
GOMPHOTARIA PUGNAX, A NEW GENUS AND SPECIES OF LATE MIOCENE DUSIGNATHINE OTARIID PINNIPED (MAMMALIA: CARNIVORA) FROM CALIFORNIA

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ABSTRACT. The nearly complete skeleton of *Gomphotaria pugnax*, a new genus and species of giant fossil pinniped, has been discovered in the latest Miocene (ca. 5 to 8.5 million years) marine Capistrano Formation in southern California, U.S.A. This remarkable pinniped is assignable to the otariid subfamily Dusignathinae and is convergent with true walruses of the subfamily Odobeninae by possessing large upper canine tusks but is unlike odobenines in other cranial and postcranial osteological features. Both upper and lower canines are enlarged, procumbent, and worn anteriorly, indicating that the animal may have probed the substrate in search of benthic invertebrates for food. Extreme breakage and subsequent wear of the large, single-rooted cheek teeth indicate that at least some, if not all of the food species (e.g., mollusks) probably had hard shells. Absence of a highly vaulted palate, present in walruses, indicates that *G. pugnax* did not suck bivalve inner tissues from the shells using the tongue-piston method employed by walruses. Although *G. pugnax* is distinguishable from type and referred specimens of all previously described odobenines and dusignathines, the continuing problem of disparate materials continues to plague interpretation of the group, and there are as yet unresolved problems of synonymies among previously described taxa.

INTRODUCTION

This is a preliminary report of a new genus and species of giant fossil pinniped from the Capistrano Formation in Orange County, southern California (see also Barnes and Raschke, 1989). The fossil was excavated from the latest Miocene (5 to 8.5 million years (Ma)) part of the siltstone facies of the Capistrano Formation. This formation is part of a thick sequence of Miocene and Pliocene marine sedimentary rocks in the southeastern part of the Los Angeles Basin that has produced important and abundant fossil marine vertebrates. The fossil was discovered in the hilly area of San Clemente, near the Pacific Ocean, in 1980, by paleontologists who were salvaging fossils during construction-related grading.

In recent years, our knowledge of the evolutionary history of sea lions, fur seals, and walruses in the family Otariidae (*sensu lato*) has increased greatly. The fossil record has had a major impact on interpretations of otariid phylogeny as is evidenced in reviews by Mitchell (1968, 1975), Re-

penning (1975, 1976), Repenning and Tedford (1977), Tedford (1976), Barnes (1979, 1987, 1989), Barnes, Domning, and Ray (1985), and Wozencraft (1989a, b). These authors have proposed several schemes of classification for the sea lions, fur seals, walruses, and their extinct relatives. As a result, the classification of the group is currently controversial (see Barnes, 1987; Barnes, Domning, and Ray 1985: 36, 38, table 1), and Wyss (1987) and Berta, Ray, and Wyss (1989) have even argued that walruses are closely related to the phocid seals.

We classify the new taxon described here in the extinct otariid subfamily Dusignathinae of Mitchell, 1968. Prior to the present study, the subfamily Dusignathinae was monotypic, *Dusignathus santacruzensis* Kellogg, 1927, being the only included species. The holotype of *D. santacruzensis* is from the latest Miocene part of the Purisima Formation near Santa Cruz in central California, and that formation is broadly correlative in age with the Capistrano Formation of southern California (Repenning and Tedford, 1977:4, 43-44; Barnes, 1976: 331, table 5, 1985:18).

Kellogg (1927) had considered *D. santacruzensis* to be a sea lion, although he recognized that it had characters of both sea lions and walruses. When Mitchell (1968:1894-1895) diagnosed the subfamily Dusignathinae, he listed characters that showed the taxon to be intermediate between sea lions and walruses, and it occupied this intermediate position in his phylogeny (Mitchell, 1968:fig. 16). Mitchell later suggested (1975:18) a somewhat different relationship when he indicated that he considered

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Dusignathus Kellogg, 1927, to be more closely related to the Desmatophocinae than to the Otariinae. Repenning and Tedford (1977), however, considered *Dusignathus* to be a member of the subfamily Imagotariinae Mitchell, 1968 (Imagotariinae being a senior synonym of Dusignathinae on the basis of page priority) and classified it within the family Odobenidae (walruses).

The importance of the new fossil described here is that it records, for the first time in a dusignathine, definitely associated cranial and forelimb bones, elements of critical importance in pinniped systematics. This information will be pivotal to the description and understanding of other taxa represented by disparate and less complete parts. Therefore, description of the taxon now is timely and will facilitate research on other taxa and specimens. The new taxon also documents previously unknown diversity in the Dusignathinae. We describe the cranium, dentaries, and some forelimb bones because they serve to differentiate the new taxon from all previously described large otariid pinnipeds of similar age. We intend to prepare a subsequent paper illustrating and describing in detail cranial variability and postcranial osteology of the new taxon based on the holotype and other specimens; however, that work is beyond the scope of this study.

METHODS AND MATERIALS

The classification used in this study is derived from those of Mitchell (1968) and Barnes (1979, 1989) in which Enaliarctinae, Otariinae, Desmatophocinae, Allodesminae, Imagotariinae, Dusignathinae, and Odobeninae are recognized as separate subfamilies within the family Otariidae, *sensu lato*. The subfamily Dusignathinae is recognized here based on characters listed by Mitchell (1968: 1894–1895) and on additional characters. We restrict our characterization and comparisons of *D. santacruzensis* to its holotype because referral of postcranial bones to the species is tenuous. Geochronologic ages of fossil pinnipeds cited herein are modified from those given by Repenning and Tedford (1977) and Barnes (1979) following the revised radiometric time scale of Dalrymple (1979).

Cranial measurements in Table 1 that were defined by Sivertsen (1954:18–20) are identified by his numbers in brackets. Other measurements are as defined by Barnes (1972:fig. 1, 1979:4–5). The anatomical terminology, including dental nomenclature, used here is adapted from that of Howell (1928), Miller, Christensen, and Evans (1964), Mitchell (1966, 1968), Mitchell and Tedford (1973), Barnes (1972, 1979, 1989), and Repenning and Tedford (1977). The bones shown in the illustrations were coated with a sublimate of ammonium chloride to make their features more visible.

Acronyms used for institutions are:

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.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Carnivora Bowdich, 1821

Family Otariidae Gill, 1866

Subfamily Dusignathinae

Mitchell, 1968

TYPE GENUS. *Dusignathus* Kellogg, 1927.

INCLUDED GENERA. *Dusignathus* Kellogg, 1927; and *Gomphotaria*, new genus.

Gomphotaria, new genus

DIAGNOSIS OF GENUS. A genus of Dusignathinae differing from *Dusignathus* by having cranium with high sagittal crest, rostrum laterally expanded distally to accommodate tusks, postglenoid process of squamosal relatively larger, mastoid–paroccipital crest more compressed anteroposteriorly and expanded dorsoventrally, relatively larger horizontal shelf projecting laterally over external acoustic meatus, external aperture of stylomastoid foramen directed anterolaterally rather than ventrolaterally; by having dentary relatively shallower dorsoventrally and relatively thicker transversely, with more recumbent coronoid process, more prominent laterally projecting angle of dentary, relatively larger and more rugose symphyseal surface, pterygoid process tabular and directed medially rather than posteromedially, and lesser degree of angular divergence from mandibular symphysis at midline (indicating longer and narrower skull); and by having upper and lower canines much larger, developed as tusks, more procumbent, and having fluted roots covered with thick cementum and exposed outside of alveoli, cheek teeth with crowns more bulbous, and upper and lower P1 more shallowly rooted.

TYPE AND ONLY INCLUDED SPECIES. *Gomphotaria pugnax*, new species, latest Miocene, California.

ETYMOLOGY. Derived from Greek; *gomphos*, for peg, nail, or bolt; in reference to the simple, round-rooted, peglike cheek teeth of this pinniped; plus *otaria*, a root derived from the generic name of the South American sea lion, the type genus of the family Otariidae, in reference to the otariid affinities of this taxon.

Gomphotaria pugnax, new species

Figures 1, 2, 3a

DIAGNOSIS OF SPECIES. The genus is presently monotypic and the generic diagnosis serves for the species.

HOLOTYPE. LACM 121508, virtually complete skeleton, including cranium, left and right dentaries, collected 21 August 1980 by L.G. Barnes, Edward D. Mitchell, Marilyn M. Morgan, Rodney E. Raschke, and Mark A. Roeder.

TYPE LOCALITY. LACM 4631, San Clemente,

Orange County, California. The holotype was excavated approximately 70 m north of Highway 101 at 10 to 12 m depth in a hill in the SW¹/₄, SW¹/₄, Sec. 28, T. 8 S., R. 7 W., San Clemente, California topographic quadrangle, USGS, 1968, 1:24,000 scale, at approximately 33°26'26" north latitude, and 117°37'20" west longitude.

FORMATION AND AGE. Siltstone facies of the upper part of the Capistrano Formation, latest Miocene, *ca.* 5 to 8.5 Ma, correlative with most of the Hemphillian North American Land Mammal Age.

The Capistrano Formation, a laterally extensive marine sedimentary rock unit in southern Orange County, includes strata of latest Miocene and early Pliocene age, consists mostly of silty shales interbedded with diatomites and sandstones, and rests conformably on the Middle and Late Miocene marine Monterey Formation (Edgington, 1974). This formation was deposited in the extreme southeastern part of the structural and depositional basin known as the Los Angeles Basin. The siltstone facies of the Capistrano Formation, described by Woodford (1925) for exposures in the San Juan Capistrano area of Orange County, consists of olive brown to gray (when weathered) and dark brown to black (when fresh), sandy siltstone, with interbedded sandstones and diatomaceous shales. There are localized occurrences of breccia at the base of this formation. The siltstone member is the deepwater, offshore (distal) facies of the Capistrano Formation, and is laterally equivalent to, and intertongues with, the nearshore (proximal) facies of the Capistrano Formation, known as the Oso Sand Member (Vedder, 1972), which has yielded horses, rabbits, and other fossils of Hemphillian age. Although the published vertebrate paleontological record of the Capistrano Formation appears to be meager (Barnes, 1976; Barnes, Raschke, and Brown, 1984, 1987), many fossils have been recovered from the rock unit and await description. The age of the rock unit has been determined partly on the basis of its stratigraphic and structural relationships with other rock units of known age and partly on the basis of published and unpublished fossils. The Capistrano Formation is broadly correlative with the lower part of the Almejas Formation on Isla Cedros, Baja California, and with the Purisima Formation near Santa Cruz in central California (Repenning and Tedford, 1977:4, 43–44; Barnes, 1976: 331, table 5, 1984, 1985:18).

ETYMOLOGY. Derived from Latin; *pugnax*, for combative or contentious; in reference to the probable appearance in life of this giant, adult, male individual with procumbent anterior teeth, large extremely worn cheek teeth, and a high forehead.

DESCRIPTION AND COMPARISONS. **Cranium.** The cranium (Fig. 1, Table 1) is massive, with large procumbent canines, stout zygomatic arches, relatively small orbits (for a pinniped), a relatively small braincase, a thick nuchal crest, and a high sagittal crest. Apparently the cranium was originally

Table 1. Measurements (in mm) of the holotype cranium of *Gomphotaria pugnax*, new genus and species, LACM 121508. See Methods and Materials for methods of measurements. Parentheses around a measurement indicate that it was estimated by doubling a half width.

Length as preserved (rostral tip to dorsal margin of foramen magnum)	466.0
Length of tooth row, C to M ¹	177.0
Width of rostrum across canines (12)	(164)
Width of rostrum across base of I ³	(65)
Width of palate across alveoli of P ⁴	(114)
Width across antorbital processes (5)	139.5
Width across greatest intertemporal constriction	45.0
Width of braincase at anterior edge of glenoid fossa (8)	(100)
Zygomatic width (17)	(280)
Auditory width (19)	(230)
Mastoid width (20)	(250)
Greatest width of anterior nares	50.9
Greatest height of anterior nares	56.2
Width of zygomatic root of maxilla (14)	38.5
Transverse diameter of infraorbital foramen	27.6
Anteroposterior diameter right I ³ alveolus	33.3
Anteroposterior diameter right canine alveolus	68.8
Anteroposterior diameter right P ¹ alveolus	21.2
Anteroposterior diameter right P ² alveolus	20.6
Anteroposterior diameter right P ³ alveolus	19.8
Anteroposterior diameter right P ⁴ alveolus	16.5
Anteroposterior diameter right M ¹ alveolus	20.3

completely preserved, but when it was exposed by earth-moving machinery, much of the ventral surface was scraped away. Because of this, the left side and posterior part of the palate, the left zygomatic arch, and most of the basicranium are missing. Remaining parts of the cranium are preserved in excellent condition.

The individual represented by the holotype was an old adult male (Group I of Sivertsen (1954)) on the basis of the following observations: (1) of the nine cranial sutures that Sivertsen considered useful for age determination, eight are closed and fused, six are obliterated, only the anterior part of the interfrontal suture and the posterior part of the premaxillary-maxillary suture are still visible, and the basioccipito-basisphenoid suture is presumed to have been fused and obliterated; (2) the cranium yields a suture age of at least 34 (see Table 2) by employing the methodology of Sivertsen (1954), thus placing it in the old range for the adult age class; (3) as in Recent adult male otariines and many fossil otariids, a sagittal crest is present; (4) the canines are fully erupted and heavily worn; (5) bones throughout the skeleton have extreme development of crests, rugosities, processes, and other secondary age and male sex characters; and (6) a bac-

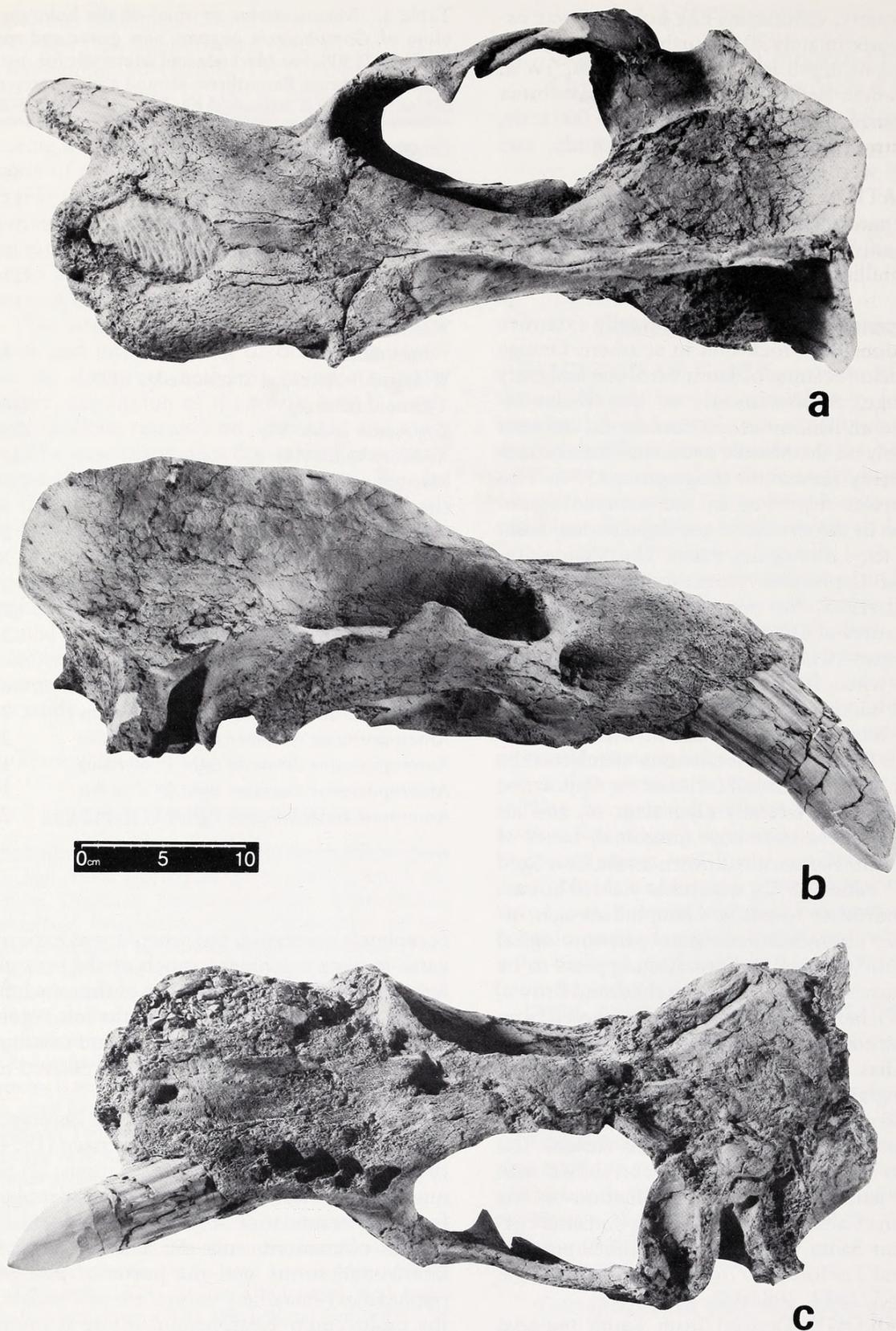


Figure 1. *Gomphotaria pugnax*, new genus and species, holotype cranium, LACM 121508, from LACM locality 4631; a, dorsal view; b, right lateral view; c, ventral view.

ulum is present. We have given the basioccipito-basisphenoid suture a score of 4 in Table 2, indicating our belief that it was closed and obliterated, even though it is not preserved on the specimen. This suture is one of the first to fuse during on-

togeny, and it definitely fuses prior to fusion of the basisphenoid-presphenoid suture, and this latter suture is fused in the holotype. The exceptionally high sagittal crest is rivaled only by that of Recent California sea lions (*Zalophus californianus* (Les-

son, 1828)) in which the crest is a diagnostic male secondary sex character (Orr et al., 1970). Males of most fossil and living otariids have at least some development of a crest, but sagittal crests are absent in odobenine walruses.

The rostrum is large and expands distally (Fig. 1a) around the roots of the large upper canines. The anterior narial opening is shaped as an elongated oval and is bordered by rounded margins of the premaxillae. Immediately anterior to the narial opening, the premaxillae protrude to form a prominent, slightly up-turned tuberosity. Such a tuberosity is primitively present in various otariid pinnipeds, especially members of the Otariinae and Imagotariinae. There is no prominent prenarial shelf as in species of *Allodesmus* (Mitchell, 1966; Barnes, 1972). The convex cheek region of the maxilla around the canine root is very rugose and perforated by many small foramina. Most parts of the sutures between the premaxillae and maxillae are obliterated by fusion. An exception to this is the part of the suture that is adjacent to the nasal bones. The ascending (posterior) process of each maxilla extends posteriorly for approximately one-half of the length of the nasals (Fig. 1a). The nasal bones are elongated and, as in *Allodesminae*, taper posteriorly to form wedges between the anterior processes of the frontals. Rather than having transversely flat anterior terminations as in most Otariidae, the anterior ends of the nasals of *G. pugnax* are oblique, with retracted medial margins, so that they are separated to form a small gap between them anteriorly.

The anterior processes of the frontals are prominent and, unlike the condition in other known kinds of otariid pinnipeds, are elevated and lap anteriorly over the posterior ends of the nasals and maxillae. Each frontal process is confluent with a prominent antorbital process. Immediately posterior to the nasals, the frontals are cleft medially by a shallow sulcus marking the interfrontal suture. The frontals are elevated and join with the parietals over the intertemporal region and the braincase to form a highly elevated and arched sagittal crest (derived character). This crest is irregular and relatively rugose, indicating prominent temporal muscle attachments, and has a fine median groove marking the course of the obliterated interparietal suture. Over the intertemporal region, the sagittal crest tapers ventrolaterally to the orbital margin, however, posteriorly its vertical sides descend abruptly to the surface of the braincase. Posteriorly the sagittal crest is confluent with the right and left parts of the nuchal crest, that flare posteriorly over and beyond the occipital shield and curve anterolaterally to join the dorsal surface of the mastoid processes. Small scattered foramina pierce the irregular surface of the braincase.

The occipital shield is high and broad. A prominent, median, vertical crest on the supraoccipital extends from immediately dorsal to the foramen magnum to the nuchal crest. A convex area lies

Table 2. Degree of closure of sutures of holotype cranium of *Gomphotaria pugnax*, new genus and species, LACM 121508. Suture nomenclature, numbers, and methods follow Sivertsen (1954).

Suture number	Suture name	Degree of closure
I.	Occipito-parietal	4
II.	Squamoso-parietal	4
III.	Interparietal	4
IV.	Interfrontal	3
V.	Coronal	4
VI.	Basioccipito-basisphenoid	4?
VII.	Maxillary	4
VIII.	Basisphenoid-presphenoid	4
IX.	Premaxillary-maxillary	3
Total (suture age)		34

dorsolateral to each condyle and extends outward to the nuchal crest. The exoccipitals flare broadly and are somewhat concave posterior to the mastoid processes. There is no indication of a large, posteroventrally projecting paroccipital process, such as occurs primitively in enaliarctine, desmatophocine, and allodesmine otariids (Barnes, 1979, 1989).

The orbit (Fig. 1b) is small compared to most fossil and Recent pinnipeds, being approximately 68 mm in diameter. In anterior view, the aperture of the large infraorbital foramen is roughly triangular. The dorsal branch of the jugal is centered above it (primitive condition), being neither retracted toward the orbit as in *Allodesminae* (see Barnes, 1972), nor flared out anteriorly over the infraorbital foramen as in Otariinae. The ventral branch of the jugal ascends from the level of the cheek tooth row, and does not depart from the snout at the level of the cheek tooth alveoli as in *Allodesminae*. The zygomatic part of the jugal is upturned into a small, thick postorbital process, which has a rather sharp, crestlike posterior margin. Ventral to the orbit, the jugal is thick, and is exceptionally deep where it curves posteroventrally ventral to the zygomatic process of the squamosal and slightly underhangs the anterolateral corner of the glenoid fossa (Fig. 1b, c).

A broad, anteroposteriorly elongate squamosal fossa separates the zygomatic process of the squamosal from the lateral wall of the braincase. This fossa is continuous laterally with a very prominent shelf that projects laterally dorsal to the external acoustic meatus. This shelf extends between the zygomatic process of the squamosal and the vertically expanded, rectangularly shaped, combined mastoid and paroccipital process. The zygomatic process of the squamosal flares anterolaterally and arches anterodorsally, becoming abruptly very slender in its anterior part dorsal to the jugal.

The right bony orbital wall is virtually complete, although the bone surface has many small cracks.

There appears to have been a moderate-sized, somewhat bilobed orbital vacuity approximately in the middle of the orbital wall. The lacrimal foramen has been lost (derived character). Directly posterior to the orbital aperture of the infraorbital foramen is a small sphenopalatine foramen. Within the posterior part of the orbit, the opposing orbital walls are closely appressed, somewhat as in derived species of Otariinae, and not widely separated as in the Recent walrus (*Odobenus rosmarus* (Linnaeus, 1758)). Because of this, the optic foramina of *G. pugnax* are relatively close together. They are located lower on the cranium than in typical Otariinae, but more dorsally than in *O. rosmarus*. The relatively small orbital fissure is ventrolateral to the optic foramen, separated from it by a strut of bone, and located immediately dorsal to the strut of the pterygoid that forms the lateral margin of the palate.

The palate (Fig. 1c) is elongated and its entire surface is perforated by numerous tiny foramina. Relatively small, paired, incisive foramina are present at the anterior end. The cheek tooth rows diverge slightly posteriorly, and between them the median part of the palate is slightly vaulted (derived character). This vaulting is different from that in *O. rosmarus*, because the vaulted portion is narrow and anteroposteriorly elongated, and easily half of the apparent vaulting results from the addition of rugose bony tissue along the lingual side of the cheek tooth alveoli. Between the P³'s are a pair of prominent palatine foramina, in the same location as in species of Enaliarctinae (see Barnes, 1979, 1989), and these foramina are likewise continuous with anteriorly directed sulci (primitive character). These sulci demarcate the medial edge of the above-mentioned areas of rugose bone medial to the cheek tooth alveoli. Unlike the homologous palatine foramina in enaliarctines, which are directed anteriorly, these are nearly vertically oriented (derived character). The infraorbital plate of the maxilla has a thick, rounded border extending posteriorly to the pterygoid region, and there is only a vestigial pterygoid process near the maxilla-palatine suture.

There are no alveoli for I¹⁻², teeth that are primitively present in most species of otariids, and in *G. pugnax* the place that such teeth occupy in other pinnipeds is merely a rugose pad of bone (derived character). The two very large I³'s were present; the alveolus for left I³ is crushed, but the uncrushed, procumbent, right one is oval in cross section and measures approximately 22.5 mm transversely by 33.3 mm anteroposteriorly. The canine, developed into a tusk, is also very procumbent and very large. Although the apex of the crown of the right canine was badly broken by earth-moving machinery, enough remains to show that it suffered extreme abrasion during life. There is no trace of any enamel remaining on it. The root is deeply fluted by alternating longitudinal grooves and ridges, and has thick deposits of cementum. To the point of breakage, the right canine of the holotype extends 135 mm

from the alveolus and we estimate that in life it extended more than 150 mm from the alveolus. At the alveolar margin, the canine root measures 69.5 mm anteroposteriorly by 49 mm transversely. The crown of the canine tapers and curves slightly ventrally and medially.

The row of five cheek tooth alveoli on either side of the palate is oblique to the sagittal plane in the mouth, extending from the posteromedial side of the canine to the lateral side of the palate near the base of the zygomatic arch. The maxilla extends ventrally along the labial border of the alveolar row, with pointed projections separating the alveoli. The alveoli are for five cheek teeth identified as P¹⁻⁴ and M¹. They are slightly procumbent and crowded, so that interalveolar septa are thin or absent. The middle tooth, P³, is deeply rooted, with an alveolus approximately 33 mm deep. The alveoli of the more anterior and posterior teeth are less deep. The alveoli of P¹⁻⁴ are circular, whereas that for M¹ is bilobed. The alveolus for P¹ is very shallow (ca. 10 mm). In fact, owing to its proximity to the root of the canine tusk, it could not have been much deeper. The alveolus for P² is approximately 30 mm deep, and that of the P⁴ is approximately 22 mm deep. The shallow, bilobed alveolus for M¹ indicates that the root of that tooth had a vestige of the double-rooted condition (primitive).

Because of the extensive damage to the basicranium (Fig. 1c), only part of the right squamosal and ear region can be described. The glenoid fossa is broad with rounded edges and with a ventrally deflected anterolateral corner. The external acoustic meatus is anteroposteriorly compressed between the postglenoid and mastoid processes (derived condition), and a space of only approximately 15 mm separates the two processes. The entrance to the external acoustic meatus is therefore narrow and high, in contrast with the situation in *Imagotaria downsi* Mitchell, 1968, for example, in which the entrance to the meatus is broad and low, even though the inframeatal lip is wrinkled from anteroposterior compression. The dorsal surface of the external acoustic meatus of *G. pugnax* is perforated by several small holes, not usually present in otariids, and these may be the result of some pathology. The inframeatal lip bears a small foramen 2.5 mm in diameter. The aperture of the stylomastoid foramen is large and, as in *I. downsi* and *Pontolis magnus* (True, 1905a), is directed anterolaterally toward the inframeatal lip.

The tympanic bulla is mostly broken away to reveal a natural internal cast of siltstone. We left this matrix cast intact because it is our only indication of the former size and shape of the bulla. The entire bulla was positioned posteromedial to the glenoid fossa, in the primitive carnivoran and otariid condition. The matrix cast indicates that the tympanic cavity was large and nearly spherical, with a somewhat flattened medial side. Its size indicates that the ventral surface of the bulla descended to a point ventral to the postglenoid and mastoid pro-

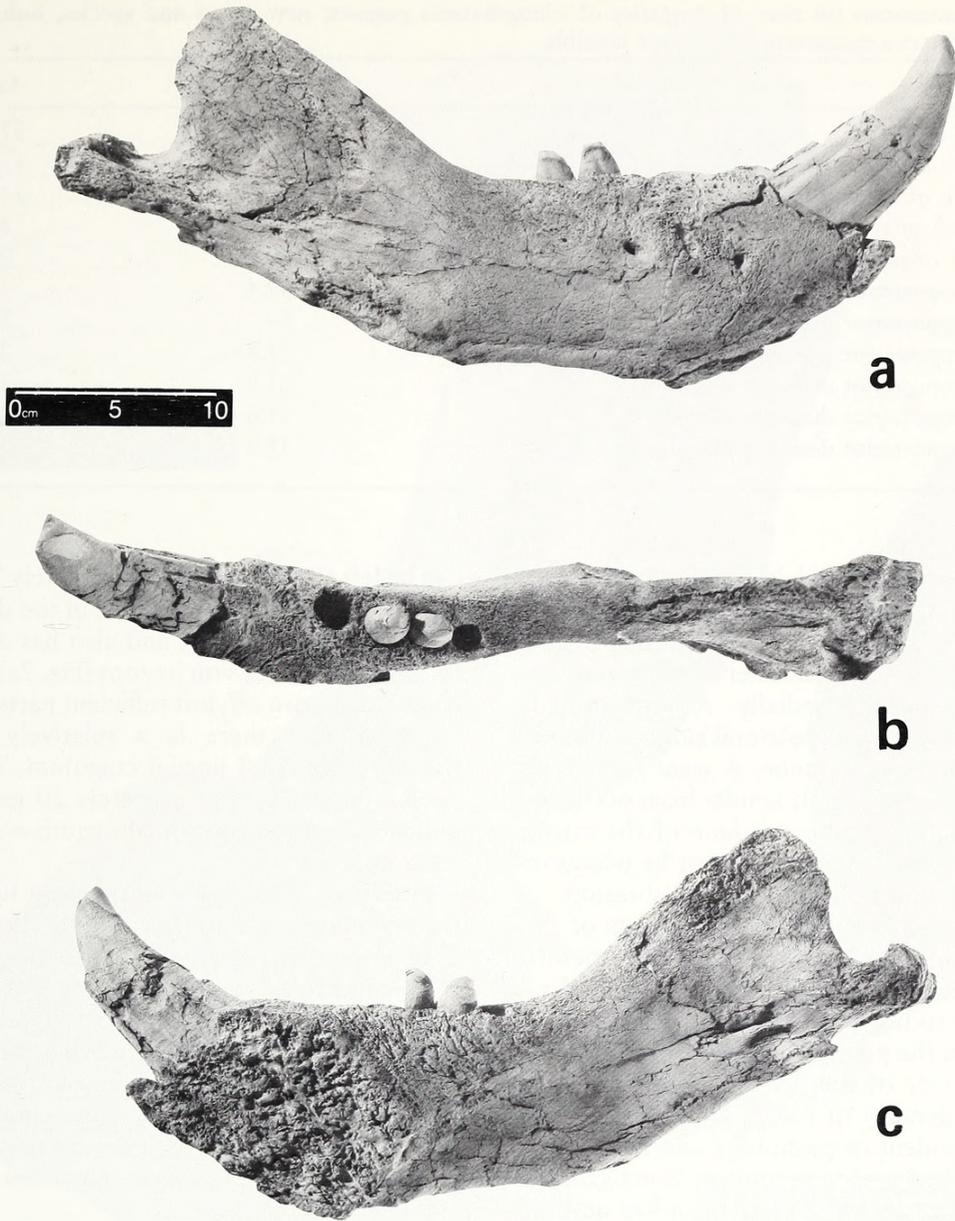


Figure 2. *Gomphotaria pugnax*, new genus and species, holotype right dentary, LACM 121508, from LACM locality 4631; a, lateral view; b, occlusal view; c, medial view.

cesses. This condition is unlike that of the imatotariine *P. magnus*, in which the bulla is flat and does not project ventral to the surrounding processes.

Dentary. The holotype of *G. pugnax* includes a complete right dentary and an incomplete left dentary (Fig. 2, Table 3). The horizontal ramus is deep dorsoventrally, like that of *Dusignathus santacruzensis*, but is much thicker transversely, with its thickest portion at the anterior end. The bone surface is very rugose and pitted. A sulcus along the ventrolateral margin of the ramus extends from the posterior margin of the symphysis to just anterior to the angle (Fig. 2a). On the lateral surface of each dentary are four mental foramina; two large, centrally located foramina, and a smaller both ante-

riorly and posteriorly. Unlike the condition in *D. santacruzensis*, there is no genial tuberosity in *G. pugnax*. The mandibular symphysis (Fig. 2c) is more oval than rhomboidal in shape, unfused, and very rugose. A large fossa is present just posterior to the ventral edge of the symphysis. The dorsal margins of both dentaries have rugose, pitted exostoses along the tooth rows. The coronoid process ascends gradually from the alveolar row and is low and rounded. The masseteric fossa is deep and elongated (Fig. 2a), unlike that of *D. santacruzensis*, in which the fossa is deep but somewhat square. The condyle is large with a laterally directed shelflike strut. A large, medially directed pterygoid process is present.

There are no alveoli for lower incisors, nor space for them, between the two enlarged canines. The lower canines are large, procumbent tusks, smaller

Table 3. Measurements (in mm) of dentaries of *Gomphotaria pugnax*, new genus and species, holotype, LACM 121508. — indicates a measurement was not possible.

	Right	Left
Total length	410.0	378.0
Length alveolar row, C-M ₁	182.0	170.0
Length of symphysis	140.5	142.0
Breadth of symphysis	92.5	86.0
Depth of ramus at P ₃	100.0	91.0
Anteroposterior diameter alveolus C	59.4	—
Anteroposterior diameter alveolus P ₁	—	19.3
Anteroposterior diameter alveolus P ₂	21.8	20.2
Anteroposterior diameter alveolus P ₃	21.9	21.8
Anteroposterior diameter alveolus P ₄	21.6	23.2
Anteroposterior diameter alveolus M ₁	15.8	—

than the upper tusks, oval in cross section, with prominent fluting below the crown. The apex of the right canine is intact and is heavily worn. Two patches of thin, smooth enamel remain; one laterally and one posteromedially. A large oblique wear surface on the posterolateral side is from occlusion with the upper canine. A wear surface on the medial side undoubtedly results from occlusion with the large I³. The anterior face of the crown also shows extreme wear, caused not by occlusion with any other tooth but by external abrasion.

The lower postcanine dentition consists of P₁₋₄ and M₁. The lower cheek tooth row is oriented slightly obliquely to the axis of the horizontal ramus. Opposite to the situation with the upper row, it extends from the posterolabial side of the canine to the lingual side of the dentary posteriorly (Fig. 2b). On each dentary of the holotype, one tooth was lost by accident or pathology and its alveolus had become filled with a secondary bony growth. On the right dentary, the P₁ had been lost and, on the left, it was the M₁. Unlike the procumbent upper cheek teeth, the lower cheek tooth alveoli are vertically oriented, and the posterior ones even slope slightly posteriorly. All of the alveoli (and roots) of the lower cheek teeth are nearly round. The largest and most deeply rooted, as with the uppers, are in the middle of the row, with the P₁ and M₁ being the smallest. The cheek teeth are crowded, progressively closer posteriorly, so that there is virtually no interalveolar septum between the P₄ and M₁.

There is a large (15 mm) diastema between the posterior margin of the canine alveolus and P₁. The left P₁ alveolus is approximately 11 mm deep. The P₂ alveoli are 24 and 28 mm deep. The left P₃ alveolus is 37.5 mm deep, and the right tooth is in place in the dentary. The root of the right P₃ has thick cementum and a longitudinal groove on the labial side (Fig. 2a), a vestige of an earlier, more primitive, two-rooted condition. The crown of this tooth is almost entirely worn off, but enough remains to indicate that it was circular in cross section and had smooth, thin enamel.

The left P₄ alveolus is approximately 28 mm deep, and the right P₄ is also in place in the dentary. This tooth resembles the P₃, and also has a faint longitudinal labial sulcus on its root (Fig. 2a). The crown is similarly worn off, but sufficient parts of it remain to show that there is a relatively prominent, smoothly rounded lingual cingulum. The right alveolus for M₁ is approximately 20 mm deep and indicates that the root of this tooth was circular in cross section.

Forelimb. Association of the right forelimb with the holotype is critical because the bones serve to differentiate this species from at least two other walrus-like fossil taxa that are not known by crania or mandibles (see comparisons in Discussion). The humerus of the holotype is fused pathologically at the elbow joint with the radius and ulna (Fig. 3a). This fusion is of unknown cause, but is an arthrosis in the general sense. Exostoses at the joint are massive; however, the diagnostic characters of the bones are clearly visible.

The humerus is relatively elongated, with an elongated, anteriorly directed deltoid crest. As in species of Otariinae and *Allodesmus*, the deltoid crest has a nearly straight anterior border, and curves rather abruptly to the shaft of the bone distally. The head of the humerus is relatively large, and the greater tuberosity extends proximally beyond it. As in walruses in general and in *Valenictus imperialensis* Mitchell, 1961, the deltoid tuberosity is on the lateral side of the deltoid crest.

The radius is relatively short and stout, although less so than the radius belonging to the forelimb of an unidentified walrus-like pinniped that was reported by Mitchell (1962) from the Purisima Formation at Santa Cruz. This specimen (LACM 3011) has limb bones that are more massive than any pinniped yet described, with the possible exception of the aberrant walrus-like *V. imperialensis*. The forelimb from Santa Cruz was identified as a possible new genus and species of odobenid by Mitchell (1962) and was tentatively assigned to *D. santacruzensis* by him (Mitchell, 1975:19) and by Repenning and Tedford (1977). Lacking associated

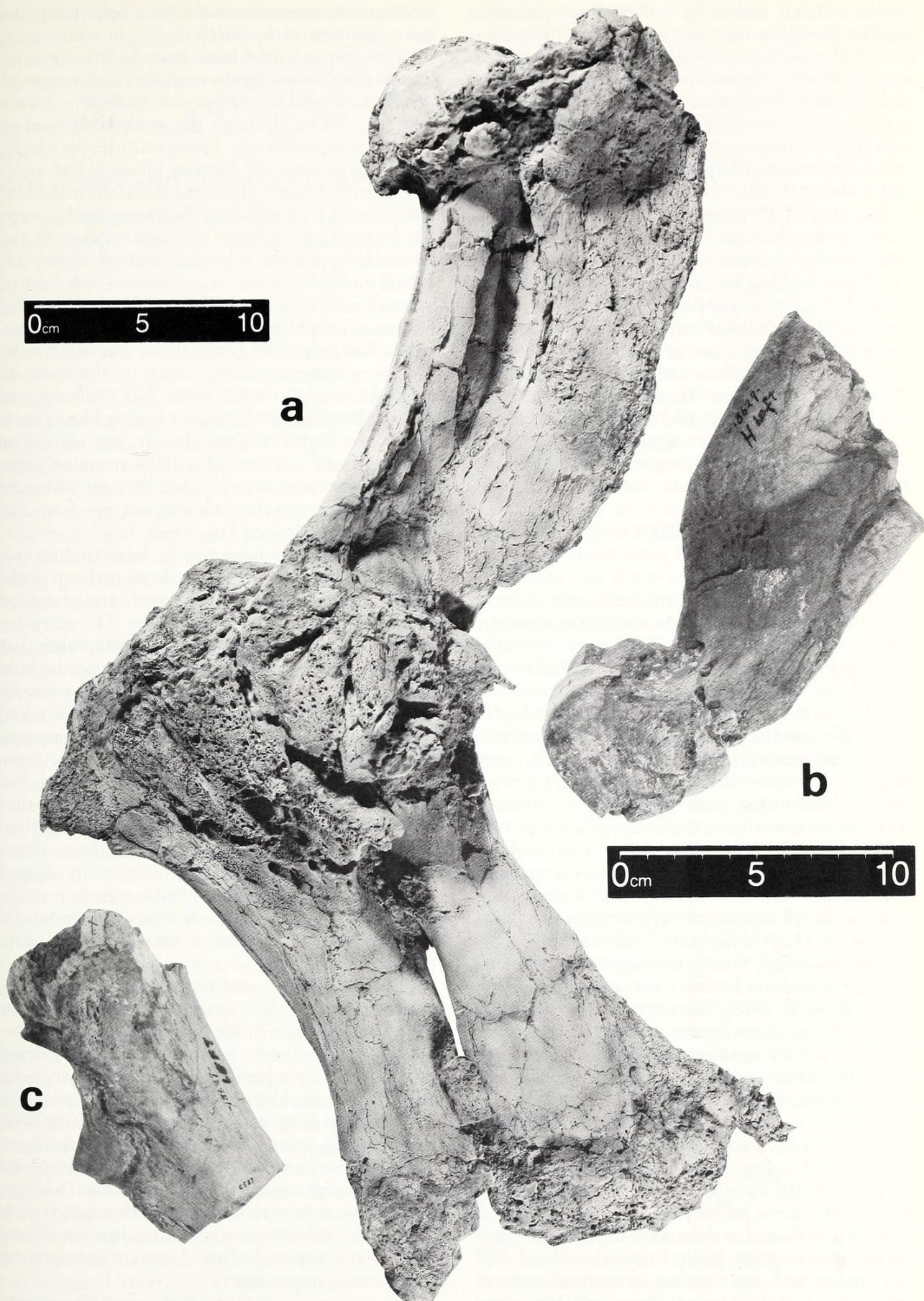


Figure 3. Forelimb bones of fossil pinnipeds; **a**, *Gomphotaria pugnax*, new genus and species, holotype, right humerus, radius, and ulna, pathologically fused at the elbow joint, LACM 121508, from LACM locality 4631, lateral view; **b** and **c**, *Pliopedia pacifica* Kellogg, 1921, holotype, USNM 13627; **b**, distal end of left humerus, lateral view; **c**, proximal part of left ulna, lateral view; to different scales—scale bar for **a** at upper left and scale bar for **b** and **c** at lower right.

cranial material, and in light of the variety of walrus-like pinnipeds now known to have existed in latest Miocene time, identification of these bones remains tenuous. The shaft of the radius of *G. pugnax* is nearly circular at midlength. Distally the radius expands anteriorly, and on its lateral surface it bears two deep ligamental grooves as is typical of Imagotariinae and Odobeninae (see Repenning and Tedford, 1977).

The ulna of *G. pugnax* is also stout, but it is more slender than the ulna that was found associated with the radius (LACM 3011) from Santa Cruz cited above. The olecranon process of the ulna is large, broad, and flares posteriorly. Its shape is very unlike the narrower and more knoblike olecranon processes on ulnae of typical fossil and Recent odobenine walruses and of the ulna (LACM 3011) from Santa Cruz. The closest similarities to *G. pugnax* among described fossil pinniped ulnae are those that have been assigned to Imagotariinae (e.g., Repenning and Tedford, 1977:pl. 13, figs. 1, 2).

DISCUSSION

PALEOBIOLOGY

The dentition of *G. pugnax* is very unusual for a pinniped, both in its composition and in its apparent use during life. As in Recent walruses, the only remaining incisors, upper or lower, are the I³'s. In *G. pugnax*, the I³'s are large and procumbent, whereas, in the Recent walrus they are small, pre-molariform, and have migrated to a position medial to the upper canine (Fay, 1982). No pinniped, fossil or living, has been described with large, procumbent upper tusks like those of *G. pugnax*, although *D. santacruzensis* has smaller upper canines that are nearly as procumbent. No walrus-like fossil has been described with the lower canines developed as tusks also. Only *D. santacruzensis* shows any tendency for elongation of both the upper and lower canines (Repenning and Tedford, 1977); although elongated, these remained caniniform and certainly would not be described as tusks (Kellogg, 1927; Mitchell, 1975). What remains of the cheek teeth of *G. pugnax* indicates that they were peglike. Their crowns are unknown, obliterated on the holotype by random breakage in life and subsequent massive wear.

Clearly *G. pugnax* was not eating fish, as do most species of living otariids (King, 1983), which have normal-sized canines and pointed cheek teeth that do not normally incur such severe wear and breakage. *Gomphotaria pugnax* did not have large eyes, as do sea lions and seals and, therefore, probably did not dive to great depths in search of food. For this reason, and also because its teeth do not resemble those of the living elephant seals (*Mirounga* spp.), it is also unlikely that it was a squid eater. The wear on the upper and lower canines, especially the anterior surfaces, indicates that these teeth probably contacted the ocean substrate during

feeding. The substrate could have been fine sediments or even rocky surfaces, but in either case, the prey items would have been benthic invertebrates. The closest living analogy to this type of food item would be the prey of the Recent walrus (see Fay, 1982), although the method of feeding must have been different. Living walruses have highly vaulted palates, no anterior incisors, and vertically oriented tusks. They feed in relatively shallow water (being the shallowest divers among the otariids) by probing sandy or silty substrates with the sensitive muzzle and vibrissae, and eat mostly bivalved mollusks as well as a variety of soft-bodied invertebrates such as tunicates, polychaete annelid worms, priapulid worms, and sea cucumbers (Fay, 1982). The soft-bodied animals are ingested whole. Walruses, however, do not chew up the shells of mollusks to get at the soft parts. The shells are held with the large lips, and using the tongue like a piston within the highly vaulted mouth, the soft inner tissues are sucked out. The shells are mostly discarded empty and nearly intact; they are not masticated by the cheek teeth and are not found in stomach contents (see Fay, 1982).

Unlike walruses, however, *G. pugnax* does not have a highly vaulted palate, indicating that it probably was unable to suck out the soft parts of shelled mollusks using its tongue as a piston. The extensive breakage and wear of its teeth indicate either that the food items with hard parts were ingested whole and chewed or that rocks were ingested with the food. It would seem that *G. pugnax* probably had a diet that included hard-shelled benthic invertebrates such as mollusks. Because the canine tusks are very procumbent and are present in both the upper and lower jaws, the angle of approach that *G. pugnax* took to the bottom and the way it probed the substrate must have been quite different from that of walruses. Because the rostrum is shaped more like that of a sea lion than a walrus, it probably did not have a broad muzzle with specialized vibrissae such as modern walruses use to locate food.

In life, *G. pugnax* was apparently a huge, heavy-bodied pinniped, with a high forehead (at least in the males, like the California sea lion, *Z. californianus*) and small eyes. It probably had a very fleshy mouth, but no proboscis like an elephant seal and no broad muzzle like a walrus. The lower lips might have been as large as the upper lips of living walruses. Its long, procumbent anterior teeth must have projected outward from its mouth, there being no way that its lips could have covered them. The large upper canines curved outward and downward with the smaller pair of procumbent I³'s between them. The lower canine tusks curved upward and outward between the upper tusks.

The extensive pathology of the right elbow joint indicates that the animal probably lived with its disability for a considerable period of time prior to its death at an extremely old age. The pathologic fusion of the joint may have inconvenienced the

animal but apparently did not prevent it from swimming and feeding. Even if there was some swimming impairment, the postulated mode of feeding in shallow water on bottom-dwelling invertebrates would not have required such agile swimming as does the capture of fish or squid.

PHYLOGENY AND CLASSIFICATION

The carnivore family Otariidae, used here in the broad sense (see Mitchell, 1968, 1975; Barnes, 1979, 1987, 1989; Barnes, Domning, and Ray, 1985:table 1), includes the living sea lions, fur seals, walruses, and their extinct fossil relatives. This broadly constructed family is equivalent to the superfamily Otarioidea as it was used by Tedford (1976), Repenning (1976), Repenning and Tedford (1977), Muizon (1978), and King (1983). The fossil record of this family, dating back to the latest Oligocene or earliest Miocene (Barnes, 1979, 1989), documents a surprising diversity of taxa. This diversity affects the classification of the extant species and our interpretation of their phylogeny.

As new fossil discoveries provided evidence of past diversity among the extinct otariids, various family groups were established to recognize the lineages (see Barnes et al., 1985). Mitchell (1968) recognized six subfamilies in a single family, the Otariidae (*sensu lato*), including walruses. In this arrangement, the dusignathines were separate from the odobenines. Later, Mitchell and Tedford (1973) added another, very primitive subfamily, the Enaliarctinae. When Repenning and Tedford (1977) reviewed the group, they merged the Dusignathinae with the subfamily Imagotariinae, a group of animals with walrus-like and dusignathine-like characters (principally postcranial) and sea lion-like dentitions and skulls. Repenning and Tedford regarded Dusignathinae as the senior synonym of Imagotariinae on the basis of page priority and classified the Dusignathinae within the family Odobenidae (walruses). Barnes (1989) presented a classification of Otariidae, to include Odobenidae, with separate subfamilies (e.g., Enaliarctinae, Otariinae, Desmatophocinae, Allodesminae, Dusignathinae, Imagotariinae, and Odobeninae), much as they were recognized by Mitchell (1968). We follow Mitchell (1968) in recognizing both Imagotariinae and Dusignathinae as subfamilies in the family Otariidae (including Odobenidae, see also Hall, 1981).

In reviewing the literature regarding fossil walrus-like pinnipeds from the west coast of North America, one finds that the species in the subfamilies Imagotariinae, Dusignathinae, and Odobeninae have been classified separately or together in a variety of subfamilies or families. Such varying classifications can be traced back as far as the original description of the type genus of the Dusignathinae, *D. santacruzensis*. Kellogg (1927) originally recognized that it had both sea lion-like and walrus-like features, but classified it in the family Otariidae, rather than in the Odobenidae. In using it to establish the new

subfamily Dusignathinae, Mitchell (1968) pointed out its unique derived characters. Repenning and Tedford (1977), influenced by its walrus-like features, assigned it to the subfamily Dusignathinae (including Imagotariinae) in the family Odobenidae with modern walruses.

Uniting *G. pugnax* with *D. santacruzensis* in the Dusignathinae, and excluding them from the Imagotariinae are the following shared characters: sagittal crest present; vertical median crest present near apex of occipital shield; tympanic bulla inflated, not flat; stylomastoid foramen round, its aperture angled anterolaterally toward external acoustic meatus; mandibular condyle located at level of alveolar border of dentary; horizontal ramus of dentary relatively short, deep dorsoventrally, and bent upward at posterior part; coronoid process recumbent; enamel on teeth relatively thin and smooth; tendency toward extreme wear on tooth crowns; tendency for accretion of cementum to tooth roots; very long I³, with long slender roots; loss of lower incisors; procumbent, elongate canines; absence of posterior crista on canine crowns; lower canine crowns with wear on anterior surfaces; lower canine roots three-sided in cross section; four premolars and one molar in each dentary; presence of a smooth lingual cingulum on cheek teeth.

Clearly, with their specialized morphologies, *D. santacruzensis* and *G. pugnax* are not walruses, although they have some walrus-like features. They also have some sea lion-like features that are derivable from the imagotariines. As Kellogg (1927) noted, *D. santacruzensis* also is intermediate in its features (see Mitchell, 1968). Dusignathinae may share a common ancestry with Odobeninae, but none of the known species could have been ancestral to them because true odobenines are contemporaneous with both *D. santacruzensis* and *G. pugnax*. Imagotariinae are still morphologically the most likely antecedents for both the Dusignathinae and the Odobeninae (Repenning and Tedford, 1977).

The work of Mitchell (1966, 1968, 1975) showed that a great number of extinct fossil animals in different lineages have acquired a sea lion-like habitus. The work of Repenning and Tedford (1977) demonstrated that an otariid need not have tusks to be related to walruses. The present study indicates that the fossil dusignathines were a relatively diverse group with members that were at least partly convergent upon walruses.

FOSSIL WALRUSES AND FOSSIL WALRUS-LIKE PINNIPEDS

Because several latest Miocene and/or Pliocene fossil pinnipeds with varying degrees of walrus affinities have been classified in the subfamilies Imagotariinae, Dusignathinae, or Odobeninae (walruses), they are summarized in Table 4 and their differences from *G. pugnax* are discussed in the following text. Although the systematics and relationships of several of these taxa remain obscure

Table 4. Nominal species of fossil Odobeninae and Dusignathinae, listed alphabetically within originally assigned genera.

Taxon	Age	Type material	Subfamily assignment
<i>Alachtherium cretsii</i>	Pliocene	Dentary	Odobeninae
<i>Alachtherium antverpiensis</i>	Pliocene	Dentary	Odobeninae
<i>Aivukus cedrosensis</i>	Latest Miocene	Skull, forelimb	Odobeninae
<i>Dusignathus santacruzensis</i>	Latest Miocene	Skull	Dusignathinae
<i>Gomphotaria pugnax</i>	Latest Miocene	Skeleton	Dusignathinae
<i>Odobenus mandanoensis</i>	Pleistocene	Dentary	Odobeninae
<i>Pliopedia pacifica</i>	Latest Miocene	Forelimb	Uncertain
<i>Pontolis magnus</i>	Latest Miocene	Braincase	Imagotariinae
<i>Prorosmarus alleni</i>	Pliocene	Dentary	Odobeninae
<i>Trichecodon huxleyi</i>	Pleistocene	Tusk	Odobeninae
<i>Trichecodon koninckii</i>	Pleistocene	Tusk	= <i>T. huxleyi</i>
<i>Valenictus imperialensis</i>	Latest Miocene	Humerus	Uncertain

because they are not known by comparable anatomical parts, *G. pugnax* can be distinguished from each of them.

Alachtherium spp.

Two nominal species from Europe have been assigned to the primitive odobenine walrus genus, *Alachtherium* DuBus, 1867: *Alachtherium cretsii* DuBus, 1867; and *A. antverpiensis* (Rutten, 1907). There are problems with the typology of these species of *Alachtherium* and the identification of referred specimens (Repenning and Tedford, 1977: 12–13). Both species have an unfused mandibular symphysis and mandibular morphology indicating that the upper canine was a tusk. The type species of the genus is *A. cretsii* DuBus, 1867. Its holotype dentary, from Early Pliocene (ca. 4 Ma) deposits in Belgium, may be compared directly with the type material of *G. pugnax*, and has been illustrated by Van Beneden (1877) and Berry and Gregory (1906).

Gomphotaria pugnax differs from *A. cretsii* by having a more horizontally elongate dentary in which the posterior end is not elevated above the cheek tooth row, a straighter horizontal ramus, a larger coronoid process, a broader symphyseal surface, by having a smaller pterygoid process, by lacking lower incisors, having an unreduced lower canine, and retaining the M_1 .

Aivukus cedrosensis Repenning and Tedford, 1977

The primitive odobenine walrus, *Aivukus cedrosensis*, is known from the latest Miocene part of the Almejas Formation on Isla Cedros, Mexico. Its holotype cranium, mandible, and forelimb bones may be compared directly with those of *G. pugnax*. Cranial characters of *G. pugnax* that distinguish it from *A. cedrosensis* are: presence of the sagittal crest; broader rostrum; border of anterior narial opening relatively rounded, not so sharply edged; frontal–maxillary suture forming a broad V, not nearly straight across; cheek surface of maxilla not so flat or so deep dorsoventrally; zygomatic process of jugal more slender with relatively smaller post-

orbital process, and longer posterior process extending posteriorly beneath squamosal; orbit smaller; palate not so highly vaulted; lateral margins of palate not extended so far ventrally; preglenoid process present (to more firmly hold mandibular condyle); external acoustic meatus more compressed anteroposteriorly between mastoid and postglenoid processes; more prominent crest projecting laterally dorsal to external acoustic meatus; exoccipital directed more posteriorly and lacking a rather well-formed lateral border that projects posteriorly; mandibular symphysis relatively much larger, more rounded in shape, and extending much further posteriorly (to a point ventral to the P_4); presence of an elongate ridge along the ventrolateral margin of the dentary; horizontal ramus of dentary nearly straight, not bowed laterally; presence of only one upper incisor in each premaxilla instead of two; I^3 not so round in cross section, but more compressed transversely; upper and lower canines relatively larger and of large diameter, more procumbent, and having fluted roots; P_1 much more shallowly rooted; and M_1 with a large round root instead of a small bilobed root. In *A. cedrosensis* the frontal–maxillary suture is nearly transverse and is aligned with the posterior part of the nasal bones (the restoration in Repenning and Tedford, 1977: fig. 1A is idealized), instead of being in the form of a splint of the maxilla projecting posteriorly into the frontal and paralleling the posterior part of the nasals as in *G. pugnax* (the primitive condition in Carnivora and Otariidae).

Dusignathus santacruzensis Kellogg, 1927

The only other species that we now assign to the subfamily Dusignathinae, *D. santacruzensis*, is from the latest Miocene part of the Purisima Formation near Santa Cruz, California. The holotype consists of a rostral fragment, a squamosal, part of the roof of the braincase, two dentaries, and teeth, all belonging to one individual. All of these parts may be compared directly with the type material of *G. pugnax*. The generic diagnosis of *Gomphotaria* lists

characters differentiating it from *Dusignathus*, and need not be repeated here.

Subsequent to Kellogg's original (1927) publication, Mitchell (1966:34–36, 1968:1888, 1894–1895, 1975:18–19) and Repenning and Tedford (1977:43–48) have discussed *D. santacruzensis*, and Mitchell (1968:fig. 16, 1975:fig. 1) and Repenning and Tedford (1977:fig. 6) showed it on phylogenies. Mitchell (1975:fig. 7) reillustrated the holotype squamosal and (1975:fig. 8) showed a possible skull reconstruction. Repenning and Tedford (1977:pl. 5, fig. 3a, b) published photographs of the holotype dentary, and (1977:pl. 15, figs. 10–17, 19, 20, 22; pl. 16, figs. 1, 3, 5) of referred and questionably referred postcranial bones from other localities. These referrals are of course subjective, because the holotype included no postcranial bones, and for our purposes, we have restricted our comparisons to the holotype.

The holotype of *G. pugnax*, which includes a baculum, is a male, and the holotype of *D. santacruzensis*, based on its small-diameter canines, might be a female. We do not believe that the two specimens represent different sexes of the same species because the relative size differential between the two holotypes is greater than the sexual size dimorphism among other species of otariids. Additionally, compared with that of *G. pugnax*, the dentary of *D. santacruzensis* is thinner transversely, less massive in overall build, the horizontal ramus is deep dorsoventrally rather than elongate as in *G. pugnax*, and the differential between the diameter of the canine and the diameters of the cheek tooth alveoli is proportionally much less.

Odobenus spp.

Although living walruses, *Odobenus rosmarus*, are Arctic in distribution (Fay, 1982), it and/or similar species were distributed farther south in both the North Atlantic and the North Pacific oceans in prehistoric, Pleistocene, and Pliocene time (e.g., Ray, 1960:137–138, 1977). One extinct Pleistocene species has been well founded on a mandible: *Odobenus mandanoensis* Tomida, 1989, from Japan.

Recent and Pleistocene *Odobenus* differ from all fossil odobenines by lacking (in adulthood) upper I^{1-2} and the lower incisors, by having an I^3 , which is premolariform and in line with the upper premolar row, by having reduced or absent posterior premolars, and by having a fused mandibular symphysis. *Gomphotaria pugnax* differs from *Odobenus* spp. by having an unfused mandibular symphysis, large, procumbent I^3 's, more procumbent upper canines, enlarged lower canines, and the suite of cranial characters used here to diagnose the genus *Gomphotaria* and the subfamily Dusignathinae.

Pliopedia pacifica Kellogg, 1921

Pliopedia pacifica, a problematic and poorly known latest Miocene, walrus-like pinniped from the Paso Robles Formation near Santa Margarita, central

California, was based only on forelimb bones, formerly Stanford University No. C. 537, now USNM 13627 (the holotype). The holotype humerus and ulna of *P. pacifica*, illustrated and described by Kellogg (1921:figs. 1a–d, 4a–c), are reillustrated here in lateral views (Fig. 3b, c). The forelimb bones of *G. pugnax* differ from the comparable bones of *P. pacifica* in the following ways: (1) the deltoid crest of the humerus is narrower transversely with a more abrupt change of slope along its anterior border than in *P. pacifica*; (2) the humerus lacks the prominent lateral crest that is confluent with the lateral epicondyle in *P. pacifica*; (3) the posterior surface of the distal end of the shaft of the humerus is distinctly convex, not flat to concave as in *P. pacifica*; (4) the shaft of the ulna is broader anteroposteriorly, with a thicker and more curved posterior border; and (5) the olecranon process is larger than it could possibly have been in *P. pacifica*, judging by the width of the ulna of the latter. The homologous bones of the two species are sufficiently different to indicate that they are not synonymous and are probably not even very closely related. Upon reexamination, the partial skeleton from the Kettleman Hills that Repenning and Tedford (1977) referred to *Pliopedia pacifica* appears (Barnes and Perry, in prep.) not to be *P. pacifica*, and we limit our consideration of *P. pacifica* to its holotype.

Pontolis magnus (True, 1905a)

Another large pinniped, of the same geologic age as *G. pugnax*, is *Pontolis magnus*. The holotype of this species is an incomplete posterior part of a cranium (see True, 1905a, b, 1909; Mitchell, 1975; Repenning and Tedford, 1977) from the latest Miocene part of the Empire Formation at Coos Bay in central coastal Oregon. At first, Mitchell (1968) was equivocal, indicating that *P. magnus* might be either an imagotariine or an odobenine. Later (1975) he considered it to be a derived imagotariine otariid (and see Barnes, 1989:23), and we agree with this. In an alternative classification, Repenning and Tedford (1977) classified it as a dusignathine (Dusignathinae including Imagotariinae) odobenid otarioid. Significantly, the broad relationships understood by Mitchell (1975) and Repenning and Tedford (1977) for this species are similar, but the hierarchical levels of their classifications differed.

Mitchell (1968:1878–1879) has suggested that an isolated squamosal and ear region (LACM 8915) from the latest Miocene part of the Capistrano Formation in Orange County, California, might represent *P. magnus* or some other large otariid pinniped. On comparing this squamosal with the more completely prepared and reillustrated holotype of *P. magnus* (see Mitchell, 1975:fig. 9; Repenning and Tedford, 1977:pl. 18, fig. 5), we concluded that the two specimens are conspecific. Therefore, the holotype and this referred squamosal serve as the basis for our comparisons between *P. magnus* and *G. pugnax*. This comparison is especially relevant be-

cause the species are contemporaneous, and both occur in the Capistrano Formation.

The holotypes of *P. magnus* and *G. pugnax* both represent large, fully adult individuals. *Gomphotaria pugnax* differs from *P. magnus* in the following ways: (1) its mastoid process is relatively smaller, more vertically oriented, and it is broad and not tapered dorsally; (2) the lateral surface of the zygomatic process of the squamosal is nearly vertically oriented, not sloping, the process is more tapered anteriorly, and is less deep dorsoventrally; (3) a shelf of squamosal bone dorsal to the external acoustic meatus is broader (i.e., extends farther laterally) and is confluent with a deeper, more anteroposteriorly elongate squamosal fossa; (4) the lateral part of the nuchal crest is broadly flaring where it merges with the squamosal bone above the mastoid process, a condition that is absent in *P. magnus*; (5) the tympanic bulla is much more inflated and extends ventrally well below the postglenoid process, whereas it is extremely flat (even somewhat concave) in *P. magnus*; (6) the aperture of the stylomastoid foramen is more round, more anterolaterally directed, and not so distinctly separated by a ridge of bone from the posteroventral border of the external acoustic meatus; (7) the dorsal part of the nuchal crest is thin and sloping posteriorly in contrast with the thickened and more vertically oriented crest of *P. magnus*; (8) a prominent, broad, vertical crest is present on the occipital shield, but is absent in *P. magnus*; (9) the occipital shield is broader than in *P. magnus*; and (10) the braincase is relatively narrower and lower vaulted than in *P. magnus*. The two species are clearly distinct and the differences cited here indicate that their separation at the subfamily level is warranted.

Prorosmarus alleni Berry and Gregory, 1906

Prorosmarus alleni, a primitive odobenine (Mitchell, 1968:1897), is known only by the holotype dentary from the Early Pliocene age (4 to 5 Ma) Yorktown Formation in Virginia. Subsequent to its original description, the species has been discussed and shown on phylogenies by Mitchell (1966:34–36, 1968:fig. 16, 1975:fig. 1) and Repenning and Tedford (1977:13–14, fig. 6). A very accurate cast of the dentary was illustrated by Repenning and Tedford (1977:pl. 2, fig. 4; pl. 5, fig. 4a, b). *Prorosmarus alleni* has an unfused mandibular symphysis, two lower incisors in a common otariid arrangement anteromedial to the lower canine, a small and premolariform lower canine, lower premolars with large, round roots, and a medial constriction of the anterior part of the dentary that indicates that the upper canine was a tusk.

Gomphotaria pugnax differs from *P. alleni* by having a differently shaped dentary, larger symphysis, no lower incisors, the lower canine developed as a tusk, and the M_1 present.

Trichecodon huxleyi Lankester, 1865

This is a large Pleistocene odobenine walrus, originally described on the basis of tusks from Great Britain and subsequently known by specimens from elsewhere in Europe and in eastern North America (see Ray, 1960). The species is sometimes classified in the genus *Odobenus* (e.g., Repenning and Tedford, 1977:55). Another nominal species, *Trichecodon koninckii* Van Beneden, 1877, is of doubtful validity (see Repenning and Tedford, 1977:55). *Gomphotaria pugnax* differs from *T. huxleyi* by having tusks that are smaller, less curved, and which lack elongate sulci on the medial sides.

Valenictus imperialensis Mitchell, 1961

Another problematical walrus-like pinniped of uncertain affinities is *V. imperialensis* Mitchell, 1961. This species is based solely on an isolated humerus, of latest Miocene age, from the Imperial Formation in Imperial County in the extreme southern part of California. Repenning and Tedford (1977:pl. 16, figs. 1, 2, 7) also illustrated and discussed the holotype and a referred humerus from the latest Miocene San Joaquin Formation in California's San Joaquin Valley. *Valenictus imperialensis* is not particularly closely related to *G. pugnax*, nor to any of the other described walrus-like otariids for that matter. It has definite walrus affinities, but more precise determination of its relationships is not possible at this time.

The humerus of *G. pugnax* is very different from that of *V. imperialensis* by: (1) being more elongate and less stout; (2) having a thinner and higher deltoid crest; (3) having a smaller deltoid tuberosity located more distally (at the midpoint) on the shaft; and (4) having the greater tuberosity extending farther proximally relative to the head (in *V. imperialensis* the greater tuberosity is more equal to the height of the lesser tuberosity and of the head).

CONCLUSIONS

Gomphotaria pugnax is a new genus and species of large fossil pinniped that inhabited the North Pacific Ocean off the coast of southern California in latest Miocene time between approximately 5 and 8.5 million years ago. We classify this remarkable new animal in the extinct subfamily Dusignathinae of the pinniped carnivore family Otariidae, and it shares some convergently acquired derived characters with Odobeninae (walruses). The species is based on a pathologic adult male skeleton found in the Capistrano Formation at San Clemente in southern California, U.S.A. (about 33 degrees north latitude). Its rarity as a fossil suggests that this pinniped may have been rare when it lived. The nearly complete holotype skeleton includes all bones necessary to differentiate *G. pugnax* from all previously named otariid pinnipeds. Most importantly, *G. pugnax* is clearly distinguishable from type and referred

specimens of all previously described odobenines and dusignathines. Some of these others, however, continue to be known only by fossil bones that are not directly comparable, and there may be some as yet unresolved synonymies among the odobenines and dusignathines.

Gomphotaria pugnax and the approximately contemporaneous *D. santacruzensis* Kellogg, 1927, are the only species that we assign to the subfamily Dusignathinae. *Dusignathus santacruzensis* is known from the Purisima Formation, which is exposed in the sea cliffs near Santa Cruz in central California. *Gomphotaria pugnax* is the more highly derived of the two species. Its cranial and mandibular features are among the most highly derived of any pinniped, but its postcranial osteology is relatively generalized. The suite of characters that distinguishes the Dusignathinae from other otariid groups includes the following: dentary deep, with broadly rounded angle, broad and low coronoid process; I^{1-2} and I_{1-2} reduced or lost; upper and lower canines procumbent and greatly elongated; and cheek teeth with relatively smooth enamel crowns and single, large, round roots.

Gomphotaria pugnax was a huge pinniped, with large procumbent upper and lower canine tusks and upper incisors projecting from its mouth, relatively small eyes, and a highly arched forehead. It probably fed in shallow water mostly on hard-shelled invertebrates such as mollusks. The wear on the anterior surfaces of its tusks indicates that it probably probed the sea floor for food, and extensive tooth breakage and wear indicate that either the food items had hard parts or that rocks were ingested with the food. The inferred food items are similar to those in the diet of Recent walruses. Unlike walruses, however, *G. pugnax* has a relatively flat palate, indicating that it did not employ a specialized method of sucking out the soft parts of shelled mollusks using its tongue as a piston. (Walruses do not chew up the shells of mollusks to get at the soft parts.)

ACKNOWLEDGMENTS

We thank J.D. Lusk and Sons, Inc., for permission to collect fossils on their property, and for support of the collecting project, which was coordinated as part of a salvage contract with Scientific Resource Surveys, Inc., of Huntington Beach, California. The Natural History Museum of Los Angeles County (LACM) and its Foundation also provided funds for field work. We thank Edward D. Mitchell, Marilyn Morgan, and Mark A. Roeder for help in collecting the holotype skeleton. Preparation by Howell W. Thomas, LACM Senior Museum Technician, was supported by the Museum, and preparation work by Raschke, was supported by National Science Foundation Grant No. BSR 82-18194. Donald Meyer of LACM prepared the photographs. The manuscript benefited greatly from comments by John M. Harris, John E. Heyning, Clayton E. Ray, Charles A. Repenning, and David P. Whistler.

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Submitted 9 January 1990; accepted 27 June 1990.



Barnes, Lawrence G. and Raschke, Rodney E . 1991. "Gomphotaria pugnax, a new genus and species of Late Miocene dusignathine otariid pinniped (Mammalia: Carnivora) from California." *Contributions in science* 426, 1-16.
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