Ann. Zool. Fennici 28:311–319
Helsinki 19 February 1992

ISSN 0003-455X

The Qualicum walrus: a Late Pleistocene walrus *(Odobenus rosmarus)* skeleton from Vancouver Island, British Columbia, Canada

C. R. Harington & Graham Beard

Harington, C. R., Paleobiology Division, Canadian Museum of Nature, Ottawa, Canada K1P 6P4.
Beard, G., Kwalikum Secondary School, P.O. Box 1000, Qualicum Beach, British Columbia, Canada VOR 2TO.

Received 12 April 1990, accepted 30 May 1990

An adult female walrus skeleton from Early Wisconsin glaciomarine clay near Qualicum Beach, Vancouver Island is the best preserved Pleistocene walrus specimen recorded from the west coast of North America. Paleoenvironmental, stratigraphic and geochronological data on the Qualicum walrus are in accord with known habits and habitat of modern walruses, as well as with knowledge of the species' past distribution — suggesting southerly advances during Pleistocene glaciations and northward withdrawals during interglacials.

1. Introduction

In May 1979, while collecting shellfish north of Qualicum Beach, Vancouver Island, William Waterhouse saw tusks protruding from the clay of a boulder-strewn beach. He tugged at the tusks and pulled up part of a skull.

Waterhouse's daughter took the skull to her teacher, the second author, who had been collecting fossils in the region for many years. She said her father had found the "lower jaw of a sea lion". Fortunately Bill Waterhouse had pinpointed the site and was able to lead the teacher there. Over the next few weeks, the second author returned several times to the site during low tide in order to excavate the rest of the specimen — most of a walrus skeleton — that had been buried lying on its back. Except for the vertebrae and ribs and pelvis, most of the bones were well preserved.

The purpose of this paper is to describe and figure the specimen, discuss its stratigraphic position, radiocarbon age, as well as its paleoenvironmental and paleobiogeographical implications. The fossil has been briefly mentioned before (Harington 1984:516–517).

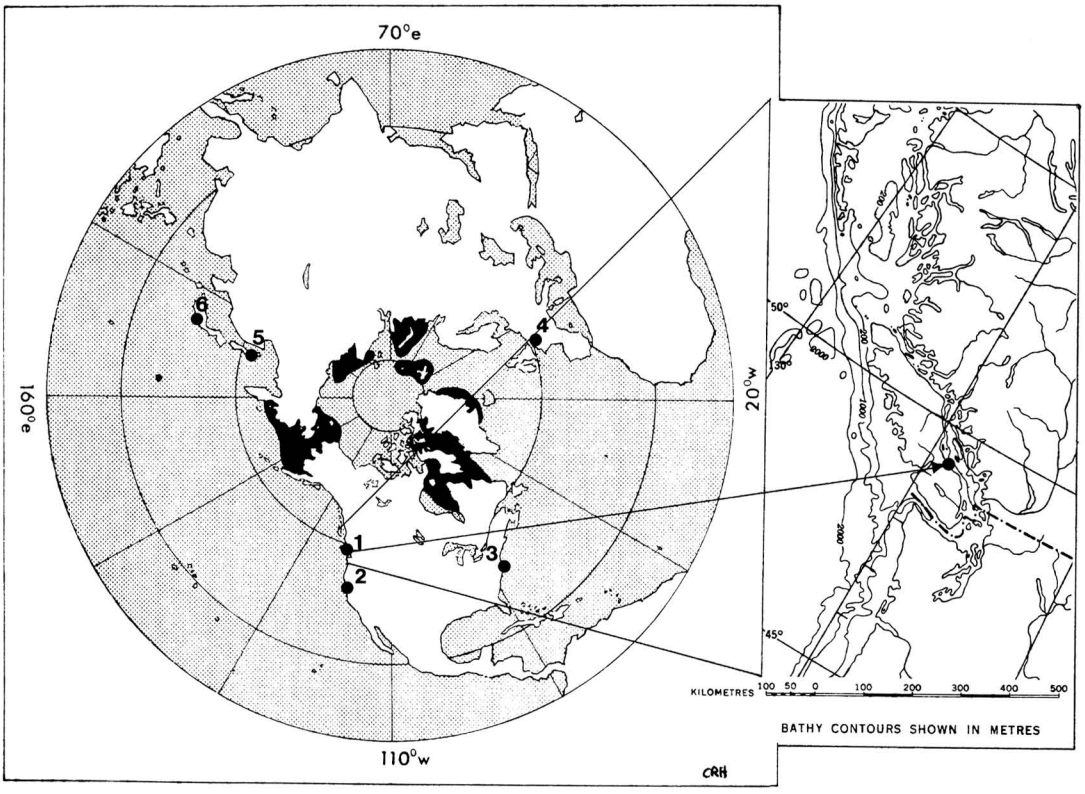

Fig. 1. Current world distribution of walruses (circumpolar black areas; after Fay 1982: fig. 3) and some of the more southerly localities where Pleistocene walrus remains have been found: 1. Qualicum Beach area, British Columbia, Canada; 2. San Francisco, California, U.S.A.; 3. Kittyhawk, North Carolina, U.S.A.; 4. Montrouge near Paris, France; 5. northern Sakhalin Island, U.S.S.R.; 6. Tokyo, Japan.

2. Locality and stratigraphic position

The specimen was found approximately 10 km northwest of Qualicum Beach (40°23′00″N, 124°34′50″W; Fig. 1), and lay about 20 m below the high tide mark in the intertidal zone (Fig. 2). The beach has a gentle slope at this point, although at low tide the water goes out nearly 45 m. In September 1980, the locality was covered with rounded boulders (apparently a lag deposit derived from the overlying Quadra Sediments), and the first author was able to confirm that the skeleton was *in situ* in bluish glaciomarine clay, containing fragments of mollusc shells and pebbles, estimated to be 20 m thick at the foot of 60 m-high coastal bluffs. The skeleton was excavated from Fyles' (1963) Unit 3 ("clay and stony clay with marine shells...") near the northern end of his Dashwood Sea Cliff section. Armstrong & Clague (1977:1473) and Hicock (1980) included both the lower stony glaciomarine sediments and the upper shell-rich marine sediments of Fyles' Unit 3 in the Dashwood Drift. Although Fyles considered the glaciomarine clay to be the basal portion of the Quadra Sediments, S. R. Hicock (pers. comm., 1981), who visited the site In July 1981, confirmed that the glaciomarine clay from which the walrus came is part of the Dashwood Drift.

Therefore, the walrus skeleton is best considered to be from a glaciomarine unit of the Dashwood Drift, and of Early Wisconsin age (Fig. 3). This age estimate based on stratigraphic study is not incompatible with a radiocarbon date on bone from the specimen.

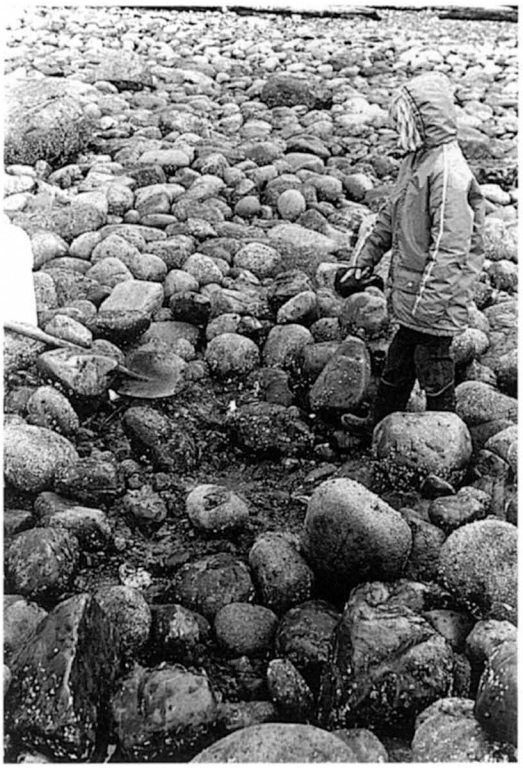

Fig. 2. Site of the Qualicum walrus find. Child points to the spot in bluish marine clay (Early Wisconsin Dashwood Drift) in which the skeleton was embedded. Overlaying boulders from the Quadra Sediments had to be removed in order to recover the fossil.

RADIOCARBON AGE (Ka)	TIME UNIT	GEOLOGIC CLIMATE UNIT	LITHOSTRATIGRAPHIC UNIT VANCOUVER ISLAND
0	HOLOCENE	POSTGLACIAL	———
10	LATE WISCONSIN	GENERAL DEGLACIATION (with local advances and retreats)	CAPILANO SEDIMENTS
13		FRASER GLACIATION	VASHON DRIFT
18			QUADRA SEDIMENTS
29	MIDDLE WISCONSIN	OLYMPIA NONGLACIAL (INTERSTADIAL)	
>62	EARLY WISCONSIN	SEMIAHMOO GLACIATION	* DASHWOOD DRIFT

Fig 3. Late Pleistocene stratigraphy of Vancouver Island, British Columbia (modified from Gascoyne et al. 1981: table 1). The asterisk indicates the source of the Qualicum walrus.

3. Radiocarbon date

Radiocarbon analysis on bone collagen derived from freshly collected rib and vertebra fragments of the Qualicum walrus yielded a date of > 40 000 B.P. (I-11617). The Libby half-life of 5568 years was used to calculate the age. No correction was made for variation in the atmospheric ^{14}C. Although this date is non-finite, a combination of the stratigraphic evidence indicating that the Dashwood Drift "is younger than Sangamon but older than classical [Late] Wisconsin" (Fyles 1963:19), Hicock's assessment of the stratigraphic position of the fossil, and the radiocarbon date of > 40 000 B.P. suggest an Early Wisconsin age for the specimen.

4. Description

Order **Carnivora** Bowdich, 1821

Family **Odobenidae** Allen, 1880

Genus ***Odobenus*** Brisson, 1762

Odobenus rosmarus (Linnaeus, 1758)

The specimen (NMC 38490; Tables 1, 2; Figs. 4, 5) consists of a large part of an adult walrus skeleton, approximately 12 years old according to a study of annuli counted in a longitudinal section through the cementum of a premolar tooth (RP^4; Fig. 6). The specimen is considered to represent a female based on the relatively small tusk dimensions. The fact that no baculum was found with the skeleton — it would have been approximately 50 cm long (Fay 1982: fig. 22), and therefore difficult to overlook had the skeleton been of a male — supports that contention. Further, F. H. Fay (pers. comm., 1984) considers that the annuli in the sectioned RP^4 have a typical female character: he has noticed that, commonly, there are about six thick internal layers followed by a rapid change to fine annuli in female walruses, as in this specimen.

Parts of the specimen that are preserved follow.

Cranium (Fig. 4). Complete except for damage to the region surrounding the occipital condyles, the central portion of the braincase, the left zygomatic arch and bone directly medial to it. Both tusks (RC^1 and LC^1) are broken near the tips; incisors (RI^3 is present but LI^3 is lacking — the socket being filled by bone); premolars (RP^1–RP^3 are present and well worn, as are LP^1–LP^2; LP^3 is missing, and traces of small, single "alveoli" posterior to the P^3 positions are filled with bone: presumably they represent P^4s present at an earlier growth stage). It is interesting to note that P^4s are present in less than half of the recent Pacific walrus *(Odobenus rosmarus divergens)* specimens examined by Fay (1982:84).

Mandible. Complete, with the following teeth: canines (RC_1 and the socket for LC_1); premolars (sockets for RP_2–RP_4; LP_2–LP_3 are present but LP_4 is lacking).

Fig. 4. Right side view of the Qualicum walrus cranium (NMC 38490). Note the relatively small tusks (with damaged tips) of an adult female. The paler areas have been restored.

Table 1. Skull measurements (mm) of the Qualicum walrus (*Odobenus rosmarus;* NMC 38490) and some comparisons with those of modern female Pacific walruses (*O. r. divergens*) derived from F. H. Fay (personal communication 1990; mean ± *SE*, sample size). Numbers in brackets are those given by the Committee on Marine Mammals, American Society of Mammalogists (1967).

	NMC 38490	Pacific Walruses (Recent)	
Cranium			
Condylobasal length (11)	341.0[a]	332.0 ± 2.5	23
Rostral width (max.)	175.0	168.0 ± 2.3	33
Interorbital width (min.) (8)	77.0	67.0 ± 1.2	26
Zygomatic width (max.) (9)	232.0[a]	212.0 ± 1.4	26
Cranial width posterior to zygomatic arches (max.)	260.0[b]	245.0 ± 2.3	25
Alveolar length (I^3–P^3)[c]	76.7	—	—
Left tusk (LC^1) / Right tusk (RC^1)			
Length (lateral), cingulum to tip	124.5[b] / 115.0[b]	—	—
Ant.-post. diameter at cingulum	47.7 / 48.6	49.0 ± 1.3	20
Med.-lat. diameter at cingulum	33.0 / 33.8	—	—
Circumference at cingulum	134.0 / 134.0	—	—
Mandible			
Length along midline (max.)	217.0	—	—
Length of dentary (max.)	237.2	233.0 ± 2.0	24
Width (max.)	226.0	—	—
Coronoid height	89.7	81.0 ± 1.7	24
Length of symphysis (max.)	91.0	—	—
Alveolar length (LCI–LP_4)	74.9	—	—

[a] Approximate measurement due to restoration of bone.
[b] Abrasion of bone makes measurements smaller than original.
[c] Anterior of RI^3 socket partly filled by bone.

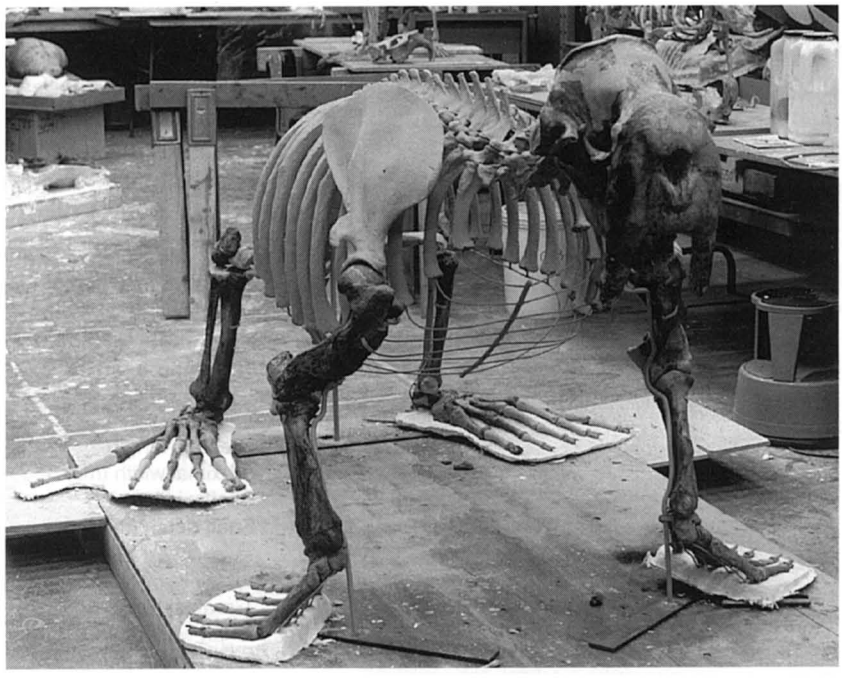

Fig. 5. Mounted skeleton of the Qualicum walrus (NMC 38490). Vertebrae, ribs and other missing parts (pale tone) were cast from a recent female walrus skeleton of similar size.

Vertebrae and ribs. Vertebral fragments are relatively small: at least 10 vertebrae seem to be represented; at least 15 ribs are represented.

Forelimbs. Left scapula (most of the proximal half); right and left humeri, radii and ulnae; all carpals except the right pisiform; all metacarpals; all first phalanges except left V; second phalanges (left I, III and IV and right I); and the left third phalanx V.

Hindlimbs. Right femur (damaged medially) and left femur (most of the distal two-thirds); right and left patellae; right tibia and fibula (damaged near the proximal ends) and the left tibia (damaged near the proximal end); all tarsals except the left navicular; all metatarsals (right I and II, left II–IV are slightly damaged); first phalanges (right II, III–V damaged near the proximal ends; left II, V); second phalanges [right I, II (damaged near the proximal end), III, and left I].

Since the skull and postcranial bones that are well preserved do not differ in any important way from those parts of a Recent adult female Pacific walrus (NMC 32182) of similar size to which they were compared, the Qualicum walrus is referred to *Odobenus rosmarus.* Despite the fact that the tusks of the fossil (NMC 38490) are abraded, they seem relatively small compared to those of recent adult female Pacific walruses (Fay 1982: fig. 81). Skull measurements of the fossil average about 6% larger than the mean of modern Pacific walrus females recorded by Fay (Table 1). So, although the fossil may well represent forerunners of the living Pacific walrus, it seems best to leave its subspecific identity in abeyance.

5. Paleoenvironment

Finding walrus remains *in situ* in Early Wisconsin glaciomarine clay is in accord with the known habits and habitat of walruses today. Fyles (1963:23) describes the paleoenvironment prevailing during deposition of this unit as epineritic (outer shallow water adjoining a sea coast) to littoral marine — the accumulating clay containing dropstones derived from floating glacial or sea ice. The clay also contains abundant, well preserved pelecypod shells (Wagner 1959:24–25) indicating a suitable source of food for walruses. Further, the mollusc assemblages recorded

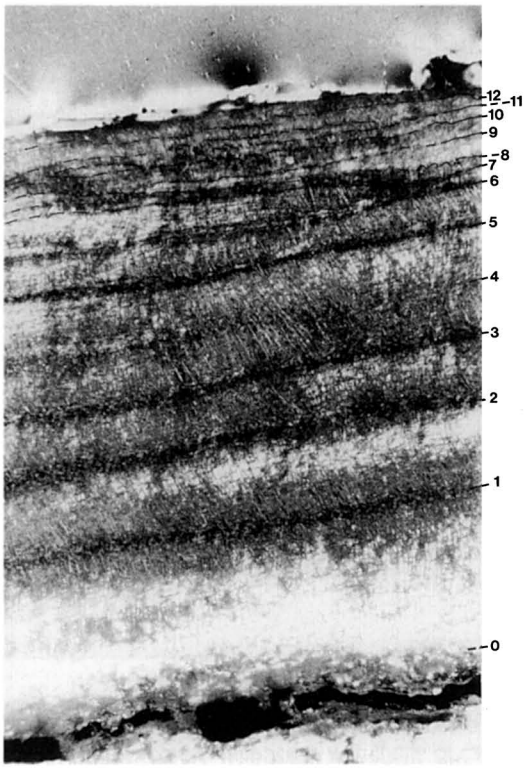

Fig. 6. Photomicrograph of part of a longitudinal section through the cementum of a premolar tooth (RP^3) from the Qualicum walrus. A count of annuli indicate the female was in her twelfth year when she died. See Fay (1982: table 2) for validation of the aging technique.

from this unit live today in the southern part of the Bering Sea, which forms approximately the southern limit of the present range of Pacific walruses (Fay 1982: fig. 17).

An examination of 17 slides produced from a sample of the bluish glaciomarine clay taken by the first author from directly beneath the skeleton yielded only four marine diatoms including two fragments (S. Federovich, Geological Survey of Canada Diatom Report 81-1): *Plagiogramma staurophorum* (Greg.) Heib. (2), *Amphora* sp.(fragment), and *Grammatophora* sp. (fragment). Although the paucity of material precludes a meaningful paleoenvironmental interpretation, it is worth noting that these taxa are typical of marine littoral conditions (S. Federovich, pers. comm., 1990), and support Fyles' (1963) paleoenvironmental conclusions mentioned previously. An examination of several slides from the same sample for pollen was fruitless (D. M. Jarzen, pers. comm., 1990).

A paleotemperature curve for this region of Vancouver Island (based on $^{230}Th/^{234}U$-dated speleothems in Cascade Cave near Port Alberni — about 16 km southwest of the fossil site)

Table 2. Measurements (mm) of main limb bones of the Qualicum walrus (*Odobenus rosmarus;* NMC 38490).

	Left	Right
Humerus		
Greatest length	343.0[a]	350.0
Proximal width (max.)	102.9[a]	93.5
Shaft width (min.)	45.4	45.2
Shaft depth (min.)	37.5	38.5
Radius		
Greatest length	274.7[a]	273.3
Shaft width (min.)	27.8	27.5
Shaft depth (min.)	25.3	26.3
Distal width (max.)	52.9	54.4
Distal depth (max.)	91.6	94.1
Ulna		
Greatest length	347.0	348.0
Olecranon depth (min.)	84.9	85.8
Shaft width (min.)	23.8	23.9
Shaft depth (min.)	40.2	40.0
Distal width (max.)	35.8	34.9
Distal depth (max.)	52.7	51.7
Femur		
Greatest length (lateral side)	—	221.8
Proximal width (max.)	—	123.2
Shaft width (min.)	51.3	51.7
Shaft depth (min.)	—	29.7
Distal width (max.)	116.0[a]	113.9[a]
Distal depth (lateral condyle)	—	63.8
Tibia		
Greatest length	373.0[a]	377.0
Shaft width (min.)	37.7	37.8
Shaft depth (min.)	28.2	28.4
Distal width (max.)	—	76.5
Distal depth (max.)	—	62.5
Fibula		
Greatest length	—	361.0
Shaft width (min.)	—	16.0
Shaft depth (min.)	—	20.0
Distal width (max.)	—	57.8
Distal depth (max.)	—	38.5

[a] Approximate measurement due to restoration of bone.

indicates that cave temperatures declined from 4°C at 64 000 years ago to about 0°C at 35 000 to 28 000 years ago. The absence of speleothems older than 67 000 year ago "suggests that beyond this limit was a period of zero growth, possibly correlated with the early Wisconsin glaciation..." (Gascoyne et al. 1981:1650) — near the end of which the glaciomarine unit discussed here was evidently deposited. So the Qualicum walrus may be close to 70 000 years old. Deposition of the Dashwood Drift from which the walrus skeleton was derived is considered to have ended more than 62 000 years ago (Gascoyne et al. 1981; Fig. 3).

6. Discussion

Evidently, walruses (Odobenidae) and fur seals and sea lions (Otariidae) were derived from North Pacific primitive aquatic bear-like carnivores (Enaliarctidae) in the Early Miocene about 20 million years ago (Repenning & Tedford 1977). Primitive walruses seem to have flourished and diversified near the end of the Miocene, but only one form, the living walrus *(Odobenus rosmarus)* has survived. King (1983:130) gives summaries of the evolution of dusignathine and odobenine walruses, but Repenning (pers. comm. 1990) notes that unpublished finds from Japan and California suggest that odobenine walruses were present continuously from latest Miocene or early Pliocene through early Pleistocene in the North Pacific and that they experienced a radiation hitherto unsuspected. Apparently the ancestor of the walrus entered the Atlantic from the Pacific via the Central American Seaway between 5 and 8 million years ago, following which the Pacific stock became extinct — perhaps by the end of the Pliocene (C. A. Repenning, pers. comm. 1990). So modern North Pacific walruses apparently arose from Atlantic animals that made their way back to the Pacific via the Arctic Ocean during the last million years (Repenning 1976). However, the discovery of three tusks from the Pliocene of Japan (the approximately 3–4 million year old Shiranuka Formation, and the 3 million year old Yotsukura Formation) suggests a considerably earlier presence of *Odobenus rosmarus* ancestors in the North Pacific (Tomida 1989). The tusks resemble those of *Odobenus huxleyi* from the late Pliocene – early Pleistocene of Europe and unidentified tusks from the Pliocene Yorktown Formation of Virginia, and particularly North Carolina (C. A. Repenning, pers. comm. 1990).

The living walrus is Holarctic in distribution and consists of two subspecies, the Atlantic walrus (*O. r. rosmarus* Linnaeus, 1758 including Hudson Bay – Davis Strait, eastern Greenland, Svalbard – Franz Josef Land, and Kara Sea – Novaya Zemlya populations) and the Pacific walrus *(O. r. divergens* Illiger, 1811 — including Laptev Sea (?) and Bering Sea – Chukchi Sea populations) (Fay 1982:6). Presumably the subspecies arose due to enduring Canadian Arctic glacial and sea ice barriers (Harington 1966:512; Dyke & Prest 1986) dividing the stocks during the late Pleistocene. The main difference between the subspecies is the larger physical size (including much larger tusks) of the Pacific group, which in part may be accounted for by the availability of richer food for walruses in the North Pacific (Harington 1975).

Probably modern walruses reached their most southerly known geographic limits (Fig. 1) near late Pleistocene glacial maxima [e.g. Kittyhawk, North Carolina (Hay 1923:29; Ray 1960:137) almost to the northern border of South Carolina — indeed, there are specimens from Edisto Island, South Carolina, that are inseparable from modern walrus (C. A. Repenning, pers. comm. 1990); Montrouge near Paris (Gratiolet 1858:620; Kellogg 1922:50); northern Sakhalin Island (Matsumoto 1926:15), possibly northeastern Hokkaido (Voronov & Voronov 1981:1118) and as far south as Tokyo, were a partial cranium was collected from the late Pleistocene Tokyo beds (Y. Hasagawa, pers. comm. 1974)]. On the Pacific coast of North America, C. A. Repenning has reported Alaskan walrus (Odobenus sp.) fossils from last (Sangamon) interglacial deposits at Nome and near Point Lay, as well as from late Pleistocene sediments south of Kuk Inlet, as well as Nelson and St. Lawrence islands (Harington 1978:72). Evidently Pacific walruses (or their forerunners) occupied more southerly waters along this coast during the Early Wisconsin stadial (Qualicum Beach, British Columbia) and even farther south (San Francisco Bay, California) in

the early Late Wisconsin. The first author (Harington 1984:517, fig. 7) obtained a radiocarbon date of 27 200 ± 950 B.P. (I-9994) on collagen from a tusk (with rostrum; California Academy of Sciences 16677) dredged up near Golden Gate Bridge in 1965. Other walrus remains have since been dredged up near San Francisco and are likewise kept in collections of the California Academy of Sciences (C. A. Repenning, pers. comm. 1990).

Perhaps a small-scale modern analogue of the suggested southerly dispersal of walruses during glacials and northward withdrawals during interglacials is their present seasonal migration in Bering Strait. There, the maximum southerly movement occurs about March, whereas the northernmost shift happens about September, when the walruses move north with the melting pack ice margin (Fay 1982: figs. 6, 12).

7. Conclusion

During the Early Wisconsin, perhaps about 70 000 years ago, an adult female walrus died and drifted through icy waters to the clay bottom near the east coast of Vancouver Island. Evidently the carcass settled belly up, head toward the present beach with the spine curving slightly southward, and decayed in situ. Following further deposition of Early Wisconsin glaciomarine clay (Dashwood Drift), Quadra sediments of Middle Wisconsin age, Vashon Drift (glacial till) and Capilano Sediments of Late Wisconsin age (Fig. 3), the land rose relative to sea level and continual coastal erosion eventually exposed the upthrusting walrus tusks in the intertidal zone near Qualicum Beach.

The Qualicum walrus is the most complete Pleistocene walrus specimen recorded from the west coast of North America. Paleoenvironmental, paleobiogeographical, stratigraphic, and geochronological evidence associated with the find seems to be in harmony. In other words, data on the Qualicum walrus fit well with our knowledge of the habits and habitat of modern walruses and of the paleoenvironment of the Qualicum area about 70 000 years ago based on various kinds of evidence.

Acknowledgements. As is often the case with important Pleistocene vertebrate finds, many people contribute to the final result. We thank particularly: William Waterhouse (Bowser, British Columbia) for relocating the site, and his daughter Micaela for reporting it; Rick Kool (Royal British Columbia Museum) for advising the first author of the discovery; Joyce Barr for kindly allowing access to the site through her property; Drs. J. G. Fyles (Geological Survey of Canada) and S. R. Hicock (University of Western Ontario) for providing stratigraphic information on the fossil locality; Dr. S. Federovich (Geological Survey of Canada) for supplying data on diatom fossils associated with the skeleton; the late Sterling L. Presley (Archaeological Survey of Canada, Canadian Museum of Civilization) for sectioning the tooth and providing a clear photomicrograph of it; G. R. Fitzgerald (Paleobiology Division, Canadian Museum of Nature), Barbara Frizzell, and Valerie Vail (student assistants, formerly of Algonquin College) for repairing damaged bones, casting missing parts and assistance in mounting the Qualicum walrus for display; and Dr. C. G. van Zyll de Jong and David Campbell (Zoology Division, Canadian Museum of Nature) for the loan of a comparative skeleton of a Pacific walrus. We are grateful to Dr. Francis H. Fay (University of Alaska) and Charles A. Repenning (United States Geological Survey) for their comments on a draft of the manuscript: the former also kindly provided comparative measurements on a series of modern Pacific walrus skulls.

The first author would like to pay tribute to the late Björn Kurtén for his valuable advice on Pleistocene faunal problems over many years, and above all for the inspiring breadth and vitality of his interest in mammalian paleontology.

References

Armstrong, J. E. & Clague, J. J. 1977: Two major Wisconsin lithostratigraphic units in southwest British Columbia. — Can. J. Earth Sci. 14(7):1471–1480.

Committee on Marine Mammals, American Society of Mammalogists 1967: Standard measurements of seals. — J. Mammal. 48(3):459–462.

Dyke, A. S. & Prest, V. K. 1986: Late Wisconsinan and Holocene retreat of the Laurentide Ice Sheet. — Geol. Survey Canada, Map 1702A.

Fay, F. H. 1982: Ecology and biology of the Pacific walrus, Odobenus rosmarus divergens Illiger. — U.S. Dept. Int. Fish Wildl. Service, North Amer. Fauna 74:1–279.

Fyles, J. G. 1963: Surficial geology of Horne Lake and Parksville map-area, Vancouver Island, British Columbia. — Geol. Survey Canada, Mem. 318:1–142.

Gascoyne, M., Ford, D. C. & Schwarcz, H. P. 1981: Late Pleistocene chronology and paleoclimate of Vancouver Island determined from cave deposits. — Can. J. Earth Sci. 18:1643–1652.

Gratiolet, P. 1858: Note sur un fragment de crâne trouvé à Montrouge, près Paris. — Bull. Soc. Geol. France 15:620–624.

Harington, C. R. 1966: Extralimital occurrences of walruses in the Canadian Arctic. — J. Mammal. 47(3): 506–513.

— 1975: A postglacial walrus (Odobenus rosmarus) from Bathurst Island, Northwest Territories. — Can. Field-Nat. 89:249–261.

— 1978: Quaternary vertebrate faunas of Canada and Alaska and their suggested chronological sequence. — Syllogeus 15:1–105.

— 1984: Quaternary marine and land mammals and their paleoenvironmental implications — some examples from northern North America. — Carnegie Mus. Nat. Hist., Spec. Publ. 8:511–525.

Hay, O. P. 1923: The Pleistocene of North America and its vertebrated animals from the states east of the Mississippi River and from the Canadian provinces east of longitude 95°. — Carnegie Inst. Washington, Publ. 322:1–499.

Hicock, S. R. 1980: Pre-Fraser Pleistocene stratigraphy, geochronology and paleoecology of the Georgia Depression, British Columbia. — Ph.D. thesis, Univ. Western Ontario, London. 231 pp.

Kellogg, R. 1922: Pinnipeds from Miocene and Pleistocene deposits of California. — Univ. California Publ., Bull. Dept. Geol. Sci. 13(4):23–132.

King, J. E. 1983: Seals of the world. — Brit. Mus. (Nat. Hist.) & Oxford Univ. Press, London. 240 pp.

Matsumoto, H. 1926: On two species of fossil Pinnipedia from Zazusa and Saghalin. — Sci. Rep. Tôhoku Imp. Univ., Sendai, Ser. 2 (Geol.) 10(1):13–16.

Ray, C. E. 1960: Trichecodon huxleyi (Mammalia: Odobenidae) in the Pleistocene of southeastern United States. — Bull. Mus. Comp. Zool., Harvard Univ. 122(3):129–142 .

Repenning, C. A. 1976: Adaptive evolution of sea lions and walruses. — Syst. Zool. 25:375–390.

Repenning, C. A. & Tedford, R. H. 1977: Otarioid seals of the Neogene. — U.S. Geol. Survey, Prof. Pap. 992:1–93.

Tomida, Y. 1989: Pliocene odobenid remains from Japan and their implication for odobenid paleobiogeography. Abstracts of papers. Forty–ninth Annual Meeting, Society of Vertebrate Paleontology. — J. Vert. Paleontol. p. 42A.

Voronov, V. G. & Voronov, G. A. (Воронов, В. Г. & Воронов, Г. А.) 1981: Restoration of geographic range and finds of walruses (Odobenus rosmarus) in the Sea of Okhotsk. (In Russian with English summary) — Zool. Zh. 60:1117–1119.

Wagner, F. J. E. 1959: Paleoecology of the marine Pleistocene faunas of southwestern British Columbia. — Geol. Survey Canada, Bull. 52:1–67.