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The Bone Joint Pathology Osteochondrosis in Extant and Fossil Marine Mammals[1]

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ABSTRACT. Osteochondrosis, a bone pathology of idiopathic origin, appears as pits and other lesions on articular surfaces of bones, and results mainly from single or repeated traumas. It has been reported in fossil hadrosaurian dinosaurs, extinct humans, and mammoths, and in extant humans, dogs, horses, cattle, camels, red deer, roan antelopes, and pigs. It has not been reported previously in any marine mammals, either Recent or fossil. Scars on articular surfaces that are consistent with osteochondrosis occur rarely on Recent and fossil bones of at least 15, and possibly 17, species of marine mammals from the North Pacific and North Atlantic oceans and the Bering Sea. The affected Recent species are *Zalophus californianus* (Lesson, 1828), the California sea lion from California; *Odobenus rosmarus divergens* (Illiger, 1815), the Pacific walrus from Alaska; *Monachus schauinslandi* Matschie, 1905, the Hawaiian monk seal from Hawaii; and *Monodon monoceros* Linnaeus, 1758, the narwhal from Greenland. Fossil occurrences from the middle Miocene Round Mountain Silt in central California, USA, the middle Miocene Rosarito Beach Formation in northern Baja California, Mexico, and the late Miocene Monterey Formation in southern California, USA include the otarioid pinnipeds *Allodesmus kelloggi* Mitchell, 1966; *Allodesmus gracilis* Barnes, 1995; an undetermined species of *Allodesmus* Kellogg, 1922; an unidentified species of gracile-boned allodesmine; a different genus and species of stout-boned allodesmine; a paleoparadoxiid desmostylian *Neoparadoxia cecilialina* Barnes, 2013; a balaenopteroid mysticete that is possibly *Tiphyocetus temblorensis* Kellogg, 1931; a mysticete that may be either *Tiphyocetus temblorensis* or *Peripolocetus vexillifer* Kellogg, 1931; the extinct sperm whale *Aulophyseter morricei* Kellogg, 1927; the long-snouted allodelphinid platanistoid odontocete *Zarhinocetus errabundus* (Kellogg, 1931); an unidentified species of medium-sized odontocete; a small species of kentriodontid delphinoid dolphin; and a larger species of kentriodontid. In pinnipeds, scars occur in both sexes on weight-bearing surfaces in the shoulder, wrist, and ankle joints and in the foot, and may result from traumas that these animals experienced at the land–sea interface, while moving on land, during fights, or during mating. The scar in the wrist joint of the desmostylian may result from trauma experienced at the land–sea interface. Among the cetaceans, scars occurring at the occipital condyle/atlas vertebra joint and in the elbow and shoulder joints are consistent with traumas possibly experienced when leaping acrobatically or during intraspecific or interspecific aggression.

INTRODUCTION

Osteochondrosis is a medical term that describes a group of relatively rare, but sometimes serious, bone disorders of idiopathic origin that affect joints of the bones of mammals and, more rarely, other vertebrates. Appearing as pits on the articular surfaces of bones, these joint pathologies usually are suffered by rapidly growing younger individuals (e.g., Osgood, 1903), and can result from both single and repeated traumas, or from developmental phenomena that disrupt the normal growth of epiphyseal cartilages in mammals.

Several phenomena can cause osteochondrosis in joints (Clanton and DeLee, 1982; Schenk and Goodnight, 1996). It can be influenced by heredity (Bernstein, 1925; Wagoner and Cohn, 1931; Smith, 1960; Jaffe, 1972), but is more commonly caused by direct or indirect trauma due to compaction (a direct force applied vertically to an articular surface), shearing (a tangential blow to a joint), avulsion (a separation caused by a cartilage fracture that produces a separated thin shell of bone) (Kennedy et al., 1966; O'Donoghue, 1966; Matthewson and Dandy, 1978; Clanton and DeLee, 1982), or by repeated, low-grade chronic traumas or microtraumas (Aufderheide and Rodríguez-Martín, 1998). Other conditions that can cause osteochondrosis are osteochondral fractures, osteonecrosis, and hereditary epiphyseal dysplasia (Schenk and Goodnight, 1996).

Trauma to a joint can disrupt the normal growth patterns in epiphyseal cartilage. The bone then necroses, or dies, due to restricted blood flow, creating a cyst, or avascular necrosis, beneath the articular surface of the bone. The cyst can ultimately break through the articular surface of the bone, leaving a pit or scar on the articular surface. The margins and bases of such scars appear nonsclerotic in acute or early-healing lesions, and become sclerotic as healing occurs, or in chronic lesions (During et al., 1994). The pathology is initially characterized by degeneration and necrosis, and is followed by regeneration and recalcification. Once the scar forms, it will remain throughout the life of the individual, even though some new bone may partially fill the pit. In modern mammal and fossil specimens osteochondrosis lesions can be detected as pits, clefts, or fissures on the otherwise normally smooth articular surfaces.

Osteochondrosis has been reported in various Recent terrestrial mammals, including cats (ulnae; Allan et al., 2008), rats (femora; Kato and Onodera, 2007), pigs (humeri, femora, ulnae, astragali; Oomah, 2008; Jørgensen et al., 1995), Japanese macaques (femora; Nakai, 2002), roan antelopes (stifle joint; Johnson et al., 2008), horses (humeri, femora, astragalus, metacarpus, and metatarsus; Nixon et al., 2004; Ytrehus et al., 2007), cattle (astragali; Baxter et al., 1991), camels (cervical and thoracic vertebrae; Hansen and Mostafa, 1958), red deer (femora; Audige et al., 1995), and dogs (humeri, femura, astragali, various tarsal bones; Rejno and Stromberg, 1978; Baker and Brothwell, 1980; Rothschild and Martin, 1993; Aufderheide and Rodríguez-Martín, 1998; Ytrehus et al., 2007). In humans it occurs especially among athletes and workers who make repetitive motions (Berndt and Harty, 1959; Brown et al., 1974; Stougaard, 1974; Woodward and Bianco, 1975; Edwards and Bentley, 1977; Canale and Belding, 1980; Pappas, 1981; Mitsunaga et al., 1982; Baur et al., 1987;

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Viegas and Calhoun, 1987; Schwarz et al., 1988; Angermann and Jensen, 1989; Fowler and Wicks, 1990; During et al., 1994; Schenk and Goodnight, 1996). It has been reported in fossil humans (mandibular condyle; Czarnetzki et al., 2003), in fossil hadrosaurian dinosaurs (pes; Rothschild and Tanke, 2007), and in mammoths (femur; Clark and Goodship, 2010).

Although theoretically any joint in the body can be affected, the joints in humans that are the most susceptible to osteochondrosis are the hip, ankle, elbow, shoulder, knee, and toe (Schenk and Goodnight, 1996; Aufderheide and Rodríguez-Martín, 1998). Osteochondrosis can be painful, cause swelling of the affected joint, and in severe cases can result in crippling. In humans, and in valuable domestic mammals, surgery is sometimes undertaken as a remedy (Edwards and Bentley, 1977; Baur et al., 1987; Schwarz et al., 1988; Angermann and Jensen, 1989; Fowler and Wicks, 1990; Nixon et al., 2004; Oomah, 2008).

Osteochondrosis has not been previously reported in any Recent or fossil marine mammal. This study reports the first evidence of its occurrence in various species of marine mammals, including Recent species as well as fossil species from Miocene marine deposits that border the eastern North Pacific Ocean. Occurrences of osteochondrosis are relatively rare, totaling only 19 affected individuals out of hundreds that were inspected. The affected bones, from four living species and from at least 11 fossil species from three different Miocene age marine formations, represent five major groups of fossil marine mammals: phocid pinnipeds, otarioid pinnipeds, a paleoparadoxiid desmostylian, mysticete (baleen) whales, and odontocete (toothed) cetaceans. The Recent specimens with apparent osteochondrosis are an ulna and tibia of *Odobenus rosmarus divergens* (Illiger, 1815) (Pacific walrus), a humerus of *Zalophus californianus* (Lesson, 1828) (California sea lion), a scapula of *Monachus schauinslandi* Matschie, 1905 (Hawaiian monk seal), and a scapula of *Monodon monoceros* Linnaeus, 1758 (narwhal). Among the fossils are seven bones of various species of allodesmine desmatophicid otarioid pinnipeds (scapula, radii, calcanea, navicular, ectocuneiform), one of a paleoparadoxiid desmostylian (ulna), two of mysticetes (atlas vertebra, radius), and five of odontocetes (occipital condyle, atlas vertebrae, humeri). The scars on these bones have rounded edges, indicating that they developed during the life of the animals and that they are not the result of postmortem, postdepositional, or man-made phenomena. The only groups of marine mammals in which we have not observed osteochondrosis are the polar bears, sea otters, and Sirenia (sea cows and manatees).

MATERIAL AND METHODS

DIAGNOSIS OF OSTEOCHONDROSIS

This pathology was first reported in the scientific literature by Paget (1870), and was subsequently given the name osteochondritis dissecans by König (1888). Considerable subsequent medical and veterinary literature exists concerning it, and through the years the name has generated considerable discussion. Osteochondrosis is a more generalized term that is currently used most commonly in preference to the earlier osteochondritis dissecans. This is because "itis", a suffix that refers to inflammation, is not the appropriate term to use in all cases, some of which are not accompanied by inflammation, and because osteochondritis dissecans is now regarded as a specific type of osteochondrosis. In some instances there is some inflammation in a joint that is affected by the pathology, but there is no inflammation in the lesion specifically.

There are several different forms of osteochondrosis, such as osteonecrosis and apophysitis. Other terms reflect specific disease sites. Examples of these are: Legg-Calve-Perthes disease (Perthes, 1910), which is epiphyseal osteonecrosis of the proximal femur; Köhler disease (Köhler, 1908), which is osteonecrosis of the astragalus, navicular or patella; Osgood-Schlatter disease (Osgood, 1903; Schlatter, 1903), which is apophysitis of the tibial tuberosity; Scheuermann disease (Scheuermann, 1920), which is epiphyseal osteonecrosis of adjacent vertebral centra in the thoracic region; Freiberg infraction (Freiberg, 1914), which is epiphyseal osteonecrosis of the second metatarsal; and Sever's disease (Sever, 1912), which is apophysitis of the calcaneum. These terms are applied to these conditions in all mammals (G.M. Davis, D.V.M., personal communication 2014).

For the present study we mostly employ the more general term, osteochondrosis, because the phenomena that we have observed on museum specimens are of uncertain origins, or possibly have multiple origins.

Our identifications and diagnoses of osteochondrosis are based on examples of the condition that have been described and illustrated by Rejno and Stromberg (1978), Baker and Brothwell (1980), Dastugue and Gervais (1992), Rothschild and Martin (1993), and Aufderheide and Rodríguez-Martín (1998). Although these previous studies did not include any examples of pathologies among marine mammals, they are the most applicable sources for describing and diagnosing the abnormalities that occur on Recent and fossil marine mammal bones.

PROGRESSION OF OSTEOCHONDROSIS

Dastugue and Gervais (1992) divided the progression of osteochondrosis into three phases. The first they termed the necrotic phase, which occurs when the bone surface first receives the damage. A damaged area of the articular surface has a pit or lesion that has a distinct border, but the bone articular surface is largely intact. The second, termed the exposition phase, occurs when the bone articular surface has become eroded through, causing a deeper pit, and thereby exposing the internal spongy part of the bone. In the third, termed the cicatrization phase, a new layer of bone has been formed within the scar. The scar will, however, typically remain present and visible throughout the remainder of the life of the individual, even though it may in some cases become partly filled with new bone. In the present study we used these three phases to characterize the status of each abnormality that we observed on various bones.

COMPARATIVE SPECIMENS

The extant species in which we found evidence of osteochondrosis are relatively well known, and have common names, which we use as well as their Linnaean names. The fossil species are less well known to most readers, and they do not have common names. We include images of skeletons and skulls of some of these fossil species to provide readers with an idea of what these animals were like when they were alive. These include some of the pinnipeds, a whale, and the desmostylian.

Some of the pathologic bones are elements of some species that previously have not been reported in the literature. To demonstrate the bases for our identifications we make comparisons and present comparative views of some bones to confirm our identifications. For some species this necessitated new identifications, new descriptions, and presentation of previously unpublished images.

ABBREVIATIONS

Specimens cited are housed in the following institutions:

BVM	Buena Vista Museum of Natural History, Bakersfield, California, USA.
CAS	Department of Geology, California Academy of Sciences, San Francisco, California, USA.
LACM(M)	Department of Mammalogy, Natural History Museum of Los Angeles County, Los Angeles, California, USA.
LACM(VP)	Department of Vertebrate Paleontology, Natural History Museum of Los Angeles County, Los Angeles, California, USA.
OCPC	The Dr. John D. Cooper Archaeological and Paleontological Center, California State University at Fullerton, Santa Ana, California, USA.
UABC	Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Ensenada, Baja California, Mexico.

UCMP Museum of Paleontology, University of California, Berkeley, California, USA.

OSTEOCHONDROSIS IN EXTANT MARINE MAMMALS

Specimens of extant marine mammals exhibiting apparent osteochondrosis in the Department of Mammalogy of the LACM belong to two species of otarioid pinnipeds, one phocid pinniped, and one cetacean, as follows.

Order Carnivora Bowdich, 1821
Family Odobenidae Allen, 1880
Odobenus rosmarus divergens (Illiger, 1815) (Pacific walrus)
Figures 1, 2

COMMENTS. Pacific walruses are extant, relatively derived, large-bodied, moderately sexually dimorphic (males are larger than females), otarioid pinniped carnivorans that live in the Bering and Chukchi seas, and are amphibious and polygynous, use all four limbs in terrestrial locomotion, and can walk and amble on sandy, icy, and rocky substrates (Fay, 1982; King, 1983:65–72).

REFERRED PATHOLOGIC SPECIMENS. LACM(M) 96762, an isolated right ulna of an adult probable male; and LACM(M) 96769, an isolated left tibia of an adult probable female; both collected by Francis H. Fay in 1963 in Alaska, USA.

REFERRED NORMAL SPECIMENS. LACM(M) 49584, an isolated left ulna of an adult probable female; LACM(M) 51100, an isolated right ulna of an adult probable male; LACM(M) 96761, an isolated left ulna of an adult probable female; LACM(M) 96767, an isolated right tibia of an adult probable female; LACM(M) 96768, an isolated left tibia of a subadult probable female; and LACM(M) 96770, an isolated right tibia of a subadult probable male; all collected by Francis H. Fay in 1963 in Alaska, USA.

DESCRIPTION. Two occurrences of damage to the articular surfaces of limb bones of Pacific walruses appear to be attributable to osteochondrosis. They both occur on isolated bones that were collected loose on beaches. They were identified as belonging to Pacific walruses by comparison with skeletons of identified individuals in the LACM Department of Mammalogy.

One occurrence is on the semilunar notch of an isolated right ulna of an adult probable male, LACM(M) 96762 (Fig. 1). The ulna is probably from a male because its size (total length 354 mm) and ontogenetic features are comparable to those of another adult probable male ulna of *O. rosmarus*, LACM(M) 51100 (total length 348 mm). In contrast, ulnae of two probable adult females of the species, LACM(M) 49584 (total length 297 mm) and LACM(M) 96761 (total length 267 mm), are from adult individuals that were notably smaller than LACM(M) 96762 and LACM(M) 51100.

The pit (Fig. 1D) on the ulna, LACM(M) 96762, that we attribute to osteochondrosis is located near the medial edge of the semilunar notch, the surface that articulates with the humerus, is oriented transversely relative to the sagittal plane of the body, measures 11.1 mm by 4.3 mm, is 2.5 mm deep, and is in phase 3 on the scale of Dastugue and Gervais (1992). It is located on a rotational surface of the joint.

The other occurrence of apparent osteochondrosis noted in a walrus is on the distal articular facet of an isolated left tibia of a subadult probable female, LACM(M) 96769 (Fig. 2). The tibia is probably from a female because its size (total length 289 mm) and ontogenetic features are comparable to those of another subadult probable female tibia of *O. rosmarus*, LACM(M) 96768 (total length 268 mm) and an adult probable female, LACM(M) 96767 (total length 302 mm). By contrast, the tibia of a probable male, LACM(M) 96770 (total length 363 mm), also from a subadult individual, is much larger.

On the tibia, LACM(M) 96769, the pit (Fig. 2D) that we attribute to osteochondrosis is located on the central part of the distal articular facet for the astragalus, is circular, measures 7.2 mm in diameter, is 2.5 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992). It is on a weight-bearing part of the articular surface.

Family Otariidae Gray, 1825
Zalophus californianus (Lesson, 1828) (California sea lion)
Figure 3

COMMENTS. California sea lions belong to the family Otariidae, the group that includes the sea lions and fur seals, a family with a fossil record dating back to late Miocene time, or approximately 11 million years ago (Koretsky and Barnes, 2006; Barnes, 2008). Various living species of otariids are equatorial to subpolar in distribution (King, 1983). California sea lions are moderately derived, medium-sized otarioid pinniped carnivorans that are noticeably sexually dimorphic (males larger than females), polygynous, amphibious, use all four limbs in terrestrial locomotion, and can walk and even run on sandy and rocky substrates (Peterson and Bartholomew, 1967; King, 1983:23–27). They live along the western coast of North America, from Baja California, Mexico, to British Columbia, Canada (Rice, 1998: 29–30).

REFERRED PATHOLOGIC SPECIMEN. LACM(M) 39652, partial skeleton of a young adult male, collected by Lawrence G. Barnes on 6 October 1968 at Drakes Beach, Point Reyes, Marin County, California, USA (field number L.G. Barnes 173).

DESCRIPTION. The pathologic specimen reported here is a young adult because most of its epiphyses are loose or only partly fused to their corresponding bones. It is a male because the baculum is present and the lower canines are relatively large, as is typical for males of otariids.

Evidence of apparent osteochondrosis in this individual is a pit (Fig. 3D) on the proximal edge of the fovea on the distal end of the right humerus where it articulates with the semilunar notch of the ulna. This pit is oriented transversely, measures 8.9 mm by 3.8 mm, is 0.7 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992). The damage is on a rotational articular surface. The articular surface of the corresponding right ulna of this individual has no damage.

Family Phocidae Gray, 1821
Monachus schauinslandi Matschie, 1905 (Hawaiian monk seal)
Figures 4, 5

COMMENTS. Monk seals are an extant group of medium-sized monachine phocid pinniped carnivorans that are not extremely sexually dimorphic (however, females are usually larger than males), relatively primitive, tropical in distribution, amphibious, and not polygynous (King, 1983:104–108; Rice, 1998:45). They are the only extant species of pinniped living around the Hawaiian Islands.

REFERRED PATHOLOGIC SPECIMEN. LACM(M) 52355, skeleton of an adult probable male, measuring 230 cm in total body length, cranial measurements are condylobasal length 234 mm and zygomatic width 131 mm, collected by Lan A. Lester in 1965 in Hawaiian Islands National Wildlife Refuge, French Frigate Shoals, Hawaii, USA.

REFERRED NORMAL SPECIMEN. LACM(M) 54384, the cranium of an adult male, body length not recorded, cranial

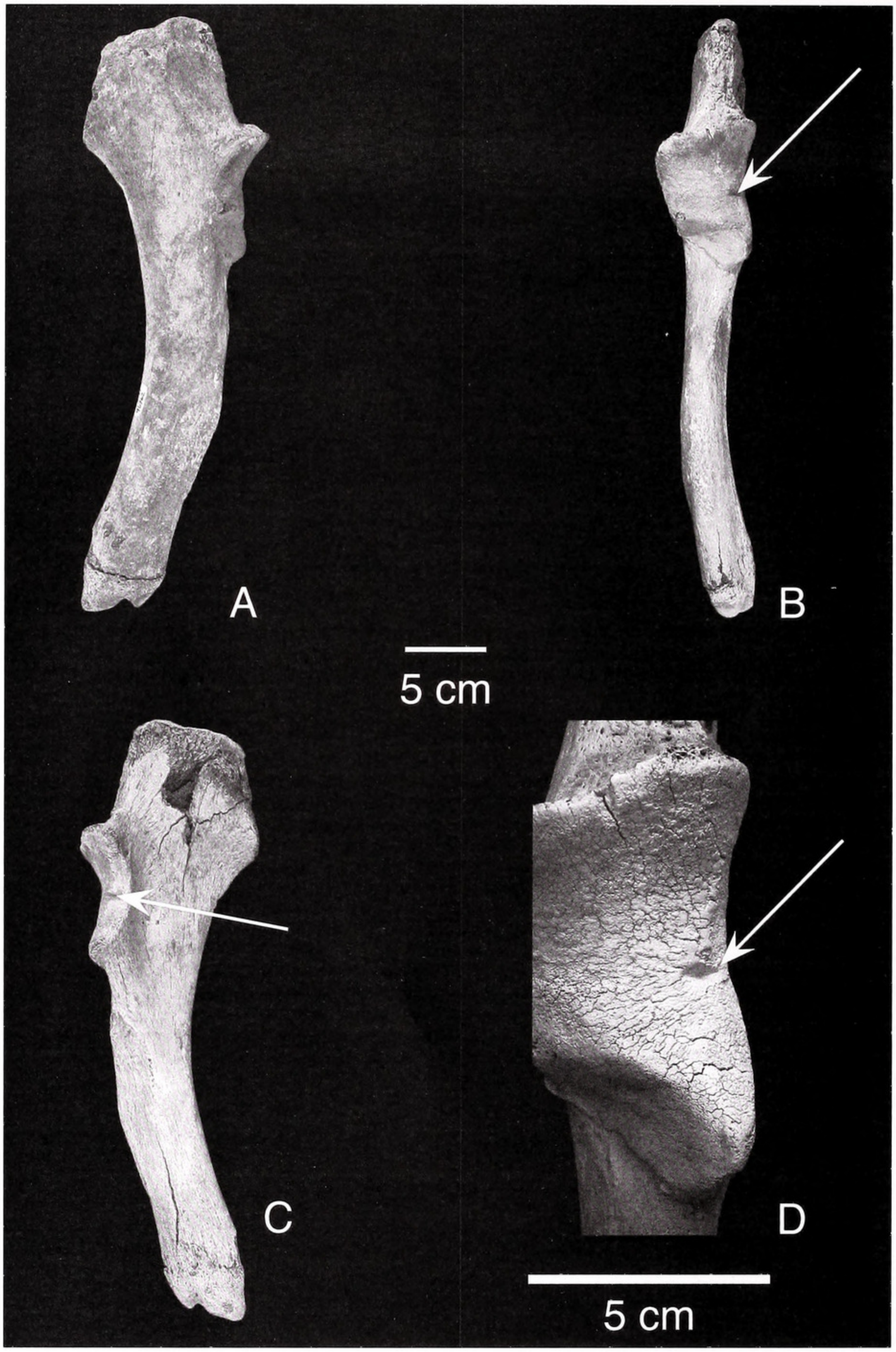

Figure 1 *Odobenus rosmarus divergens* (Illiger, 1815) (Pacific walrus), right ulna, isolated bone of an adult probable male, LACM(M) 96762, from Alaska, USA. **A,** lateral view; **B,** anterior (cranial) view; **C,** medial view; **D,** enlarged anterior (cranial) view of semilunar notch. Arrows in **B–D** point to pit attributed to osteochondrosis. Scale bars = 5 cm, but **D** enlarged to three times the scale used for **A–C.** Checking and cracking of bone surface is the result of postmortem weathering on the beach.

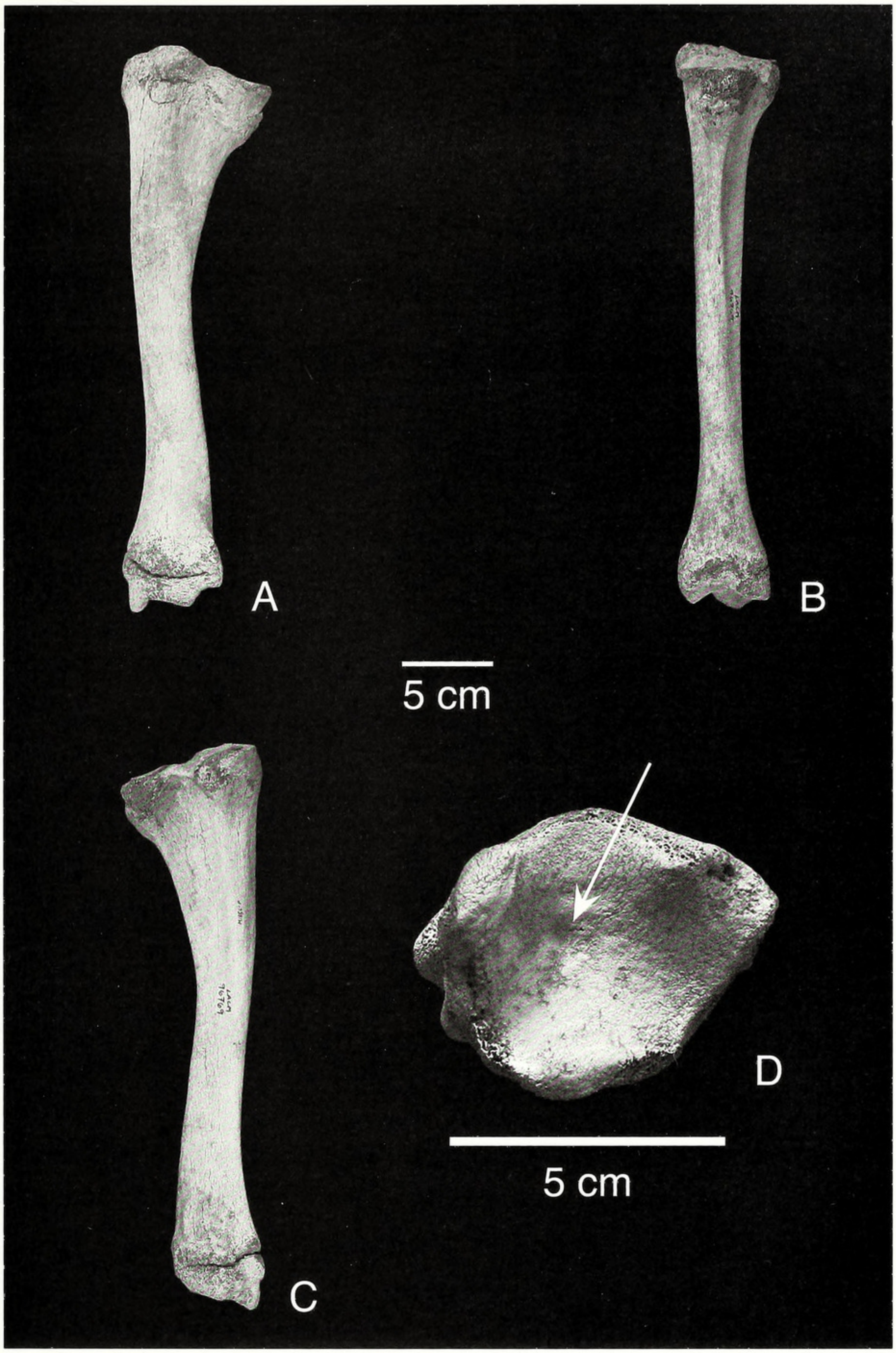

Figure 2 *Odobenus rosmarus divergens* (Illiger, 1815) (Pacific walrus), left tibia, isolated bone of an adult probable female, LACM(M) 96769, from Alaska, USA. **A,** anterior (cranial) view; **B,** lateral view; **C,** posterior (caudal) view; **D,** enlarged view of distal articular surface showing pit attributed to osteochondrosis indicated by arrow. Scale bars = 5 cm, but **D** enlarged to three times the scale used for **A–C.** Checking and cracking of bone surface is the result of postmortem weathering on the beach.

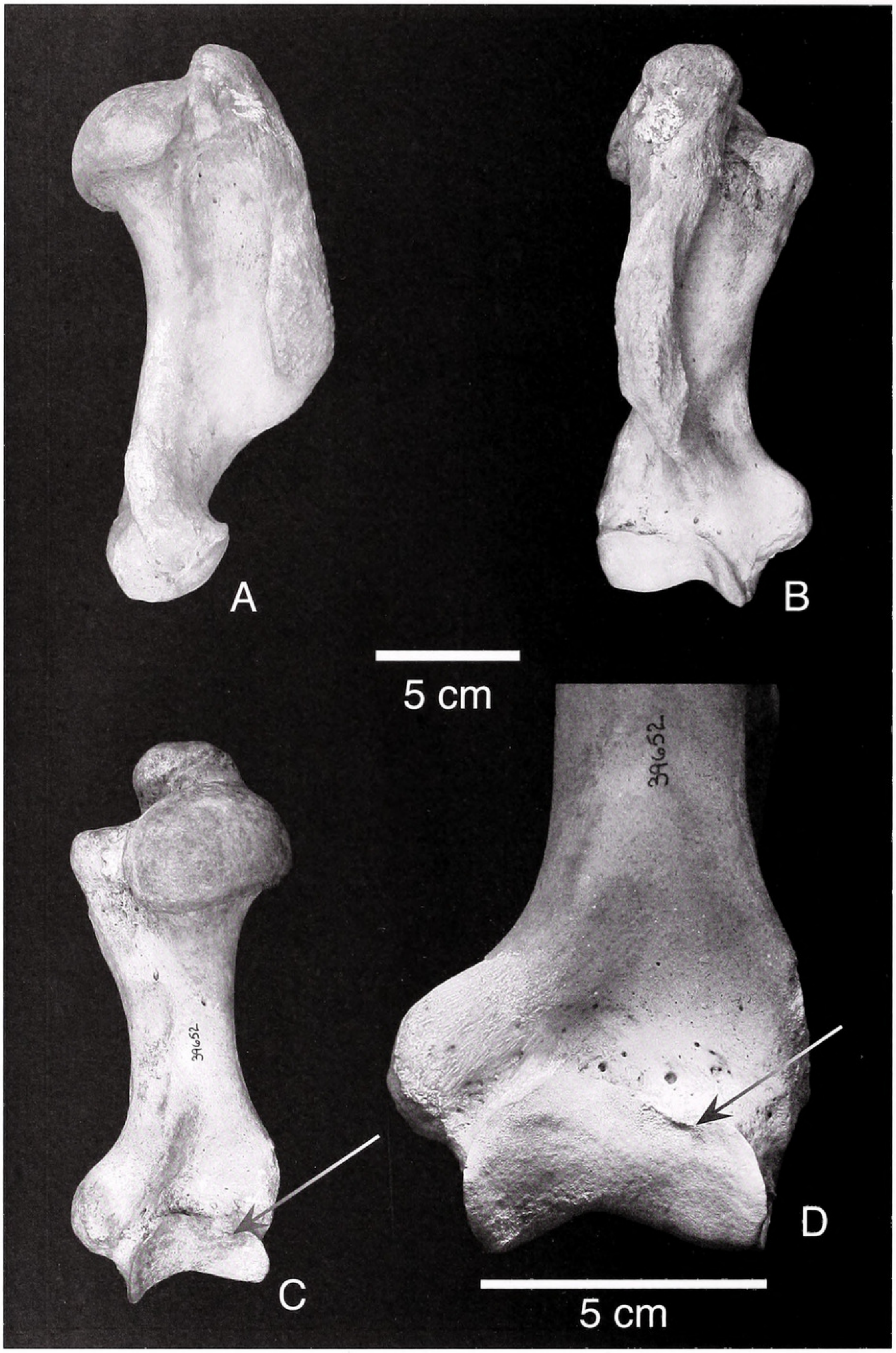

Figure 3 *Zalophus californianus* (Lesson, 1828) (California sea lion), right humerus from partial skeleton of young adult male, LACM(M) 39652, from Drakes Beach, Marin County, California, USA. **A**, lateral view; **B**, anterior (cranial) view; **C**, posterior (caudal) view; **D**, enlarged posterior (caudal) view of distal end. Arrows in C–D point to pit attributed to osteochondrosis. Scale bars = 5 cm, but D enlarged to approximately two times the scale for A–C.

Figure 4 *Monachus schauinslandi* Matschie, 1905 (Hawaiian monk seal), crania. **A** and **B**, LACM(M) 54384, adult confirmed male from Kure Atoll, Hawaii, USA. **A**, dorsal view; **B**, ventral view. **C** and **D**, LACM(M) 52355, adult presumed male with possible osteochondrosis from Hawaiian Islands National Wildlife Refuge, French Frigate Shoals, Hawaii, USA. **C**, dorsal view; **D**, ventral view.

Figure 4 Continued.

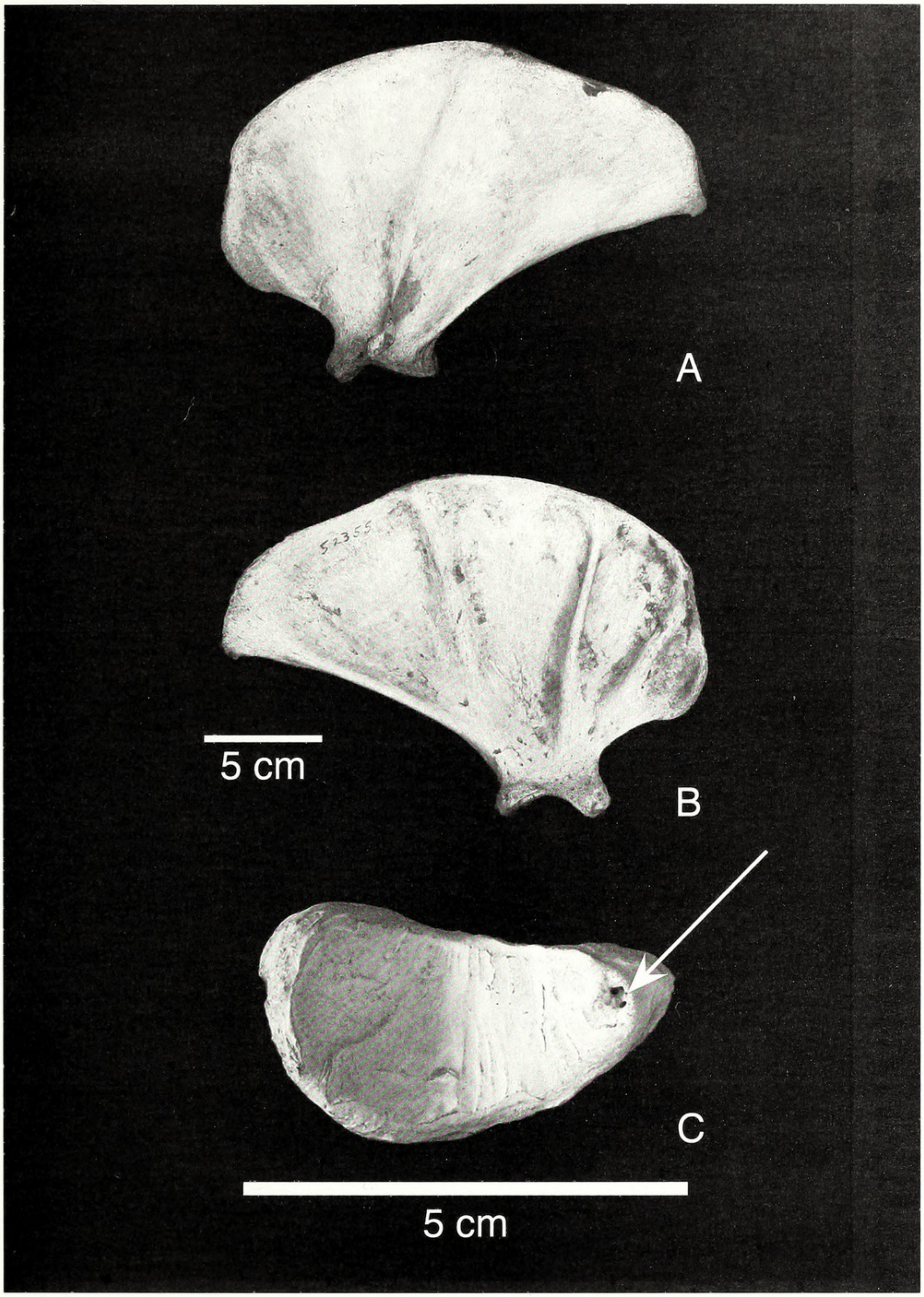

Figure 5 *Monachus schauinslandi* Matschie, 1905 (Hawaiian monk seal), left scapula of skeleton of adult presumed male, LACM(M) 52355, same individual as cranium shown in Figures 4C-D, from French Frigate Shoals, Hawaii, USA. **A**, lateral view; **B**, medial view; **C**, enlarged distal view of glenoid fossa showing pit attributed to osteochondrosis indicated by arrow. Scale bars = 5 cm, but **C** enlarged to four times the scale used for **A** and **B**.

measurements are condylobasal length 228 mm and zygomatic width 136 mm, originally captured live at Kure Atoll, Hawaii, USA, and died 15 February 1965 in Hawaii Sea Life Park, Oahu, Hawaii, USA (field number Robert L. Brownell, Jr., 245).

DESCRIPTION. The Hawaiian monk seal specimen LACM(M) 52355 has a pathology that we attribute to osteochondrosis. The gender of this specimen is not recorded in Lan A. Lester's field notes or in the collection records of the LACM Department of Mammalogy.

The cranium of the specimen with the pathology, LACM(M) 52355, is similar in size to that of an adult confirmed male of this species, LACM(M) 54384 (Figs. 4A–B), and the two specimens are very similar in their development of maturation-related and secondary adult sex-related characters (tooth eruption, tooth crown wear, suture fusion, canine tooth size, sagittal and lambdoidal crest heights, and mastoid process size). Thus LACM(M) 52355 (Figs. 4C–D) most likely is a male individual. The absence of a baculum curated among the bones of this specimen might simply be because the bone was not retained during the flensing of the animal. It is an adult because its cranial sutures are closed and epiphyses are fused to their respective bones.

A pathology on the left scapula (Fig. 5) of LACM(M) 52355 is a pit (Fig. 5C) that is on the anterior part of the glenoid fossa is oriented transversely to the long axis of the bone, measures 5.4 mm by 3.4 mm, is 2.2 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992). The area of damage is near the margin of the weight-bearing articular surface.

The corresponding articular surface on the head of the left humerus of this same individual shows no damage. This indicates that trauma occurred to the weight-bearing articular surface of the scapula without leaving any detectable signs of damage to the articular surface of the corresponding humerus to which it articulated. The articular surface of the humeral head would have rotated through various arcs of several degrees relative to the single affected site on the scapula, thus no single place on the humeral head would have been affected.

Order Cetacea Brisson, 1762
Family Monodontidae Gray, 1821
Monodon monoceros Linnaeus, 1758 (narwhal)
Figure 6

COMMENTS. Narwhals are an extant group of medium-sized, sexually dimorphic, delphinoid odontocete cetaceans that are Arctic in distribution, and at times of the year become gregarious and actively interact (Heide-Jørgensen, 2002, 2009).

REFERRED PATHOLOGIC SPECIMEN. LACM(M) 72329, the scapulae of an adult of unknown gender, collected by Donald R. Patten in 1976 at Qeqertat, Inglefield Bredning Fjord, Greenland (field number D.R. Patten 2285).

DESCRIPTION. Damage that appears to be osteochondrosis is on the right scapula of LACM(M) 72329 (Fig. 6), occurring as a pit near the center of the glenoid fossa (Fig. 6C). This pit is elongated transversely, measures 10.9 mm by 3.4 mm wide, is 2.2 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992).

OSTEOCHONDROSIS IN FOSSIL MARINE MAMMALS

EXAMPLES FROM THE MIDDLE MIOCENE SHARKTOOTH HILL BONEBED

GEOLOGY AND AGE. The middle middle Miocene age Sharktooth Hill Local Fauna (named by Mitchell and Tedford, 1973:fig. 3) is derived from the Sharktooth Hill Bonebed (named by Barnes, 1977:326–327), a stratum that is in the upper part of the Round Mountain Silt, a marine near-shore shelf deposit that crops out to the northeast of Bakersfield, in Kern County, central California, USA. This bonebed is approximately between 14.5 and 16.1 million years old (MA), is correlated with the Temblor Provisional Provincial mega-invertebrate stage of Addicott (1972), the Relizian and/or Luisian foraminiferal stages, and the Barstovian North American Land Mammal Age. The Sharktooth Hill Local Fauna is a global standard of comparison for fossil marine vertebrates of its age (Barnes, 1977; Barnes and Mitchell, 1984; Barnes et al., 1999; Prothero et al., 2008a, 2008b; Pyenson et al., 2009). Fossil bones from this bonebed that show apparent osteochondrosis belong to several extinct species of marine mammals as follows.

Order Carnivora Bowdich, 1821
Family Desmatophocidae Hay, 1930
Subfamily Allodesminae (Kellogg, 1931) Mitchell, 1966
Allodesmus kelloggi Mitchell, 1966
Figures 7, 8, 11A, 12A

COMMENTS. Allodesmines are an extinct group of highly derived otarioid pinniped carnivorans that were large-bodied, sexually dimorphic (males significantly larger than females), most likely amphibious, deep-diving, ambulatory on land, and polygynous. All species in this subfamily (and likewise in the entire family Desmatophocidae) are extinct, and these animals were distantly related to extant sea lions and walruses. Allodesmines were taxonomically diverse and geographically widespread in the North Pacific Ocean during middle Miocene time (Mitchell, 1966; Barnes, 1972, 2008; Barnes and Hirota, 1995; Koretsky and Barnes, 2006).

The type species of the genus *Allodesmus* Kellogg, 1922, is *Allodesmus kernensis* Kellogg, 1922. The holotype specimen (CAS 2472) of *A. kernensis* is a weathered and broken partial dentary that was collected from the Round Mountain Silt in the Kern River district, Kern County, California, USA. This dentary may have been collected from a horizon that is stratigraphically lower than, and therefore geochronologically older than the Sharktooth Hill Bonebed (see Mitchell, 1966:5; Barnes and Hirota, 1995:341). The holotype dentary of *A. kernensis* differs from those of *A. kelloggi* and *A. gracilis* (another species that is discussed below), both of which definitely occur in the Sharktooth Hill Bonebed, by being much more stout, and by having a transversely thicker horizontal ramus; a larger, wider, and less procumbent mandibular symphysis; and a more vertically implanted lower canine. The holotype of *A. kernensis* differs further from the holotype dentary of *A. kelloggi* by being larger and by having two separate roots on the m1 rather than a single root.

Mitchell's (1966:5) description of *Allodesmus kelloggi* was based upon the nearly complete holotype skeleton of an adult male individual, LACM(VP) 4320, which was collected from the Sharktooth Hill Bonebed. Barnes and Hirota (1995) later concluded at the time of their writing that the holotype skeleton was the only confidently identified specimen of *A. kelloggi*.

PATHOLOGIC HOLOTYPE SPECIMEN. LACM(VP) 4320, a nearly complete skeleton of an adult male, collected by Edward D. Mitchell, Jr., Joseph F. Arndt, Jere H. Lipps, and Archer Warne on 1 October 1960 at locality LACM 1557 (field number E.D. Mitchell 193).

DESCRIPTION. The holotype skeleton (Fig. 7) has two occurrences of damage to articular surfaces that appear to be attributable to osteochondrosis. One occurrence is in the glenoid fossa of its right scapula (Fig. 8A). Mitchell (1966:pl.15, figs. a, d) illustrated the medial and lateral views of this scapula, but not the

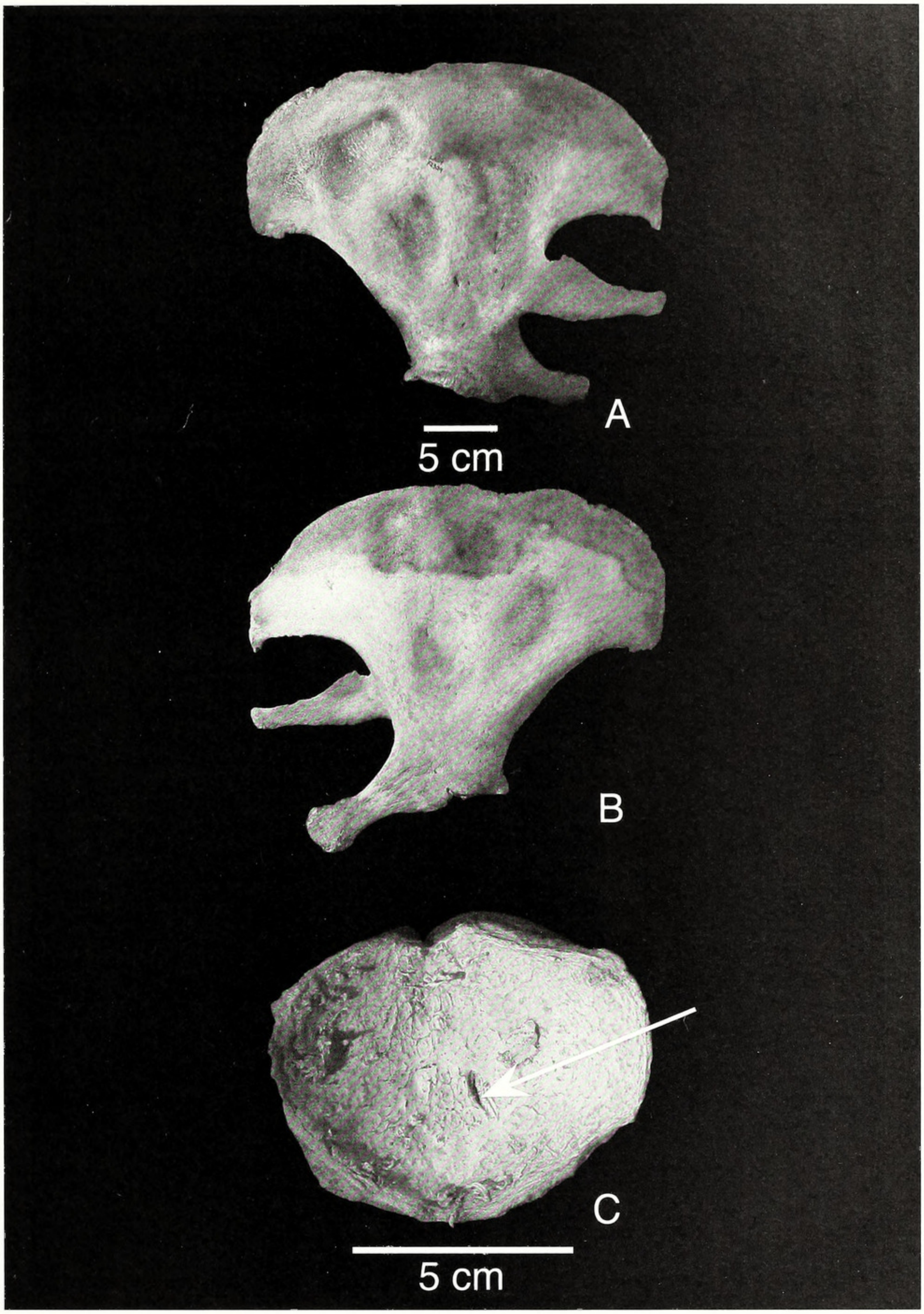

Figure 6 *Monodon monoceros* Linnaeus, 1758 (narwhal), right scapula of adult of unknown gender, LACM(M) 72329, from Qeqertat, Inglefield Bredning Fjord, Greenland. **A**, lateral view; **B**, medial view; **C**, enlarged distal view of glenoid fossa showing pit attributed to osteochondrosis indicated by arrow. Scale bars = 5 cm, but **C** enlarged to three times the scale for **A** and **B**.

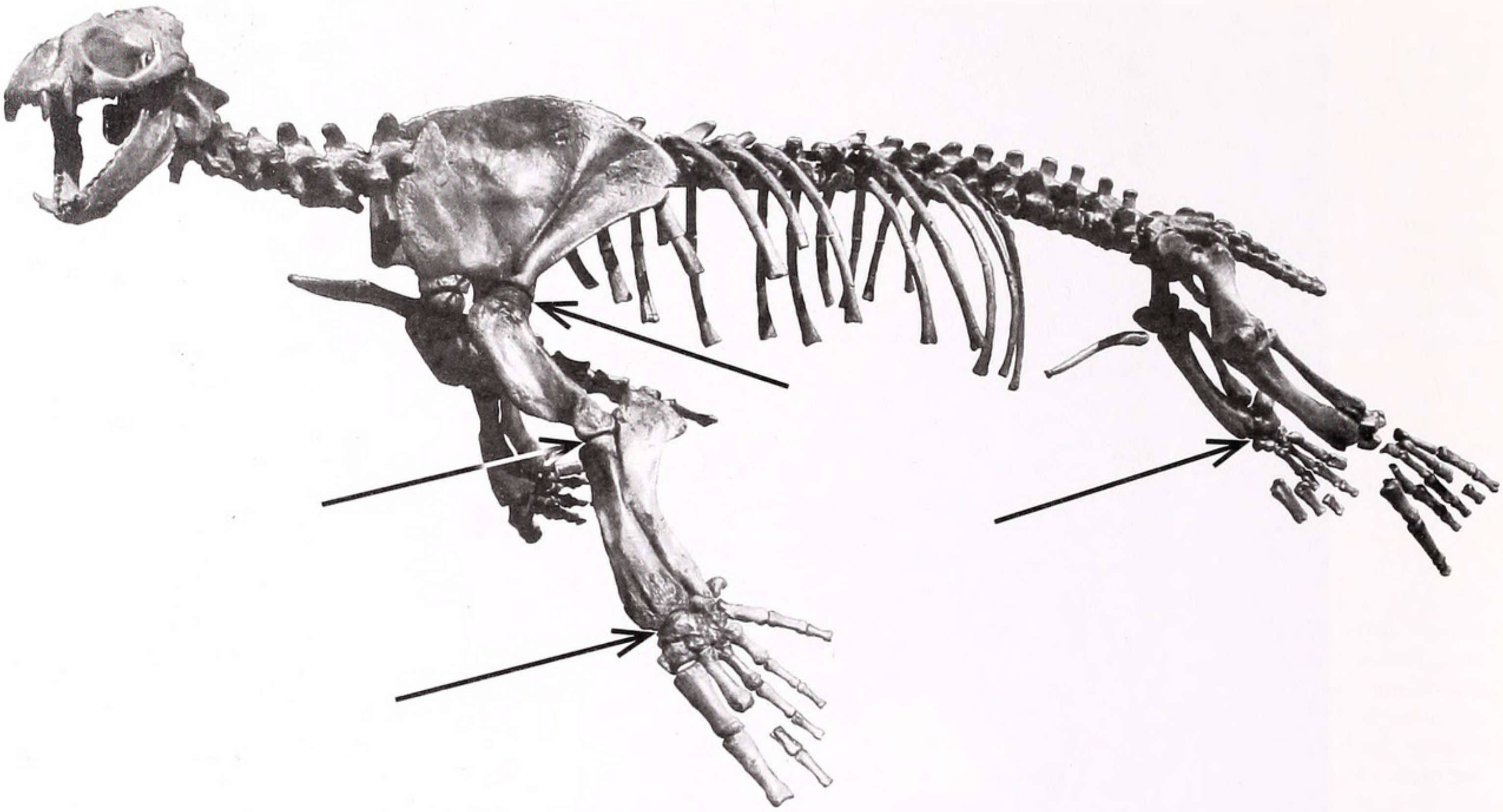

Figure 7 *Allodesmus kelloggi* Mitchell, 1966, holotype skeleton of adult confirmed male, LACM(VP) 4320, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA, left lateral view, arrows point to bones of this individual that have pits attributed to osteochondrosis (the right scapula and the left ectocuneiform) and to other areas of the body in other pinnipeds that are affected apparently by osteochondrosis. View is the right lateral view that was reversed. Total body length as restored and mounted is approximately 2.58 m (Mitchell, 1966:21).

glenoid articular surface. The pit that is attributable to osteochondrosis is approximately rectangular in shape, measures 12.5 mm by 10.7 mm in its maximum dimensions, is 4.1 mm deep, and is in Phase 2 on the scale of Dastugue and Gervais (1992).

This is one of the few fossil specimens on which it is possible to observe both sides of an affected joint and, as with the Recent specimen of a *Monachus schauinslandi* (Hawaiian monk seal) described above, the articular surface on the head of the corresponding right humerus shows no damage. This suggests that in pinnipeds trauma can occur on the weight-bearing articular surface of the scapula without leaving any detectable signs of damage on the head of the corresponding rotational surface of the humerus with which it articulated. This may be explained by the fact that the articular surface of the humeral head would have rotated through various arcs of several degrees relative to the single affected spot on the scapula, thus no single place on the humerus would have been affected.

The other instance of apparent osteochondrosis in the same individual of *A. kelloggi*, LACM(VP) 4320, is on its left ectocuneiform (Fig. 8B; also shown by Mitchell, 1966:pl. 22, figs. i, j). A pit on the articular surface of this ectocuneiform is approximately triangular in outline; its three sides measure 4.0 mm, 5.4 mm, and 2.7 mm; it is 2.1 mm deep; and it is in Phase 3 on the scale of Dastugue and Gervais (1992).

Because these two occurrences of possible osteochondrosis in the same individual are on fore and hind limbs on opposite sides of the animal, and because they are in different phases of the healing process, the traumatic events that caused them most likely happened at different times during the life of the individual. The fact that the animal was an old adult individual may have contributed to the cumulative damage that it experienced to its articular surfaces.

Allodesmus gracilis Barnes, 1995 (in Barnes and Hirota, 1995)
Figures 9, 10, 12B

COMMENTS. *Allodesmus gracilis* appears to be the most abundant species of allodesmine pinniped in the Sharktooth Hill Local Fauna (Barnes and Hirota, 1995). It was originally described on the basis of the holotype cranium and dentary, UCMP 81708, and some additional dentaries from the Sharktooth Hill Bonebed were referred to it. A normal adult confirmed male specimen, LACM(VP) 9723 (Fig. 9), which we now also refer to this species, includes several bones that were previously unknown for the species, and it confirms our referrals to this species of the other pathologic bones that are described herein. This partial skeleton represents a male, based on its large body size, proportionally large upper canine teeth, and presence of a baculum. It is a relatively old adult because all of the epiphyses in its skeleton are fused to their corresponding bones and the crowns of its upper cheek teeth are extremely worn.

This skeleton was first described by Barnes (1972), who identified it at the time of that writing as *Allodesmus kernensis*. Following the naming of *Allodesmus gracilis* Barnes, 1995, we now refer this individual to that species. Subsequently this skeleton has been restored and articulated (Fig. 9).

A referred pathologic partial skeleton, LACM(VP) 34944, is presumed to be a female based on its smaller body size and

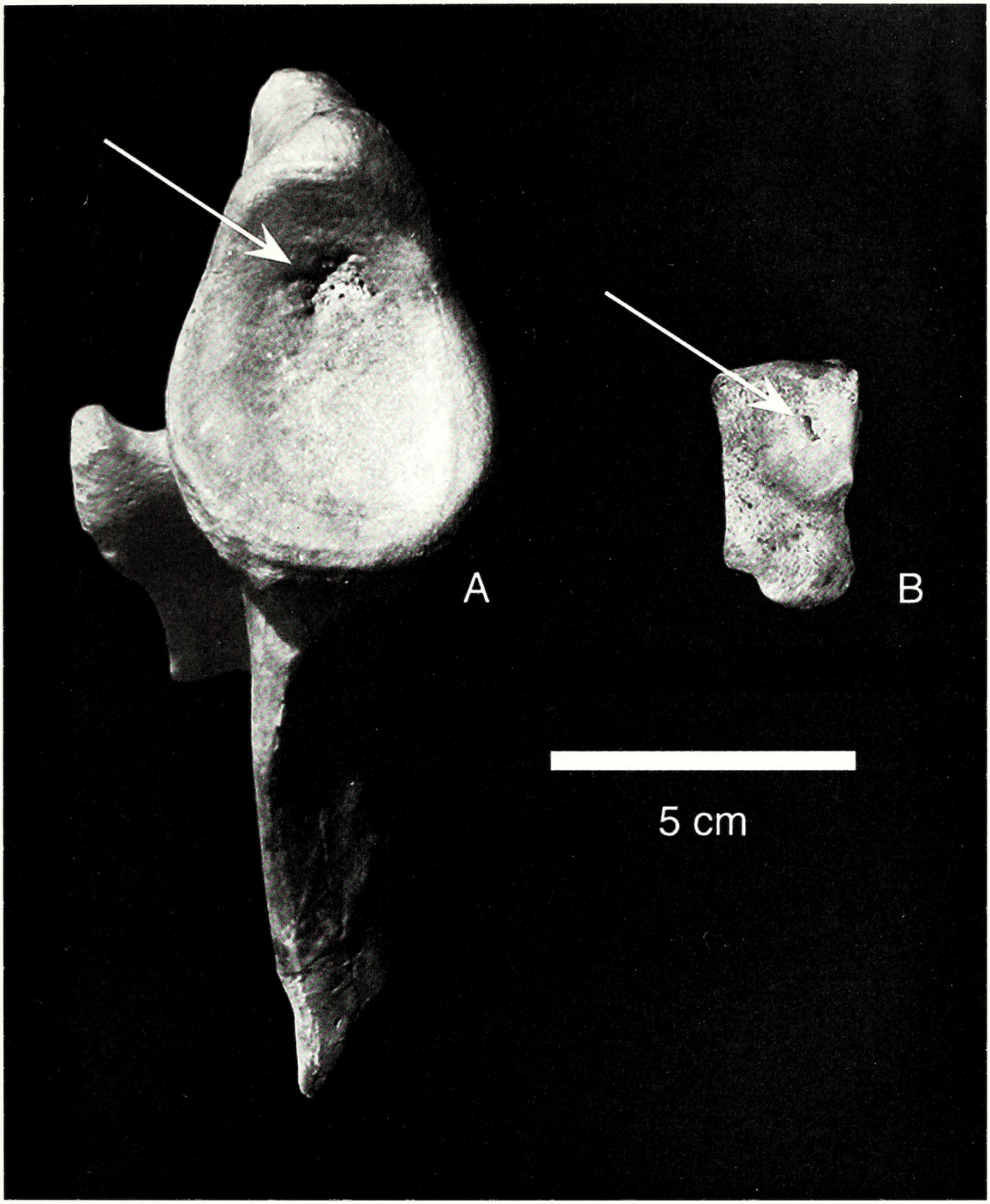

Figure 8 *Allodesmus kelloggi* Mitchell, 1966, holotype, adult confirmed male, LACM(VP) 4320, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA, bones of the same individual as shown in Figure 7 that have two occurrences of joint trauma attributed to osteochondrosis. **A**, right scapula in distal view with arrow pointing to pit in glenoid fossa; **B**, left ectocuneiform in lateral view with arrow pointing to pit on articular surface.

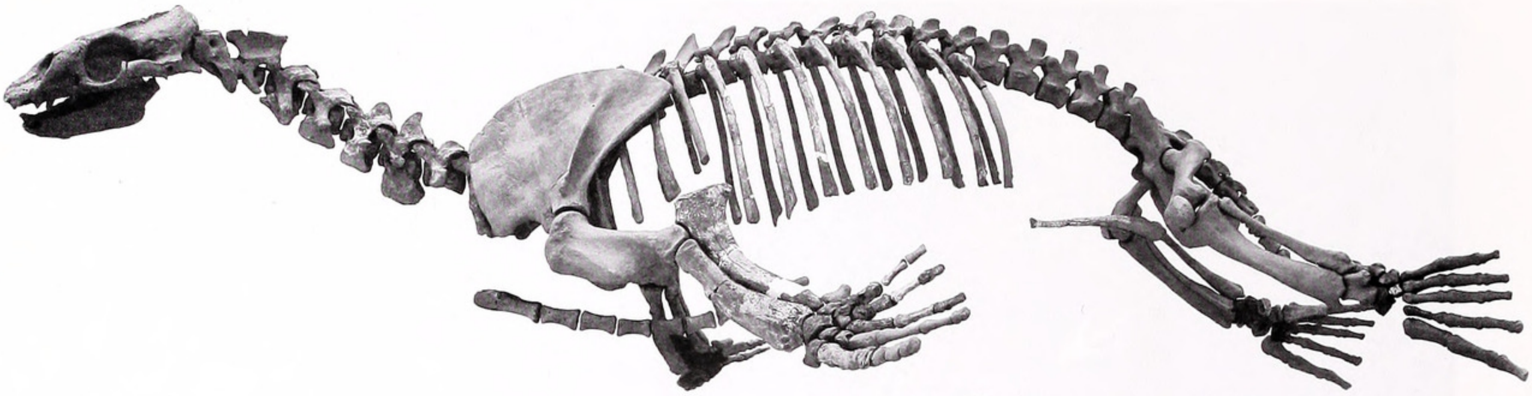

Figure 9 *Allodesmus gracilis* Barnes, 1995, referred skeleton of adult confirmed male, LACM(VP) 9723, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA, left lateral view. Total body length as estimated from vertebral centrum lengths was 3.30 m (Barnes, 1972:35), and as the restored skeleton as mounted is 3.73 m.

proportionally smaller canine teeth. It is identified as *A. gracilis* because its dentary shares with the dentary of the subadult male holotype (UCMP 81708; see Barnes, 1972:figs. 7, 10), and with other dentaries from the Sharktooth Hill Bonebed that have been referred by Barnes (1970, 1972) and Barnes and Hirota (1995) to *A. gracilis*, the following species-diagnostic characters: transversely relatively thin horizontal ramus, procumbent mandibular symphysis, relatively narrow mandibular symphyseal surface, procumbent root of the lower canine tooth, and two roots present on the m1. It is an adult because all of the epiphyses in its skeleton are fused to their corresponding bones and the crowns of its premolars are considerably worn.

The only radius of *A. gracilis* that has been previously illustrated (see Barnes, 1972:pl. 6d; but identified therein as *A. kernensis*) is part of the large adult male skeleton, LACM(VP) 9723 (Fig. 10A). The radius (Fig. 10B, D) of the smaller presumed female skeleton, LACM(VP) 34944, that has apparent osteochondrosis, resembles that of the male skeleton by having a relatively large and oblong distal articular facet for the scapholunar bone that is expanded anteroposteriorly (Fig. 10D). These radii both differ from the radii with the holotype (LACM(VP) 4320) of *A. kelloggi,* which have relatively smaller and more circular distal articular facets.

An isolated distal radial epiphysis, LACM(VP) 49539, can also be assigned to *A. gracilis* because its articular surface for the scapholunar is oblong (Fig. 10C), expanded anteroposteriorly in the same manner as the same articular surfaces on the radii of both the adult female skeleton, LACM(VP) 34944, and the adult male skeleton, LACM(VP) 9723, and differs from the more circular facets on the radii of the holotype, LACM(VP) 4320, of *A. kelloggi*. This unfused epiphysis is from a subadult individual, and is most likely from a male because it is slightly larger than the corresponding part of the adult male holotype of *Allodesmus kelloggi*. Similarly, the subadult male holotype of *A. gracilis,* UCMP 81708, is from a larger individual than the old adult male holotype of *A. kelloggi*, LACM(VP) 4320, adding to the evidence that adult males of *A. gracilis* were larger than adult males of *A. kelloggi*.

REFERRED PATHOLOGIC SPECIMENS. LACM(VP) 34944, a right radius belonging to a partial associated skeleton of an adult presumed female individual, collected by Joseph F. Arndt in 1966 at locality LACM 6688, and LACM(VP) 49539, the distal epiphysis of a right radius of a subadult presumed male, collected by Edward D. Mitchell, Jr., in August 1963 at locality LACM 1625.

REFERRED NORMAL SPECIMEN. LACM(VP) 9723, a partial associated skeleton of an adult confirmed male, collected by Michael K. Hammer on 5 and 6 December 1964 at locality LACM 1621.

DESCRIPTION. A medium-sized scar (Fig. 10D) that we attribute to osteochondrosis is located in the center of the articular surface for the scapholunar bone on the distal end of the right radius with the female skeleton, LACM(VP) 34944. The scar is oblong, with its long axis oriented anteromedially to posterolaterally, measures 10.2 mm by 5.0 mm, is 1.9 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992). The location of the scar is in the center of the weight-bearing surface of the bone.

A scar that we attribute to osteochondrosis is located on the anterior part of the articular surface for the scapholunar bone on the isolated distal radial epiphysis, LACM(VP) 49539 (Fig. 10C). The scar is approximately rectangular, measures 3.4 mm by 2.3 mm, is 1.1 mm deep, and is in Phase 2 on the scale of Dastugue and Gervais (1992). The location is on a weight-bearing surface of the bone.

Both of these scars could be described as representing classic occurrences of osteochondritis (B.M. Rothschild, personal communication, 2013), but we prefer to describe them here using the more general term, osteochondrosis.

Allodesmus, species undetermined
Figure 11B

COMMENTS. An isolated navicular (Fig. 11B) differs from the navicular (Fig. 11A) that is part of the adult male holotype skeleton, LACM(VP) 4320, of *Allodesmus kelloggi* by being slightly thicker proximodistally, having a deeper (more concave) facet for the astragalus, and having differently shaped distal articular facets. This navicular could belong to *A. gracilis,* but a navicular has not yet been identified for this species and, as will be shown in following text, at least two other unnamed species of Allodesminae occur in the Sharktooth Hill Bonebed (Figs. 12C, D). Thus, we identify LACM(VP) 49055 as belonging to an undetermined species of *Allodesmus*. It is probably from an adult male individual because it is approximately the same size as the navicular of the holotype skeleton of *A. kelloggi,* LACM(VP) 4320 (compare Figs. 11A and B).

REFERRED PATHOLOGIC SPECIMEN. LACM(VP) 49055, a left navicular of an adult presumed male, collected by Edward D. Mitchell, Jr., in October 1960 at locality LACM 1557 (field number E.D. Mitchell F-200).

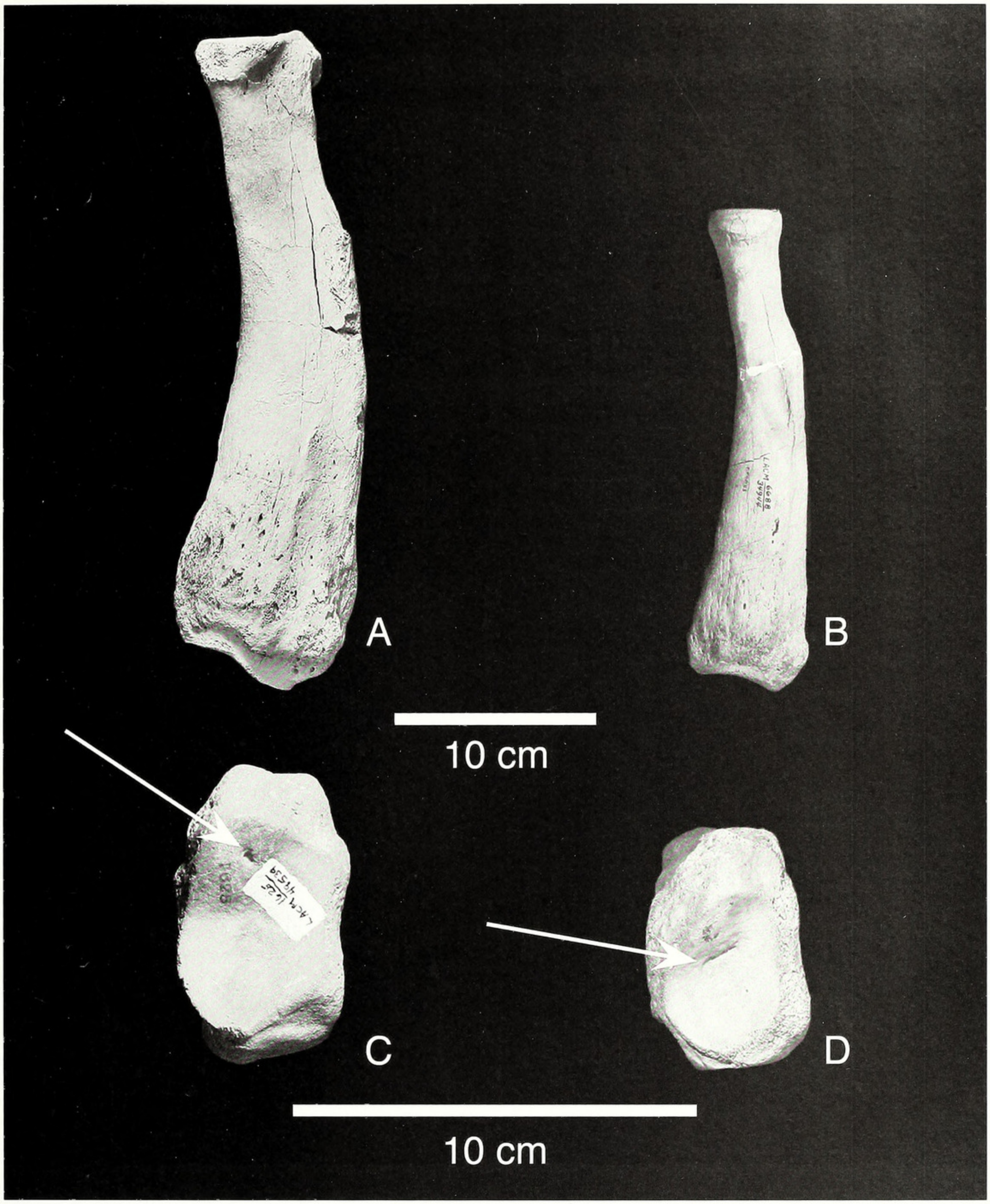

Figure 10 *Allodesmus gracilis* Barnes, 1995, referred right radii from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA. **A**, LACM(VP) 9723, adult confirmed male, the same individual as shown in Figure 9, lateral view; **B**, LACM(VP) 34944, adult presumed female, lateral view; **C**, LACM(VP) 49539, distal epiphysis of subadult presumed male, distal view, with arrow pointing to pit attributed to osteochondrosis; **D**, LACM(VP) 34944, adult presumed female, distal view, with arrow pointing to pit attributed to osteochondrosis. Scale bars = 10 cm, but **C** and **D** enlarged to two times the scale used for **A** and **B**.

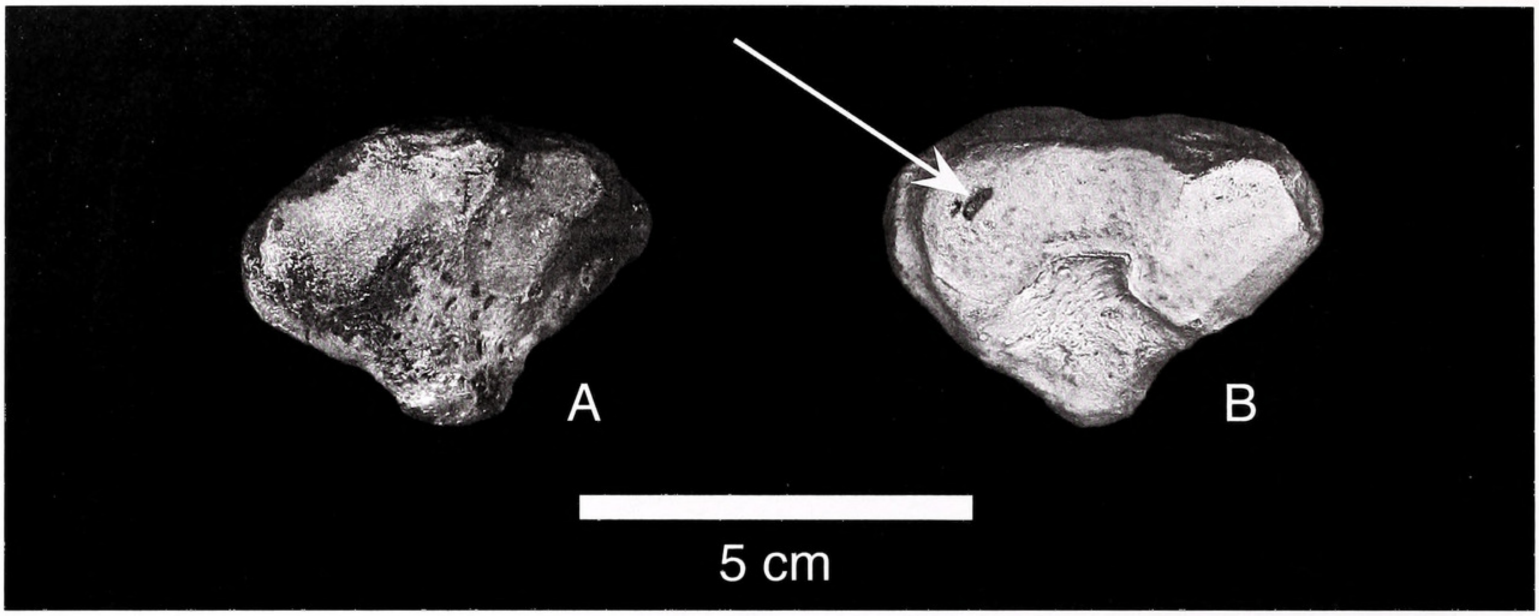

Figure 11 Allodesminae left naviculars, in distal views, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA. **A,** *Allodesmus kelloggi,* holotype, adult confirmed male, normal navicular, LACM(VP) 4320, the same individual as shown in Figure 7; **B,** *Allodesmus,* species undetermined, adult presumed male, LACM(VP) 49055, with arrow pointing to pit attributed to osteochondrosis.

DESCRIPTION. Two connected scars that we attribute to osteochondrosis are located on the distal surface of the navicular, LACM(VP) 49055, on the facet for articulation with the ectocuneiform (Fig. 11B). The smaller scar is approximately rectangular and the other is approximately square and is located dorsomedial to the smaller scar. The larger scar measures 5.3 mm by 2.2 mm, and the smaller scar measures 3.4 mm by 1.4 mm. Each scar is surrounded by several much smaller, round scars. These are in Phase 3 on the scale of Dastugue and Gervais (1992). They are located in a part of the foot that would have been subjected to flexion and extension during both terrestrial and aquatic locomotion.

Allodesminae, genus and species undetermined A
Figure 12D

COMMENTS. This species is represented by a complete calcaneum, LACM(VP) 154568, that is approximately the same size as the one that is part of the adult presumed female skeleton, LACM(VP) 34944, referred above to *Allodesmus gracilis*, but is smaller than the calcaneum that is part of the adult confirmed male skeleton, LACM(VP) 9723, of *A. gracilis* (see Fig. 12), and therefore is most likely from an adult female. It differs from these calcanea that we refer to *A. gracilis* (Fig. 12B) and from the calcanea of the holotype (LACM(VP) 4320) of *A. kelloggi* (Fig. 12A) by being much less stout and by having differently oriented articular facets for the astragalus, a more slender calcaneal tuber, and a larger posteromedially projecting process on the calcaneal tuber. Thus, LACM(VP) 154568 is probably not from a species of *Allodesmus,* but more likely is from another species of Allodesminae, probably unnamed, that has limb bones that are more gracile than those of *A. kelloggi, A. gracilis,* and the species identified in following text as Allodesminae, genus and species undetermined B.

REFERRED PATHOLOGIC SPECIMEN. LACM(VP) 154568, a right calcaneum of an adult presumed female, collected by Howell W. Thomas and William Hawes, Jr., approximately 1979 at locality LACM 3162.

DESCRIPTION. A very small scar that we attribute to osteochondrosis is located on the astragalar articular surface of the sustentacular process (Fig. 12D) of LACM(VP) 154568. The scar is approximately rectangular, measures 2.1 mm by 1.0 mm, and is in Phase 1 on the scale of Dastugue and Gervais (1992). It is located on a weight-bearing part of the bone. This scar could be described as a classic occurrence of osteochondritis (B.M. Rothschild, personal communication), but we choose to describe it by the more general term, osteochondrosis.

Allodesminae, genus and species undetermined B
(? = Desmatophocine B, Barnes, 1972)
Figure 12C

COMMENTS. This species is represented by an isolated calcaneum, LACM(VP) 21081 (Fig. 12C), which was broken during collecting and is missing its calcaneal tuber and parts of the sustentacular process. When complete it would have been approximately the same size as the calcanea that are part of the holotype adult male skeleton (LACM(VP) 4320) of *Allodesmus kelloggi* (Fig. 12A; and see Mitchell, 1966:pl. 22 q,r), but smaller than the calcaneum of the male of *A. gracilis* (LACM(VP) 9723; see Barnes, 1972:pl. 6c; and Fig. 12B herein), and thus it is probably from an adult male. It is a more robust bone than the calcaneum, LACM(VP) 154568, (Fig. 12D) of the other unnamed species of allodesmine identified above, and its sustentacular process is relatively larger and more medially directed than the same processes on the calcanea of both *A. kelloggi* and *A. gracilis*.

Thus, LACM(VP) 21081 most likely does not represent a species of *Allodesmus,* nor the unnamed gracile-boned species identified above as Allodesminae, genus and species undetermined A.

Barnes (1972:57) reported from the Sharktooth Hill Local Fauna an unnamed robust-boned allodesmine pinniped that is likewise not a species of *Allodesmus*, a species which at that time he identified as "Desmatophocine B." This latter species has a large and very stout dentary, and differs from species of *Allodesmus* by

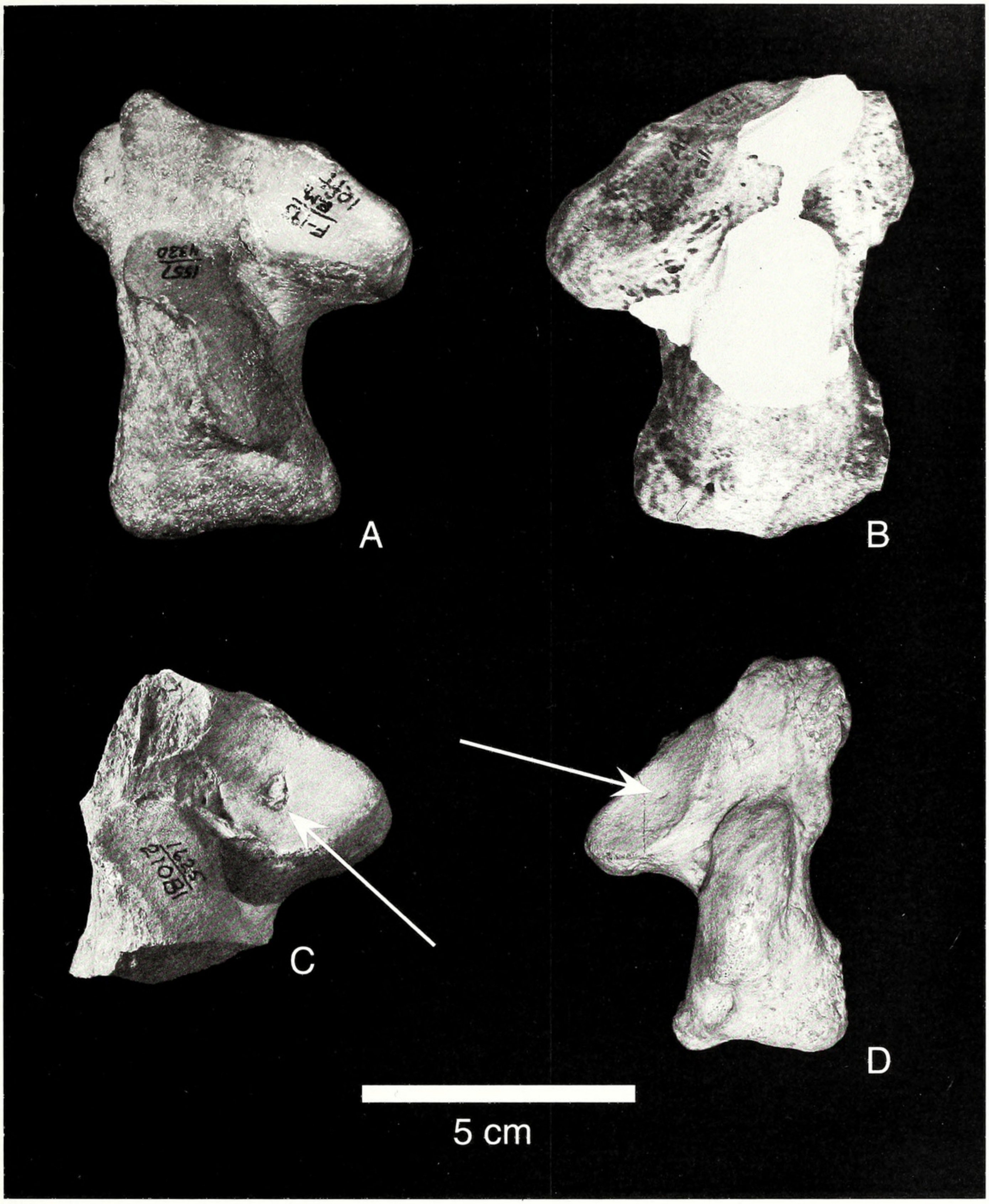

Figure 12 Allodesminae calcanea, in dorsal views, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA. **A**, *Allodesmus kelloggi* Mitchell, 1966, holotype, adult confirmed male, left calcaneum, LACM(VP) 4320, the same individual as shown in Figure 7; **B**, *Allodesmus gracilis* Barnes, 1995, adult confirmed male, referred right calcaneum, LACM(VP) 9723, the same individual as shown in Figure 9; **C**, Allodesminae, genus and species undetermined B, adult presumed male, distal part of left calcaneum, LACM(VP) 21081, with arrow pointing to pit attributed to osteochondrosis; **D**, Allodesminae, genus and species undetermined A, adult presumed female, right calcaneum, LACM(VP) 154568, with arrow pointing to pit attributed to osteochondrosis. **A** modified from Mitchell (1966:pl. 22, fig. r); **B** modified from Barnes (1972:pl. 6, fig. c).

lacking the m1–2 (see Barnes, 1972:fig. 23). It is possible that the relatively robust calcaneum, LACM(VP) 21081, belongs to the species that has been identified as "Desmatophocine B."

REFERRED PATHOLOGIC SPECIMEN. LACM(VP) 21081, the distal part of a left calcaneum of an adult presumed male, collected by Edward D. Mitchell, Jr., in August 1963 at locality LACM 1625 (field number ED Mitchell 499-30).

DESCRIPTION. The scar attributable to osteochondrosis on this calcaneum is located in the lateral part of the sustentacular surface that articulated with the astragalus (Fig. 12C). The scar is approximately triangular, measures 9.2 mm on the medial side, 7.3 mm on the lateral side, 3.9 mm on the proximal side, is 1.9 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992). It is located on a weight-bearing part of the bone. This scar could be interpreted as being a classic case of osteochondritis (B.M. Rothschild, personal communication, 2013), but we choose to describe it here using the more general term, osteochondrosis.

Order Cetacea Brisson, 1762
Suborder Mysticeti Flower, 1865
Superfamily Balaenopteroidea Gray, 1868
Family undetermined
?*Tiphyocetus temblorensis* Kellogg, 1931
Figure 13

COMMENTS. At least five species of mysticetes have thus far been identified in the Sharktooth Hill Local Fauna (Barnes, 1977:327, table 3). These include a probable balaenid (extinct right whale) that has not yet been identified to genus or species and four primitive balaenopteroid whales of uncertain relationships: *Parietobablena securis* Kellogg, 1931; *Tiphyocetus temblorensis* Kellogg, 1931; *Peripolocetus vexillifer* Kellogg, 1931; and aff. *Aglaocetus* sp. The first three of these Kellogg (1931) called cetotheres. These whales are not referable to the family Cetotheriidae, *sensu stricto* (*fide* Whitmore and Barnes, 2008), and thus we identify them here as balaenopteroids (*sensu* Fordyce and Marx, 2013) for which family relationships have not been ascertained.

A medium-sized mysticete is represented by an isolated complete radius, LACM(VP) 120052. Its laterally bowed diaphysis indicates that it is from the right side. In size and morphology it is similar to the proximal end of a left radius, CAS 4438, that Kellogg (1931:336, figs. 86, 87; and see Figs. 13A and 13C herein) referred to *Tiphyocetus temblorensis*. Kellogg's identification of CAS 4438 is possibly correct; however, because the bone was not found associated with the holotype cranium, CAS 4355, of *T. temblorensis*, there is no way to objectively confirm that identification. No other limb bones from the Sharktooth Hill Bonebed have ever been attributed to any particular species of mysticete.

Because the complete radius with a pathology, LACM(VP) 120052, appears to belong to the same species as the partial radius, CAS 4438, which Kellogg referred to *Tiphyocetus temblorensis*, it is identified here as questionably belonging to *T. temblorensis*. These two radii are too large to have belonged to the diminutive species *Parietobalaena securis*, and they are too small to have belonged to the rather large whale identified by Barnes (1977) as aff. *Aglaocetus* sp. The proximal epiphysis of LACM(VP) 120052 is fully fused to the diaphysis, and the distal epiphysis is partly fused to the diaphysis, indicating that this radius is from a young adult individual.

REFERRED PATHOLOGIC SPECIMEN. LACM(VP) 120052, the right radius of a young adult of undetermined gender, collected by Paul Kirkland and Roberta Kirkland on 23 October 1976 at locality LACM 1622 (field number P. Kirkland 9M9).

REFERRED NORMAL SPECIMEN. CAS 4438, proximal end of left radius of an adult of undetermined gender, collected by G Dallas Hanna and Charles Morrice in 1924 at CAS locality 905.

DESCRIPTION. On the radius LACM(VP) 120052 (Fig. 13D), a relatively large and deep scar attributable to osteochondrosis is located on the proximal articular surface for the humerus. Bruce M. Rothschild (personal communication, 2013) concurred with our diagnosis of this pathology, because it appears that a piece of cartilage on the articular surface was literally broken out. This scar is approximately triangular, its medial side measures 8.5 mm, its anterior side measures 11.0 mm, its posterior side measures 11.5 mm, it is 8.3 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992).

A radiograph (Fig. 13E) of the proximal end of this radius, made with the bone placed in same orientation as it is shown in Figure 13C, shows the depth of this pit. A cyst, or an area of avascular necrosis, lies within the bone distal to (beneath) the pit. This area of osteonecrosis appears in the radiograph as a semicircular "halo" that mimics the shape of this pit. This semicircular necrotic area results from impaired circulation that was probably related to the area that was affected by osteochondrosis.

?*Tiphyocetus temblorensis* Kellogg, 1931, or
?*Peripolocetus vexillifer* Kellogg, 1931
Figure 14

COMMENTS. An isolated atlas vertebra, LACM(VP) 154570, could have come from a whale similar in size to those having the above-described radii, and it therefore possibly represents *Tiphyocetus temblorensis*. However, *Peripolocetus vexillifer* is a similar-size mysticete in the Sharktooth Hill Local Fauna. Atlas vertebrae have not been identified for either of these species, and this atlas could thus pertain to either of them. It is too large to belong to an individual of *Parietobalaena securis*, and it is too small to belong to the species that was identified by Barnes (1977) as aff. *Aglaocetus* sp.

REFERRED PATHOLOGIC SPECIMEN. LACM(VP) 154570, an atlas vertebra of an adult individual of undetermined gender, collected by Lawrence G. Barnes on 17 March 1973 at locality LACM 1625 (field number L.G. Barnes 792).

DESCRIPTION. The articular surfaces and processes of the vertebra are well-formed, indicating that it is from an adult individual. A scar attributable to osteochondrosis is located on the articular facet for the right occipital condyle (Fig. 14). It is approximately circular, measures 4.8 mm by 4.3 mm, and is in Phase 2 on the scale of Dastugue and Gervais (1992).

Suborder Odontoceti (Flower, 1865) Flower, 1867
Family Physeteridae Gray, 1821
Subfamily Aulophyseterinae Kazár, 2002
Aulophyseter morricei Kellogg, 1927
Figures 15, 16

DISCUSSION. *Aulophyseter morricei* is a relatively small extinct sperm whale that differs from the extant giant sperm whale, *Physeter macrocephalus* Linnaeus, 1758, by having a relatively smaller head and smaller teeth. Currently these two species are classified in separate subfamilies. *Aulophyseter morricei* is known only from the Sharktooth Hill Bonebed. Few specimens of the species have been documented in the scientific literature, and Figure 15 shows a composite articulated skeleton of a juvenile individual.

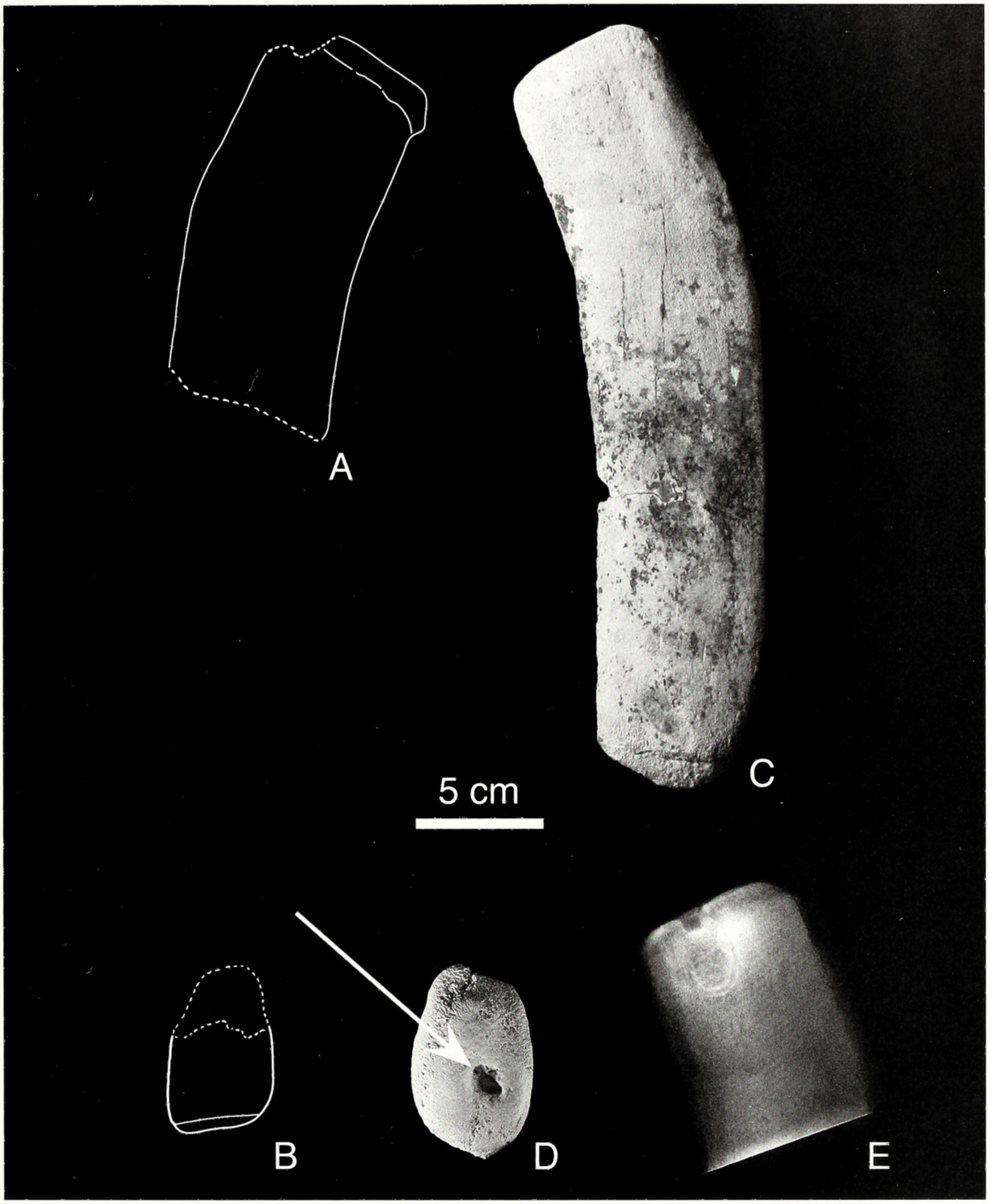

Figure 13 ?*Tiphyocetus temblorensis* Kellogg, 1931, referred radii from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA. **A** and **B**, proximal part of left radius, adult of undetermined gender, CAS 4438. **A**, lateral view; **B**, proximal view of proximal articular facet. **C–E**, right radius, adult of undetermined gender, LACM(VP) 120052. **C**, lateral view of complete bone; **D**, proximal view of proximal articular facet with arrow pointing to pit attributed to osteochondrosis; **E**, radiograph of proximal part of radius in lateral view showing a cyst, or an area of avascular necrosis, distal to the pit, in cranio-caudal section. **A** and **B** modified from Kellogg (1931:figs. 86, 87).

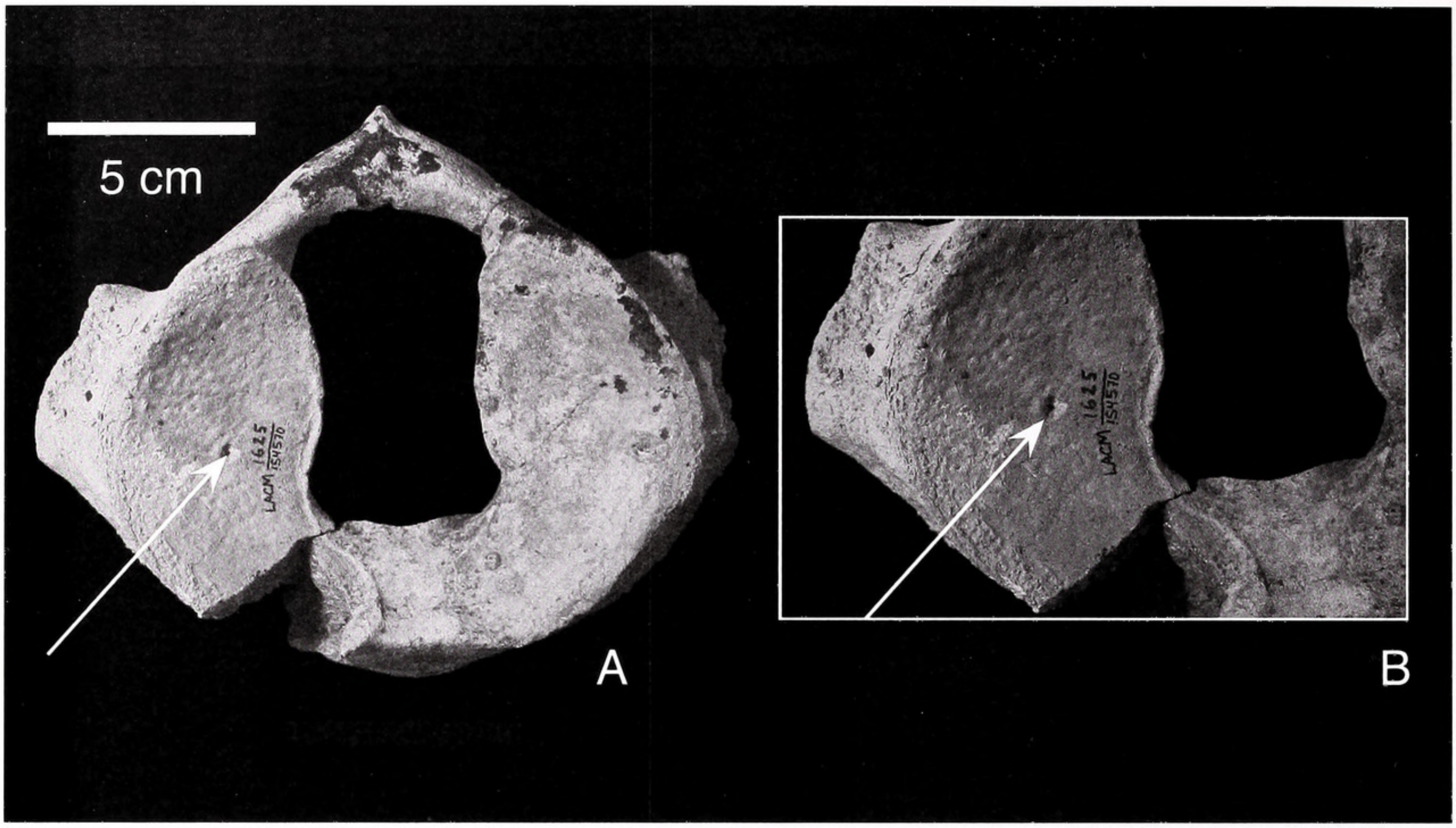

Figure 14 ?*Tiphyocetus temblorensis* Kellogg, 1931, or ?*Peripolocetus vexillifer* Kellogg, 1931, atlas vertebra, adult of undetermined gender, LACM(VP) 154570, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA, with pit attributed to osteochondrosis. **A**, anterior (cranial) view, arrow points to pit located on the right articular facet; **B**, enlarged view of right articular facet with close-up of pit. Scale bar pertains only to **A**.

The pathologic specimen, BVM 10737, of *A. morricei* that we report here differs from published images of the holotype and previously referred crania of this species. The tip of its rostrum does not have the morphology that was described by Kellogg (1927, 1931), and various features of this cranium differ from those of another cranium (UCMP 81661) from the Sharktooth Hill Bonebed that was referred to this same species by Kimura et al. (2006). Following, we explain our assignment of this pathologic specimen to the species *A. morricei.*

The holotype of *A. morricei* is a partial cranium, USNM 11230, of a large adult individual (Kellogg, 1927:5). It is missing the anterior part of the rostrum, the left side of the facial region, and the dorsal part of the nuchal crest that surrounds the posterior part of the supracranial basin. Although the anterior part of the rostrum is missing (see Kellogg, 1927:pls. 1, 2), it is evident that this individual had a relatively stout and dorsoventrally deep rostrum. This is in contrast with the dorsoventrally flattened and anteriorly tapered rostrum of extant *P. macrocephalus* (see Flower, 1868). The distal end of the holotype cranium was shown in published photographs as being restored with plaster (Kellogg, 1927:pl. 3; pl. 5, fig. 1), and this specimen appeared similarly restored in a subsequent publication as a line art illustration (Kellogg, 1931:fig. 106). The cranium that we here refer to this species, BVM 10737, demonstrates that although the length of the rostrum of the holotype was nearly correct as it had been restored, the shape of the distal end of the rostrum had been incorrectly restored.

The referred cranium, BVM 10737, demonstrates that the distal end of the rostrum of this species is even more stout than was shown in Kellogg's (1927:pl. 3; pl. 5, fig. 1; 1931:fig. 106) reconstructions. The distal end of the rostrum is unusually wide and blunt, the distal tip being flattened anteriorly. This flattening is unique among known sperm whales. In other fossil species for which the anterior tip of the rostrum has been discovered, it is narrow and tapered anteriorly, forming a relatively sharp point, similar to that in extant *P. macrocephalus* (see Flower, 1868:pl. 57).

The cranium, BVM 10737 (Fig. 16), is from an adult individual, and its preserved anatomy is similar to that of the holotype, USNM 11230. As with the holotype, it is missing the nuchal crest; that of the holotype removed by geologic processes, that of BVM 10737 removed by a tractor. BVM 10737 is slightly smaller than the holotype, its estimated zygomatic width (estimated because the lateral surfaces of the zygomatic processes of the squamosals are abraded) being 69.9 cm compared to 71.8 cm for the holotype. BVM 10737 measures 121.9 cm in condylobasal length, from the complete tip of the rostrum to the posterior surfaces of the occipital condyles. The holotype cranium, USNM 11230, measures 111.4 cm as preserved. Thus, BVM 10737 appears to represent the correct cranial morphology of adult males of *A. morricei.*

A slightly smaller adult cranium, UCMP 81661, from the Sharktooth Hill Bonebed was referred to *Aulophyseter morricei* by Kimura et al. (2006:10, fig.10), who suggested that the specimen was that of a female because it has a less massive anterior extremity of the rostrum. Unlike the supposed male crania, USNM 11230 and BVM 10737, it has a relatively gracile and anteriorly tapered rostral extremity. The tip of the rostrum, however, is very slightly flared and widened transversely, being almost a miniature version of the rostral tip of the presumed male specimen, BVM 10737. UCMP 81661 does have a complete nuchal crest, which is missing on both of the other specimens. Its thickened nuchal crest has the shape of a dorsally curved arch where it surrounds the posterior part of the supracranial basin.

REFERRED PATHOLOGIC SPECIMEN. BVM 10737, nearly complete cranium of an adult, probably of a male, collected by Robert Ernst between approximately 1993 and 1996 at locality LACM 6069 (field number Robert Ernst B.E. 7737/2).

NORMAL HOLOTYPE AND REFERRED SPECIMENS. USNM 11230, holotype partial cranium of an adult, probably of a male, collected by Charles Morrice during the first week of April 1924 at locality CAS 905; LACM(VP) 154100, associated partial juvenile skeleton of undetermined gender, articulated and mounted, including parts of another juvenile individual, LACM(VP) 154106, both specimens collected by Robert L. Clark in April 1982 at locality LACM 4956, and parts of other individuals from the same bonebed; UCMP 81661 (replica catalogued as LACM(VP) 154597), cranium of an adult, probably of a female, collected by Lawrence G. Barnes, Donald E. Savage, and J. Howard Hutchison on 17 May 1968 at locality UCMP V68131 (field number L.G. Barnes 151).

DESCRIPTION. A relatively large scar that we attribute to osteochondrosis is located near the dorsal margin of the left occipital condyle of the referred supposed male cranium, BVM 10737 (Fig. 16C). The scar is approximately oval, measures 30 mm wide transversely, 13 mm dorsoventrally, and 3 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992).

Family Allodelphinidae Barnes, 2006
Zarhinocetus errabundus (Kellogg, 1931)
Figures 17, 18

COMMENTS. *Zarhinocetus errabundus* is a large-bodied, long-necked, long-snouted, platanistoid odontocete. The species was originally named *Squalodon errabundus* by Kellogg (1931) on the basis of two isolated petrosals, USNM 11573 and USNM 11574, belonging to two different individuals, both from the Sharktooth Hill Bonebed. Two crania, LACM(VP) 21258 and LACM(VP) 149588, have been collected from the same bonebed, each with a petrosal lying adjacent to its basicranium. These petrosals are both conspecific with the holotype, USNM 11573, of *Squalodon errabundus.* Based on the identifications of these two crania it is evident that the species belongs neither in the genus *Squalodon* Grateloup, 1840, nor in the family Squalodontidae.

Thus, Barnes and Reynolds (2009) assigned this species to the new genus *Zarhinocetus,* and to the extinct platanistoid family Allodelphinidae (and see Barnes et al., 2010). *Zarhinocetus errabundus* is the only platanistoid odontocete that is currently known from the Sharktooth Hill Local Fauna, and fossils of the species have thus far been reported only from the Sharktooth Hill Bonebed.

We refer to *Z. errabundus* a pathologic atlas vertebra, LACM(VP) 119370. No postcranial bones have previously been referred to this species, the pathologic vertebra is extensively remodeled, and the basis for our identification of this atlas vertebra is as follows.

The partial cranium, LACM(VP) 21258, which lacks its rostrum, shares with the other referred cranium, LACM(VP) 149588 (Fig. 17), the following species-diagnostic characters: a wide facial surface, large and nearly vertically oriented occipital shield, asymmetrical cranial vertex, oval dorsal nares, very small nasal bones that are fused to the underlying frontal bones, narrow exposures of the frontal bones on the cranial vertex, anteroposteriorly aligned supraorbital maxillary crests, posterior ends of the premaxillae atrophied and retracted anteriorly to a location lateral to the nares, dorsal surface of each premaxilla depressed anterior to the nares, lateral side of the rostrum expanded laterally anterior to the antorbital notch and bearing a hemispherical tuberosity, zygomatic process of the squamosal nearly rectangular in lateral view, glenoid fossa facing anteroventrally, posterior part of the palatal surface convex, and lateral lamina of pterygoid (see Mead and Fordyce, 2009:86) large and fully ossified within the medial part of orbit.

The identification of cranium LACM(VP) 21258 as belonging to *Z. errabundus* allows assignment to this species of a complete nonpathologic atlas vertebra, LACM(VP) 13981 (Figs. 18A, C, D), of an old adult individual. This atlas articulates correctly with the occipital condyles of cranium LACM(VP) 21258, and the two might have belonged to the same individual because they were fossilized relatively near one another, being excavated only a few meters apart in the Sharktooth Hill Bonebed.

Finally, the pathologic atlas vertebra, LACM(VP) 119370 (see Fig. 18B), we refer to *Zarhinocetus errabundus* because it shares with the larger normal referred atlas vertebra, LACM(VP) 13981, such characters as overall relatively large size, separate and enlarged dorsal and ventral transverse processes, relatively large and widely spaced anterior articular facets for the occipital condyles that have prominent and flaring lateral margins, large fossa to accommodate the relatively large odontoid process of the axis vertebra, and large transverse foramina. This pathologic atlas differs from the normal one by being smaller overall and relatively shorter anteroposteriorly. Its transverse processes are broken off, and their original sizes thus cannot be determined. It likely belonged to a subadult individual of the species.

REFERRED PATHOLOGIC SPECIMEN. LACM(VP) 119370, an atlas vertebra of a juvenile of undetermined gender, collected by William Hawes, Jr., in January 1977 at locality LACM 3499.

REFERRED NORMAL SPECIMENS. LACM(VP) 13981, an atlas vertebra of an adult of undetermined gender, collected by William Harold Barnes in April 1965 at locality LACM 1625 (field number L.G. Barnes Locality 15); LACM(VP) 21258, cranium that is lacking the rostrum, and associated with a left petrosal and a right tympanic bulla, of an old adult of undetermined gender, collected by Edward D. Mitchell, Jr., on 8 September 1963 at locality LACM 1625 (field number E.D. Mitchell 581, Locality 499, square 39); LACM(VP) 149588, cranium and mandible with associated petrosal and tympanic bulla of an adult of undetermined gender, collected by Gregory Art in 1976 at locality LACM 4314 (field number L.G. Barnes 1818).

DESCRIPTION. A very large and deep scar attributable to osteochondrosis on the pathologic atlas vertebra, LACM(VP) 119370, is located on the ventral part of the articular facet for the right occipital condyle (Fig. 18B). This scar is approximately teardrop-shaped, the point of the "teardrop" being oriented dorsolaterally, and is 12.5 mm long, 8.7 mm wide, and 6.6 mm deep, and in Phase 2 on the scale of Dastugue and Gervais (1992).

In addition to this scar, the vertebra has other very severe pathologies and anomalies. Large areas of the bone are deformed and damaged by advanced osteoarthritis, resulting in bilateral asymmetry and damaged anterior articular facets. The scar that we attribute to osteochondrosis may have resulted from a piece of cartilage, or perhaps of bone, becoming detached during an impact injury. The osteochondrosis may have initiated the development of the osteoarthritis as well. These pathologies, being located in an anatomically critical area, where the spinal nerve cord joins the cranium, may have caused the death of this relatively young individual.

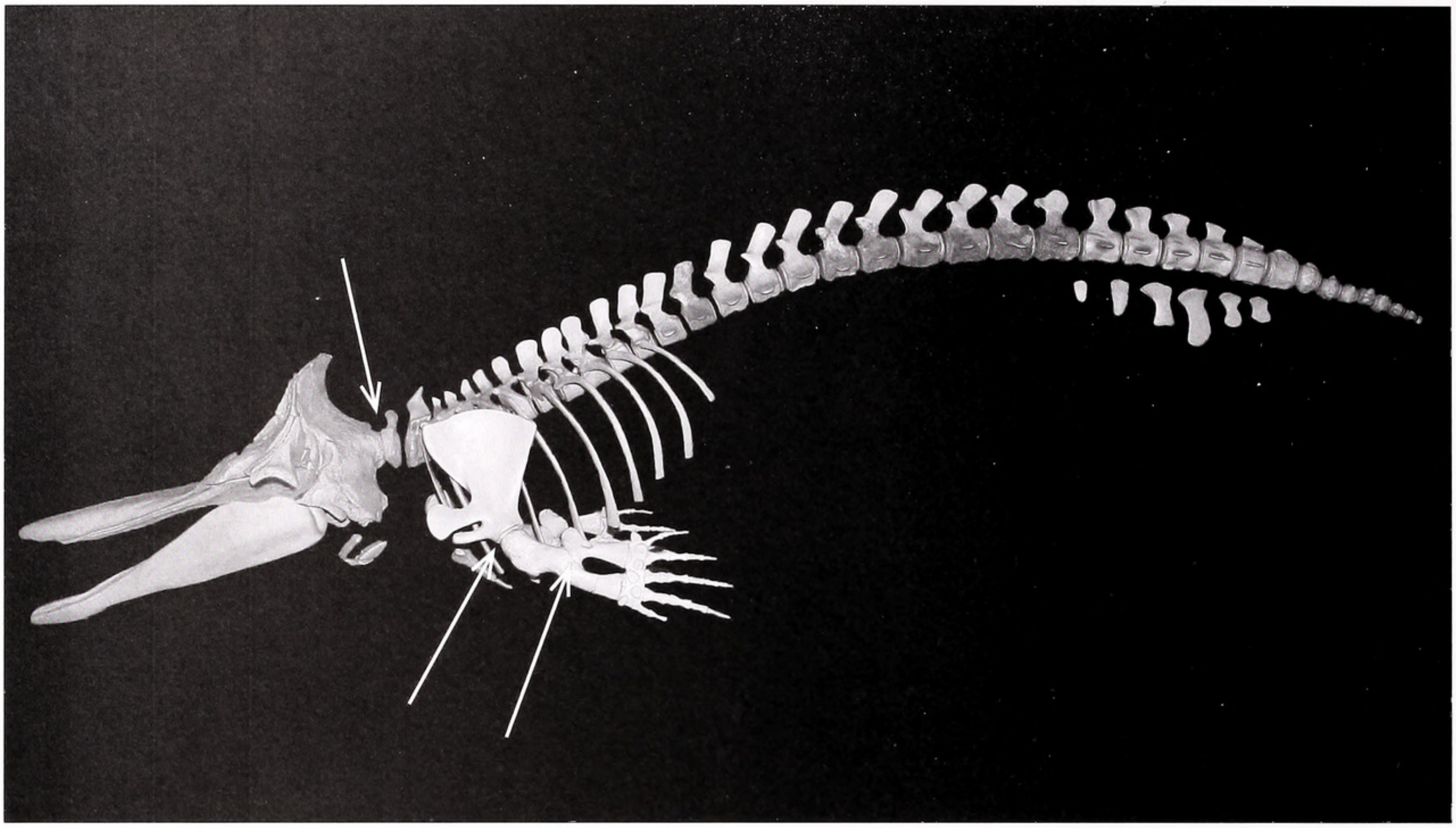

Figure 15 *Aulophyseter morricei* Kellogg, 1927, referred composite skeleton of juvenile of undetermined gender, based primarily on LACM(VP) 154100, with parts from another individual, LACM(VP) 154106, of similar size and ontogenetic age, and other specimens, all from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA, left lateral view. Arrow pointing to cranium–atlas joint indicates area where a pathology occurs in another referred specimen, BVM 10737 (shown in Fig. 16). Other arrows point to parts of the body that in other species of Cetacea are affected by osteochondrosis. Total body length of restored skeleton as mounted is approximately 2.99 m.

Family Kentriodontidae (Slijper, 1936) Barnes, 1978
Genus and species undetermined A
Figures 19A, 19C

COMMENTS. The size of the humerus LACM(VP) 98659, which measures 66.8 mm from the proximal surface of the head to its distal end, and 69 mm in overall length, suggests that it is from a relatively small dolphin that was approximately 2 m in body length. Kellogg (1931) named ten species of nonphyseterid odontocetes from the Sharktooth Hill Local Fauna, all of them based on isolated petrosals. One of these ten species is now understood to be the large allodelphinid platanistoid, *Zarhinocetus errabundus* (noted above).

In the same publication in which Kellogg (1931) named these odontocetes on the basis of petrosals he mentioned six isolated small odontocete humeri, four of which were illustrated (Kellogg, 1931:figs. 95–100). These humeri, which, then as now, are impossible to assign to species (as Kellogg, 1931:349, clearly stated), nonetheless do support the diversity of small odontocetes in the Sharktooth Hill Local Fauna that is indicated by the isolated petrosals that Kellogg named.

One of these humeri, CAS 4362 (see Kellogg, 1931:350–351,figs. 98, 99), closely resembles the pathologic humerus, LACM(VP) 98659, by being stout, having anterior and posterior borders of the diaphysis nearly parallel rather than converging proximally, and by having a relatively large deltopectoral crest. These two specimens may represent the same species.

Because no humeri have been assigned to any of the various small delphinoid odontocete species in the local fauna, the isolated pathologic humerus, LACM(VP) 98659, can be identified only as possibly belonging to a small species of the family Kentriodontidae. Fusion of its epiphyses to the diaphysis and its rugose surface texture both indicate that it is from an adult individual.

REFERRED PATHOLOGIC SPECIMEN. LACM(VP) 98659, a left humerus of an adult of undetermined gender, collected by Paul Kirkland and Roberta Kirkland on 17 or 18 January 1973 at locality LACM 3205.

REFERRED NORMAL SPECIMEN. CAS 4362, right humerus, collected by G Dallas Hanna and Charles Morrice in 1924 at CAS locality 905.

DESCRIPTION. On the isolated humerus, LACM(VP) 98659, a scar attributable to osteochondrosis is located near the posterior margin of the articular facet for the radius (Fig. 19C). It is oval, 5.2 mm long and 2.4 mm wide, and is in Phase 2 on the scale of Dastugue and Gervais (1992).

Genus and species undetermined B
Figures 19B, 19D

COMMENTS. Another isolated humerus, LACM(VP) 154569, from a delphinoid odontocete most likely represents a different species of Kentriodontidae. It is larger than the kentriodontids that are described above. This humerus measures 95.0 mm from the

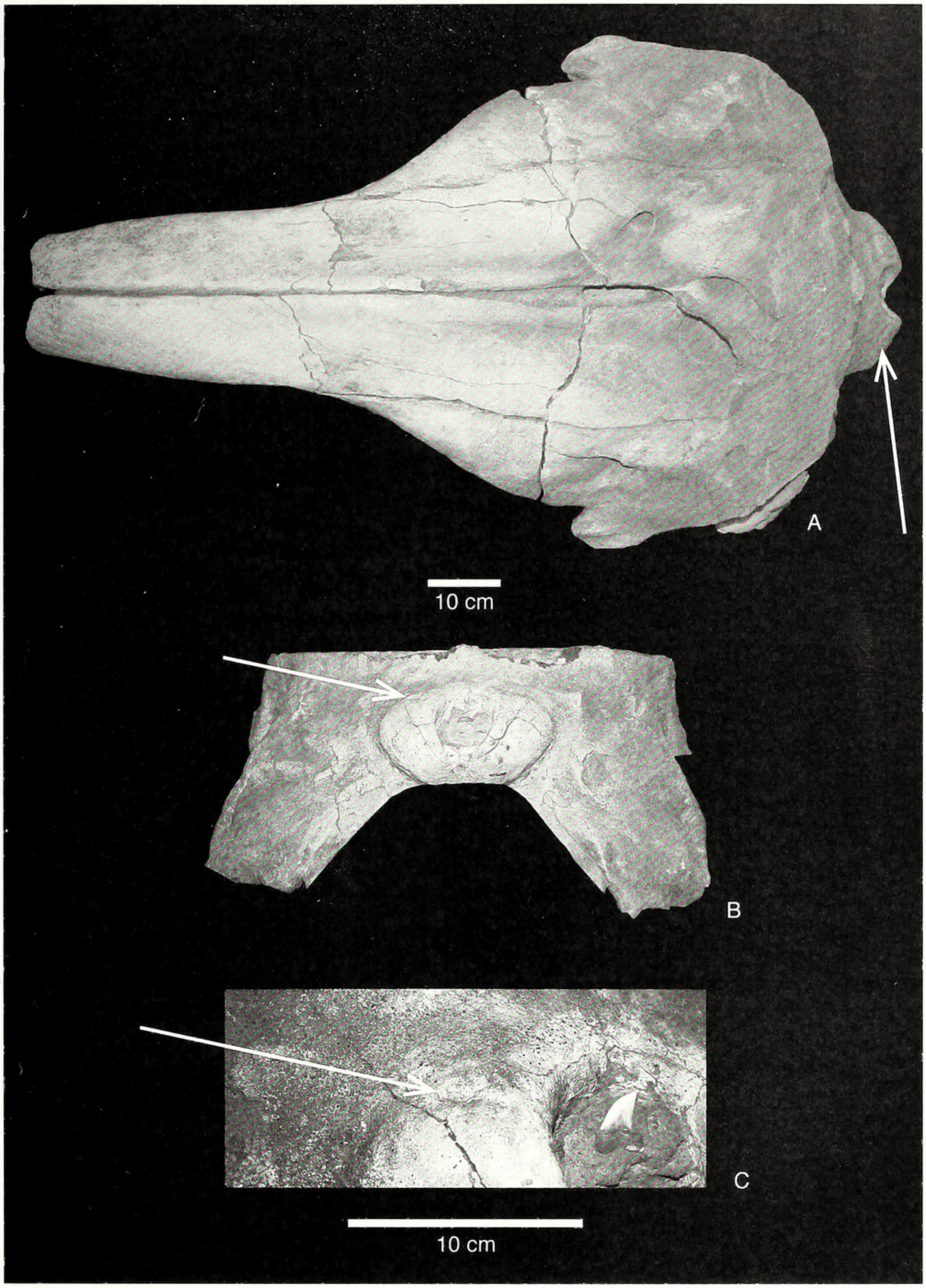

Figure 16 *Aulophyseter morricei* Kellogg, 1927, referred cranium of adult presumed male individual, BVM 10737, of the same species as shown in Figure 15, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA. **A**, dorsal view; **B**, posterior view; **C**, enlarged view of dorsal part of left occipital condyle. Arrow in each view points to pit attributed to osteochondrosis, which is located at apex of left occipital condyle. Scale bars = 10 cm, but **C** is enlarged to approximately 3.25 times the scale used for **A** and **B**.

Figure 17 *Zarhinocetus errabundus* (Kellogg, 1931), referred cranium and associated mandible of adult of undetermined gender, LACM(VP) 149588, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA, left lateral view.

proximal surface of the head to its distal end and 98.2 mm in total length. It is from a smaller animal than the large kentriodontid from the Calvert Formation in Maryland, *Hadrodelphis calvertense* Kellogg, 1966, which has a humerus that is approximately 156 mm long, its length being estimated from the scale that was provided by Dawson (1996:fig. 8). Thus, LACM(VP) 154569 apparently is from an intermediate-sized odontocete.

Species in the Sharktooth Hill Local Fauna to which this humerus could belong, based on the sizes of their petrosals because no other parts have been referred to them, are *Loxolithax sinuosa* Kellogg, 1931, and *Platylithax robusta* Kellogg, 1931. As with the above-mentioned smaller odontocetes, in the absence of identified postcranial bones of the various named odontocetes from the Sharktooth Hill Local Fauna, we identify this humerus as belonging to an undetermined genus and species of the family Kentriodontidae.

REFERRED PATHOLOGIC SPECIMEN. LACM(VP) 154569, a left humerus of an adult of undetermined gender, collected by William Hawes, Jr., and Howell W. Thomas in approximately 1979 at locality LACM 3162.

DESCRIPTION. A scar on the humerus LACM(VP) 154569 that we attribute to osteochondrosis is located on the articular facet for the ulna (Fig. 19D). It is approximately triangular, measures 6.9 mm on its lateral side, 7.1 mm on its anterior side, 7.3 mm on its posterior side, and is in Phase 2 on the scale of Dastugue and Gervais (1992).

EXAMPLE FROM THE MIDDLE MIOCENE ROSARITO BEACH FORMATION

GEOLOGY AND AGE. The marine middle Miocene Los Indios Member of the Rosarito Beach Formation (named by Minch, 1967), which is exposed south of La Misión and north of Ensenada in northern Baja California, Mexico, has yielded an extensive assemblage of fossil invertebrates and marine and terrestrial vertebrates (Minch et al., 1970, 1984; Deméré et al., 1984; Aranda-Manteca, 1990; Stewart and Aranda-Manteca, 1993; Barnes, 1998, 2002; Flores-Trujillo et al., 2000; Salinas-Márquez et al., 2014), which has been named the Mesa La Misión Local Fauna by Barnes (1998). Marine sediments of the Los Indios Member overlie a basalt that has yielded a radiometric date of 16.1 MA ± 2.1 MA (Minch et al., 1984:35). Mollusks from the Rosarito Beach Formation indicate a middle Miocene age (Minch et al., 1970; Aranda-Manteca, 1990). Minch et al. (1970) had suggested that camel species identified from the formation tentatively indicate a correlation with the Hemingfordian North American Land Mammal Age (early middle Miocene). Most of the marine vertebrate species in the Mesa La Misión Local Fauna are similar to, but not exactly the same as, those in the middle middle Miocene (Barstovian correlative) Sharktooth Hill Local Fauna in central California (Barnes, 1977, 1998, 2002; Aranda-Manteca, 1990).

Suborder Odonticeti (Flower, 1865) Flower, 1867
Family undetermined
Genus and species undetermined
Figure 20

COMMENTS. Two humeri, UABC 2877 and UABC 2878, which represent the same odontocete species, have been collected from the Rosarito Beach Formation. One of these humeri is pathologic and the other is normal. These humeri are unusual among those of known species of Odontoceti by having a relatively elongated and posteriorly curved diaphysis, an oval-shaped head that is oddly expanded proximodistally, a relatively large fossa in the midpart of the lateral side of the diaphysis, and a proximo-distally expanded deltopectoral tuberosity. They are from a species that was larger than both of the kentriodontids from the Sharktooth Hill Local Fauna described above. They are also too large and not of the appropriate morphology to have belonged to *Kentriodon diusinus* Salinas-Márquez, Barnes, Flores-Trujillo, and Aranda-Manteca, 2014, a small kentriodontine kentriodontid from the Rosarito Beach Formation. They do not appear to be readily assignable to any described species of the odontocete superfamilies Physeteroidea, Ziphioidea, Eurhinodelphinoidea, Platanistoidea, or Delphinoidea, and it is uncertain to what family of Odontoceti they might belong. Such humeri as these have not been discovered in the Sharktooth Hill Bonebed, nor, thus far, apparently in any other middle Miocene age

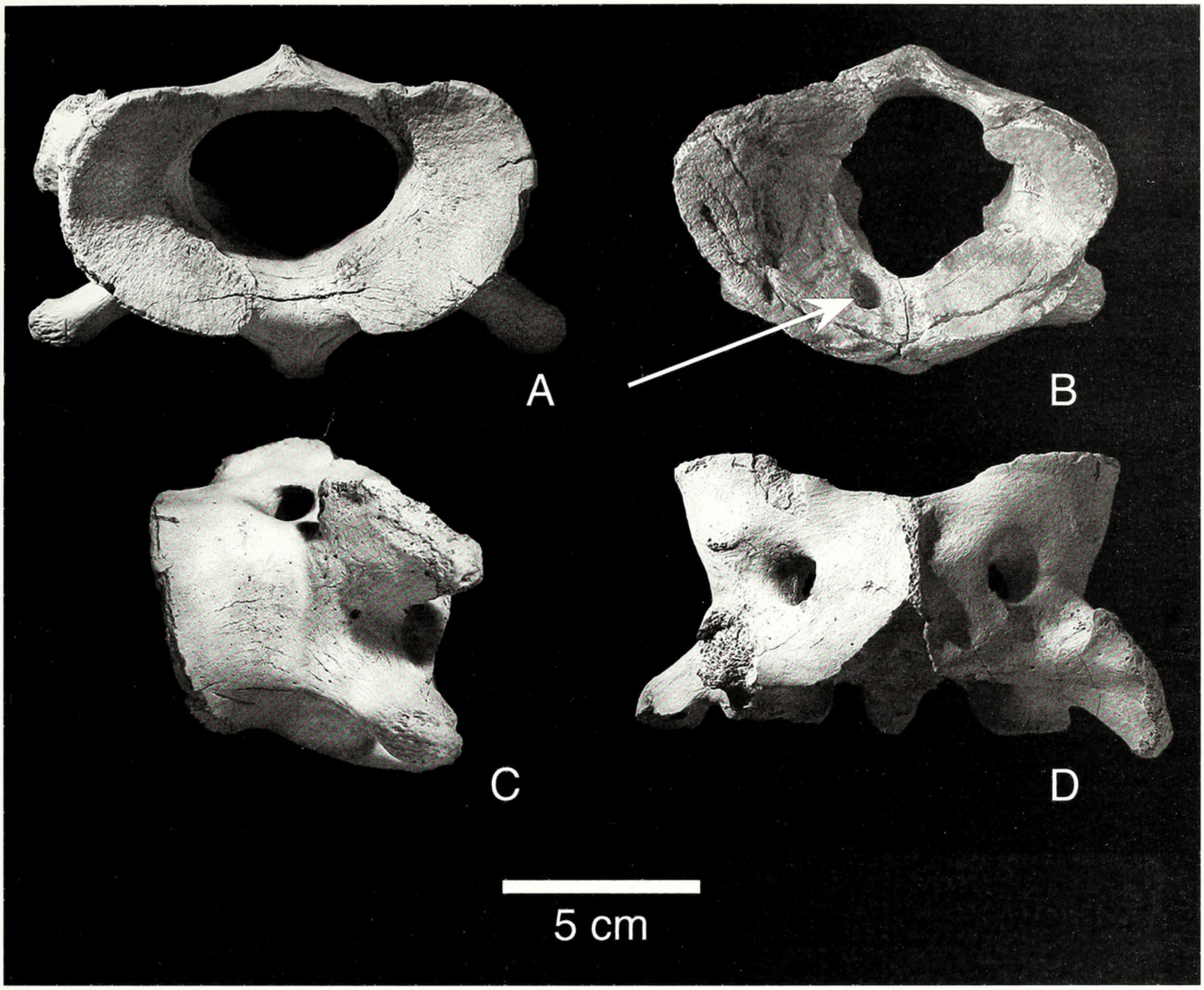

Figure 18 *Zarhinocetus errabundus* (Kellogg, 1931), referred atlas vertebrae of the same species as shown in Figure 17, from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA. **A**, **C**, **D**, LACM(VP) 21258, normal atlas vertebra of old adult of undetermined gender. **A**, anterior view; **C**, left lateral view; **D**, dorsal view. **B**, LACM(VP) 119370, pathologic and distorted atlas vertebra of juvenile of undetermined gender, with apparent osteoarthritis, with arrow pointing to pit attributed to osteochondrosis.

deposits in the North Pacific realm and they indicate the presence of an interesting and most likely undescribed species of odontocete in the Rosarito Beach Formation. Both specimens are from adults because their proximal and distal epiphyses are firmly fused to their diaphyses.

REFERRED PATHOLOGIC SPECIMEN. UABC 2878, an isolated left humerus of an adult of undetermined gender, collected by Francisco Javier Aranda-Manteca in January 1998 at locality UABC 103, in Bed G of the Rosarito Beach Formation, at Mesa La Misión, Baja California, Mexico.

REFERRED NORMAL SPECIMEN. UABC 2877, an isolated left humerus of an adult of undetermined gender, collected by UABC students from the Rosarito Beach Formation, at Mesa La Misión, Baja California, Mexico.

DESCRIPTION. A scar that we attribute to osteochondrosis is located on the articular facet for the radius on the distal end of humerus UABC 2878 (Fig. 20D). This scar can be interpreted as being specifically a case of osteochondritis (B.M. Rothschild, personal communication, 2013), but we choose here to describe it by the more general term, osteochondrosis. The scar is approximately rectangular, with the corners of the rectangle being oriented dorsoventrally and medio-laterally; it measures 5.7 mm by 5.0 mm, is 2.5 mm deep, and is in Phase 3 on the scale of Dastugue and Gervais (1992).

EXAMPLE FROM THE LATE MIOCENE MONTEREY FORMATION

GEOLOGY AND AGE. The part of the Monterey Formation that was deposited in the Capistrano Embayment, which is the southern part of the Los Angeles Basin in southern California (see Vedder et al., 1957; Fife, 1974), is early late Miocene in age,

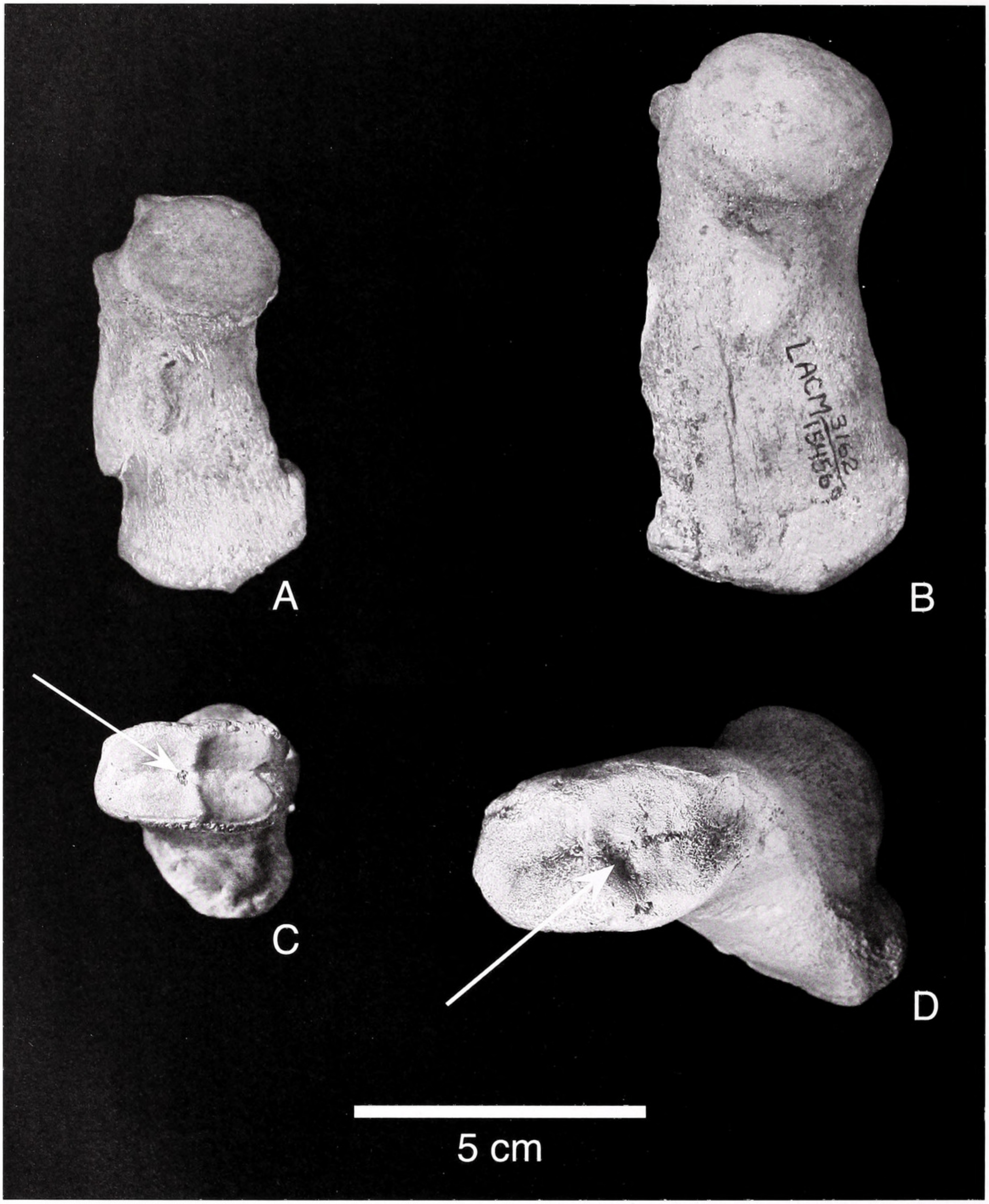

Figure 19 Kentriodontidae humeri from the middle middle Miocene Sharktooth Hill Bonebed, central California, USA, with joint traumas attributed to osteochondrosis. **A** and **C**, genus and species undetermined A, left humerus of adult of undetermined gender, LACM(VP) 98659. **A**, lateral view; **C**, distal view with arrow pointing to pit attributed to osteochondrosis. **B** and **D**, genus and species undetermined B, left humerus of adult of undetermined gender, LACM(VP) 154569. **B**, lateral view; **D**, distal view with arrow pointing to pit attributed to osteochondrosis.

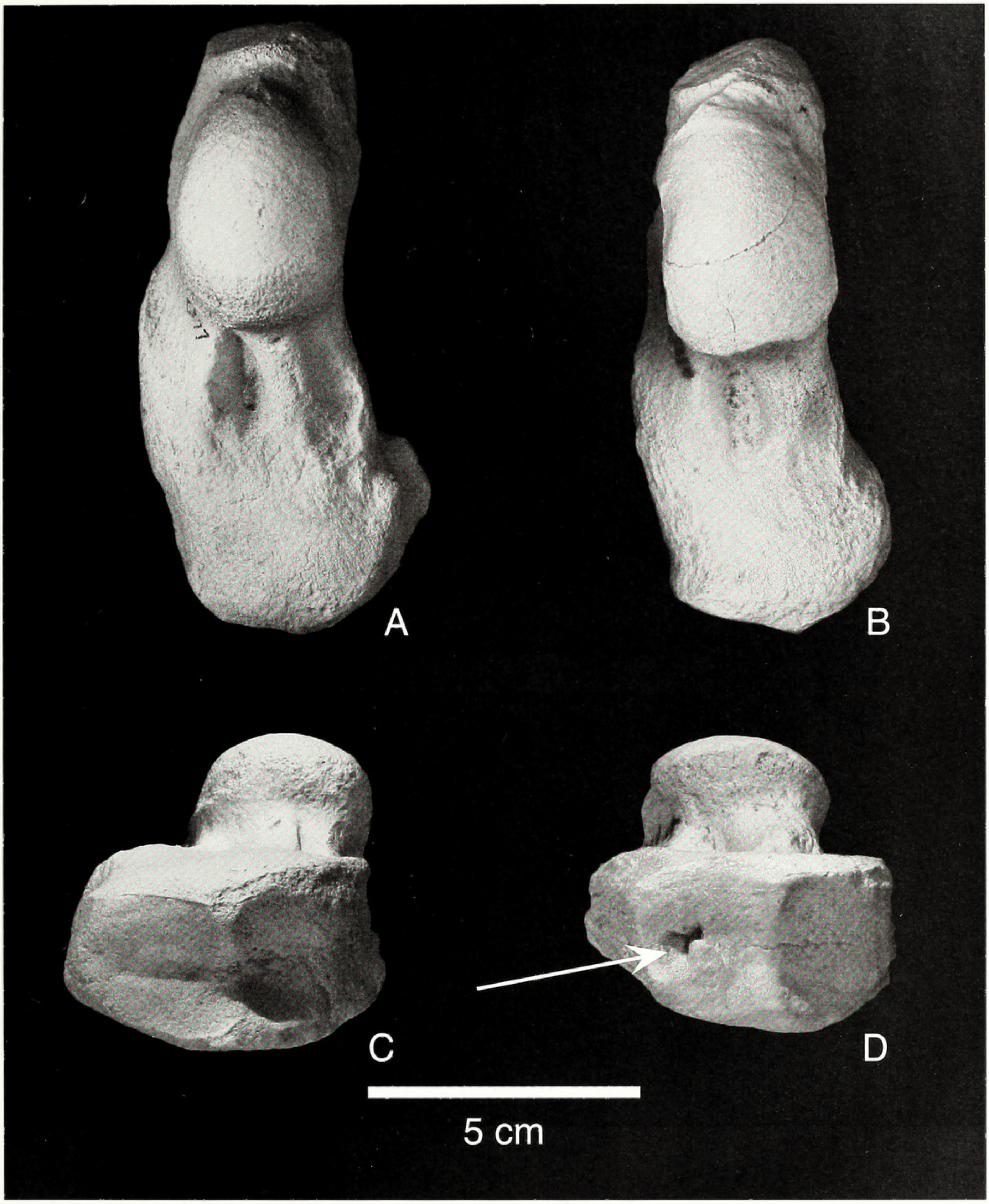

Figure 20 Odontoceti, family, genus, and species undetermined, two left humeri of adults of undetermined gender, from the middle Miocene Rosarito Beach Formation, Baja California, Mexico; one specimen normal and the other pathologic. A and C, UABC 2877, normal humerus. A, lateral view; C, distal view. B and D, UABC 2878, pathologic humerus. B, lateral view; D, distal view with arrow pointing to pit attributed to osteochondrosis.

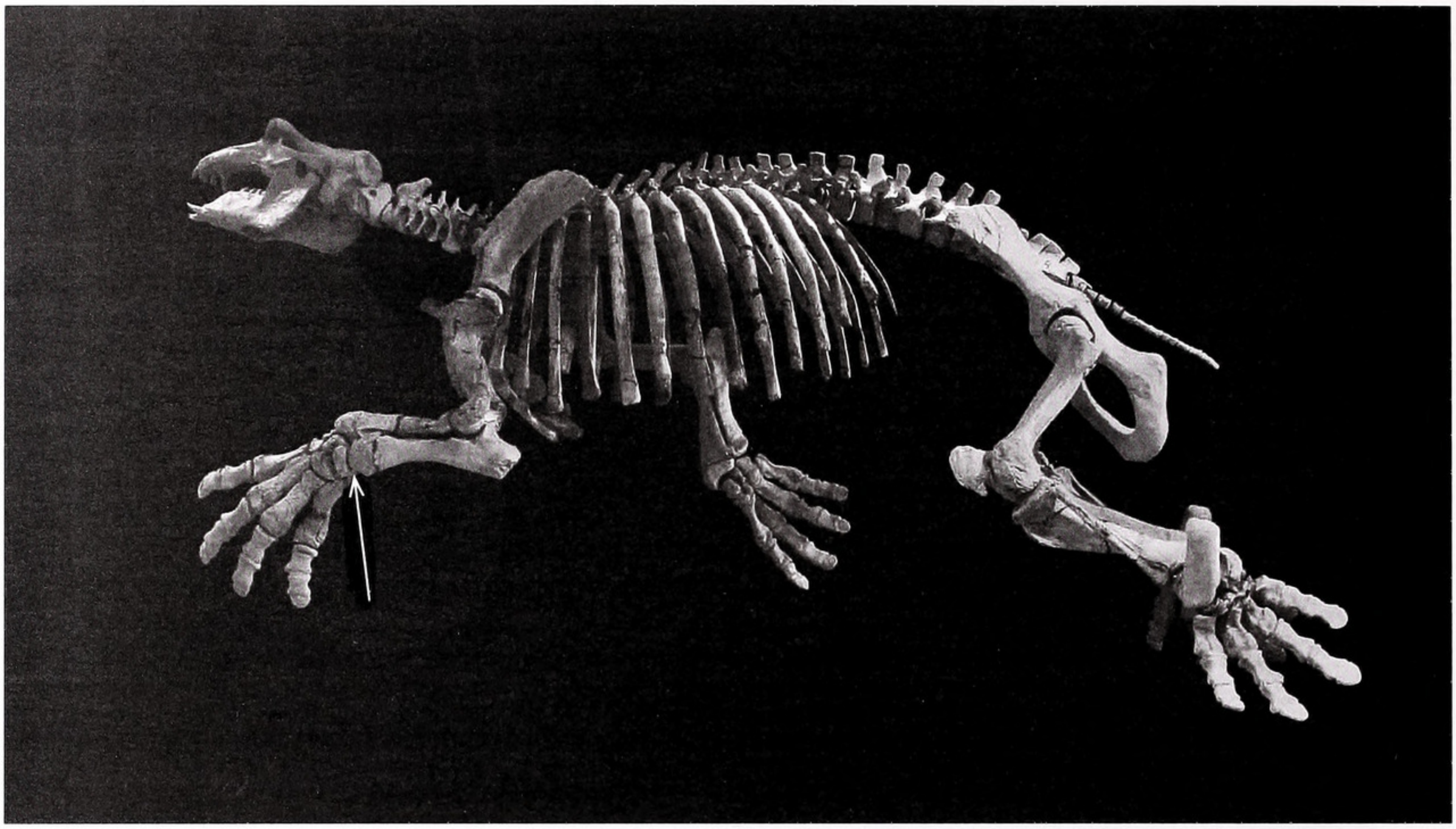

Figure 21 *Neoparadoxia cecilialina* Barnes, 2013, articulated restored holotype skeleton of a juvenile of undetermined gender, LACM(VP) 150150 (= OCPC 1892), from the early late Miocene Monterey Formation, California, USA; right lateral view. Arrow points to part of the body affected by apparent osteochondrosis. Total body length of restored skeleton as mounted is approximately 2.44 m.

approximately 9 to 12 million years old, and is correlated to the Mohnian foraminiferal stage and the "Margaritan" provisional mega-invertebrate stage (Addicott, 1972; Barnes, 1977:330, 1985:3, 2013), and indirectly to the middle part of the Clarendonian North American Land Mammal Age (see Repenning and Tedford, 1977:table 1; Tedford et al., 2004:fig. 6.2).

The pathological paleoparadoxiid specimen reported here is the holotype of *Neoparadoxia cecilialina* Barnes, 2013. It is from finely laminated, semiconcretionary diatomites, mudstones, and siltstones that are mapped as the upper part of the Monterey Formation (Vedder et al., 1957; Fife, 1974; Barnes, 1977:fig. 1, "area 20"). Strata from slightly higher in the same formation, and to the east of the type locality across Aliso Creek, contain the diatom *Denticulopsis dimorpha* (Schrader, 1973), which is an index species for the North Pacific Diatom Zone NDP 5D, which spans from 9.16 to 9.9 million years (Maruyama, 2000; Ventimiglia, 2010:16, fig. 14). Thus, the holotype of *Neoparadoxia cecilialina* is slightly older than 9.9 MA, and may be approximately 10 to 11 million years old.

Order Desmostylia Reinhart, 1953
Family Paleoparadoxiidae Reinhart, 1959
Subfamily Paleoparadoxiinae (Reinhart, 1959) Barnes, 2013
Neoparadoxia cecilialina Barnes, 2013
Figures 21, 22

COMMENTS. Members of the extinct mammalian order Desmostylia were distantly related to elephants and their relatives, and to the sirenians (Inuzuka, 2000). Their geochronologic range is from the Oligocene to late Miocene (Barnes, 2013). They were endemic to the North Pacific Ocean, amphibious and herbivorous, and apparently never very abundant or very diverse taxonomically. Through time, most species of the desmostylian family Paleoparadoxiidae progressively evolved larger body size, larger tusks, and more dorsally placed eyes (Barnes, 2013).

Currently recognized species of the paleoparadoxiid subfamily Paleoparadoxiinae are the small and primitive *Archaeoparadoxia weltoni* (Clark, 1991), known only by a subadult partial holotype skeleton from the latest Oligocene Skooner Gulch Formation in Mendocino County, California, USA, approximately 24 million years old (Addicott, 1967); *Paleoparadoxia tabatai* (Tokunaga, 1939), a species whose adult individuals were larger than *A. weltoni,* best known by the juvenile neotype skeleton (the "Izumi Specimen") from the early Middle Miocene Aoki Formation on Honshu, Japan, and approximately 18 million years old (Hasegawa et al., 1995, 2006; Inuzuka, 2000; Domning and Barnes, 2007); the relatively large and highly derived species, *Neoparadoxia repenningi* (Domning and Barnes, 2007), known only from the old adult holotype partial skeleton (the "Stanford Skeleton"), which is from the middle Miocene age Ladera Sandstone (see Skjei et al., 1965) that is exposed near Stanford University, San Mateo County, California, USA, and is approximately 14 million years old; and the relatively derived *Neoparadoxia cecilialina* Barnes, 2013, known only by the juvenile holotype partial skeleton, which is from the late Miocene Monterey Formation in southern California and is approximately 10 to 11 million years old. This latter species is the geochronologically youngest named paleoparadoxiid desmostylian.

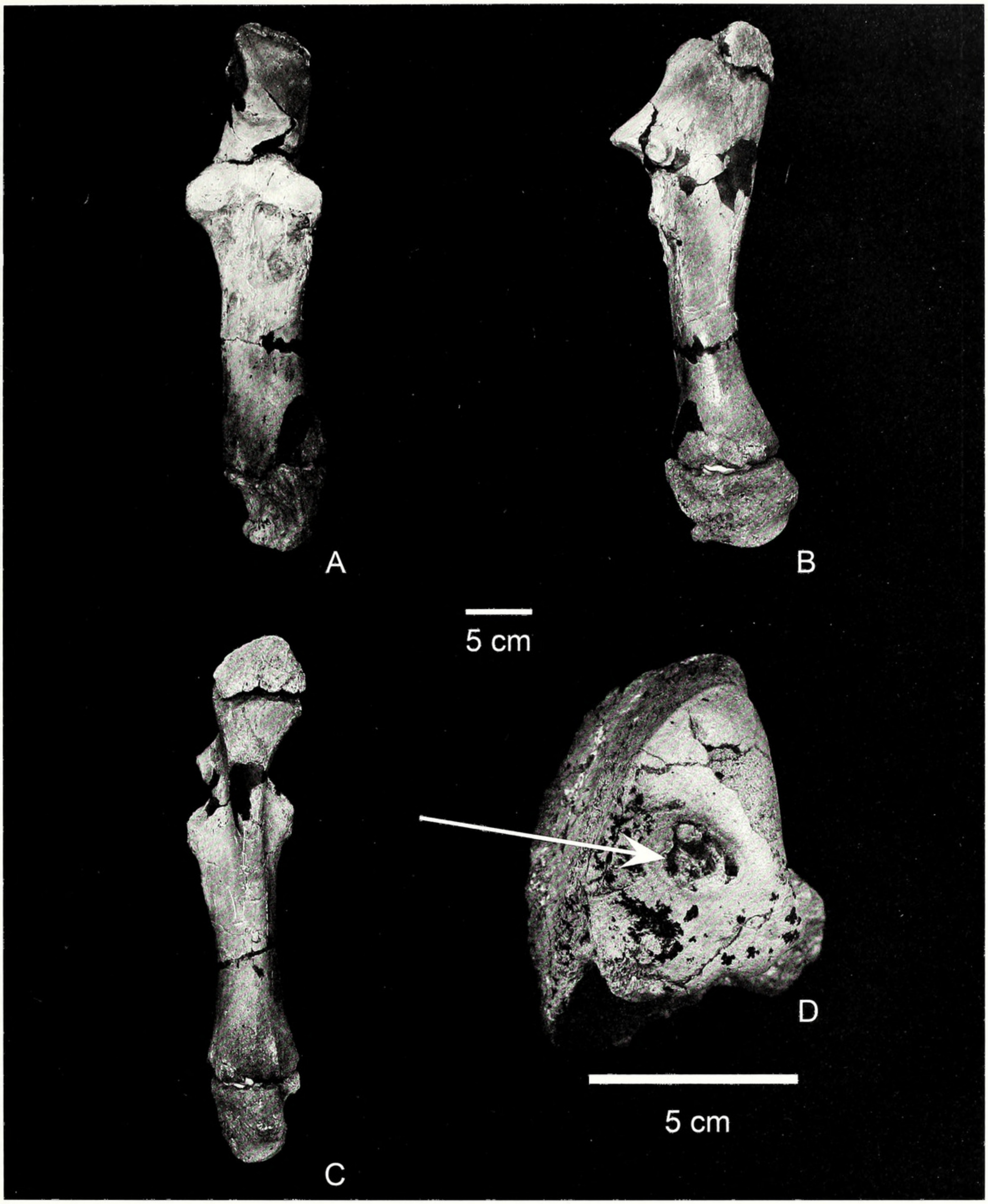

Figure 22 *Neoparadoxia cecilialina* Barnes, 2013, left ulna of holotype skeleton of a juvenile of undetermined gender, LACM(VP) 150150 (= OCPC 1892), the same individual as shown in Figure 21, from the early late Miocene Monterey Formation, California, USA. **A**, anterior (cranial) view; **B**, lateral view; **C**, posterior (caudal) view; **D**, distal view of distal epiphysis showing pit attributed to osteochondrosis indicated by arrow. Scale bars = 5 cm, but **D** is enlarged to three times the scale used for **A–C**.

PATHOLOGIC HOLOTYPE SPECIMEN. LACM(VP) 150150 (= OCPC 1892), a nearly complete skeleton of a juvenile of undetermined gender, collected by David N. Stevens, Scott Armstrong, Diana M. Weir, Marilyn Morgan, Sherri Gust, and others on 25 March 1998 at locality LACM 7506 (= OCPC 1002), Laguna Niguel, Orange County, California, USA.

DESCRIPTION. The holotype skeleton (Fig. 21) of *N. cecilialina* (see Barnes et al., 2011; Harris, 2011; Barnes, 2013) was a juvenile individual at the time of its death because its canine teeth were only partly erupted, its M3s and m3s were unerupted, and the epiphyses of its vertebrae and limb bones were still unfused to their respective bones. Based on its as-mounted total body length of approximately 2.44 m, had this juvenile grown to be an adult, it would have been larger than adults of any other named species of paleoparadoxiid. Among the other named species, it most closely resembles *N. repenningi* by having relatively very stout limb bones (Barnes, 2013).

A scar that we attribute to osteochondrosis is located on the distal articular surface of the left ulna of the holotype (Fig. 22D). It is oval, measures 24.15 mm by 18.93 mm, is 7.06 mm deep, and is in Phase 2 on the scale of Dastugue and Gervais (1992). Bruce M. Rothschild (personal communication) concurred with our diagnosis, noting that the reactive and resorbed bone in this pit, which almost looks as though the bone were "melted," is what would be expected in a case of osteochondritis.

An alternative diagnosis could be that the unusually large and deep scar on this bone is a result of spondyloarthropathy. However, spondyloarthropathy is a form of inflammatory arthritis that is characterized by a group of symptoms, including marginal syndesmophytes, vertebral squaring, reactive bone formation, asymmetrical erosive joint and bone disease, bone fusion, and sacroiliac joint disease. An example of a fossil marine mammal that does exhibit all of these conditions (Barnes et al., 2002) is the holotype skeleton of the dusignathine otarioid pinniped *Gomphotaria pugnax* Barnes and Raschke, 1991. The relatively complete and well-preserved holotype skeleton of *N. cecilialina* exhibits none of these other pathologies, its only pathology being the scar on the distal end of the ulna that we here attribute to osteochondrosis.

SUMMARY AND CONCLUSIONS

GENERAL OBSERVATIONS

Osteochondrosis (in earlier literature also referred to as osteochondritis dissecans) is, without surgical intervention, an irreversible abnormality of the joints of vertebrates, occurring principally in mammals, and primarily in young individuals. It can result from single or repeated traumas, osteochondral fractures, osteonecrosis, or hereditary epiphyseal dysplasia, and results in irregularly shaped shallow scars on the articular surfaces of bones. This pathology has been widely reported in humans, in both wild and domesticated living mammals, in extinct mammoths, and in fossil hadrosaurian dinosaurs. The condition can produce pain and debility, and sometimes surgery is undertaken to remedy it in humans and in valuable domestic mammals. It is unclear how osteochondrosis affects the well-being or survival of wild mammals.

Osteochondrosis has not been reported previously in any marine mammals, either fossil or Recent. This study indicates that this pathology does occur in both extant and fossil marine mammals. Among marine mammals, scars indicating occurrences of osteochondrosis appear on the articular surfaces of bones, range from 2.1 mm to 24.15 mm in diameter and the phases of lesion development range from active bone necrosis to complete new bone growth within the lesion.

PINNIPEDS. Osteochondrosis occurs in fossil and extant pinnipeds in their shoulders, elbows, wrists, ankles, and feet (see Fig. 7), probably resulting from injuries that the animals might have sustained when they were entering or leaving the ocean, clambering on rocks, fighting, or mating. These injuries occur in both rotational and flexible joints. In each skeleton, whether fossil or Recent, where it was possible to observe both sides of a joint, the damage exists on one bone and not on the corresponding articulating bone. This may indicate that damage is less likely to be spread over the larger articular surface of an opposing bone, but remains localized on an affected weight-bearing articular surface of a bone. This is the case in both observed individuals in which a pit is present on a scapula but not on the articulating surface of the corresponding humeral head.

DESMOSTYLIANS. One observed occurrence of apparent osteochondrosis in a paleoparadoxiid desmostylian is in the wrist, being a pit in the distal articular surface of the ulna (see Fig. 21). This could have been created when the animal was injured while entering or exiting the water.

CETACEANS. All observed occurrences of apparent osteochondrosis in fossil and extant cetaceans are on the occipital condyle of the cranium, on the anterior articular surface for the cranium on the atlas vertebra, in the shoulder, or in the elbow (see Fig. 15). The only observed occurrence of this pathology in a Recent cetacean is in the shoulder. Somewhat unexpected are the occurrences in the nonrotational and relatively immobile elbow joints of fossil cetaceans. Based on these occurrences in fossil cetaceans, osteochondrosis likely also occurs in the elbow joints of extant cetaceans. However, in many museum osteological specimens the humerus is preserved in articulation with the radius and ulna, connected by fibro-cartilage, and thus the articular surfaces in question usually cannot be readily observed. Damage to the elbow of cetaceans may result from tangential blows to the flipper. The injuries to the cranium–atlas joint and pectoral flippers of cetaceans may have occurred during aerial leaps, followed by impact with the water, or from active interactions, either intraspecific or interspecific. Such behaviors are common among both living mysticetes and odontocetes.

OSTEOCHONDROSIS IN RECENT (EXTANT) MARINE MAMMALS

Damage attributed to osteochondrosis totals only five observed occurrences, in four species, among 4,552 catalogued individual specimens of extant pinnipeds and cetaceans in the LACM Department of Mammalogy collections. This rate of occurrence, in only approximately 0.11% of the specimens observed, may indicate the approximate rate of incidence of osteochondrosis in marine mammal populations in general. The condition was found in otarioid pinnipeds, a phocid pinniped, and a cetacean. Its apparent absence in any of the inspected specimens of Sirenia (sea cows and manatees) may reflect the facts that (1) sirenians are not amphibious and thus do not experience trauma at the land–water interface, and (2) sirenians are typically not aggressive and thus are less prone to this type of injury.

PACIFIC WALRUS (*Odobenus rosmarus divergens*). Two isolated bones that were collected on beaches have pits attributable to osteochondrosis. An ulna, probably of a male, has a pit on the articular surface of the semilunar notch where it articulates with the humerus. The other, a tibia, probably of a female, has a pit on the articular surface were it articulates with the astragalus. In each occurrence the corresponding articulating bone is not present, so it is impossible to determine if both sides of the joint were affected.

CALIFORNIA SEA LION (*Zalophus californianus*). One young adult male individual was observed to have a pit attributable to osteochondrosis on the distal end of the humerus where it articulates with the ulna. The corresponding articular surface of the ulna of the same individual was not affected.

HAWAIIAN MONK SEAL (*Monachus schauinslandi*). An adult probable male individual has a pit attributable to osteochondrosis located on the glenoid fossa of the scapula where it articulates with the humerus. The corresponding articular surface of the humerus of the same individual was not affected.

NARWHAL (*Monodon monoceros*). One adult individual of unknown gender has a pit attributable to osteochondrosis present on the glenoid fossa of the scapula where it articulates with the humerus.

OSTEOCHONDROSIS IN FOSSIL MARINE MAMMALS

Osteochondrosis is the most plausible diagnosis for scars that occur on the articular surfaces of some bones of various fossil marine mammal species from middle and late Miocene age marine deposits along the eastern margin of the North Pacific Ocean. Specimens showing this condition are relatively rare, for example totaling only 11 individuals among 4,567 catalogued marine mammal specimens from the fossil-rich middle middle Miocene Sharktooth Hill Bonebed, which yields the Sharktooth Hill Local Fauna, in the Round Mountain Silt, in central California, USA, that are conserved in the collection of the LACM Department of Vertebrate Paleontology. Some of these catalogued specimens represent partial skeletons, and they thus include multiple bones, and one, the holotype skeleton of *Allodesmus kelloggi,* has two bones bearing scars attributable to osteochondrosis. The pathology occurs in approximately 0.24% of the fossil marine mammal specimens in the observed sample.

OTARIOID PINNIPEDS. From the Sharktooth Hill Bonebed, seven limb bones (scapula, radii, navicular, calcanea, entocuneiform) of adult male and female allodesmine otarioid pinnipeds, representing *Allodesmus kelloggi, A. gracilis, Allodesmus* sp., and two unidentified species, have abnormalities probably indicating occurrences of osteochondrosis.

DESMOSTYLIANS. The damaged articular surface on the ulna of a juvenile of the paleoparadoxiid desmostylian, *Neoparadoxia cecilialina,* from the early late Miocene Monterey Formation in southern California, USA, possibly resulted from trauma experienced while it was entering or leaving the ocean. Domning (2002) postulated that desmostylians were slow-moving, heavy-bodied, graviportal, amphibious animals that clambered over rocks and slippery surfaces in the intertidal zone along ocean shorelines while they foraged for algae or sea grasses. Such a lifestyle and environment undoubtedly subjected these animals to limb injuries. Indeed, the holotype skeleton of another species of paleoparadoxiid, *Neoparadoxia repenningi,* which is of an old adult, has healed fractures in both of its hind limbs (Repenning and Packard, 1990). Thus, it is significant that two of the three published paleoparadoxiid skeletons from California exhibit damage to their limb bones.

CETACEANS. Examples of damage attributable to osteochondrosis occur in fossil bones of both mysticetes (baleen whales) and odontocetes (echolocating toothed whales) from the Sharktooth Hill Local Fauna. A radius, questionably identified as the balaenopteroid mysticete whale, *Tiphyocetus temblorensis,* has such abnormalities on its proximal end. An atlas vertebra, possibly representing either *Tiphyocetus temblorensis* or another species of mysticete, *Peripolocetus vexillifer,* also has such an abnormality on its anterior articular surface. From the same bonebed a cranium of an adult probable male of the extinct sperm whale, *Aulophyseter morricei,* has an apparent occurrence of osteochondrosis on its occipital condyle. Also from the same bonebed, an atlas vertebra of a subadult individual of the large, long-necked, long-snouted allodelphinid platanistoid odontocete, *Zarhinocetus errabundus* has such an abnormality on its anterior articular surface. Two humeri from the Sharktooth Hill Bonebed, probably of kentriodontid delphinoid odontocetes, one a small species and the other a larger one, both have such abnormalities on their distal articular surfaces.

From the middle Miocene Mesa La Misión Local Fauna in the Rosarito Beach Formation in northern Baja California, Mexico, a humerus of an unidentified medium-sized odontocete cetacean has this same type of abnormality on its distal articular surface.

NEW FAUNAL AND TAXONOMIC RECORDS

The following new records for fossil Miocene marine mammals in the eastern North Pacific Ocean result from the identifications of bones that were used for this study:

An apparently unnamed species of allodesmine desmatophocid otarioid pinniped that has gracile limb bones is added to the Sharktooth Hill Local Fauna in central California, USA, which is middle middle Miocene in age, between approximately 14.5 and 16.1 million years old. In the present study this species is represented by an isolated calcaneum.

An enigmatic unidentified odontocete species is added to the middle Miocene age Mesa La Misión Local Fauna from the Rosarito Beach Formation in northern Baja California, Mexico. The species is known thus far only by two humeri that have very distinctive morphologies.

NEW ANATOMICAL RECORDS

The following anatomical records for Miocene marine mammal species result from identifications of bones that were used for this study:

Two partial skeletons, one of an adult male and another of an adult female, are referred to the allodesmine desmatophocid otarioid pinniped *Allodesmus gracilis* from the middle middle Miocene Sharktooth Hill Local Fauna, which is derived from the Sharktooth Hill Bonebed in the upper part of the Round Mountain Silt in central California. This species was previously known only by crania and mandibles.

An isolated calcaneum is referred to another unnamed species of allodesmine in the Sharktooth Hill Local Fauna, this one having robust limb bones. This bone may represent the same species that has been previously identified in this local fauna as "Desmatophocine B."

A complete radius, possibly belonging to the balaenopteroid mysticete whale *Tiphyocetus temblorensis,* is reported from the Sharktooth Hill Bonebed. This species was known previously by the holotype partial cranium and by a questionably referred partial radius.

A complete atlas vertebra, possibly belonging to either of the mysticete whales, *Tiphyocetus temblorensis* or *Peripolocetus vexillifer*, is reported from the Sharktooth Hill Bonebed.

A composite skeleton of a juvenile and a cranium of a large adult apparent male are referred to the extinct sperm whale, *Aulophyseter morricei*, from the Sharktooth Hill Local Fauna. This species was known previously by the holotype incomplete adult apparent male cranium, a referred adult apparent female cranium, isolated petrosals, and isolated humeri.

Two crania, one with its associated mandible, and two atlas vertebrae are referred to the long-snouted, long-necked allodelphinid platanistoid odontocete, *Zarhinocetus errabundus,* from the Sharktooth Hill Local Fauna. This species was known previously by the holotype and paratype isolated petrosals, and by a referred cranium.

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