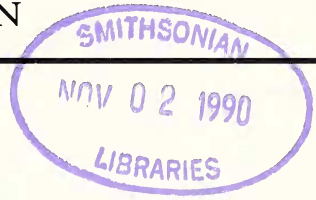


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# A NEW MIOCENE ENALIARCTINE PINNIPED OF THE GENUS *PTERONARCTOS* (MAMMALIA: OTARIIDAE) FROM THE ASTORIA FORMATION, OREGON

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**ABSTRACT.** The eastern North Pacific fossil otariid pinniped genus *Pteronarctos* Barnes, 1989, includes the geologically youngest known species in the subfamily Enaliarctinae and is close to the ancestry of modern sea lions and fur seals of the otariid subfamily Otariinae. The type species of *Pteronarctos*, *P. goedertae* Barnes, 1989, known only from the basal part of the late Early Miocene to early Middle Miocene age Astoria Formation in coastal Oregon, is late Early Miocene in age (circa 19 million years old). Recently discovered fossil crania from higher in the same formation document a new species of *Pteronarctos*, *P. piersoni*, of early Middle Miocene age (circa 16 million years old). Because *Pteronarctos piersoni* has more primitive cranial morphology than the earlier *P. goedertae*, it could not have evolved from the latter species. There must be at least two lineages of *Pteronarctos* represented by fossils in the Astoria Formation, and the genus must have had a significant prior evolutionary history.

## INTRODUCTION

Fossiliferous outcrops of Tertiary marine sediments along the central Oregon coast continue to yield important new pinniped fossils. From such deposits, I have described the late Early Miocene *Pteronarctos goedertae* as a new genus and species of derived enaliarctine pinniped, a member of the family Otariidae, apparently near the ancestry of modern fur seals and sea lions of the subfamily Otariinae (Barnes, 1989). This discovery modified previous ideas (see Repenning and Tedford, 1977; Barnes, 1979) that the geochronologically older earliest Miocene (24 to 25 million years (Ma) old) *Enaliarctos mealsi* Mitchell and Tedford, 1973, from southern California was a likely ancestor of the otariines. The fossil cranium of *Pteronarctos goedertae* was discovered in strata about 19 Ma old near the base of the Astoria Formation near Newport, Oregon. This was the first pinniped taxon to have been named from coastal Oregon since Condon (1906) described *Desmatophoca oregonensis*.

The otariid subfamily Enaliarctinae, to which I assigned *Pteronarctos*, was originally named to contain *Enaliarctos mealsi* from Kern County, California. Other specimens and taxa of enaliarctines were subsequently described (Barnes, 1979), but prior to the discovery of *Pteronarctos goedertae* from coastal Oregon, the entire published record of the subfamily had been based on California fos-

sils, principally on specimens from the earliest Miocene age Pyramid Hill Sand Member of the Jewett Sand in Kern County (Mitchell and Tedford, 1973; Barnes, 1979). For a review of my classification of otariid pinnipeds, the reader is referred to Barnes (1989).

The present article describes recently acquired fossil crania from coastal Oregon that represent a second species of *Pteronarctos*, *P. piersoni*, new species. These fossils were discovered at a higher stratigraphic level in the Astoria Formation and at a locality farther north along the coast than the type locality of *P. goedertae*. The new species is from the early Middle Miocene part of the Astoria Formation, circa 16 Ma. Because the new species and *P. goedertae* are based on virtually complete crania, all known characters used to define the two species are directly comparable.

## METHODS AND MATERIALS

Both crania of *Pteronarctos piersoni* were found in indurated calcareous sandstone concretions. The bulk of the matrix was removed from both specimens using rock-cutting saws and pneumatic chisels. Fine surface preparation was accomplished by removing the last remaining matrix from the bone using formic acid. When laboratory preparation revealed all of the critical structures in the left orbit of each specimen, it was decided not to remove the matrix filling the right orbit.

Anatomical terminology used here is adapted from that of Howell (1928), Miller, Christensen, and Evans (1964), Mitchell (1966, 1968), Hershkovitz (1971), Mitchell and Tedford (1973), Barnes (1972, 1979), and Repenning and Tedford (1977). Character polarity (primitive versus derived) was determined based on comparisons using primitive or generalized fissiped carnivores (especially canids

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and amphicyonodontine ursids) as outgroups. Indications of what are commonly considered to be derived cranial characters among otariids may be obtained by consulting Howell (1928), Mitchell and Tedford (1973), Tedford (1976), Repenning and Tedford (1977), and Barnes (1979, 1989).

The suture ages of crania, calculated following the methods of Sivertsen (1954), are relative ages and not necessarily the same as ages in years. To determine a suture age, the extent of ontogenetic closure of each of nine cranial sutures is rather subjectively graded on a scale of 1 to 4 (from open to completely closed), then the scores of these nine sutures are added together to yield a relative individual age. This method is useful for comparing the relative individual ages of specimens for which teeth have not been sectioned to reveal annual growth layers.

I have identified which cranial measurements in Table 1 are the same as those that were defined by Sivertsen (1954:18–20) by appending to them the numbers that were given them by Sivertsen. Other measurements are as defined by Barnes (1972:fig.1; 1979:4–5). Crushing of the paratype cranium necessitated omitting some measurements in Table 1.

Geologic ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979), following the revised radiometric scale of Dalrymple (1979) and the correlations proposed by Armentrout (1981). Millions of years is abbreviated Ma. The acronym LACM is for the Natural History Museum of Los Angeles County, Los Angeles, California.

The crania were coated with a sublimate of ammonium chloride for photography. Cranial restorations are based primarily on the holotype of *P. piersoni*, supplemented by the paratype. The braincase of the holotype cranium is crushed by a few mm dorsoventrally, and the restorations (Figs. 3, 6, 9) compensate for this. Anatomical abbreviations in the illustrations are as follows:

- ac—alisphenoid canal (posterior aperture)
- at—auditory tube (= musculotubular canal, including Eustachian tube)
- Bo—basioccipital
- Bs—basisphenoid
- cc—carotid canal
- eam—external acoustic meatus
- fh—hypoglossal foramen
- fi—incisive foramen (= palatine fissure)
- fio—infraorbital foramen
- fl—lacrimal foramen
- fla—anterior lacerate foramen (joined with foramen rotundum as an orbital fissure)
- flp—posterior lacerate foramen
- fo—foramen ovale
- fop—optic foramen
- fpal—palatine foramen
- fpg—postglenoid foramen
- Fr—frontal
- fs—sphenopalatine foramen
- fsm—styломastoid foramen
- g—glenoid fossa
- hf—tympanohyal pit (= hyoid fossa)
- Ju—jugal
- mp—mastoid process
- Mx—maxilla
- Na—nasal
- nf—nasolabialis fossa
- Oc—occipital
- occ—occipital condyle
- Pa—parietal

- Pal—palatine
- Pmx—premaxilla
- pp—paroccipital (= jugular) process
- Ps—presphenoid
- Pt—pterygoid
- sop—supraorbital process
- sp—fossa corresponding to pseudosylvian sulcus of brain
- Sq—squamosal
- tb—tympanic bulla

## SYSTEMATICS

- Class Mammalia Linnaeus, 1758
- Order Carnivora Bowdich, 1821
- Infraorder Arctoidea Flower, 1869
- Parvorder Ursida Tedford, 1976
- Family Otariidae Gill, 1866
- Subfamily Enaliarctinae  
Mitchell and Tedford, 1973
- Pteronarctos* Barnes, 1989

**TYPE SPECIES.** *Pteronarctos goedertae* Barnes, 1989.

**INCLUDED SPECIES.** *Pteronarctos goedertae* Barnes, 1989, late Early Miocene, Oregon; and *P. piersoni*, new species, early Middle Miocene, Oregon.

### *Pteronarctos piersoni*, new species

Figures 1–9, 10a, 11a, 12a

**DIAGNOSIS OF SPECIES.** A species of *Pteronarctos* differing from *P. goedertae* by having cranium with rostrum deeper dorsoventrally, nasolabialis fossa deeper and more distinct, anterior ends of nasal bones less deeply emarginated (= more concave), dorsal surface of rostrum anteroventrally sloping, ascending (nasal) process of premaxilla shorter and transversely broader, infraorbital foramen of larger diameter, zygomatic arch more bowed dorsally, pterygoid process of palatine smaller, bony palate shorter, auditory region (including tympanic bulla and petrosal) located farther posteriorly on basicranium (indicated by styloform process of bulla, lateral to anterior end of auditory tube, extending only as far anteriorly as the anterior border of the postglenoid process), tympanic bulla smaller, mastoid process relatively thicker antero-posteriorly, crest between mastoid process and paroccipital process thicker, occipital condyles projecting farther and more prominently from occipital shield, canine crown more vertically oriented, cheek tooth rows more laterally bowed, and posterior root of M<sup>1</sup> distinctly bilobed instead of nearly circular.

**HOLOTYPE.** LACM 127972, complete cranium with canines, collected by Guy E. Pierson, 2 April 1983.

**TYPE LOCALITY.** LACM 4851, among loose boulders on Moolack Beach between the mouths of Schooner Creek and Moolack Creek, Lincoln County, Oregon. (Moolack is the locally used spell-

ing of the names of both the beach and the creek, although both are shown as Moloch on the U.S. Geological Survey, Yaquina, Oregon, 15 minute topographic map, 1959 edition.)

**PARATYPE.** LACM 128002, complete cranium with left P<sup>4</sup>; from LACM locality 4850, found among loose boulders on the beach on the north flank of Schooner Point, just north of the mouth of Schooner Creek, Lincoln County, Oregon; collected by Guy E. Pierson, 11 November 1985.

**FORMATION AND AGE.** The strata that yielded both the holotype and paratype of *Pteronarctos piersoni* are part of a stratigraphic section that has been referred to the Astoria Formation and are early Middle Miocene in age and approximately 16 Ma old. They represent the Newportian Molluscan Stage and are correlated with the Hemingfordian North American Land Mammal Age.

The name Astoria Formation was originally proposed for late Early Miocene rocks exposed farther north, at Astoria, Oregon, on the south side of the Columbia River, and the formation name has been subsequently applied to the slightly younger strata of late Early Miocene to early Middle Miocene age that were deposited in the Newport Embayment along the coast of Oregon (Howe, 1926; Packard and Kellogg, 1934; Ray, 1976:fig. 2; Colbath, 1985: 849). The Astoria Formation is the only Tertiary age rock unit that crops out in the sea cliffs at Moolack Beach at the collecting localities of the holotype and paratype. The geology of this area has been discussed by Schenck (1928), Packard and Kellogg (1934:4-7), Moore (1964), and Colbath (1985). The locality where Colbath (1985) studied molluscan paleoecology is approximately 4 km north of the localities that produced *P. piersoni*.

Both specimens of *P. piersoni* were found in rounded, extremely hard, fine-grained gray concretions that typically weather out of the sea cliff at Moolack Beach from an easily recognizable concretionary horizon in the Astoria Formation that has become known as the "Iron Mountain bed" (see Munthe and Coombs, 1979:78-79; Armentrout, 1981:141 (note 29)).

The entire thickness of the Astoria Formation and its contained molluscan fauna at this part of the Oregon coast were used by Addicott (1976:102, 104, fig. 4) to characterize the Newportian Molluscan Stage (and see Armentrout, 1981). This stage, correlated with the early part of the "Temblor" provisional provincial mega-invertebrate stage as characterized by Addicott (1972) on the basis of Californian fossils and the Saucesian foraminiferal stage (Addicott, 1976; and see Moore, 1964:20-21), has also been correlated with the Hemingfordian North American Land Mammal Age and the Burdigalian Stage of Europe (see Barnes, 1989:8, and references cited therein). The same "Iron Mountain bed" that yielded the *Pteronarctos piersoni* fossils also produced the cranium of the dome-headed Hemingfordian chalicothere, *Tylocephalonyx* sp., described by Coombs (1979) and Munthe

and Coombs (1979) and estimated in the latter reference to be between 15 and 16 Ma old. The Depoe Bay Basalt, which unconformably overlies and intrudes the Astoria Formation in this area, has yielded dates originally published as  $15.2 \pm 0.6$  Ma,  $14.5 \pm 1.0$  Ma, and  $14.0 \pm 2.7$  Ma (Turner, 1970; and see Munthe and Coombs, 1979). When these dates are corrected using the factors supplied by Dalrymple (1979), the age of the Depoe Bay Basalt is still calculated at about 14.4 to 15.6 Ma, and these dates would postdate deposition of the uppermost part of the Astoria Formation. The age of the base of this section of the Astoria Formation is more difficult to estimate. Armentrout (1981:139) placed the lower boundary of the Newportian Stage (and therefore of the Astoria Formation in this area) at approximately 20 Ma. The Oregon coastal section of the Astoria Formation therefore spans from approximately 15 to 20 Ma (see Ray, 1976:fig. 2; Repenning and Tedford, 1977:table 1; Munthe and Coombs, 1979:78-79; Armentrout, 1981; Barnes, 1989). Because the holotype and paratype of *P. piersoni* are from a horizon that is stratigraphically high within the stratotype of the Newportian Stage, the age of these specimens is undoubtedly coincident with the younger parts of all of the above ages and is estimated at 16 Ma.

**ETYMOLOGY.** The species is named in honor of Mr. Guy E. Pierson of South Beach, Oregon, who collected both the holotype and paratype.

**DESCRIPTION AND COMPARISONS.** The cranium of *Pteronarctos goedertae* has been described, illustrated, and compared with those of other enaliarctines (Barnes, 1989). It is unnecessary to duplicate here the description of cranial anatomy that is identical in *P. goedertae* and the previously described enaliarctines. Therefore, I will describe the characters that differentiate *P. piersoni* from related taxa and interpret the similarities and differences.

The holotype apparently represents a young adult male (Group I of Sivertsen (1954)) based on the following observations: (1) the only cranial suture that is obliterated by fusion is the occipito-parietal, all other sutures are unfused and are readily visible because of matrix that fills them; (2) the cranium yields a suture age of at least 23 (see Table 2) by employing the methodology of Sivertsen (1954), thus placing it in the adult age class; (3) as in Recent adult male otariines, a sagittal crest is present; and (4) the canines are fully erupted but not heavily worn, with only slight wear on the apex of the right one.

The paratype apparently represents a slightly older adult male than the holotype (Group I of Sivertsen) based on the following observations: (1) suture fusion is more advanced than in the holotype, four cranial sutures are obliterated by fusion (the occipito-parietal, coronal, basioccipital-basiphenoid, and maxillary), the interparietal and premaxillary-maxillary sutures are comparatively more closed, and all other sutures are unfused and are readily visible



Figure 1. *Pteronarctos piersoni*, new species, holotype cranium, LACM 127972, from LACM locality 4851, dorsal view.



Figure 2. *Pteronarctos piersoni*, new species, paratype cranium, LACM 128002, from LACM locality 4850, dorsal view.

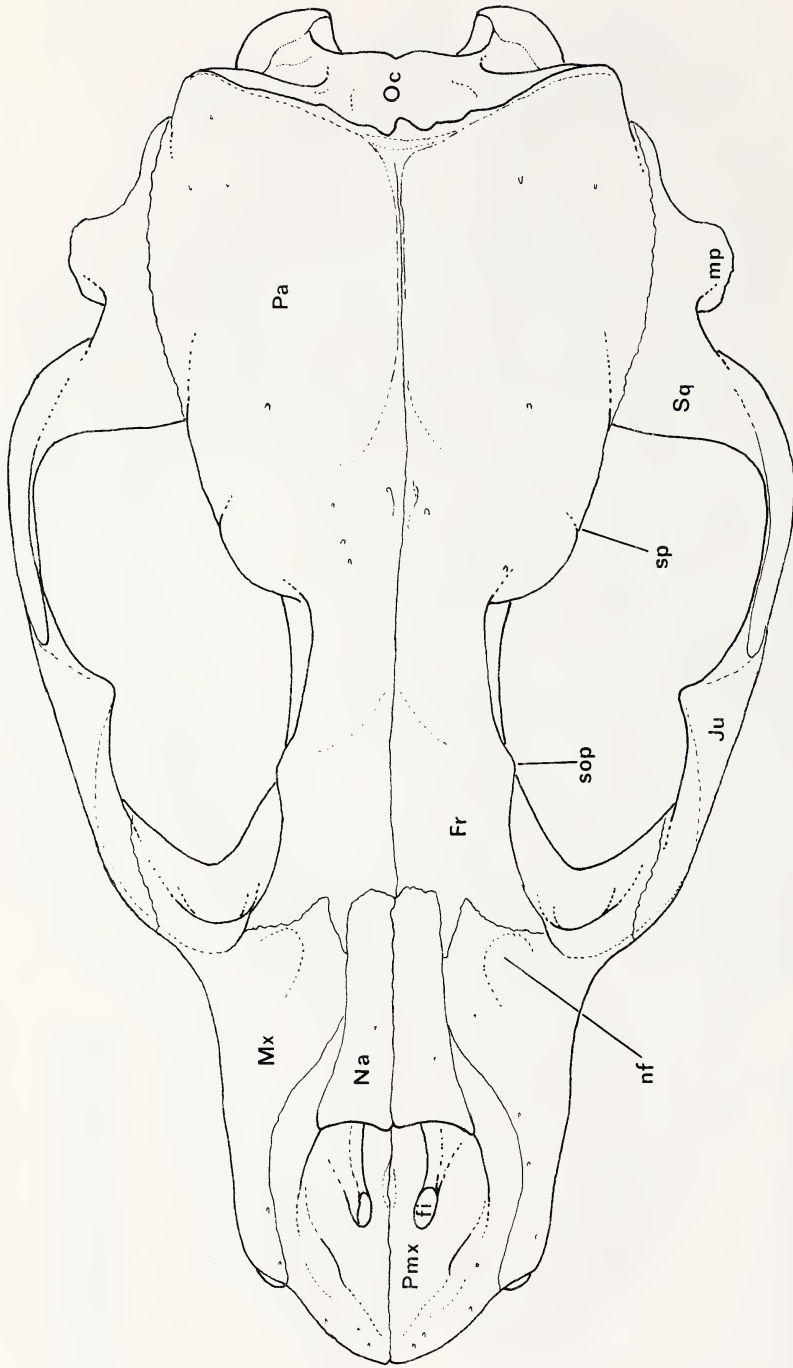


Figure 3. *Pteronarctos piersoni*, new species, restoration of cranium based on holotype and paratype, dorsal view; for explanation of abbreviations see Methods and Materials.



Figure 4. *Pteronarctos piersoni*, new species, holotype cranium, LACM 127972, from LACM locality 4851, left lateral view.



Figure 5. *Pteronarctos piersoni*, new species, paratype cranium, LACM 128002, from LACM locality 4850, left lateral view.



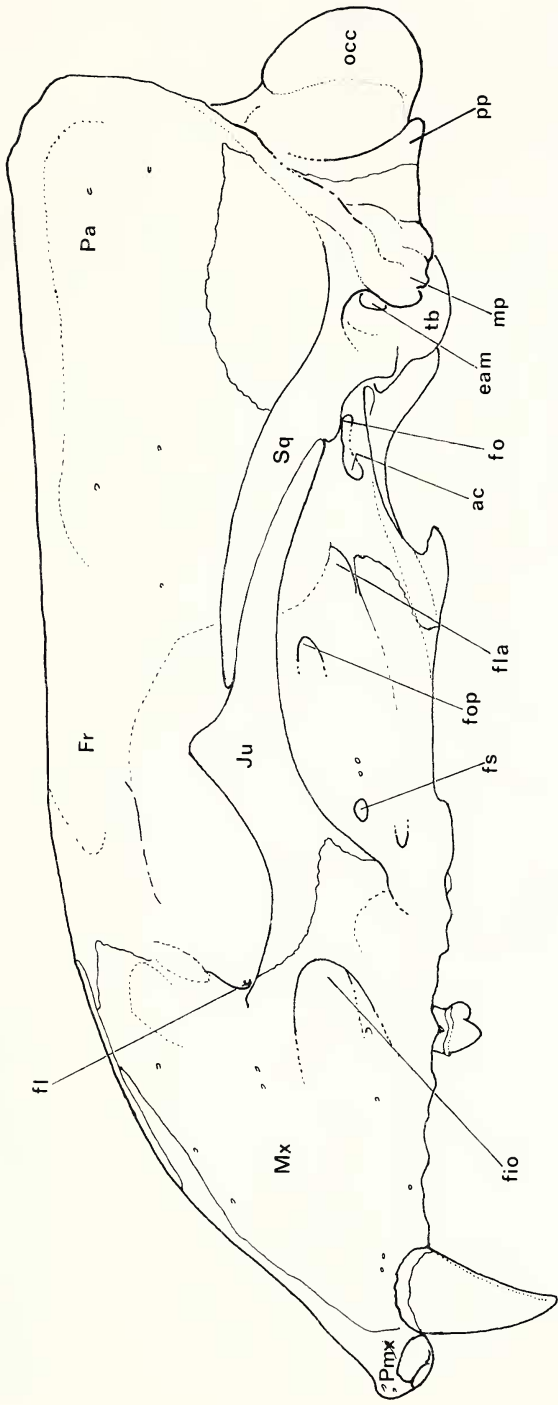


Figure 6. *Pieronarctos piersoni*, new species, restoration of cranium based on holotype and paratype, left lateral view; for explanation of abbreviations see Methods and Materials.



Figure 7. *Pteronarctos piersonti*, new species, holotype cranium, LACM 127972, from LACM locality 4851, ventral view.



Figure 8. *Pteronarctos piersoni*, new species, paratype cranium, LACM 128002, from LACM locality 4850, ventral view.

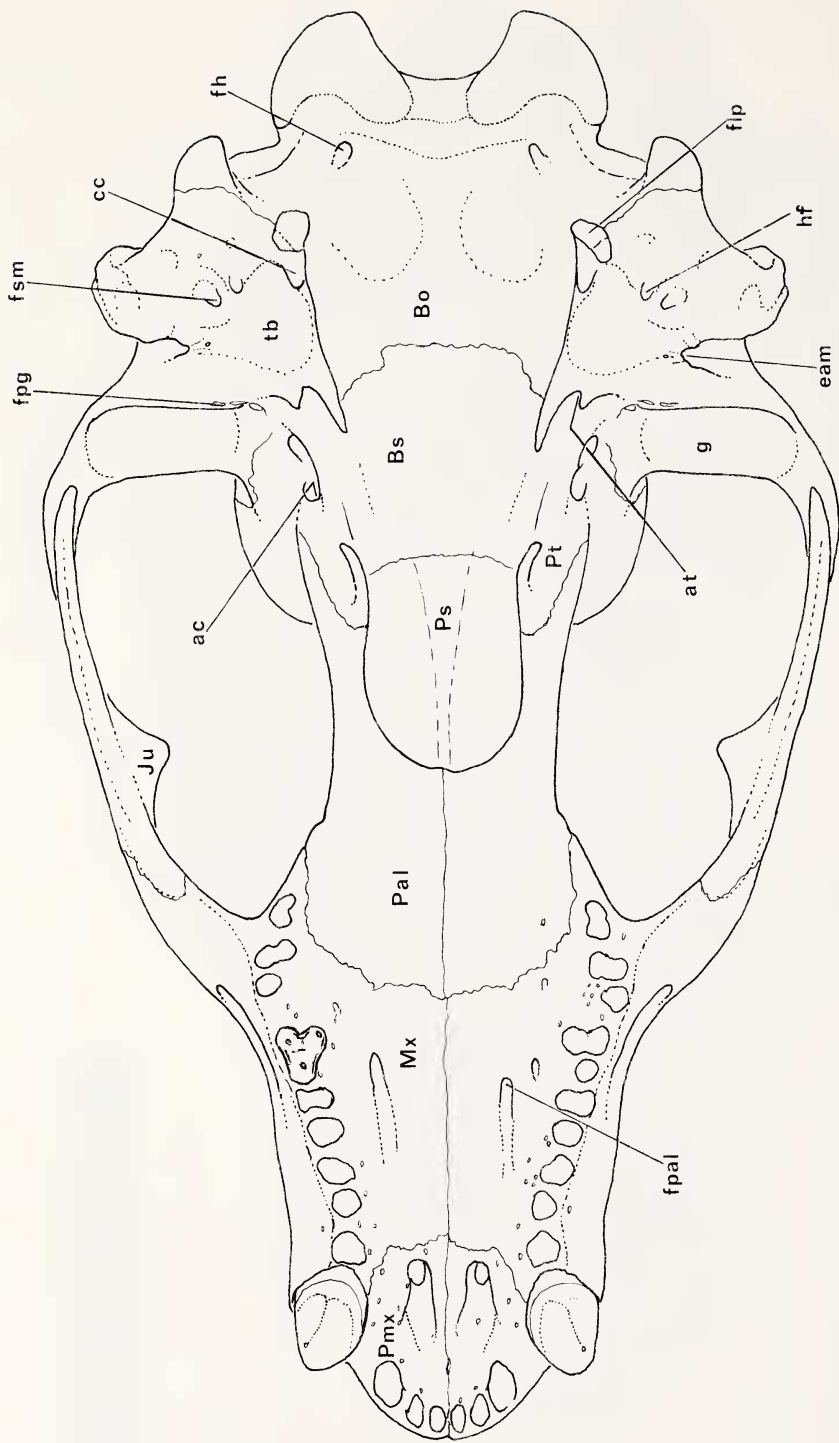


Figure 9. *Pteronarctos piersoni*, new species, restoration of cranium based on holotype and paratype, ventral view, for explanation of abbreviations see Methods and Materials.

**Table 1.** Measurements (in mm) of crania of *Pteronarctos piersoni*, new species. See Methods and Materials section for methods of measurements.

	Holo- type LACM 127972	Para- type LACM 128002
Total length (condylobasal length) (0)	212.5	212.2
Post-palatal length (palatal notch to basion)	102.5	101.2
Basion to anterior edge of zygomatic root (18)	142.0	142.2
Length of tooth row, C to M <sup>2</sup>	70.7	69.1
Width of rostrum across canines (12)	47.2	47.6
Width of palate across anterior alveoli of P <sup>4</sup>	48.4	47.6
Width between infraorbital foramina	50.2	—
Width across antorbital processes (5)	47.8	—
Width across greatest interorbital constriction (6)	36.5	38.0
Width across supraorbital processes (7)	37.0	39.2
Width across greatest intertemporal constriction	26.6	29.1
Width of braincase at anterior edge of glenoid fossa (8)	68.1	67.9
Zygomatic width (17)	121.8	124.8
Auditory width (19)	93.4	96.8
Mastoid width (20)	103.8	109.0
Paroccipital width	79.0	86.2
Greatest width across occipital condyles	52.1	51.3
Greatest width of anterior nares	25.2	—
Greatest height of anterior nares	26.6	—
Width of zygomatic root of maxilla (14)	13.0	13.6
Greatest width of foramen magnum	26.1	23.6
Greatest height of foramen magnum	16.0	15.1
Transverse diameter of infraorbital foramen	8.4	7.4

because of matrix that fills them; (2) the cranium yields a suture age of at least 30 (see Table 2) by employing the methodology of Sivertsen (1954), thus placing it in the adult age class; (3) a sagittal crest is present; and (4) the left P<sup>4</sup> shows moderate wear.

I have suggested (Barnes, 1979:16) that species of *Enaliarctos* were sexually dimorphic, with females having canines that are 20 to 32 percent smaller than those of males. The canines of the holotype of *P. piersoni* are nearly equal in size to those attributed to male (= the larger dimorph) *Enaliarctos* sp. from near the type locality of *E. mealsi*. Additionally, both the holotype and paratype crania of *P. piersoni* are approximately the same size and have canines (or canine alveoli) equal in size to those of the holotype of *P. goedertae*,

which was interpreted as being from a male (see Barnes, 1989).

Both crania apparently indicate the typical skull size for mature males of the species. Even though the paratype cranium demonstrates a significantly more advanced stage of suture fusion (Table 2), the two crania are nearly identical in size and proportions (Table 1).

Both known crania of *P. piersoni* are virtually complete, but the holotype (LACM 127972) is the least distorted of the two. Postdepositional sediment compaction has resulted in the dorsoventral compression of the brain case of the holotype (Fig. 4) and of the rostrum and anterior part of the braincase of the paratype (LACM 128002, Fig. 5). The latter has thus undergone breakage and outward displacement of the lateral surfaces of the rostrum, the braincase, and the orbital wall. Both crania apparently underwent preburial transport that resulted in loss of teeth and slight abrasion prior to fossilization. The holotype has both canines in place, and the paratype has only the left P<sup>4</sup>. All other teeth of both specimens fell out before final burial.

As with *P. goedertae*, the rostrum tapers smoothly anteriorly and the canine roots do not form prominent bulges in the cheek region. In anterior view, the widest part of the external narial opening of *P. piersoni* is at a higher point than in *P. goedertae*. The anterior narial opening is smaller in *P. piersoni* than in *P. goedertae* (Fig. 10). In contrast with *P. goedertae*, the anterior margin of each nasal bone is less concave, the rostrum is deeper and more arched (derived condition), and the nasolabial fossa is more distinct (primitive condition). In *Pteronarctos piersoni* the ascending (nasal) process of the premaxilla is broader transversely and does not extend as far posteriorly (Fig. 10) as in *P. goedertae* (which has the primitive condition as in primitive arctoid carnivores). The suture between the maxilla and premaxilla is clearly visible on both specimens. On the holotype, the maxillary-frontal suture is visible as it trends laterally toward the orbit, between the nasolabial fossa and the small antorbital process. In *P. piersoni*, the diameter of the infraorbital foramen is approximately 1.5 times that of the same foramen in *P. goedertae*. The larger diameter of this foramen in *P. piersoni* is a derived character. The zygomatic arch is more bowed dorsally at midpoint in *P. piersoni* than in *P. goedertae*, and this is a more primitive character.

The posterior part of the interorbital region is more constricted in the holotype of *P. piersoni* than in the paratype, and such differences are characteristic of the variability within Recent otariine species (see King, 1954:table 1 for *Arctocephalus australis*; Orr, Schonewald, and Kenyon, 1970:table 3 for *Zalophus californianus*; and Itoo, 1985:table 1 for *Zalophus californianus japonicus*). Although both known crania of *P. piersoni* have low sagittal crests on the braincase, neither has an anterior extension of this crest over the interorbital area, a derived condition that exists in *P. goedertae*.

Both the holotype and paratype have undergone breakage of the braincase along the parietal-squamosal suture, and this suture can be traced on both specimens and is shown in the restorations (Figs. 3, 6). The nuchal crests on both crania of *P. piersoni* are broader and not directed so far posteriorly as they are in *P. goedertae* (which has the primitive condition). In *P. piersoni* the occipital condyles project farther posteriorly than they do in *P. goedertae*. They are set off from the occipital shield more prominently (primitive condition), and they are thus visible extending beyond the nuchal crest in dorsal view (see Figs. 1–3).

The holotype has the typically flat palate of *Pteronarctos*, although the palate of the paratype has been distorted by sediment compaction and its slight arch is an artifact of preservation. All of the palatal sutures shown in Figure 9, including the pterygoid-palatine sutures, are observable on the holotype. The paratype has two very distinct palatine foramina that continue anteriorly, just as in *P. goedertae* (Fig. 8). On the holotype of *P. piersoni*, the same grooves are more shallow (Fig. 7). Located at the posterior margin of the palate ventral to the orbit, the pterygoid process is smaller than in *P. goedertae* (Figs. 12a, b), a more primitive condition. The bony palate is shorter in *P. piersoni* than in *P. goedertae*, so that the internal narial opening is 6 to 7 mm farther anterior on the cranium relative to the anterior end of the zygomatic arch. Concomitant with the shorter palate of *P. piersoni* is a longer pterygoid-palatine strut.

The canines of the holotype of *P. piersoni* are virtually the same size and have the same morphology as those of the holotype of *P. goedertae*. However, in *P. piersoni* the canine crowns are more vertically oriented relative to the plane of the palate (more primitive condition, see Figs. 11a, b). The locations, sizes, and shapes of the alveoli for P<sup>1-4</sup> are virtually identical to those of *P. goedertae*. In contrast with the condition in *P. goedertae*, the cheek tooth row of *P. piersoni* is more bowed laterally in the region of the P<sup>4</sup> and M<sup>1</sup> (Figs. 12a, b; primitive condition).

A left P<sup>4</sup> remains in the paratype cranium (Figs. 5, 8), and this is the first cheek tooth positively identified for the genus. (Barnes (1989) described an isolated M<sup>1</sup> from California that had the appropriate root morphology for *P. goedertae*.) The crown of the P<sup>4</sup> of *P. piersoni* is nearly an equilateral triangle in occlusal view (Fig. 9). The paracone is the major cusp and is broad anteroposteriorly and transversely compressed. It lies near the lateral part of the crown, and the smaller metacone lies directly posterior to it. An undulating labial cingulum (Fig. 6) curves apically around both the anterior and posterior ends of the crown to produce, at each location, a small cusp. The protocone is reduced to a low cusp separated from the paracone by a trigon basin and bordered lingually by a cingulum that is confluent with the labial cingulum. The tooth is less sectorial than is the homologous carnassial

**Table 2.** Degree of closure of sutures and suture ages of crania of *Pteronarctos piersoni*, new species. Suture nomenclature, numbers, and methods follow Sivertsen (1954).

	Holotype LACM 127972	Paratype LACM 128002
I. Occipito-parietal	4	4
II. Squamoso-parietal	3	3
III. Interparietal	2	3
IV. Interfrontal	2	2
V. Coronal	3	4
VI. Basisoccipito- basisphenoid	2	4
VII. Maxillary	2	4
VIII. Basisphenoid- presphenoid	3	3
IX. Premaxillary-maxillary	2	3
Total (suture age)	23	30

in *Enaliarctos mealsi*, and this is consistent with the cheek dentition of *Pteronarctos* being more nearly homodont than that of *Enaliarctos*. In comparison with the (more primitive) P<sup>4</sup> of *E. mealsi*, the metacone in *P. piersoni* is much smaller and has moved more anteriorly, and the protocone has moved more posteriorly relative to the paracone. As in *P. goedertae*, the anterior root above the paracone remains separate, and the posterior root above the metacone has merged with the medial one above the protocone to form a single bilobed root. In size and shape, the P<sup>4</sup> of *P. piersoni* is very similar to the P<sup>4</sup> in the holotype cranium of the Early Miocene enaliarctine *Pinnarctidion bishopi* Barnes, 1979. On the P<sup>4</sup> of *Pteronarctos piersoni*, the protocone is slightly higher, the labial margin is slightly bowed lingually, and the posterior margin of the crown, posterior to the trigon basin, is more concave. The overall aspect of the P<sup>4</sup> of *P. piersoni* shows a tooth form that is more like the anterior premolars, with the paracone becoming the principal cusp, in a cheek tooth row that is in the process of achieving homodonty.

The M<sup>1</sup> of *P. piersoni* has differently configured roots than that of *P. goedertae*. In *P. goedertae*, the posterior root is elongate anteroposteriorly, the elongation reflecting two originally separate roots, one above the protocone and one above the metacone. In *P. piersoni*, this same double posterior root is much more distinctly bilobed, and the elongation is oriented obliquely to the sagittal plane (Figs. 12a, b), a more primitive condition.

The basioccipital-basisphenoid suture is most distinct on the holotype, whereas the basisphenoid-presphenoid suture and the presphenoid-ptyergoid sutures are most distinct on the paratype. The entire auditory region of *P. piersoni* is positioned on the basicranium in a location that is typical of otariids and generalized fissipeds (the primitive condition).

Only the styliform process of the tympanic bulla projects farther anteriorly than the anterior surface of the postglenoid process. This is in contrast to the relatively unusual and derived condition in *P. goedertae*, in which the entire ear region is positioned more anteriorly on the basicranium, and the anterior part of the tympanic bulla, ventral to the auditory tube, extends anteromedial to the postglenoid process. In *P. goedertae*, the tympanic bullae are broad and most inflated in their centers. In contrast, the bullae on both crania of *P. piersoni* are relatively smaller and most inflated in their medial parts. On the holotype cranium, the most inflated part of each bulla bulges medially toward the basioccipital, whereas neither bulla of the paratype bulges in this fashion, and the inflated part of each bulla is aligned anteroposteriorly. Similar variation in bullae exists among samples of Recent species of Otariinae.

On both crania of *P. piersoni*, the mastoid process is thicker anteroposteriorly than in *P. goedertae*, and the crest of bone that joins the mastoid process with the paroccipital process is also thicker (derived condition) than it is in *P. goedertae*. In *P. goedertae*, the lateral margin of this crest is nearly straight between the two processes, whereas in *P. piersoni* the margin is concave. On the holotype of *P. goedertae*, the posterior extremities of both paroccipital processes are missing, so the crania of *P. piersoni* provide the first indication of their true shapes in the genus *Pteronarctos*. These processes are relatively broad, and their laterally bowed lateral margins give them the appearance of bending medially at the posterior ends. On both the holotype and paratype, the exoccipital-squamosal suture is visible as it extends across the lateral surface of the paroccipital process (Fig. 6), thence on the ventral surface of the process to the posterolateral side of the posterior lacerate foramen (Fig. 9).

## DISCUSSION AND CONCLUSIONS

*Pteronarctos piersoni* is the third named species of otariid pinniped described from the Astoria Formation in coastal Oregon. The first species was the large desmatophocine, *Desmatophoca oregonensis* Condon, 1906. Thus, members of at least two distinct subfamilies of otariid pinnipeds are found in this same stratigraphic interval of the Astoria Formation. One subfamily is represented by the *Desmatophoca* lineage, the other by the more otariine-like *Pteronarctos* lineage, and they both apparently occupied this area of coastal Oregon during early Middle Miocene time. Without more data, however, it is not possible to determine if populations of these pinnipeds lived at the site at different times of the year, because of differing seasonal migrations, or if they were truly sympatric to the point of using the same beaches on which to haul out simultaneously.

The dentition of *Pteronarctos piersoni*, based on the canines, the P<sup>4</sup>, the empty alveoli for other

teeth, and inferred from the known I<sup>3</sup> of *P. goedertae*, was apparently somewhat like that of Recent otariines. Although the P<sup>4</sup> retained some sectorial function, on the whole the cheek dentition was becoming homodont. *Pteronarctos piersoni* might have been able to feed on squid or crustaceans, but its main diet, like that of most Recent Otariinae, probably was mostly fish. *Desmatophoca oregonensis* has a somewhat different type of dentition, with more bulbous cheek tooth crowns. It might have also been partly or largely piscivorous, and the two species certainly could have been competing for the same type of food resources.

Although the type locality of *D. oregonensis* is near Newport, farther south along the coast and stratigraphically lower in the Astoria Formation, the only published referred cranial material of the species (see Barnes, 1987) is from the same locality and approximately the same stratigraphic horizon as the holotype of *P. piersoni*. The referred specimen of *D. oregonensis* and the holotype and paratype of *P. piersoni* are all from the 1.5 km section of Moolack Beach extending from Schooner Point, at the mouth of Schooner Creek, northward toward the mouth of Moolack Creek. A cranium referred to the cetotheriid mysticete whale, *Cophocetus oregonensis* Packard and Kellogg, 1934, and a cranium of the bizarre dome-headed chalicothere, *Tylocephalonyx* sp. (see Coombs, 1979; Munthe and Coombs, 1979), were found along the same section of Moolack Beach. These fossils are all derived from essentially the same beds, within a few meters stratigraphically of one another, relatively high in the Astoria Formation and are early Middle Miocene in age (circa 16 Ma).

The fossil mollusks from this part of the Astoria Formation indicate an environment of deposition in warm-temperate true marine conditions on an open shelf in shallow to moderate depths over a substrate of silty mud to fine sand (Moore, 1964: 17; Colbath, 1985:849, 867). These are the conditions in which the holotype of *P. goedertae* was buried and might have been indicative of its living environment.

The type species of *Pteronarctos*, *P. goedertae*, was collected from a much lower stratum, very close to the base of the Astoria Formation near Newport, Oregon, and is late Early Miocene in age. This lower part of the Astoria Formation represents the lower part of the Newportian molluscan stage and because the chalicothere found higher in the formation at Moolack Beach indicates a correlation with the Hemingfordian North American Land Mammal Age (Coombs, 1979), the age of *P. goedertae* is probably older and close to 19 Ma (Barnes, 1989).

*Pteronarctos piersoni* is therefore known only from strata that are approximately 3 Ma younger than the horizon that yielded *P. goedertae*. It is interesting and phylogenetically significant, therefore, that the chronologically younger of the two species, *P. piersoni*, has a greater number of prim-

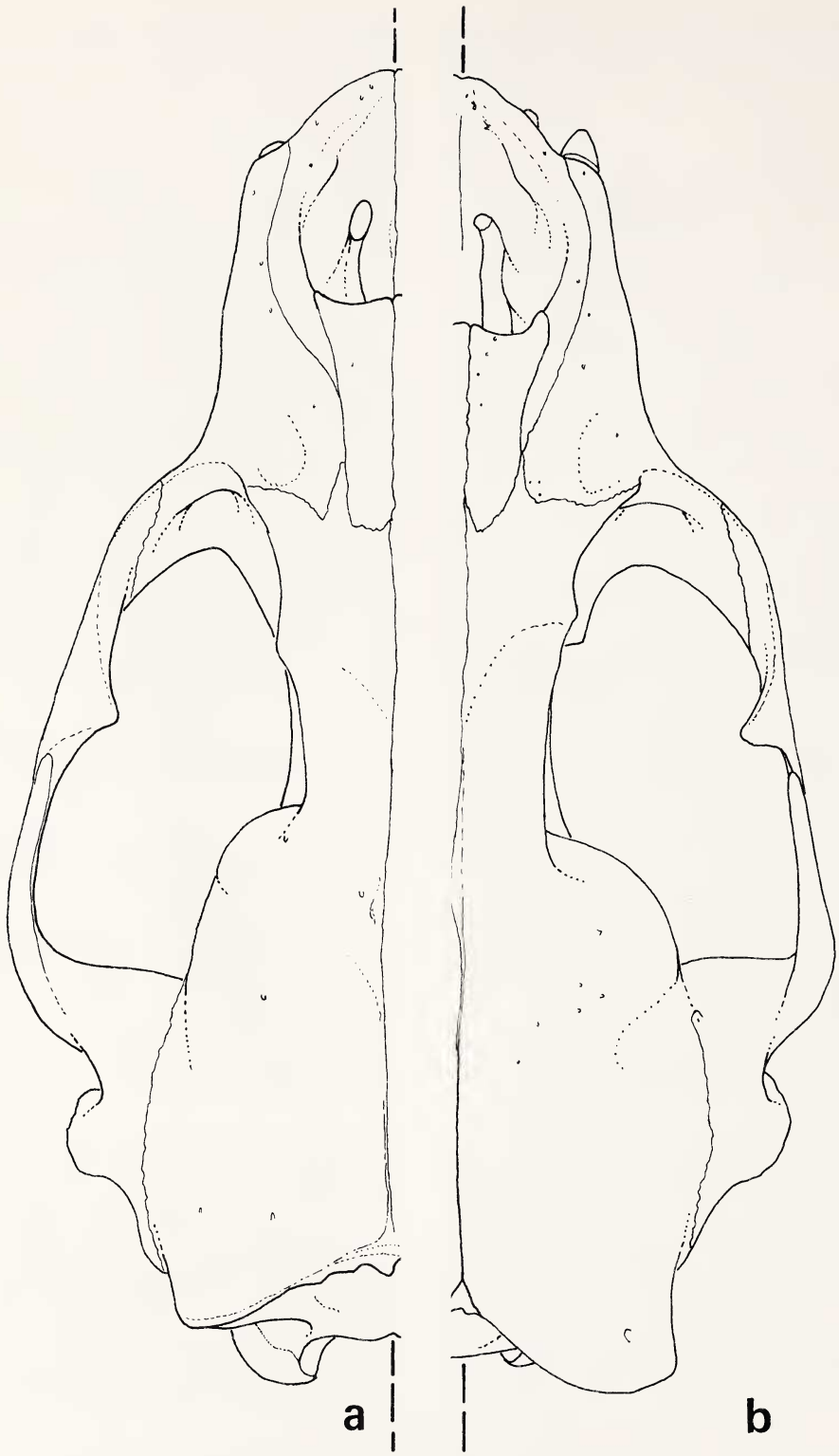


Figure 10. Comparative dorsal views of crania of species of *Pteronarctos*; a, *P. piersoni*, new species; b, *P. goedertae* Barnes, 1989 (after Barnes, 1989:fig. 2).



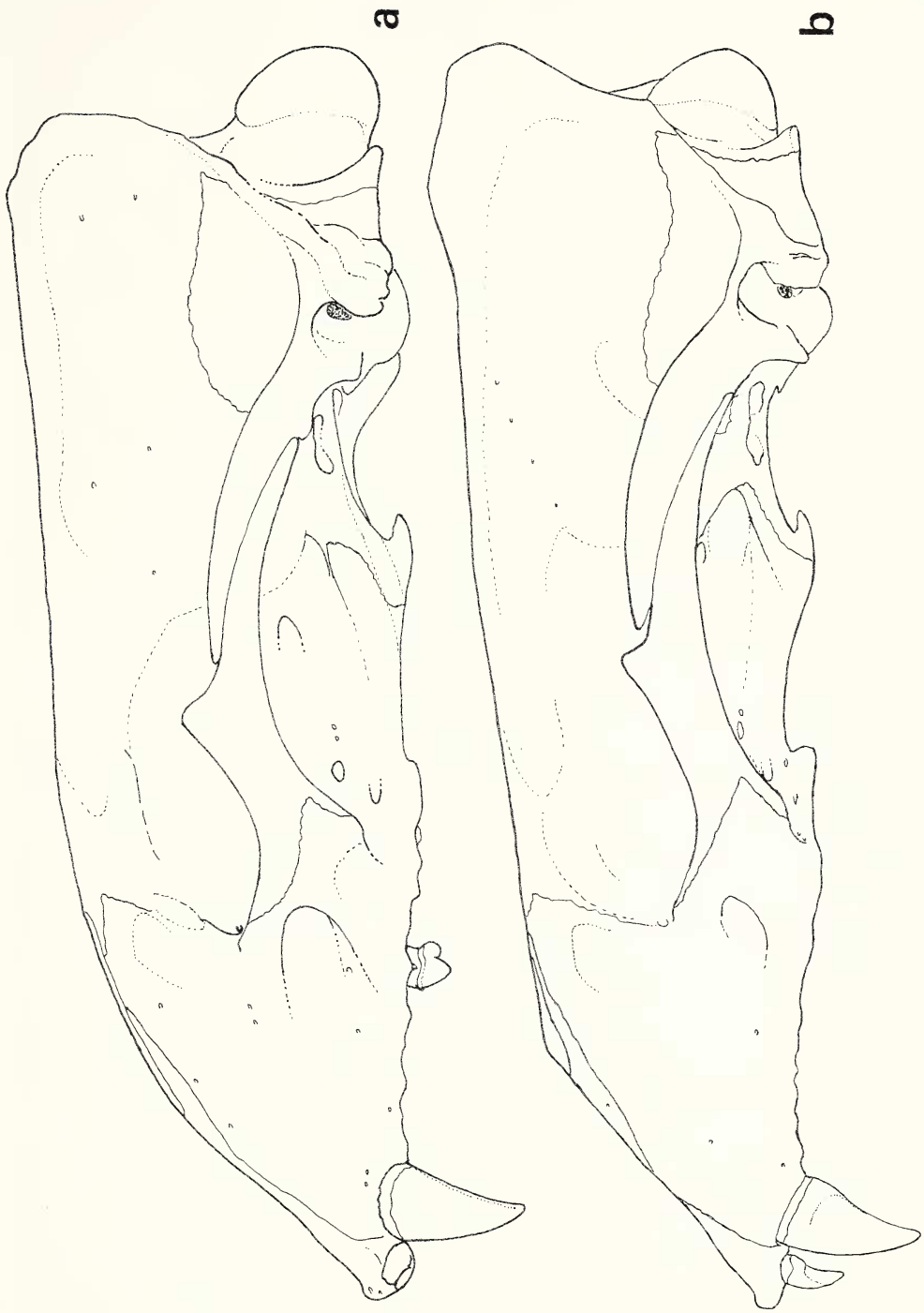


Figure 11. Comparative lateral views of crania of species of *Pteronartcos*: a, *P. piersoni*, new species; b, *P. goedertae* Barnes, 1989 (after Barnes, 1989:fig. 3b).

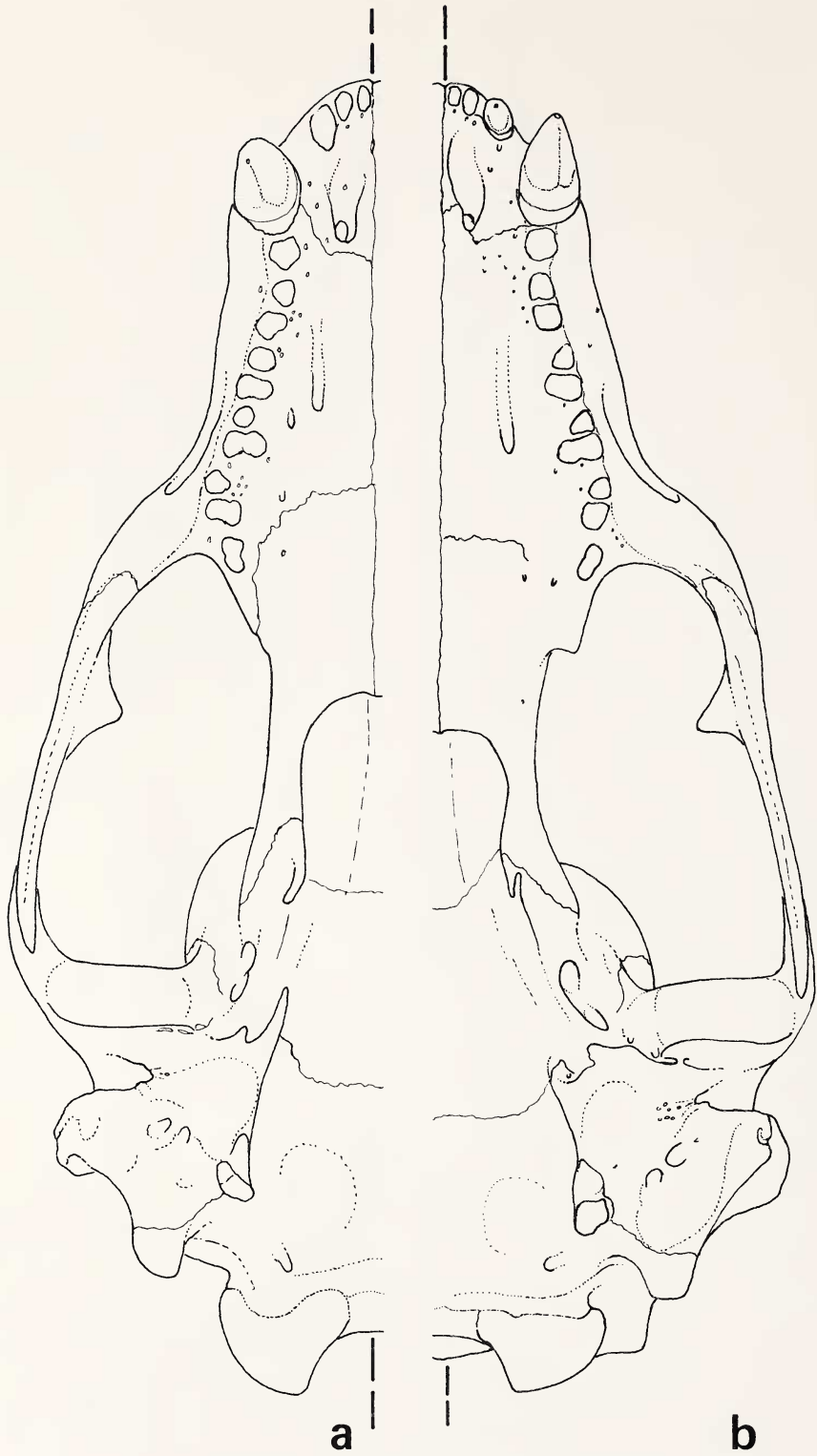


Figure 12. Comparative ventral views of crania of species of *Pteronarctos*; a, *P. piersoni*, new species; b, *P. goedertae* Barnes, 1989 (after Barnes, 1989:fig. 6).

itive cranial characters than *P. goedertae*. These characters are interpreted to be primitive because they are more like those of fissioned carnivores than like those of derived Otariidae. They include, but are not limited to, deeper nasolabialis fossa on the cheek, more dorsally curved zygomatic arch, smaller pterygoid process at the back of the palate, more vertically oriented canine crowns, more strongly laterally bowed cheek tooth rows, distinctly bilobed posterior root of M<sup>1</sup>, shorter palate, posteriorly positioned auditory region of the basicranium, smaller tympanic bulla, and more prominently projecting occipital condyles (Figs. 10–12). *Pteronarctos piersoni* does have a few derived characters compared with *P. goedertae*, and these are the greater depth of the rostrum, shorter and broader ascending (nasal) process of the premaxilla, larger diameter of the infraorbital foramen, and less prominent and more dorsally directed nuchal crest. The interesting situation exists, therefore, that the geochronologically earlier species, *P. goedertae*, has a greater number of derived characters than the later species, *P. piersoni*.

Clearly, the most parsimonious interpretation is that the older, yet more highly derived, *P. goedertae* could not have been ancestral to the more primitive, yet chronologically younger, *P. piersoni*. This interpretation avoids invoking evolutionary reversals in several character states. The two species undoubtedly evolved from a common ancestor, and this suggests that the genus *Pteronarctos* includes more than one lineage, that at least two such lineages are represented by fossils in the Astoria Formation, and that the first appearance of the genus probably will prove to be prior to the late Early Miocene occurrence of *P. goedertae*. A parallel situation was reported by Barnes (1987) for the genus *Desmatophoca* Condon, 1906, in which the older species, *D. brachycephala* Barnes, 1987, from the Early Miocene Astoria Formation in Washington is more derived than early Middle Miocene *D. oregonensis* from the coastal Oregon exposures of the Astoria Formation. The characters differentiating *P. piersoni* from *P. goedertae* are similar in kind and magnitude to differences between Recent species of arctocephaline fur seals of the polytypic genus *Arctocephalus* (see Repenning, Peterson, and Hubbs, 1971; Bonner, 1981).

The P<sup>4</sup> of *Pteronarctos piersoni* indicates that the cheek tooth row of the species was more nearly homodont than in *Enaliarctos mealsi*. Because *P. piersoni* is in general more primitive than *P. goedertae*, the latter species retains its position as the enaliarctine that shares the greatest number of derived characters in common with the living fur seals and sea lions of the subfamily Otariinae.

It must be re-emphasized that although *Enaliarctos mealsi* is, on the whole, the most primitive species of otariid pinniped yet described, in some character states *Pteronarctos goedertae* is more primitive (e.g., a shorter posterior extension of the palate ventral to the choana, a smaller posterior lacerate foramen,

a bilobed posterior root on P<sup>3</sup> representing a remnant relic of the medial (protocone) root, and a large M<sup>2</sup> alveolus; see Barnes, 1989:15). Now *P. piersoni* is known to have been yet more primitive than *P. goedertae*. The presence of these primitive characters in species of *Pteronarctos* prohibits consideration of any known species of *Enaliarctos* as being ancestral to either species of *Pteronarctos* (unless evolutionary reversals of several characters were invoked). *Pteronarctos* could share a common ancestry with *Enaliarctos*, however (see Barnes, 1989:fig. 9).

The classification of nominal species in the subfamily Enaliarctinae is summarized below. The genus *Enaliarctos* is listed first because of its preponderance of primitive characters. The subfamily Enaliarctinae, as used here, is paraphyletic (see also Berta, 1989), representing a basal group of primitive Otariidae from which several more derived lineages appear to have arisen. The diagnosis given for the subfamily in Barnes (1979) still pertains to all included species.

Family Otariidae Gill, 1866

Subfamily Enaliarctinae Mitchell and Tedford, 1973

*Enaliarctos* Mitchell and Tedford, 1973

*Enaliarctos mealsi* Mitchell and Tedford, 1973

*Enaliarctos mitchelli* Barnes, 1979

*Pteronarctos* Barnes, 1989

*Pteronarctos piersoni*, new species

*Pteronarctos goedertae* Barnes, 1989

*Pinnarctidion* Barnes, 1979

*Pinnarctidion bishopi* Barnes, 1979

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