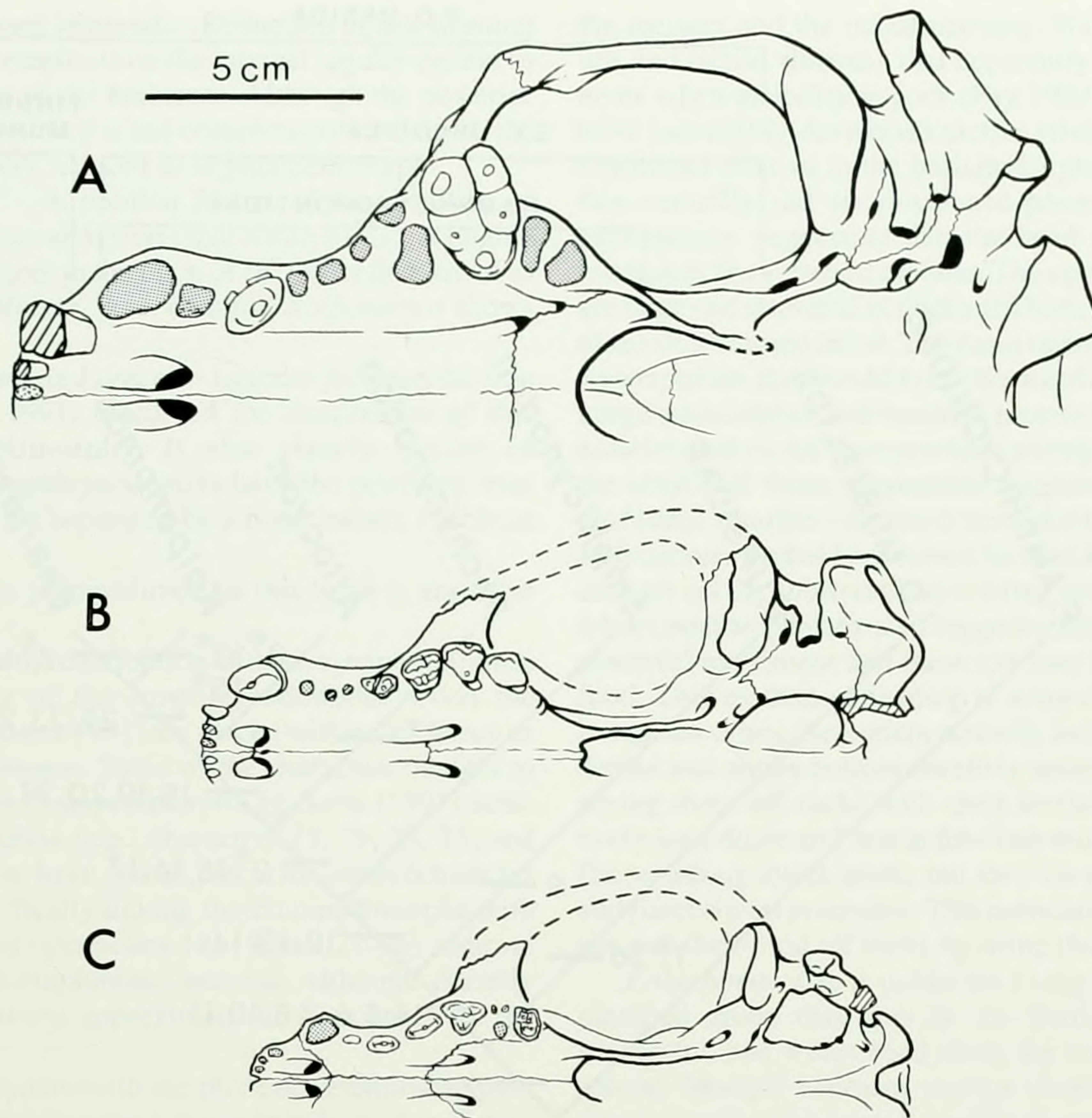
Figure 14. Comparative outline drawings of ventral side of crania. A, *Kolponomos clallamensis* Stirton, 1960, referred, LACM 131148; B, *Allocyon loganensis* Merriam, 1930, holotype, UCMP 24106, from Merriam (1930: fig. 3); C, *Pachycynodon boriei* (Filhol, 1877), holotype, from Filhol (1877: fig. 60).

posteriorly into the squamosal contribution to the mastoid process seems to be the most primitive state of this feature. In ursids and amphicynodontids this structure is shallow primitively and is lost in derived taxa rather than being obliterated by growth of the tubular external auditory meatus.

3. *M^3 absent.*—A feature uniting all arctoids above the Amphicyonidae.

4. *Basioccipital wide posteriorly.*—The greater width of the basioccipital across the posterior lacerate foramen versus its width at the basisphenoid suture is a derived feature of ursids and higher arctoids. This feature was cited by Wyss (1987) as a pinniped synapomorphy, later modified by Berta (1991: table 7, no. 44) to indicate the short and wide basioccipital that describes the condition of pinnipeds above the Otariidae.

5. *Fourth upper premolar with large protocone.*—All ursoids have an upper carnassial with a broad protocone that is usually shelflike because of incorporation of the lingual cingulum. Further enlargement of this cusp in *Kolponomos* relative to the labial cusps is an autapomorphy that serves to "molarize" the carnassial.

6. *Second upper molar with "heel."*—All ursoids have an M^2 that differs from the tribosphenic form of that of other arctoids by the posterior shelf or "heel" formed by a well-developed posterior cingulum, often incorporating the metaconule. This appears to be the case in *Kolponomos* and probably *Allocyon*. Although the M^2 of *Enaliarctos* is very reduced it seems to include a shelflike heel behind the trigon (as in *E. emlongi*; Berta 1991) and so is coded as

derived in this feature.

7. *Reduction and loss of parastyle on M^{1-2}.*—Early parastyle reduction and loss is a feature of ursines and hemicyonines. Amphicynodontids lost this cusp later in phylogeny as similarly hypocarnivorous forms (e.g., *Pachycynodon*) arose.

8. *Reduction and loss of paraconule on M^{1-2}.*—Full loss of the paraconule took place at different times in the ursine, hemicyonine, and amphicynodontid lineages, but reduction in the size of this cusp characterizes the early members of all groups. Curiously, *Kolponomos* retains this cusp, inflated like all the molar cusps, to form the broad grinding surface as in another molluscivore, *Enhydra*.

9. *Lingual position of M^1 metaconule.*—The ursid metaconule is strongly connected to the longitudinally elongated protocone in M^1 (and M^2). It has lost its primitive connection with the metacone and occupies a more lingual position on the crown (Cirot and de Bonis 1992). *Amphicynodon* retains a primitively labial position of the M^1 metaconule but this cusp is large and well connected to the protocone by a crista. *Kolponomos* also retains a primitive tribosphenic form of M^1 but all cusps are inflated and lack connecting cristae.

10. *Reduction of paraconid of M_2.*—Modification of M_2 in ursoids involves enlargement of the talonid relative to the trigonid. Reduction and loss of the paraconid accompanies attainment of subequal size of the metaconid and protoconid and their assumption of a more transverse relationship. Again, *Kolponomos* appears to retain a paraconid in its large M_2 trigonid.
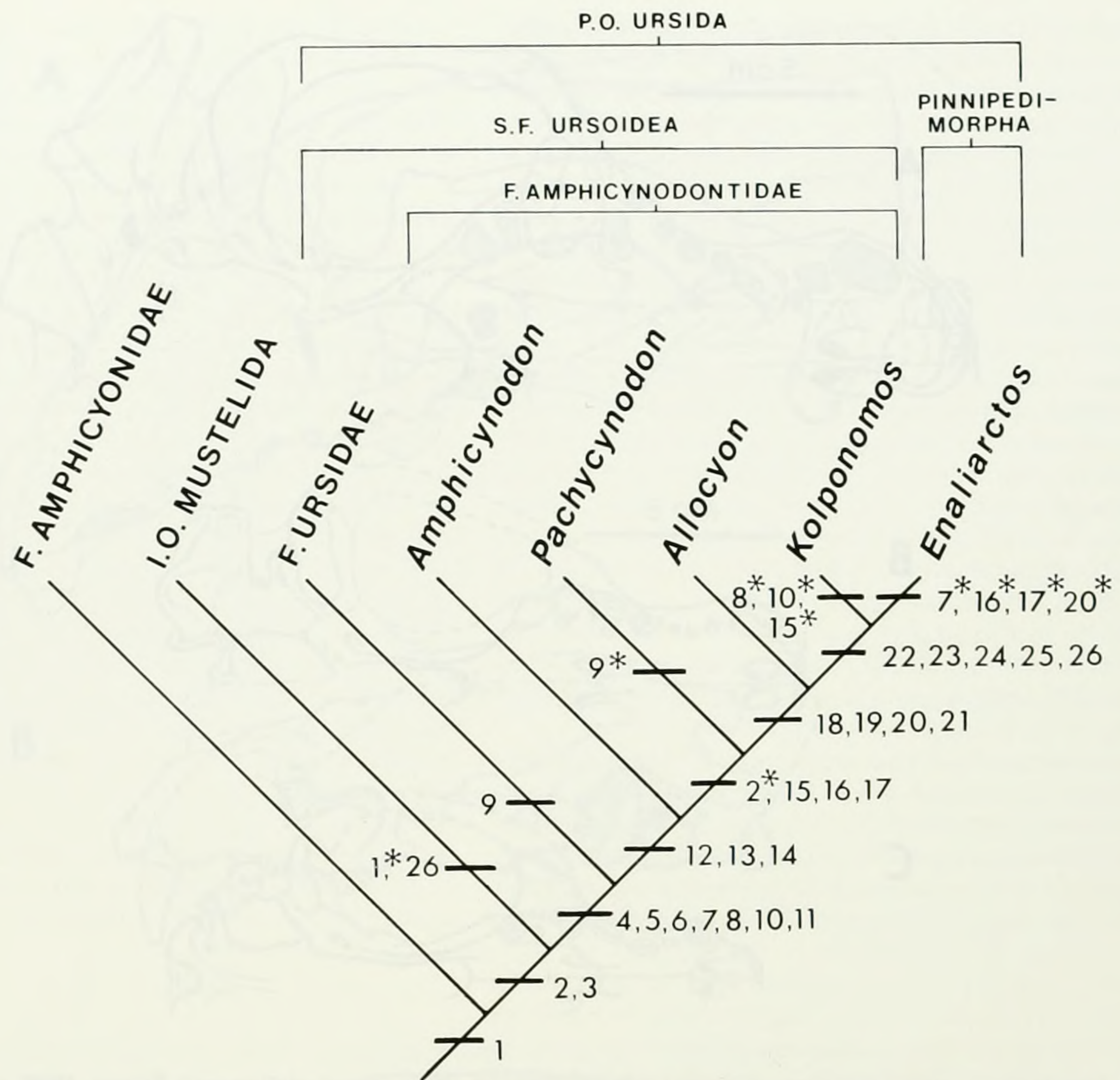
Figure 15. Phyletic relationships of taxa discussed in the text. For character numbers see text and Table 3. Asterisks indicate reversal to primitive state.

11. *Size of metaconid equal to protoconid on M₂.*—The reduction of the trigonid relative to the talonid in the M_2 of ursids and amphicynodontids involves enlargement of the metaconid to the same size as the protoconid.

12. *Infraorbital canal short.*—The distance from the anterior edge of the orbit to the opening of the canal is unusually abbreviated in the amphicynodontid ursoids and pinnipedimorphs.

13. *Infraorbital foramen large.*—Amphicynodontid ursoids and pinnipedimorphs also have a very large anterior opening of the short infraorbital canal.

14. *Metastyle of P⁴ short.*—In a trend toward hypocarnivory the amphicynodontids shorten the carnassial blade by reduction of the metastyle.

15. *Palate posteriorly extended.*—The palate is prolonged in the midline by posterior extension of the palatine bones so that the internal nares lie at a considerable distance behind the tooth row. This condition is derived in the Ursoidea but has an independent distribution that implies some homoplasy (i.e., it is present in the Ursinae and some amphicynodontids but not in *Kolponomos* or pinnipedimorphs generally).

16. *M₁ talonid as wide as or wider than trigonid.*—Corresponding to modification of the M¹ talon (character 9), amphicynodontids enlarge the talonid of the lower carnassial to accommodate the longitudinal protocone and associated metaconule of M¹.

17. *M₁ metaconid large.*—Modification of the M₁ trigonid more for crushing in derived amphicynodontids involved enlargement of the metaconid relative to surrounding cusps. In volume it comes to match the paraconid and is nearly as high in the unworn crown as the protoconid.

18. *Nasolabialis fossa present.*—A prominent fossa just dorsoanterior to the orbital rim, presumably for the nasolabialis muscle, is a derived condition in *Allocyon, Kolponomos,* and primitive pinnipedimorphs. From the perspective of pinniped evolution Berta (1991) coded the loss of this feature in pinnipeds as derived, i.e., a reversal to the primitive arctoid state.

19. *Infraorbital fossa present.*—This broad depression lies just anterior to the opening of the infraorbital canal onto the face. It is not correlated with the large foramen of amphicynodontids but characterizes *Allocyon, Kolponomos,* and pinnipedimorphs.

20. *Mastoid process hypertrophied.*—This is a synapomorphy for *Allocyon* and *Kolponomos*, although the latter has greatly elongated the process ventrally. The massive backward-pointing paroccipital process in *Allocyon* is an autapomorphy for that genus.

21. *Postorbital process lacking.*—In contrast to other arctoids, in *Allocyon* and *Kolponomos* the postorbital processes of the frontals are lacking. Low supraorbital ridges at the anterior ends of the parasagittal crests represent the position of the processes in these genera and in primitive pinnipedimorphs (Berta 1991).

22. *Alisphenoid "strut" present.*—A reinforced region extends from the palatine process of the alisphenoid dorsoanteriorly to a correspondingly reinforced pterygoid process of the palatine. These elements combine to form a strut bracing the posterior part of the palate against the braincase. Such a structure is present in *Kolponomos* and pinnipedimorphs.

23. *Postglenoid foramen vestigial.*—Reduction of this opening is correlated with greater emphasis on the internal jugular system as the main venous drainage of the braincase. Although the posterior lacerate foramen in *Kolponomos* is not conspicuously enlarged, the postglenoid foramen is very reduced as in pinnipedimorphs.

24. M^2 *lingual to* M^1.—A peculiar feature of the dentition of pinnipedimorphs (and *Potamotherium*) that retain M^2 is the lingual position of this tooth adjacent to the talon of M^1 rather than labial as in most carnivores (M. Wolsan, pers. comm.). *Kolponomos* shows this feature.

25. *Foramen rotundum and anterior lacerate foramen lie in a common fossa.*—Berta (1991) discussed the distribution of this pinnipedimorph synapomorphy. It also clearly occurs in *Kolponomos*, but other amphicynodontids have the primitive state in which these foramina are separated by a bony lamina visible in lateral view of the skull.

26. M_3 *absent.*—As in pinnipedimorphs this tooth is absent in *Kolponomos*.

Figure 15 summarizes the distribution of these synapomorphies, indicating the paraphyly of the Amphicynodontidae when the Pinnipedimorpha (sensu Berta 1991) are placed within this group as the sister taxon of *Kolponomos*. Some of the characters thought to be synapomorphies of the Pinnipedimorpha by Berta (1991) actually have a wider distribution (e.g., characters 13, 21, 23, 25, and 26) within the Ursoidea or have ursoid precursor states (character 4). Synapomorphies specifically linking the Pinnipedimorpha with *Allocyon* and *Kolponomos* (characters 18, 19, and 21–26) indicate that these terrestrial and amphibious arctoids, although dentally specialized for hypocarnivory, approximate the stem group for the pinnipedimorphs.

A classification consonant with the phyletic relationship postulated for the carnivorans discussed above is indicated in Figure 15. The Pinnipedimorpha were not ranked by Berta (1991) and are so indicated on Figure 15 as an unranked taxon within the parvorder Ursida of Tedford (1976). Since the traditional "suborder" Pinnipedia is subsumed in the Pinnipedimorpha it too must remain unranked in the present attempt to construct a taxonomy that expresses the phylogenetic conclusions of this paper.

Speculations About the Mode of Life of *Kolponomos*

The few postcranial bones presently known indicate that *Kolponomos* was not fully aquatic, at least in the sense that the pinnipeds are. Its foot bones clearly indicate retention of significant ability for terrestrial locomotion and an amphibious existence. It was probably littoral in distribution. All known specimens are from near-shore, shallow-water marine deposits that contain abundant fossil mollusks, including large mussels and giant pectinids. The broad, sea-otterlike crushing cheek teeth would have been ideally suited to a diet of hard-shelled marine invertebrates. The teeth are well worn, indicating that the diet included very hard-shelled animals, possibly mussels, limpets, abalone, pectinids, and echinoids. Coupled with accidentally ingested abrasive sediment, these would account for the heavily worn condition of the cheek teeth. The orbits are directed anteriorly rather than laterally as in living bears, suggesting that *Kolponomos* probably could view objects directly in front of its head. This would be of benefit to an animal selectively eating rock-dwelling benthic or attached (sessile) marine invertebrates. The infraorbital foramen is large, quite so in *K. clallamensis*, and the mental foramina on the lateral side of the dentary of *K. newportensis* are also large. These probably indicate enhanced tactile sensitivity of the lips and muzzle. *Kolponomos* might also have had a large upper lip approaching that in living walruses, and this would be concomitant with the depth of the premaxilla between the incisors and the narial opening. Walruses have very sensitive lips and tactile vibrissae that apparently aid in distinguishing prey items when visibility is poor (Fay 1982). *Kolponomos* might also have had highly developed tactile vibrissae. The palate is flexed downward relative to the basicranial plane; the occipital condyles face ventrally and are positioned posteroventrally relative to the basicranium, suggesting that the head was carried downward in relation to the vertebral column. The upper canine and incisor teeth are large and clustered in thickened bone at the extreme anterior end of the downturned snout. The nasal opening is retracted posteriorly, an adaptation that would keep the nostrils away from the substrate. Large paroccipital and mastoid processes indicate powerful neck muscles that could have provided strong downward movements of the skull. All these adaptations suggest that *Kolponomos* fed on epifaunal marine invertebrates living on rocky substrates. *Kolponomos* probably obtained its food by levering tightly clinging animals off the substrate and twisting and prying with its head. The robust median phalanx also suggests that the digits were capable of powerful movement and these too may have been used to procure food. This method of feeding is somewhat different from that of living sea otters. Sea otters actively swim in shallow to moderate depths and obtain bottom-dwelling animals, largely by pulling and prying them off rocks with their forelimbs. Sea otters have relatively long digits and strong forelimb musculature. They have large, flat, crushing cheek teeth, but they do not have enlarged mastoid and paroccipital processes. This correlates with the fact that they do not pull their food off rocks by using their heads.

Kolponomos also is unlike the living walrus, which belongs to a pinniped group that later in the Tertiary became very diverse, successful, and widespread along the coasts of the northern hemisphere. Modern walruses occupy shorelines, at least part of the time, when they haul out at specific locations along the shore. When feeding, however, they are offshore, diving pinnipeds. They typically dive only to shallow or moderate depths, where they exploit food resources for the most part different from those of other pinnipeds, mostly benthic shelled and nonshelled invertebrates. They do not crush mollusk shells by chewing (Fay 1982) but rather use the tongue in a pistonlike method to suck the soft parts out of gaping bivalve shells. They also use the tongue as a piston to direct a jet of water from the mouth onto the substrate in a method of hydraulic mining of infaunal prey. Walruses do not chew up shells of their prey and they do not swallow shells or broken shells, so, although the general category of food of walruses is the same as that proposed for *Kolponomos*, the locating of the food and manner of gathering and eating it is apparently different.

The specialized dusignathine otariid *Gomphotaria pugnax* may be a relatively close functional counterpart to *Kolponomos*. This large pinniped is known from upper Miocene rocks of the California coast. Like *Kolponomos*, *Gomphotaria* had elongated upper as well as lower canines, even more fully developed as tusks. Also like *Kolponomos*, *Gomphotaria* had large cheek teeth, which although not expanded transversely were broken and worn during life from feeding on resistant prey. Barnes and Raschke (1991) proposed that *Gomphotaria* was a shallow-water or littoral pinniped that pried its food off rocks, the food presumably being shelled mollusks as we have postulated for *Kolponomos*, and that rather than sucking its food into the mouth it crushed the animals with the cheek teeth.

Kolponomos appears to be an ursid variation on the sea otter adaptation. On the west coast of North America, middle and upper Miocene horizons bearing fossil marine vertebrates have been extensively prospected, much more extensively than have the lower Miocene deposits. Nothing related to *Kolponomos* has as yet been found in these younger deposits. *Kolponomos* might very well be the end of its lineage.

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LITERATURE CITED

Addicott, W.O. 1976a. Neogene molluscan stages of Oregon and Washington. Pp. 95–115 *in* A. E. Fritsche, H. Ter Best, Jr., and W. W. Wornardt (eds.). The Neogene Symposium. Society of Economic Paleontologists and Mineralogists (Annual Meeting, Pacific Section), San Francisco, California.

———. 1976b. New molluscan assemblages from the Upper Member of the Twin River Formation, western Washington: Significance in Neogene chronostratigraphy. United States Geological Survey Journal of Research 4:437–447.

———. 1976c. Molluscan paleontology of the lower Miocene Clallam Formation, northwestern Washington. United States Geological Survey Professional Paper 976.

Armentrout, J. M., D. A. Hull, J. D. Beaulieu, and W. W. Rau (eds.). 1983. Correlation of Cenozoic stratigraphic units of western Oregon and Washington. Oregon Department of Geology and Mineral Industries Oil and Gas Investigations 7, Portland, Oregon.

Barnes, L. G. 1987. *Aetiocetus* and *Chonecetus*, primitive Oligocene toothed mysticetes and the origin of baleen whales. Journal of Vertebrate Paleontology 7 (3) supplement:10A.

———. 1989. *Aetiocetus* and *Chonecetus* (Mammalia: Cetacea); primitive Oligocene toothed mysticetes and the origin of baleen whales. Abstracts of Posters and Papers, Fifth International Theriological Congress, Rome, Italy, 22–29 August 1989, 1:479.

———, and R. E. Raschke. 1991. *Gomphotaria pugnax*, a new genus and species of late Miocene dusignathine otariid pinniped (Mammalia: Carnivora) from California. Natural History Museum of Los Angeles County Contributions in Science 426.

———, D. P. Domning, and C. E. Ray 1985. Status of studies on fossil marine mammals. Marine Mammal Science 1:15–53.

Berta, A. 1991. New *Enaliarctos** (Pinnipedimorpha) from the Oligocene and Miocene of Oregon and the role of "enaliarctids" in pinniped phylogeny. Smithsonian Contributions to Paleobiology 69.

Carroll, R. L. 1988. Vertebrate Paleontology and Evolution, W. H. Freeman, New York, New York.

Cirot, E. 1992. Etude phylogénétique de quelques genres d'Arctoidea de l'Oligocène eurasiatique. Comparaison des données morphologiques et moléculaires. Ph.D. Dissertation, Faculté des Sciences Fondamentales et Appliquées de Poitiers, Poitiers, France.

———, and L. de Bonis, 1992. Revision du genre *Amphicynodon*, carnivore de l'Oligocène. Palaeontographica, Pt. A, 220:103–130.

Dalrymple, B. 1979. Critical tables for conversion of K–Ar ages from old to new constants. Geology 7:558–560.

Domning, D. P., C. E. Ray, and M. C. McKenna. 1986. Two new Oligocene desmostylians and a discussion of tethytherian systematics. Smithsonian Contributions to Paleobiology 59.

Fay, F. H. 1982. Ecology and behavior of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. North American Fauna 74.

Feldmann, R. M., A. B. Tucker, and R. E. Berglund. 1991. Fossil crustaceans, paleobathymetry and decapod crustaceans, Washington. National Geographic Research and Exploration 7:352–363.

Flynn, J. J., N. A. Neff, and R. H. Tedford. 1988. Phylogeny of the Carnivora. Pp. 73–116 *in* M. J. Benton (ed.). The Phylogeny and Classification of the Tetrapods, vol. 2. Systematics Association Special Volume 35B. Clarendon Press, Oxford, England.

Hunt, R. M., Jr. 1977. Basicranial anatomy of *Cynelos* Jourdan (Mammalia: Carnivora), an Aquitanian amphicyonid from the Allier Basin, France. Journal of Paleontology 51:826–843.

———, and L. G. Barnes. 1994. Basicranial evidence for ursid affinity of the oldest pinnipeds, *in* A. Berta and T. A. Deméré (eds.) Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History 29:57–68.

Merriam, C. W. 1930. *Allocyon*, a new canid genus from the John Day beds of Oregon. University of California Publications, Bulletin of the Department of Geological Sciences 19:229–244.

Moore, E. J., and W. O. Addicott. 1987. The Miocene Pillarian and Newportian (Molluscan) stages of Washington and Oregon and their usefulness in correlations from Alaska to California. United States Geological Survey Bulletin 1664A.

Olson, S. L. 1980. A new genus of penguin-like pelecaniform bird from the Oligocene of Washington (Pelecaniformes: Plotopteridae). Natural History Museum of Los Angeles County Contributions in Science 382.

Piveteau, J. 1961. Mammifères: Origine reptilienne, evolution. Traité de Paléontologie 6:1–1138.

Rau, W. W. 1964. Foraminifera from the northern Olympic Peninsula, Washington. United States Geological Survey Professional Paper 374-G.

Ray, C. E., D. P. Domning, and M. C. McKenna. 1994. A new specimen of *Behemotops proteus* (order Desmostylia) from the marine Oligocene of Washington, *in* A. Berta and T. A. Deméré (eds.) Contributions in marine mammal paleontology honoring Frank C. Whitmore, Jr. Proceedings of the San Diego Society of Natural History 29:207–224.

Romer, A. S. 1966. Vertebrate Paleontology. University of Chicago Press, Chicago, Illinois.

Schmidt-Kittler, N. 1981. Zur stammesgeschicte der marderverwandten Raubtiergruppen (Musteloidea, Carnivora). Eclogae Geologicae Helvetiae 74:753–801.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85:1–350.

Snavely, P. D., Jr. 1983. Peripheral rocks: Tertiary geology of the northwestern part of the Olympic Peninsula, Washington. Geological Association of Canada, Victoria, British Columbia. Field Trip Guidebook 12:6–31.

———, A. R. Niem, N. S. MacLeod, J. E. Pearl, and W. W. Rau. 1980. Makah Formation—a deep-marginal-basin sequence of Late Eocene and Oligocene age in the northwestern Olympic Peninsula, Washington. United States Geological Survey Professional Paper 1162-B.

Stirton, R. A. 1960. A marine carnivore from the Clallam Miocene Formation, Washington. Its correlation with nonmarine faunas. University of California Publications in Geological Sciences 36:345–368.

Tabor, R. W., and W. M. Cady. 1978. Geologic map of the Olympic Peninsula, Washington. United States Geological Survey Miscellaneous Investigations Series Map I-994.

Tedford, R. H. 1977. Relationships of pinnipeds to other carnivores (Mammalia). Systematic Zoology 25 (for 1976):363–374.

Thenius, E. 1969. Stammesgeschichte der Säugethiere (Einschliesslich der Hominiden). Handbuch der Zoologie, Band 8, Teil 2, Vol. 1:1–368.

Wyss, A. R., 1987. The walrus auditory region and the monophyly of pinnipeds. American Museum Novitates 2871.