A Primitive Seal (Mammalia: Phocidae) from the Early Middle Miocene of Central Paratethys

Irina A. Koretsky and Peter Holec

ABSTRACT

A well-preserved skull from the early middle Miocene (approximately 15 Ma) at Devinska Nova Ves (formerly Neudorf an der March), Slovakia, herein named *Devinophoca claytoni*, new genus and new species, is morphologically the closest common ancestor of all true seals. It shows a mixture of subfamilial characters. Features shared with Phocinae are the number of incisors and the lack of a strongly pronounced mastoid process. Characters similar to Monachinae are the shape of maxillae and the ratio between frontal and maxillary contacts of nasal bones. Characters shared with Cystophorinae are the ratio between interorbital width and mastoid width and (also shared with Phocinae) the ratio between length of auditory bullae and distance between them. Moreover, this skull has primitive features that are not known in any of the three subfamilies: M1 is triangular, with three cusps and three roots; in P2–P4 the larger posterior roots are clearly made up of two fused roots; the incisors form a curved line; the anterior palatal foramina are deep and oval; and the sagittal crest is very well developed.

The traditional separation of the family Phocidae into the subfamilies Phocinae, Monachinae, and Cystophorinae has been intensively debated during the past 40 years and debate continues today, but we herein follow the traditional classification. The plesiomorphic *D. claytoni* is thus considered a sister taxon to the three extant subfamilies of Phocidae and is referred to a new subfamily, Devinophocinae. Because of its late age, *D. claytoni* cannot be ancestral to the more advanced phocids. Its primitive characters in combination with the characters it shares with the other subfamilies suggest, however, that it might approximate the common ancestral morphotype.

Introduction

Around Devínska Kobyla Hill near Bratislava, Slovakia (Figure 1), fossil mammals are found at eight localities. A brief

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description and a list of all vertebrate species from these localities were given by Holec and Sabol (1996). These assemblages contain a mixture of marine and terrestrial vertebrates. Fossil seals are found at three of the localities at Devínska Nová Ves: Sandberg, Bonanza (a newly discovered fissure-filling at the quarry of the former Stokerau limekiln), and Wait's Quarry. The first locality discovered was Sandberg, the history of which was discussed in detail by Thenius (1952). The original independent township Devínska Nová Ves (Neudorf an der March in the earlier literature) is now a suburb of Bratislava.

In the quarry of the former Stokerau limekiln, two localities with mammalian faunas are found. The first is Zapfe's classical locality, consisting of two fissures in the western part of the quarry filled with terra fusca with many fossil bones of terrestrial mammals; marine mammals have never been found there. At present, only the more western of the two fissures can be seen. At the eastern end of the limestone quarry a new, second locality, called Bonanza, was discovered more recently; there, abundant fossil bones of terrestrial and marine vertebrates (fishes and seals) are mixed in the same deposit.

The knowledge of the mammalian assemblage found in the two western fissures at the Stokerau limekiln is the result of the efforts of Helmuth Zapfe. His father, I.B. Zapfe, saved the fossils that were discovered in the fissure-filling during exploitation of the limestones in 1943. From the large-mammal fauna, Zapfe (1953) determined the age of the filling to be "Helvetian." Fejfar (1974) also carried out research there, focused mainly on the small mammals. He identified five species of insectivores and fifteen species of rodents, on the basis of which he determined the age of the assemblage to be early Badenian. Some species of rodents were mentioned also by Holec (1986).

The Bonanza locality was discovered in 1984 by the amateur paleontologist Š. Mészáros. Its vertebrate fauna was described by Holec et al. (1987). In addition to the mammals, abundant remains of fishes and frogs also were found there.

Remains of seals also were found at Wait's Quarry; a short description of the locality by Holec and Sabol (1996) mentioned the occurrence.

FIGURE 1.—Map of Central Europe. Study area indicated by black square.

Zapfe's (1937) description of *Miophoca vetusta* from the Sandberg locality (early middle Miocene; Badenian) was based upon a mandible. He noted that this specimen may be related to *Pristiphoca* Gervais, 1848–1852, and also is very close to the living Monachinae. Later, Thenius (1950), using Zapfe's hypothesis, transferred this material to the genus *Pristiphoca*. As explained below, we do not accept this transfer because this genus is a nomen dubium.

A preliminary description of the pinniped skull described herein has already been published by Holec with a list of the other fossil mammals from the early Miocene of Slovakia (Holec et al., 1987). When Koretsky visited the Slovak National Museum in Bratislava in 1995, she recognized the unusual morphology of a this skull and its importance to phocid evolution.

In this paper, we accept a traditional classification (Simpson, 1945; Chapskii, 1955, 1974; Scheffer, 1958; King, 1966; Heptner et al., 1976) in which the family Phocidae is divided into three subfamilies: Phocinae, Monachinae, and Cystophorinae.

For our morphometric analysis of the skull, we used the methods of Dornesco and Marcoci (1958), Piérard (1971), von den Driesch (1976), and Trelea and Simionescu (1985). Osteological terminology in this paper follows the *Illustrated Veterinary Anatomical Nomenclature* (Schaller, 1992).

GEOLOGY

Rising to 514 m above sea level, Mt. Devínska Kobyla is the highest peak in the Devínske Karpaty Mountains, which constitute the southernmost tip of the Malé Karpaty Mountains in

Slovakia. Devínska Kobyla lies near the southern edge of the mountains, close to the Vienna Basin. The Devínske Karpaty range is bounded by the Danube River on the south and southeast, the Morava River on the west, Dúbravský Potok creek on the north, and the Lamaè Fault, which separates these mountains from the rest of the Malé Karpaty, on the north-northeast. The whole area lies in the territory of greater Bratislava City, which includes once-separate villages such as Devínska Nová Ves, near which are several important fossil vertebrate localities, and the village of Devín (Figures 1, 2).

The Devínska Kobyla area was emergent at the beginning of the late Miocene, and terrestrial sediments being produced by erosion were sometimes trapped and preserved in fissures and caverns in the subjacent limestones. This is exemplified by loamy fillings in a quarry of the former Stockerau lime plant. The early middle Miocene (early Badenian, 16.0–13.6 Ma) fillings contain many bones of various vertebrates, described mainly by Zapfe between 1949 and 1983. The terrestrial loam in these fissures is overlain by transgressive sandy marine sediments of late Badenian age.

Late Badenian sediments occur (along with early and middle Badenian sediments) in drillhole DNV-1 (Bonanza locality), as well as in outcrops. The lithostratigraphic unit, Sandberg Sands, had been defined there by Baráth et al. (1994). The base of this formation consists of gravels with pebbles of variable size intercalated with sands. The sands reflect a transgressive stage of deposition on the eastern edge of the Vienna Basin. Calcareous clays and friable siltstones, which account for the entire late Badenian in the basin are found in a brick plant in Devínska Nová Ves. These sediments are typically rich in micro- and macrofauna and include terrestrial flora (Holec, 1987; Holec and Sabol, 1997).

The late Badenian marine transgression reached the slopes of Devínska Kobyla, whose summit at that time protruded as an island or peninsula. Littoral deposits (carbonate breccias) of late Badenian age are found in numerous outcrops: sands, sandstones, algal limestones, and carbonate breccia. Coarse breccia and conglomerates, with clasts as much as 1 m in size, are exposed in the former Wait's Quarry on the western slope of Devínska Kobyla, where they were deposited on the inundated ridge (Andrusov, 1969). The signs of a seacoast also are very clearly visible at the renowned Sandberg locality, where almost 300 species of fossils including marine algae, invertebrates, marine vertebrates, and terrestrial mammals have been found (Holec, 1985; Holec and Sabol, 1996; Švagrovský, 1981). The presence of red algal sandy limestones at Sandberg proves that the sea here was shallow during the time of late Badenian deposition.

The whole Devínska Kobyla area is rich in fossil remains of invertebrates and vertebrates alike. The three Badenian localities yielding fossil seals (Figure 2) are (1) Wait's Quarry, an abandoned quarry on the western slope of Devínska Kobyla, (2) Sandberg, a sand pit located about 700 m north of Wait's Quarry, and (3) the Bonanza sublocality of the Stockerau limekiln.
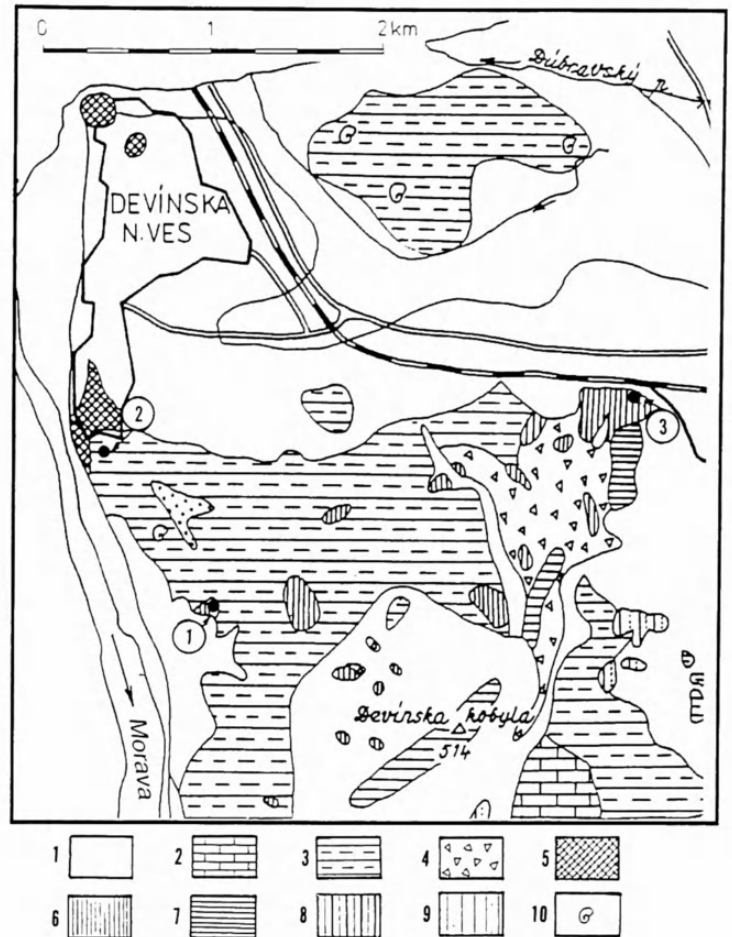

FIGURE 2.—Geological map of Devínska Kobyla: 1=Quaternary, undifferentiated: fluvial, proluvial, and man-made sediments. 2=Sarmatian: Bryozoan-serpulid limestones, oolitic sands, calcareous and variegated clays, sands. 3=Studienka Formation, late Badenian: algal limestones, sands with sandstone beds and gravel intercalations, conglomerates dominated by granite pebbles. 4= Devínska Nová Ves, middle Badenian and undifferentiated Badenian: granite conglomerates, carbonate breccias cemented by sinter, conglomerates. 5= Mesozoic, Albian?: shales; Neocomian: mildly marly, cherty limestones; Dogger-Malm: siliceous limestones and silicites; Lias: brecciated limestones with carbonate extraclasts. 6=Envelope unit, Middle Triassic: massive, locally dolomitic limestones, massive intraclast breccia dolomites interlayered with limestones. 7=Early Triassic: bedded siliceous limestones and dolomites. 8=Late Devonian–Early Carboniferous: aplite and pegmatite dikes. 9=Pre-Devonian: crystalline schists, primarily metapelites. 10=Fossil occurrences. Localities (circled numbers): Wait's Quarry (1), Sandberg (2), Bonanza (3).

The former Stockerau lime plant and its quarry are situated on the northern slope of Devínska Kobyla. Dark gray, fairly strongly recrystallized limestone of Jurassic age is exposed there. It is dissected by north-south trending fissures, many of them filled with sinter, terra rossa, and terra fusca. Overlying all of these is late Badenian marine sand. A rich vertebrate fauna was described largely by Zapfe (1937–1983) from two of these fissures in the western part of the Stockerau quarry. Bonanza is a third fissure located nearby on the quarry's eastern edge. Unlike the preceding two fissures, which yielded only terrestrial vertebrates, this one also contains a wealth of remains of fish, seals, and marine invertebrates (Holec et al.,

1987). The holotype skull of *Devinophoca claytoni* described below was found there.

Systematic Paleontology

Superfamily PHOCOIDEA Smirnov, 1908

Family PHOCIDAE Gray, 1825

Subfamily DEVINOPHOCINAE, new subfamily

DIAGNOSIS.—Upper dental formula I3, C1, P4, M1 (shared with Phocinae). Incisors forming U-shaped arcade; P2–P4 double rooted (as in Phocinae and Monachinae, in contrast to Cystophorinae), with posterior root larger than anterior; P4 with two fused posterior roots and with carnassial notch on metastyle blade; M1 triangular with three cusps and three roots (no other phocid has teeth with three cusps and three roots in triangular arrangement); preorbital part of maxilla with very short, pronounced concavity (similar to Monachinae); antorbital process well defined; frontal contact of nasal bones much shorter than maxillary contact (shared with Phocinae); interorbital space slightly broader anteriorly than posteriorly; interorbital width less than 25% of width of skull at mastoid processes (as in Cystophorinae); sagittal crest very well developed (more than in Monachinae) and not forming triangle with lambdoidal crests; diameter of infraorbital foramen less than diameter of alveolus of upper canine (as in *Monachus schauinslandi*, unlike Phocinae and Cystophorinae); anterior palatal foramina oval-shaped and deep (as in Cystophorinae), with well-pronounced palatal groove; anteroposterior length of tympanic bullae greater than distance between them (similar to Phocinae and Cystophorinae); width of mastoid process less than one-half length of tympanic bulla; mastoid convexity not turned down behind mastoid process (as in Phocinae).

TYPE AND ONLY INCLUDED GENUS.— *Devinophoca*, new genus

Genus *Devinophoca*, new genus

Pristiphoca.—sensu Holec et al., 1987:350, fig. 3.—[Not *Pristiphoca* Gervais, 1852:272 (nomen dubium)].—[Not *Pristiphoca* Thenius, 1950:1–9; 1952: 60–63; 1969:402, figs. 420, 421; 1979:171; 1992:73].

TYPE SPECIES.—*Devinophoca claytoni*, new species.

ETYMOLOGY.—From *Devin*, in reference to Devínska Nová Ves, Slovakia; and *phoca* (Latin), seal.

DIAGNOSIS.—As for the subfamily until other genera are described.

REMARKS.—According to Koretsky and Ray (in prep.), the name *Pristiphoca occitana* Gervais and Serres, 1847, in Gervais, 1848–1852 is a nomen dubium because it was based upon an illustration of the canine tooth of an indeterminate carnivore.

Devinophoca claytoni, new species

FIGURES 3–8, TABLES 1, 2

Miophoca vetusta Zapfe, 1937.—Holec et al., 1987:350, fig. 3 [assignment to *Pristiphoca*].

HOLOTYPE.—Incomplete skull with right M1 and left P2–M1; collected by the amateur paleontologist Š. Mészáros in 1984; catalog number Z14523 of the Museum of Natural History, Slovak National Museum, Bratislava, Slovak Republic.

TYPE Locality.—Stokerau lime quarry, Bonanza Hill, Devínska Kobyla, Slovak Republic.

ETYMOLOGY.—Named in honor of Clayton E. Ray, in recognition of his numerous contributions to the study of fossil pinnipeds.

AGE AND DISTRIBUTION.—Badenian, early middle Miocene, 14.8 Ma (Steininger and Nevesskaya, 1975; Steininger et al., 1989; Rögl and Daxner-Höck, 1996); Vienna Basin of Slovakia.

DIAGNOSIS.—As for the subfamily and genus.

DESCRIPTION AND COMPARISON.—The obliterated sutures and heavily worn premolars indicate that the holotype cranium of *D. claytoni* represents an adult individual. All of the incisors and both canines have fallen out. On the right side of the skull all teeth have fallen out except M1. The anterior part of the premaxillae around the incisors, the palatine, parts of the palatine processes of the maxilla, and much of the orbital parts of the frontal bones are missing. Part of the basicranium is broken away also, and the vomer, pterygoid, presphenoid, and basisphenoid bones are missing. Both jugal (=zygomatic) bones are missing, the paroccipital (=jugular) processes are broken away, and the supraoccipital part of the occipital shield is largely absent.

The pre- and postorbital parts of the skull are approximately equal in length (Figure 3). The lateral outline of the braincase is rounded. In lateral profile, the top of the skull is slightly concave. The braincase is widest (84.5 mm) above the external auditory meatus. The preorbital parts of the maxillae, between the nasal aperture and the orbits, are short and concave, the same shape as in the Monachinae (Chapskii, 1974). The palatal parts of the premaxilla-maxillary sutures are fused and completely obliterated, but lateral to the nares, near the nasal bones, the sutures are clear. The tongue-like ascending process (pnp) of the premaxilla has a short (at least 4.0 mm) contact with the lateral edge of the nasal bones (Figure 4A,B); it cannot be determined with certainty whether this process of the premaxilla is complete.

The supraorbital process (sop) of the frontal bone is represented only by a small tubercle (Figure 3A,B). On the maxilla at the anterior margin of the orbit is a small but distinct antorbital process (aop). The fronto-maxillary suture is slightly forward of the anterior rim of the orbit.
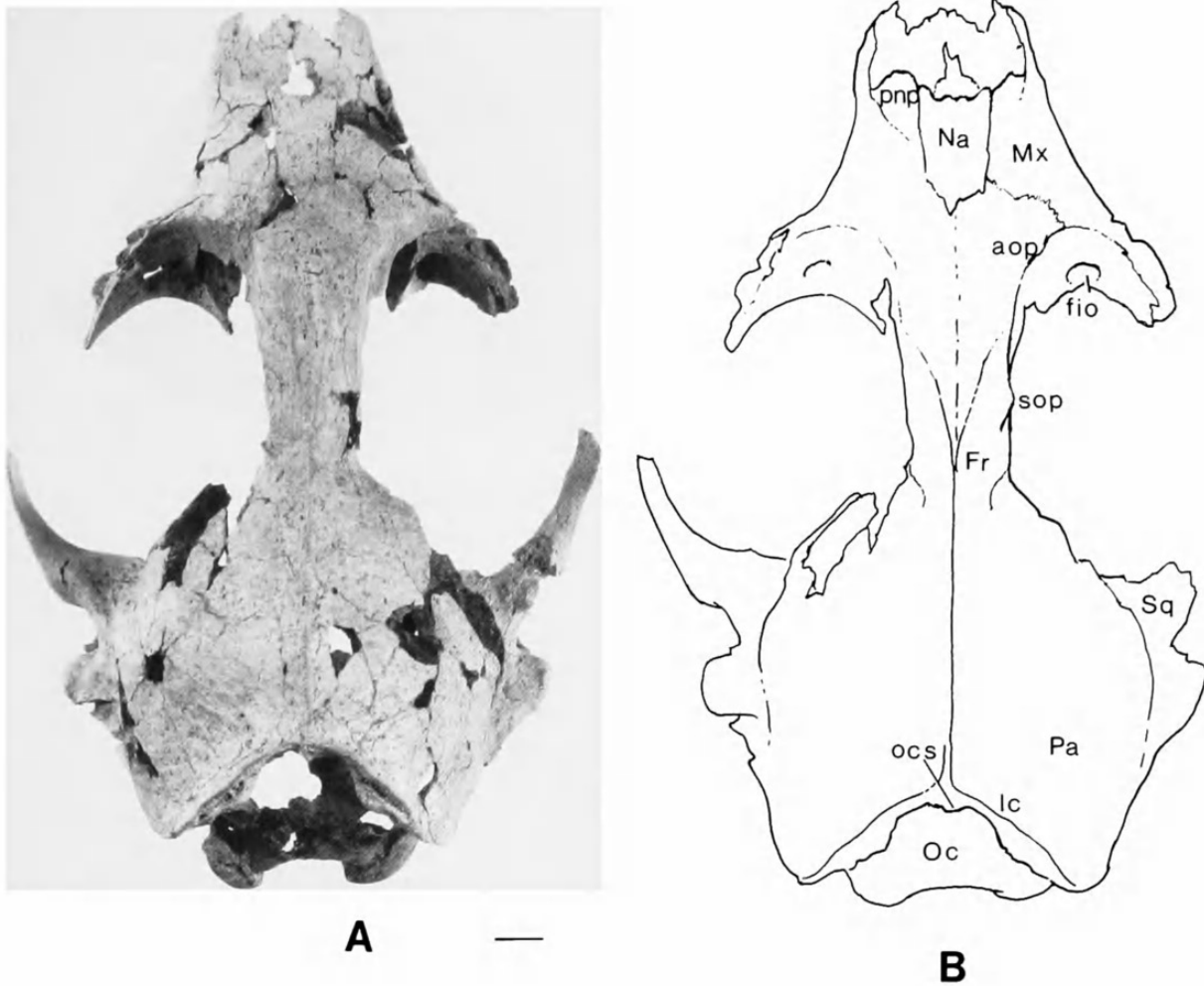
FIGURE 3.—*Devinophoca claytoni,* new genus and species, holotype skull Z14523: A, dorsal view; scale bar= 0.75 cm; B, outline drawing of the photograph of dorsal view. (Abbreviations for Figures 3–7: aop=antorbital process; Bo=basioccipital; cc=carotid canal; cf=carotid foramen; ch=hypoglossal canal; cma=anterior musculotubular canal; coc=condyloid canal with transverse venous sinus; eam=external acoustic meatus; ec=ectotympanic; en=entotympanic; fi=incisive foramen; fio=infraorbital foramen; flp=posterior lacerate foramen; fml= median lacerate foramen; fpal=palatine foramen; fpg=postgelenoid foramen; Fr=frontal; fsm=stylomastoid foramen; g=glenoid fossa; ju=jugal process of squamosal; lc=lambdoidal crest; mp=mastoid process; mt= meatal tube of the bulla; Mx=maxilla; Na=nasal; Oc=occipital; occ=occipital condyle; ocs=supraoccipital crest; Pa=parietal; Pal=palatine; Pmx=premaxilla; pnp=nasal process of the premaxilla; pp=paroccipital process; Sq=squamosal; sips=sulcus for inferior petrosal sinus; sop=supraorbital process; spt=transverse palatal suture; tb=tympanic bulla.)

Neither jugal bone is present, but the maxillary-jugal suture is complete on the left side; it slopes posterolaterally from the anteroventral edge of the orbit.

The nasal bones (Figures 3, 4A) are very short and completely fused to each other along the midline; their frontal contact is much shorter than their maxillary contact. Posteriorly the nasal bones together form a V-shaped projection about 5 mm long inserted between the frontal bones. The posterior limit of the nasal bones is immediately behind the broad frontal-maxillary contact. The width of the nasal bones is approximately constant for their whole length except for the small pointed frontal process. The nasal opening is circular (Figure 4A,B).

The lateral edge of each nasal bone projects farthest anteriorly; the anterior edge of each nasal bone is concave, and together the two nasals form a short median anterior projection. This shape of the anterior border of the nasal bones is more similar to that of the Phocinae (especially *Erignathus*) than to that of other members of the Phocidae. The ratio between the lengths of the frontal and maxillary contacts of the nasal bones, however, is more similar to that of Monachinae.

The interorbital region is slightly wider anteriorly and narrows posteriorly to where the braincase begins. The least interorbital width occurs in the most posterior portion of the interorbital area. Berta and Wyss (1994) noted that this very primitive
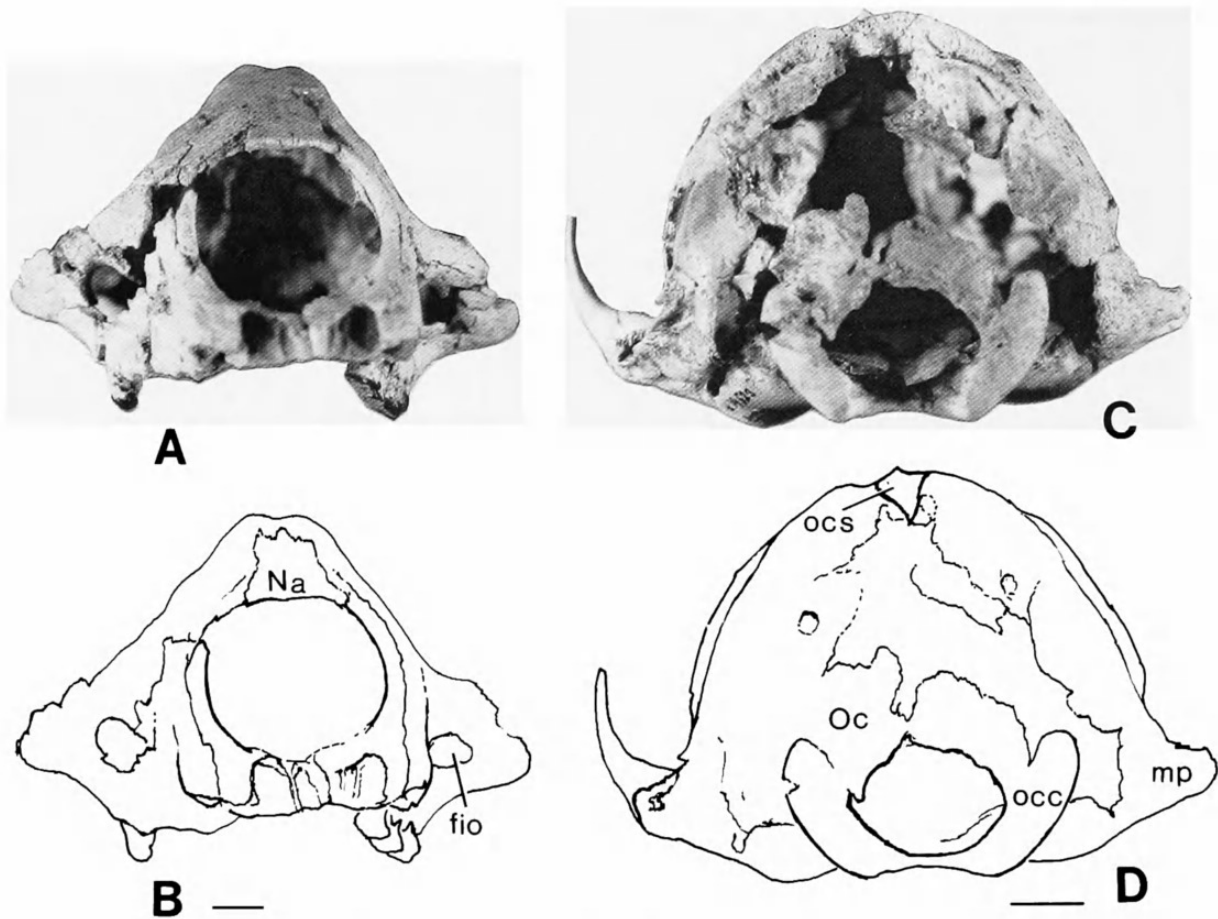
FIGURE 4.—*Devinophoca claytoni*, new genus and species, holotype skull Z14523: A, anterior view; B, outline drawing of the photograph of anterior view; scale bar=0.75 cm; C, posterior view; D, outline drawing of the photograph of posterior view, scale bar=1.0 cm. For explanation of abbreviations see Figure 3.

feature is typical for terrestrial carnivorans. The widest part of the interorbital area (24.0 mm) is about 21% of the width of the skull across the mastoid processes (113.0 mm; Table 1), which is very similar to the ratio in Cystophorinae (including *Cystophora* and *Mirounga*).

The sagittal crest is much better developed than in other Phocidae; it begins at the narrowest part of the interorbital area, even with the posterior ends of the orbit, and continues to the lambdoidal crest. At its anterior end the sagittal crest divides into two much smaller, indistinct temporal crests that disappear at the dorsal edge of the orbit. The depressions on either side of the sagittal crest become deeper where they meet the lambdoidal crests. The sagittal and lambdoidal crests join at a point, without the triangle seen in the monachines. The maximum height of the sagittal crest is about 2 mm.

The infraorbital foramen (Figures 4A,B, 6B) is located above the posterior P4–anterior M1; it is circular and relatively small. The diameter of the alveolus of the upper canine (13.2 mm) is greater than the diameter of the infraorbital foramen, in contrast to Phocinae. When the skull is viewed dorsally, the posterior opening of the infraorbital canal cannot be seen in the orbits. The ventral root of the zygomatic process of the maxilla originates posterolateral to M1, at the same level as the palatal

process of the maxilla. The medial wall of the infraorbital canal is continued posteriorly by the vertical interorbital plate of the maxilla, which is very similar to the condition in *Enaliarctos mealsi* Mitchell and Tedford, 1973.

The palatine process of the maxilla (Figure 6) is a flat plate. The anterior palatal foramina (=fissurae palatinae) are located between the canines and are oval and deep, in contrast to the condition stated by Wozencraft (1989) for other phocids. Between the canines the palate is narrow and concave (18.5 mm wide and 11 mm high) and descends abruptly to the posterior margin of the incisor arcade. The lingual alveolar margins of the canines and incisors are at the same level as those of the cheek teeth (Figure 5). From the anterior palatal foramina to the level of P2 the palate is broken; posterior to P2 the palate is flattened transversely. The maxillary-palatine suture (=sutura palatina transversa, spt) lies medial to M1; the palatine bones are missing. The posterior palatine foramina (=canali palatine major, fpal) are medial to P4 (Figure 6), anterior to the palatine/ maxilla suture; each is divided into two openings by a tiny bridge. The anterior and posterior palatine foramina are connected by a relatively shallow anteroposteriorly aligned groove (=sulcus palatinus) (Figure 6A). Wyss and Flynn (1993) theorized that this primitive condition characterized phocid ances-

TABLE 1.—Cranial measurements (in mm) in the holotype skull Z14523 of *Devinophoca claytoni,* new genus and new species.

Character	Measurement
1. Total length	119.9
2. Condylobasal length	119.3
3. Length of processus palatinus	71.0
4. Length of rostral part, measured from antero-upper corner of orbit	49.0
5. Length of braincase, measured from anterior corner of orbit	93.5
6. Length of bulla tympanica	38.5
7. Length of tooth row, P1 to M1	49.0 (L), 53.2 (R)
8. Length of tooth row, P2 to P4	32.5 (L), 34.5 (R)
9. Maximum diameter of infraorbital foramen	7.5 (L), 11.2 (R)
10. Length of temporal fossa	61.5
11. Width of rostrum across canines	40.0
12. Maximal infraorbital width	25.5
13. Minimal infraorbital width	14.0
14. Width of skull across of processus zygomaticus of squamosal	124.0
15. Width of braincase	88.0
16. Mastoid width	113.0
17. Width of processus palatinus between P1s	10.5
18. Maximum width of processus palatinus	55.5
19. Maximum width of foramen infraorbitale	9.0 (L), 10.0 (R)
20. Width of bulla tympanica	49.3
21. Width of rostrum	37.0
22. Height of skull in region of bulla tympanica	80.0
23. Distance from center of stylomastoid foramen to center of postglenoid foramen	15.1
Ratios of measurements	
character 14/ character 1	103.4
character 4/ character 5	52.4
character 18/ character 9	160.9

tors. The posterior border of the horizontal plate of the maxilla is sharp edged, turning ventrally about 2 mm behind M1. Posterior to M1, the ventrolateral border of the maxilla (inside the orbits) is flattened, and a very distinct separation can be defined between the horizontal and vertical surfaces of the palatine bones. The thickness of the maxilla between the posterior alveolus of M1 and the ventral border of the infraorbital canal is about 12.5 mm.

The anterior edge of the orbit is above the middle of P4 (Figure 5). The jugal process (ju) of the squamosal ascends anteriorly, as a long tapered process; the length of this process in front of the glenoid fossa is at least 36 mm. The glenoid fossa (g) measures 11 mm anteroposteriorly and 23.5 mm transversely. The postglenoid process itself is located about 4 mm forward of the meatal tube. A postglenoid foramen (fpg) is present in the fossa between the postglenoid process and the meatal tube (Figures 6, 7B). In contrast to the opinion of Wyss and Flynn (1993), we consider the presence of this foramen to be primitive in Phocidae; it is present and large in terrestrial carnivorans. Between the meatal tube and the postglenoid foramen is a deep, narrow groove in the tympanic bone; this groove is parallel to the meatal tube and floored by the tympanic. The presence or absence of a suprameatal fossa cannot be determined.

Laterally, the bulla (Figure 6) is extended as a long tube, with a prominent ventral lip forming the ventral margin of the external auditory meatus (eam); this opening is slightly oval (Figures 5, 6). The rim of the external auditory meatus is separated by a shallow notch from the mastoid process on the left side (as in other carnivorans), whereas on the right side these are in contact, with no notch present. The middle part of the auditory tube (on both sides) is completely fused to the anteromedial portion of the mastoid. A distinct shallow groove extends anterolaterally from the stylomastoid foramen (fsm) between the meatal tube of the bulla and the mastoid process (mp); this groove is present in all phocids and absent in all otarioids, including the enaliarctines. The groove has a different prolongation on the two sides of the skull: it starts from the vagina processus hyoidei (for this terminology see Mitchell, 1966, and Burns and Fay, 1970); on the right side of the skull this groove disappears at the middle of the meatal tube (mt), whereas on the left side, the groove continues to the lateral one-third of the tube, where it disappears. A deep cleft continues from the hyoid fossa around the posterolateral border of the bulla; this is the typical phocid structure, unlike any otarioid pinniped. The pit for the tympanohyal ligament is separated from the stylomastoid foramen (Figure 6B) and is medial to the latter (a primitive character).

In ventral view (Figure 6), the tympanic bulla (tb) is roughly triangular in outline, has a smoothly convex ventral surface, is slightly inflated in its anterolateral (=ectotympanic) parts, and slopes uniformly toward the external auditory meatus (eam).
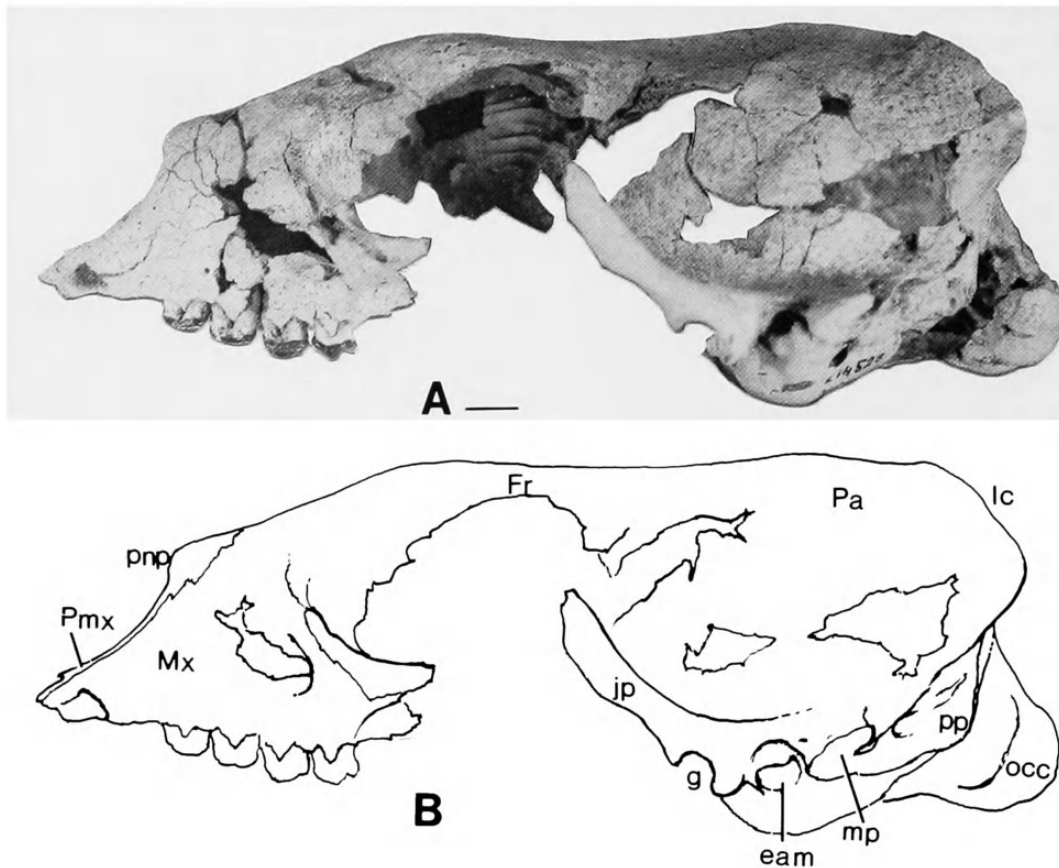
FIGURE 5.—*Devinophoca claytoni*, new genus and species, holotype skull Z14523: A, left lateral view, scale bar= 0.75 cm; B, outline drawing of the photograph of left lateral view. For explanation of abbreviations see Figure 3.

The anteroposterior length of the tympanic bulla is 1.38 times greater than the distance between the bullae (27 mm); this size relationship is similar to that of Cystophorinae and Phocinae. The length of the auditory bulla (37.5 mm) is 3.4 times the anteroposterior width of the glenoid fossa (11 mm), whereas in phocines it is 2.5–3.0 times this width. The long axis of the bulla is slightly oblique to the midline of the skull. The median lacerate foramen (fml) and musculotubular canal (=canalis musculotubaris, cma) are internally separated by a septum above the anteromedial corner of the bulla (Figures 6, 7B). The entotympanic part is much larger (more than two-thirds of the bulla) than the ectotympanic (ec). Caudally, the entotympanic (en) is more flattened than the ectotympanic along an anteroposterior axis, and it is separated from the ectotympanic part of the bulla by a distinct ridge instead of a sulcus. The flatter entotympanic is in contrast to the more inflated entotympanic of Mustelinae and other Phocidae, as noted by Wozencraft (1989).

The medial portion of the entotympanic close to the petrosal forms a deep, long fissure around the medial side of the bulla, and the carotid foramen (cf) is separated from the posterior lacerate foramen by a tiny lip. The carotid canal (cc) (Figures 6, 7) is partially concealed in the posteromedial wall of the bulla, considerably anterior to the posterior lacerate foramen (the primitive state; see Tedford, 1977). In contrast to phocines (Berta and Wyss, 1994), in *Devinophoca claytoni* the posterior

opening and the posteromedial process of the carotid canal (cc) are visible in ventral view. In *D. claytoni* the posterior aperture of the carotid canal is horizontal by lateral to the basioccipital, opens in a posteroventral direction, and has a fully formed margin on the right bulla at its medial side. This is the primitive condition, in contrast to that of other phocids, in which the posterior opening of the carotid canal is directed ventrally. It can be seen clearly on an X-ray (Figure 7) that the carotid canal is quite long; on the right side of the skull it is parallel to the sagittal plane of the skull, but on the left side the canal curves in an anterolateral direction. In the wall of bone dividing the carotid canal from the basioccipital bone (Bo) on the left bulla is a small canal (=inferior tympanic canaliculus), whereas on the right bulla this canaliculus is found inside (medial to) the posteromedial process of the carotid foramen.

The posterior lacerate foramen (flp) does not reach the base of the paroccipital process (pp) as it does in other phocids (Mitchell and Tedford, 1973). The posterior lacerate foramen (flp) at the posteromedial corner of the bulla is transversely bilobed and formed of two fenestrae; through the posterior lacerate foramen a septum is visible (Figure 6A). The posterior carotid foramen (cf) (Figure 6B) does not open into a common fossa with the posterior lacerate foramen (such a common opening is characteristic of ursids, otariids, and also of primitive musteloids) (see Mitchell and Tedford, 1973; Tedford,
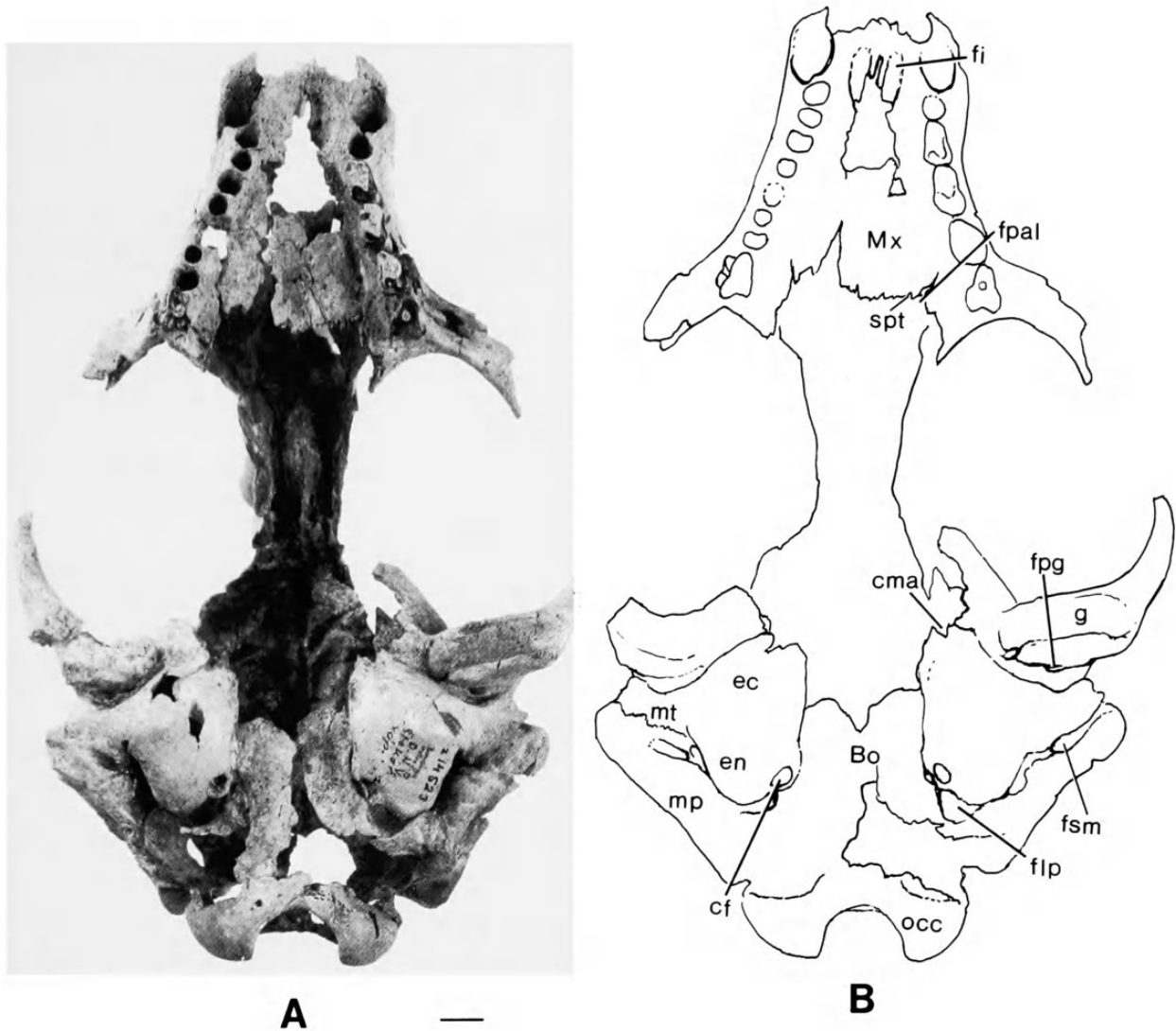
FIGURE 6.—*Devinophoca claytoni,* new genus and species, holotype skull Z14523: A, in ventral view scale bar= 0.75 cm; B, outline drawing of the photograph of ventral view. For explanation of abbreviations see Figure 3.

1977; Wolsan, 1993). The anterior part of the posterior lacerate foramen is expanded anteroposteriorly, whereas its posterior part extends mediolaterally (=transversely), a condition unknown in any other phocid (Wyss, 1988; Barnes, 1989; Berta and Wyss, 1994) (Figure 6). The posterior extremity of the petrosal is visible inside the posterior lacerate foramen, behind the bulla (King, 1966; Burns and Fay, 1970; Ray, 1976; Berta and Wyss, 1994) (Figure 6A). On the lateral margin of the basioccipital is a sulcus for the inferior petrosal sinus (sips) (see outline drawing from the X-ray on Figure 7B).

The mastoid process (mp) does not extend far laterally as it does in Monachinae, but it does form a pronounced prominence lateral to the auditory bulla. The mastoid is not so inflated that it obscures the bulla in lateral view; this is the condition described by Chapskii (1974) and King (1983) for phocines. According to Mitchell and Tedford (1973), a unique phocid feature, especially well developed in the Phocinae, is the inflation of the lateral side of the squamosal between the paroc-

cipital and mastoid processes, joining the two in a crest (Figure 6A). This is present also in *Devinophoca claytoni.* A continuous crest extends from the mastoid process over the paroccipital process (pp; jugular process in the terminology of Burns and Fay, 1970) to the supramastoid crest and connects to the lambdoidal crest (lc); it is rounded and weakly developed. Posteriorly the bulla is separated from the base of the paroccipital process by a distance of 10 mm, whereas it contacts both mastoid and exoccipital bones. The bases of the paroccipital (= jugular) processes are small, but the processes themselves are broken away.

In his analysis of the functional morphology of the inner and middle ear regions, Repenning (1972) concluded that phocids, otariids, and odobenids have different patterns of environmental adaptation in their auditory apparatus. Unfortunately, the middle ear cavity of *D. claytoni* is impossible to examine directly without destroying the tympanic bulla. An X-ray (Figure 7A) does not adequately display the middle ear cavity, but it

FIGURE 7.—*Devinophoca claytoni,* new genus and species, holotype skull Z14523: A (left), X-ray of skull in ventral view; B (below), outline drawing based upon Figure 7A and other X-rays of skull in ventral view. Scale bars=1.0 cm. For explanation of abbreviations see Figure 3.
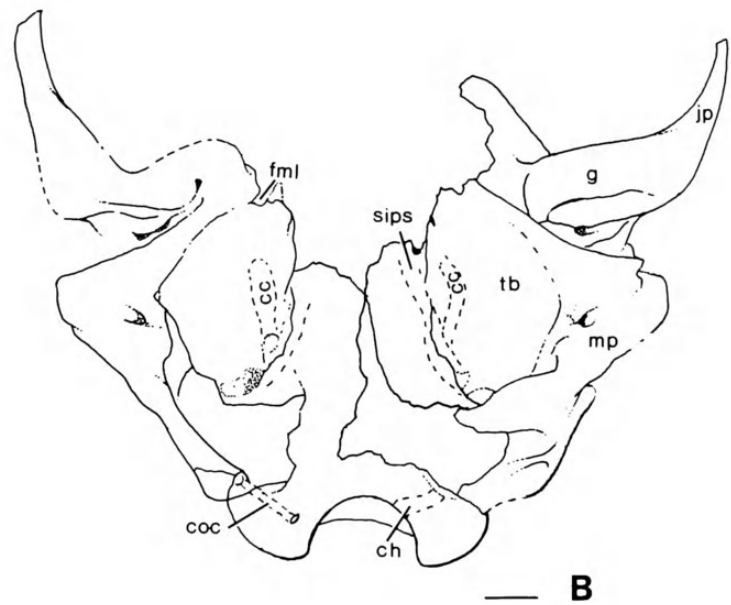
does allow us to learn that in *Devinophoca claytoni* the inner ear has a phocid construction; i.e., the oval window is a small, slim fissure, not round as in otariids. Along its ventral path to the oval window, the basal whorl of the cochlea extends transverse to the orientation of the skull as in other phocids, rather than posterolaterally as in otariids and odobenids. The fossa of the round window is partially shielded by the bony lip of the entotympanic.

The occipital shield (oc) is partially broken away (Figure 4C,D). A thin, median supraoccipital crest (ocs), only the dorsal part of which is preserved, extends dorsally to meet the thick lambdoidal crest. Lateral to the occipital condyles, the lambdoidal crests become very thin and continue as sharp ridges to the posterodorsal corners of the mastoid processes. The occipital condyles are 27 mm apart in the upper part of the foramen magnum and are approximately 18 mm apart below the foramen. The border of the intercondylar notch is thick (4.5 mm). The dorsal border of the foramen magnum is semicircular. The foramen for the transverse venous sinus is located medially in-

side of the occipital condyle, and the condyloid canal runs anterolaterally (Figure 7B).

The upper dental formula is I3, C1, P4, M1 (Figures 5B, 8). The incisor alveoli form a narrow U-shaped arcade. Cingula traverse the lingual sides of the crowns of the maxillary teeth and extend around to the buccal sides both anteriorly and pos-

TABLE 2.—Measurements (in mm) of the upper dentition in the holotype skull Z14523 of *Devinophoca claytoni,* new genus and new species.

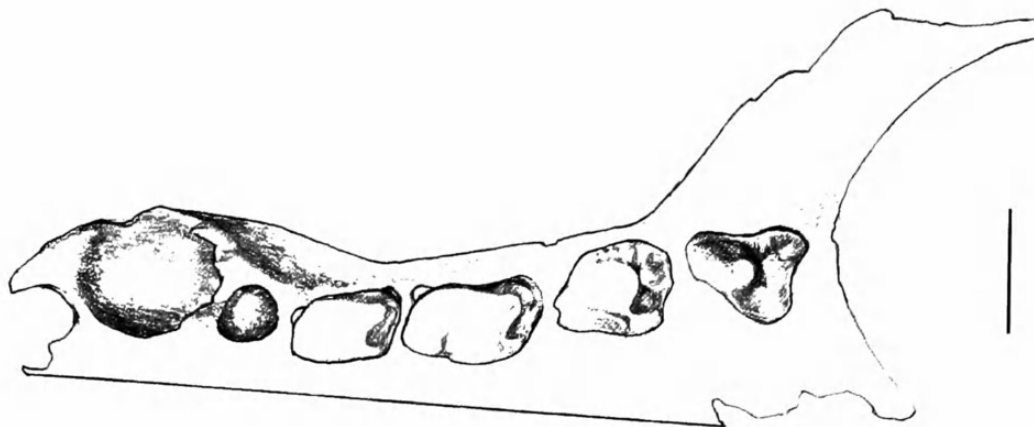| Teeth	length	width
I1 alveolus	–	3.0
I2 alveolus	–	3.0
I3 alveolus	–	5.7
C alveolus	13.2	10.5
P1 alveolus	6.5	5.6
P2 crown	10.0	6.5
P3 crown	10.0	8.0
P4 crown	10.6	8.2
M1 crown	9.3	7.5

FIGURE 8.—*Devinophoca claytoni*, new genus and species, holotype skull Z14523: Drawing of teeth in occlusal view. Scale bar=1.5 cm.

teriorly. As a result, the cingula nearly encircle the crowns of the teeth, as in the Enaliarctinae (Barnes, 1992), in *Kolpono-mos* (Tedford et al., 1994), and in other primitive arctoid carnivorans (Wolsan, 1993). The number of upper incisors is six, the same as in Phocinae, whereas Monachinae and Cystophori-nae have four. Preserved alveoli indicate that I3 is much larger than both I1 and I2, and that I1 and I2 are approximately equal in size (Table 2). The canines were relatively small and projected ventrally more than forward, judging from the curvature of the anterior surfaces of their alveoli. P1 has a single root, circular in cross section. P2 and P3 each have two roots; the anterior roots are round in cross section, but the posterior roots are expanded transversely and bilobed in cross section. The crowns of P2 and P3 are oval in occlusal view and heavily worn. P3 has a distinct lingual cusp (protocone).

The crown of P4 is subtriangular in occlusal view, and the buccal side is convex. Its metacone is present as a distinct cusp; the paracone and protocone are heavily worn. P4 has two roots, with the posterior alveolus bigger than the anterior and bilobate in cross section, indicating that the posterior root is made up of two fused roots, one above the protocone and one above the metacone. The bilobed posterior roots of P4 are very similar to the primitive condition in terrestrial carnivores (Berta and Wyss, 1994), unlike most pinniped teeth. A shallow notch (carnassial notch) is present between the paracone and metacone (Figure 8). The protocone of P4 and M1 is posteromedial to the paracone, and its buccal side is longer than the lingual, as in terrestrial arctoid carnivorans (Wolsan, 1993; Wyss and Flynn, 1993).

The M1 of *D. claytoni* is unlike that of any other known pinniped, but some similarity can be seen with the same tooth in the Enaliarctinae (Mitchell and Tedford, 1973; Barnes, 1979, 1992). The crown is triangular in occlusal view and is composed principally of the paracone, which is flanked by the much smaller metacone and protocone (Figure 8). These three cusps are supported respectively by the three roots. A three-rooted M1 has not been reported previously in any phocid. The

paracone is long anteroposteriorly and compressed transversely, and the small metacone lies posterolateral to it. The protocone is smaller than on the P4 but equal in size to those on P2 and P3. It is separated from the paracone by a trigon basin (as in enaliarctines, according to Barnes, 1989). The metacone and protocone connect to the paracone by sharp ridges, but a stronger ridge connects the apex of the paracone to the anterior angle of the tooth where it joins the anterior end of the buccal cingulum without a parastyle. The axis of this ridge is parallel to the sagittal plane.

Cladistic Analysis

CHARACTERS USED IN FAMILY PHOCIDAE

For this cladistic analysis, 32 characters were scored (Table 3). 0 designates the most primitive state among the taxa studied; 1 and 2 are alternate derived states; – indicates unknown or missing data.

1. Tympanic bulla: (0) small; (1) large (Chapskii, 1974:300, fig. 12).
2. External auditory meatus: (0) inframeatal lip well developed; (1) poorly developed.
3. Mastoid process: (0) not united with paroccipital process; (1) united with paroccipital process.
4. Mastoid process: (0) axis of mastoid convexity not directed ventrally; (1) directed ventrally.
5. Mastoid process: (0) prominence lateral to auditory bullae not strongly pronounced; (1) pronounced.
6. Mastoid process: (0) narrow (width of process less than length of process itself); (1) wide (Chapskii, 1974).
7. Mastoid process: (0) bulbous; (1) cylindrical.
8. Mastoid process: (0) width less than or equal to one-half of length of tympanic bulla; (1) width greater than one-half of length of tympanic bulla.
9. Mastoid convexity: (0) not turned down; (1) moderately turned down behind mastoid process; (2) directed sharply downward behind mastoid process.

TABLE 3.—Matrix of character-state data for Phocidae taxa and outgroups analyzed. (*=outgroup taxa.)

Species	Character number																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
*Allodesmus kelloggi**	0	1	0	1	0	0	1	1	1	1	0	2	2	1	0	1	0	0	1	0	0	0	0	2	1	0	0	1	1	0	1	0
*Lutra canadensis**	1	0	0	0	1	1	1	0	2	0	1	0	0	1	0	1	2	1	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Devinophoca claytoni	0	0	1	0	0	0	0	0	0	0	1	2	1	0	0	–	1	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0
Cystophora cristata	1	0	1	1	0	1	1	1	2	0	0	1	1	1	0	0	1	1	0	0	0	2	0	1	1	0	1	1	1	0	1	1
Mirounga leonina	1	0	1	1	1	1	0	0	2	1	0	1	0	1	0	0	2	1	0	0	0	2	0	1	1	0	0	1	1	0	1	1
Monachus monachus	0	0	1	0	1	1	0	1	1	1	1	2	2	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0
Monachus schauinslandi	0	0	1	0	1	1	0	1	0	1	1	2	2	0	1	0	0	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0
Callophoca obscura	1	1	1	0	0	0	1	1	1	0	1	2	2	0	0	0	1	0	1	0	0	1	1	1	0	0	1	0	0	1	0	2
Phoca vitulina	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	2	1	0	1	1	0	0	1	1	0	0	0
Erignathus barbatus	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	2	1	0	1	1	1	1	1	1	0	1	0
Leptophoca lenis	0	0	–	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	0	0	0	0	0

10. Nasal bones: (0) anterior ends form one common termination; (1) anterior ends separated.

11. Nasal bone: (0) maxillary contact longer than frontal contact; (1) frontal and maxillary contacts almost equal in length.

12. Maxilla: (0) very pronounced convexity anterior to orbits; (1) short concavity; (2) long concavity (Chapskii, 1974).

13. Anterior palatine foramina: (0) round and deep; (1) oval and shallow; (2) indistinctly marked (Burns and Fay, 1970).

14. Palatal groove: (0) present; (1) absent.

15. Palatal process of maxillary bone: (0) flat; (1) convex.

16. Foramen ovale: (0) hidden under hamular process of pterygoid bone; (1) exposed.

17. Interorbital width: (0) less than 25.0% of mastoid width of skull; (1) less than 30.0% but equal to or greater than 25.0% of mastoid width; (2) equal to or greater than 30.0% of mastoid width (Burns and Fay, 1970; Chapskii, 1974).

18. Paroccipital process: (0) well developed, large, hook-shaped; (1) poorly developed or absent, small conical projection.

19. Rostrum: (0) short, relative to cranium; (1) elongated (Chapskii, 1974).

20. Diameter of infraorbital foramen: (0) less than diameter of alveolus of upper canine; (1) equal to diameter of alveolus of upper canine; (2) greater than diameter of alveolus of upper canine.

21. Length of auditory bullae: (0) equal to or greater than distance between them; (1) less than distance between them (Burns and Fay, 1970; Chapskii, 1974).

22. Number of incisors: (0) 3/2; (1) 2/2; (2) 2/1 (Chapskii, 1974).

23. Roots of postcanine teeth (P2, P3): (0) one (fused); (1) two (according to Berta and Wyss, 1994).

24. Roots of P4: (0) three; (1) two; (2) one.

25. Crowns of postcanine teeth: (0) multicusped; (1) single cusped.

26. Relative dimensions of postcanine teeth as compared with longitudinal diameter of alveolus of upper canine: (0) more than 60% of longitudinal diameter of upper canine; (1) less than 60% or subequal.

27. Longitudinal diameter of alveolus of upper canine compared with maximal width of infraorbital foramen: (0) subequal in size; (1) more than one-half of maximal width.

28. Basal cingulum of postcanine teeth: (0) well developed; (1) not developed.

29. Number of additional cusps of premolars: (0) more than two; (1) no additional cusps.

30. Premolar crown: (0) aligned parallel to axis of tooth row; (1) seated obliquely.

31. Upper incisors: (0) arranged in a curved arcade; (1) arranged in a straight line.

32. Second and third upper incisors: (0) third larger than second; (1) second larger than third, (2) all upper incisors subequal in size.

The matrix of character-state data for nine species of fossil and modern phocids is given in Table 3; in addition, these characters were scored for two outgroup taxa. These outgroup taxa are the fossil otarioid *Allodesmus* and the living mustelid *Lutra*, reflecting the competing hypotheses of pinniped relationships, monophyly (Wyss and Flynn, 1993; Berta and Wyss, 1994) or diphyly (McLaren, 1960; Mitchell, 1966; Tedford, 1977). Allodesmines are highly evolved otariids, widely diversified in the middle Miocene, and possess many derived marine carnivore features (Barnes and Hirota, 1995).

The analysis of the phocid taxa using these 32 unweighted cranial and dental characters and the bb*; ie* routines in Hennig86 (Farris, 1988) produced two maximally parsimonious trees, each 79 steps long with a consistency index of 0.51 and a retention index of 0.68.

Use of Hennig86's successive-weighting option reduced the number of trees from two to one, leaving this part of the tree much better resolved (Figure 9). Points where the nodes of the present tree correspond, the clades, traditionally recognized as subfamilies, are indicated. Only one new higher taxon name is introduced here: inclusion of *Devinophoca* within the Phocidae requires recognition of the new subfamily Devinophocinae.

The nodes of the cladogram shown in Figure 9 are supported by the following character transformations:
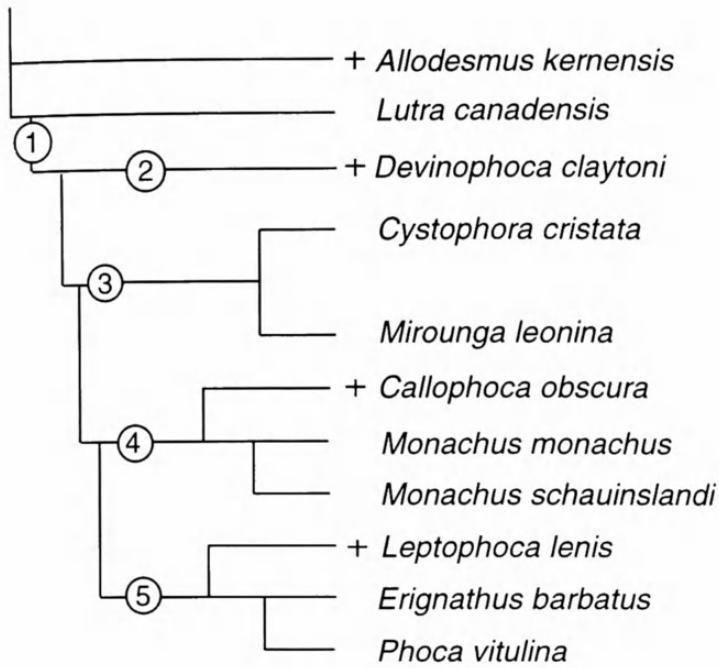
FIGURE 9.—Nelson consensus tree of two trees of the hypothesized phylogenetic relationships among taxa of true seals and two outgroups, generated by Hennig86 using 32 cranial characters and the successive weighting option. Tree length, 79 steps; consistency index, 0.51; retention index, 0.68. Character states are given in Table 3.

Node 1 (Family Phocidae): 3(1); 23(1); 24(1). These apomorphic characters (relative size of the mastoid process and its lack of union with the paroccipital process; two roots on postcanine teeth) are treated as synapomorphies of the family Phocidae.

Node 2 (subfamily Devinophocinae, possibly paraphyletic): 24(0). Autapomorphy of *D. claytoni*: three roots of the posterior postcanine teeth fused.

Node 3 (subfamily Cystophorinae): 9(2); 22(2); 29(1). The mastoid convexity directed sharply downward behind the mastoid process; reduced number of incisors; no additional cusps on premolars.

Node 4 (subfamily Monachinae): 11(1); 13(1). The relative dimensions of the frontal and maxillary parts of the nasal bones; the shape of the anterior palatine foramina. Also, character 13(2) is homoplasious in *Phoca vitulina* and *Erignathus barbatus*.

Node 5 (subfamily Phocinae): 20(1, 2); 21(1). The diameter of the infraorbital foramen is equal to or greater than the diameter of the alveolus of the maxillary canine; the length of the auditory bullae is less than the distance between them. Also, character 20(1) is homoplasious in *Monachus schauinslandi* and *Leptophoca lenis*.

Discussion and Conclusions

The traditional separation of Phocidae into subfamilies Phocinae, Monachinae, and Cystophorinae has been inten-

sively debated during the past 40 years, but overall it is the system still used today.

The well-preserved skull of *Devinophoca claytoni* from the early middle Miocene (16.4 Ma) shows a mix of subfamilial characters. The features it shares with Phocinae are weakly pronounced mastoid process, 5(0); six incisors, 22(0); and poorly developed paroccipital process, 18(1) (also shared with Cystophorinae). The characters similar to Monachinae are the shape of maxillae, 12(2) and the ratio between frontal and maxillary contacts of the nasal bones, 11(0) (shared with Phocinae also). Characters shared with Cystophorinae are ratio between interorbital space and mastoid width, 17(1); ratio between the length of auditory bullae and distance between them, 21(0); and oval-shaped and deep anterior palatine foramina, 13(1).

Moreover, this skull has primitive features that are not known in any of the three subfamilies: M1 is triangular, with three cusps and three roots; in P2–P4 the larger posterior roots are clearly made up of two fused roots; and the sagittal crest is very well developed for a phocid, though weak compared with some carnivorans. This plesiomorphic pinniped is therefore considered a sister taxon to the other three subfamilies of Phocidae. Because of its late geologic age, *Devinophoca* might represent a very primitive relict of the common ancestor of the groups of Phocidae.

Wozencraft (1989) identified the shortened and narrowed contact between the premaxilla and the nasal, as seen in phocids and lutrines, as a primitive condition. Barnes (1989), Berta and Wyss (1994), and Wyss and Flynn (1993) had the opposite opinion and suggested that this character is derived. The supraorbital process of the frontal is a small, rounded knob that is the primitive condition seen in terrestrial carnivorans (Berta and Wyss, 1994).

In *Devinophoca claytoni,* the nasals bones end near the frontal-maxillary contact. According to Berta and Wyss (1994), this is a primitive condition among terrestrial carnivorans, and among otariids and odobenids, as exemplified by the enaliarctine otarioids *Enaliarctos* and *Pteronarctos*. In the more-derived phocids, the nasals extend far posterior to the frontal-maxillary suture between the frontals, and they share this feature convergently with the otarioids *Desmatophoca* and *Allodesmus*. Our material supports that statement; this plesiomorphic representative of phocids, i.e., *Devinophoca*, shares the primitive form of the nasals with terrestrial carnivorans, especially with Mustelidae.

Computer-assisted phylogenetic analysis of some fossil and living phocids supports the monophyly of the family and recognizes four principal clades, including the new subfamily Devinophocinae. This phylogenetic framework supports the classification used by Chapskii (1955, 1974), Scheffer (1958), and Koretsky and Grigorescu (2002), and it conflicts with the various arrangements proposed by King (1966), Burns and Fay (1970), Wyss (1994), and McKenna and Bell (1997). We are reluctant to name a new higher-level taxon, but the very unusual morphology of *Devinophoca* does not allow us to assign

it to any known subfamily. We thus erect a new taxon at the subfamilial level.

The interorbital construction in *Devinophoca claytoni,* the large size of the orbits, and the loss of the lacrimal bone also are found in other aquatic species, including the Enaliarctinae among the otarioids, as advanced aquatic adaptations (Howell, 1928; Savage, 1957; Mitchell and Tedford, 1973). The development of the dorsal sagittal sinus (as clearly seen in the X-ray; Figure 7) for venous drainage of the brain is suggested by Mitchell and Tedford (1973) to be related to diving adaptations.

Striking similarities between the skulls of *Devinophoca* and *Enaliarctos* include a short rostrum. Although the ventral part of the skull is not preserved in *Devinophoca,* we presumed that the interorbital part of the skull has the shape of an l-beam, as

seen in *Enaliarctos* and other Phocidae. Mitchell and Tedford (1973) suggested that this construction is an adaptation for structural rigidity, while accommodating the large eyes (as in desmatophocines also). The presence of a sagittal crest and strong lambdoidal crests, the complexity of the teeth, and the short rostrum all indicate that the feeding mechanism of *Devinophoca claytoni* was adapted for slower and more powerful closing of the jaws, rather than the rapid action of the fish-eating pinnipeds. We conclude that *Devinophoca claytoni* was adapted to eating mollusks and crustaceans.

Some of the features mentioned above, such as the paroccipital process separated from the mastoid and a single-chambered bulla with large entotympanic and much smaller ectotympanic, are more similar to the primitive Mustelidae or Procyonidae than to Ursidae (in accord with Tedford, 1977).

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