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A NEW SPECIES OF THE SUBFAMILY DEVINOPHOCINAE (CARNIVORA, PHOCIDAE) FROM THE CENTRAL PARATETHYS

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Abstract. Several excavations in Slovakia resulted in the finding and description of a new species of the extinct phocid subfamily Devinophocinae from the early Badenian, early Middle Miocene (16.26-14.89 Ma). Material of *Devinophoca*, including the skull, mandibles and teeth, presents distinguishing characters of the subfamily as well as mixed characters with the three extant phocid subfamilies (Cystophorinae, Monachinae and Phocinae). Detailed descriptions of dentition reveal that true seals ranging from 16 million years ago to the present have a generally uniform dental formula within each subfamily, based on total number of incisors: Phocinae (10 incisors; 3/2), Cystophorinae (6 incisors; 2/1); Monachinae (8 incisors; 2/2), and Devinophocinae (also 8 incisors as Monachinae, but in different combination: 3/1). The newly described *Devinophoca emryi* is represented by the second known skull of this subfamily, with *D. claytoni* being the first. Certain derived characters in pinnipeds were clearly noticeable on this skull, supporting the phylogenetic analysis that showed *D. claytoni* as its sister taxon. Stratigraphical examinations suggest that these Paratethyan seals (*D. claytoni* and *D. emryi*) from the Vienna Basin, specifically from the Devínska Nová Ves-Bonanza locality, occupied shallow marine water with coral-reef zones. Over time, they transitioned from a humid, tropical shallow shore zone in the early Badenian (16.26 – 14.89 Ma) to a subtropical climate in the middle Badenian (14.89 -13.82 Ma) and a warm temperate climate during the late Badenian (13.82 -12.73 Ma).

Introduction

During excavations at the base of the Malé Karpaty Mountains, specifically at the Bonanza site near the junction of the Morava and Danube rivers (Fig. 1), a single skull and numerous teeth, mandibles and multiple postcranial bones were collected. The assemblage comprises a mixture of marine and terrestrial vertebrates derived from the southern slope of Devínska Kobyla Hill (geographic coordinates of the site are 48° 12’ 34” N and 16° 58’22” E), located on the opposite side of the hill and situated not far from the village of Devínska Nová Ves (= Neudorf an der March, vicinity of Bratislava, western Slovakia). In addition to terrestrial and marine mammals, fossils from different species of fish and frogs were also found at this site. A brief description and a list of all species of vertebrates from this site have been previously published (Holec et al. 1987; Holec & Sabol 1996; Holec et al. 1997; Schultz 2004; Fejfar & Sabol 2009). Additionally, detailed descriptions of the geology and history of this site and nearby localities can be found in Koretsky and Holec (2002) and Domning and Pervesler (2012).

The found material was discovered in 1984 by the amateur paleontologist Š. Mészároš, who called this location “Bonanza” (dated to the Middle Miocene, early Badenian, lower part of MN 6). He and another amateur paleontologist, Miroslav Hornacek, donated all their collected material to the Slovak National Museum, including the skull of *Devinophoca claytoni* previously described by Koretsky and Holec (2002).

A scientific excavation at this site was performed in 1997-98 through the help of the Paleobiology Department of the Smithsonian Institution (Washington, D.C., USA) in collaboration with the Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University, and with the Department of Paleontology of the Slovakian National Museum (Bratislava, Slovak Republic), leading to the discovery of cranial and multiple mandibular and postcranial elements.

Here, we describe a new species of the Subfamily Devinophocinae from the early Badenian, early Middle

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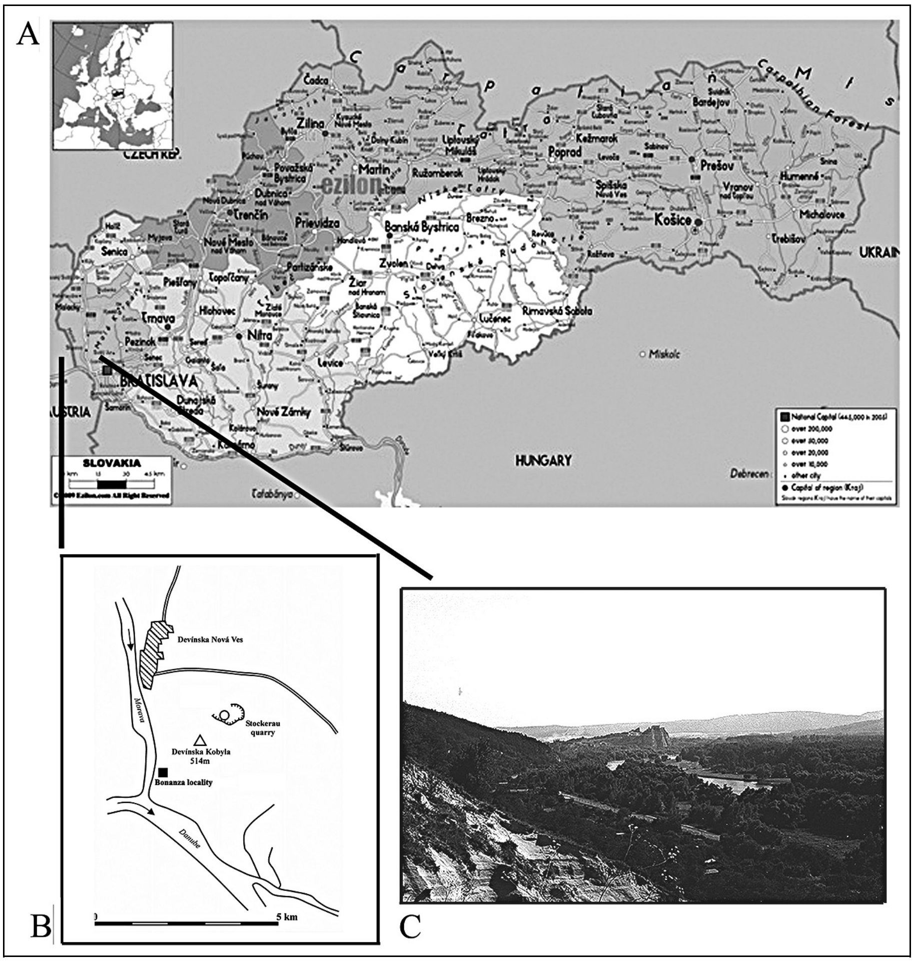

Fig. 1 - A) Map of Slovakia. B) Location and C) Outcrop of the Devínska Nová Ves Bonanza site (~ 16.5 Ma) near Bratislava, Slovakia (Map modifed after Fejfar & Sabol 2009).

Miocene (16.26-14.89 Ma). As mentioned in numerous previous publications (Koretsky 2001; Koretsky & Grigorescu 2002; Koretsky & Holec 2002; Koretsky & Rahmat 2013), we accept a "traditional" classification of seals (Simpson 1945; Scheffer 1958; Chapskii 1955, 1974; King 1964; Heptner et al. 1976), in which the Family Phocidae is divided into three extant subfamilies: Phocinae, Monachinae, and Cystophorinae. Although this classification opposes the current view of some investigators (Wyss 1994; Muizon 1982, 1992; King 1983; Berta & Sumich 1999; Amson & Muizon 2014), detailed discussion of interpreting systematics and taxonomic history of seals has been provided in Koretsky and Rahmat (2013: 325-327).

In this paper, we focus only on the skull, mandibles, and teeth (collected by I.A. Koretsky and R.J. Emry). Descriptions of postcranial elements will be detailed in a separate paper.

Abbreviations

SNMZ, Department of Paleontology, Slovakian National Museum, Bratislava, Slovak Republic; **USNM,** National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Systematic Paleontology

Order **Carnivora** Bowdich, 1821
Superfamily Phocoidea Gray, 1825
Family Phocidae Gray, 1825
Subfamily Devinophocinae Koretsky & Holec, 2002

Type Genus: Type and only included genus by monotypy, *Devinophoca* Koretsky & Holec, 2002.

Distribution: Early Badenian (MN 6), early Middle Miocene (16.26 -14.89 Ma); Central Paratethys, Vienna Basin of western Slovakia.

Emended Diagnosis: Dental formula I3/1, C1/1, P4/4, M1/1 (presenting a unique combination of incisors that differ from Phocinae, Monachinae and Cystophorinae). Alveoli of upper incisors form wide u-shaped arcade; P2/2 – M1/1 double-rooted (as in Phocinae, Monachinae, and Cystophorinae), with posterior root larger than anterior; pre-orbital part of maxilla with wide, pronounced concavity (similar to Monachinae); antorbital process well defined; frontal contacts of nasal bones much shorter than maxillary contact (shared with Phocinae); interorbital space slightly broader anteriorly than posteriorly; interorbital width less than 25% of skull width at mastoid processes (as in Cystophorinae); sagittal crest very well developed (more than in Monachinae), and does not form triangle with lambdoidal crests; diameter of infraorbital foramen less than diameter of alveolus of upper canine (as in *Monachus schauinslandi*, unlike in Phocinae and Cystophorinae); anterior palatal foramina oval and deep (as in Cystophorinae), with well-pronounced palatal groove; anteroposterior length of tympanic

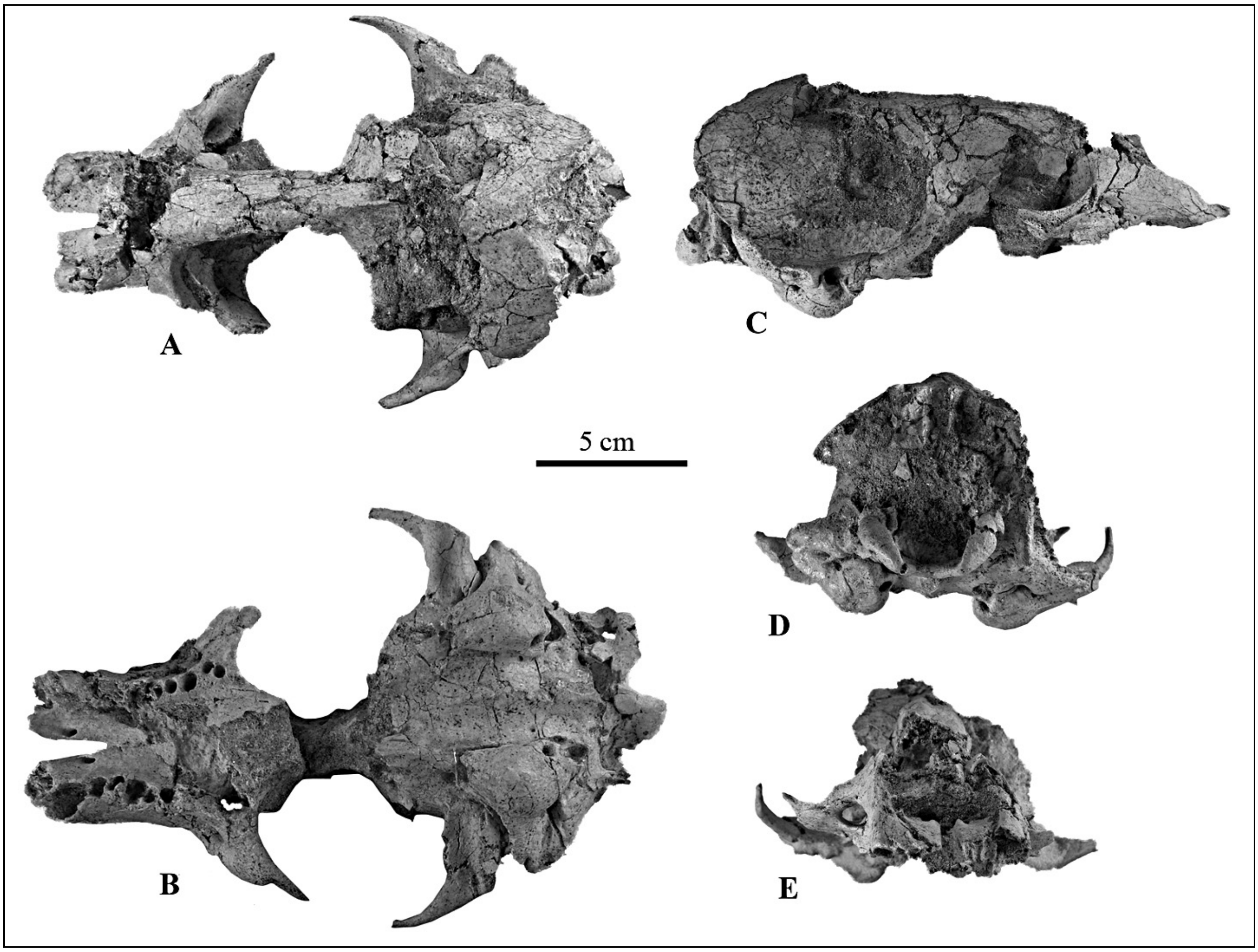

Fig. 2 - Skull of the holotype of *Devinophoca emryi* sp. n. (Early-Middle Miocene; ~16 Ma; Badenian, Vienna Basin, Slovakia; holotype, USNM 553684) in A) dorsal, B) ventral; C) lateral, D) caudal, and E) cranial views.

bullae greater than distance between them (similar to Phocinae and Cystophorinae); width of mastoid process less than half length of tympanic bulla; mastoid convexity does not turn ventrally behind mastoid process (similar to Phocinae).

Body of mandible shallow; mental process absent; symphyseal part not pronounced, symphysis reaches middle of alveolus p2; posterior (=distal) alveoli bigger than anterior (=mesial); postcanine teeth multicusped; alveoli of p4 bigger than those of m1; teeth with long metaconid and strongly developed basal cingulum; no diastemata.

Devinophoca emryi sp. n.

Figs 2, 3, 4, 6, 7; Tabs 1-4

Etymology: "emryi" in honor of Dr. Robert J. Emry (National Museum of Natural History, Smithsonian Institution, Washington, D.C.), in recognition of his contributions to the discovery and collecting of this fossil material.

Holotype: Incomplete skull without teeth; USNM 553684 of the Museum of Natural History. The closed sutures suggest a fully mature individual.

Paratypes: In addition to the holotype, the following specimens were found in the Devínska Nová Ves – Bonanza site: R. mandible (USNM 553687), with p2 and p3; L. mandible (SNMZ 25502), without teeth; R. mandible (USNM 553683), with p2 and p3; R. condyloid process of mandible (SNMZ 25503). Morphologically, the condyloid processes of these mandibles fit perfectly into the glenoid fossa of the *D. emryi* skull and their length correspond to the size of this skull, and not to the *D. claytoni* skull.

Six isolated cheek teeth: right P1 (SNMZ 14529), left P3 (SNMZ 14529), and left P4 (SNMZ 14529); right p1 (SNMZ 14529); left p1 (SNMZ 14529), left p4 (SNMZ 14698).

Type Locality: The holotype and the paratypes (see below) are from the locality of the Stockerau lime plant, Bonanza Devínska Kobyla, outskirts of Bratislava, Slovak Republic.

Range: Badenian, early Middle Miocene (16.26 -14.89 Ma); Central Paratethys, Vienna Basin of western Slovakia.

Diagnosis: Infraorbital foramen oval and large (in contrast to *D. claytoni* where it is small and circular); length of palatine process shorter, but length of tooth-row longer than in *D. claytoni*; anteroposterior length of tympanic bulla shorter than in *D. claytoni,* same as groove which extends anterolaterally from stylomastoid foramen between meatal tube of bulla and mastoid process; distance between base of paroccipital process and bulla greater than in *D. claytoni*, and base of paroccipital process larger. I3 much larger than I2, which in turn is larger than I1; upper canine roots relatively large and crown projected more anteriorly than ventrally.

Body of mandible thin and shallow, with long, wide, and oval teeth; metaconid and basal cingulum strongly developed; mental process absent; symphyseal part not pronounced, symphysis reaches middle of alveolus p2; postcanine toothrow oriented parallel to axis of mandible; posterior alveoli larger than anterior; postcanine teeth multicusped; p4 shorter, but wider than m1; no diastemata.

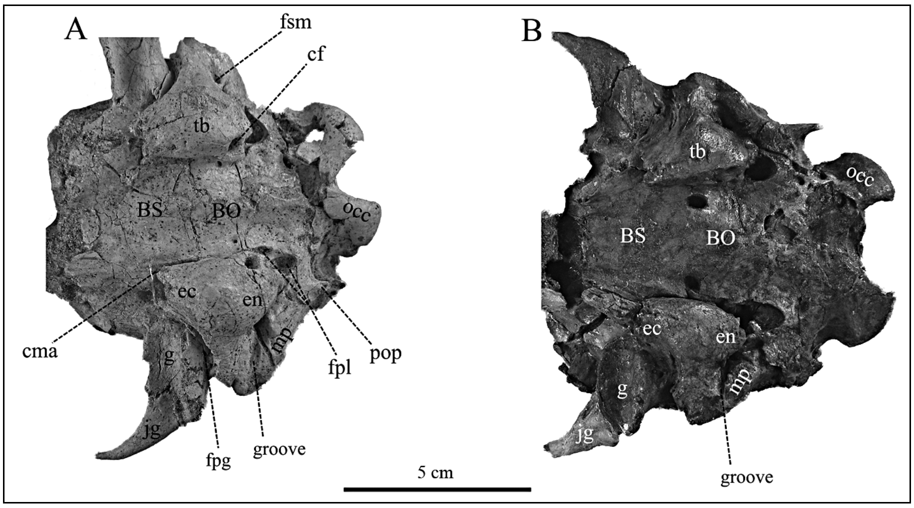

Fig. 3 - Detailed views of basicrania of A) *Devinophoca emryi* sp. n. (Early-Middle Miocene; ~16 Ma; Badenian, Vienna Basin, Slovakia; holotype, USNM 553684) and B) *Leptophoca lenis* (Late-Early Miocene; ~18 Ma; Calvert Formation, Maryland, USA; CMM-V 2021) in ventral view.
Abbreviations: BO = basioccipital; BS = basisphenoid; cf = carotid foramen; cma = anterior musculotubular canal; ec = ectotympanic; en = entotympanic; fpl = posterior lacerate foramen; fpg = postglenoid foramen; fsm = stylomastoid foramen; g = glenoid fossa; jg = jugal process; mp = mastoid process; occ = occipital condyle; pop = paraoccipital process; tb = tympanic bulla.

Description and comparisons

The complete description of the *Devinophoca* skull has been detailed for *D. claytoni* in Koretsky and Holec (2002). All of the teeth of the holotype of *D. emryi* have fallen out. The cranial material (Fig. 2) and mandibles are well preserved and bear morphological and phylogenetic information, making possible a precise assessment of the affinities of *Devinophoca emryi*. In the following description and discussion, morphological implications are based on several previous publications on extant seals and other carnivores (Howell 1928; Miller et al. 1964; Piérard 1971; Koretsky & Holec 2002; Amson & Muizon 2014).

While the palatal parts of the premaxilla-maxillary sutures are fused and completely obliterated in *D. claytoni*, in the new species there is a groove, likely for the neurovascular bundle. The nasal bones, the palatal bone (Fig. 2A, B), parts of the palatine processes of the maxilla and a segment of the orbital part of the frontal bones are missing in *D. emryi*. While both species have equal condylobasal lengths, *D. claytoni* has a shorter palatine process and longer tooth-row than *D. emryi*. Part of the basicranium is broken away also, and the vomer, pterygoid, and presphenoid bones are missing. Overall, the *D. emryi* skull is more complete than that of *D. claytoni*. Both jugal (= zygomatic) bones are missing, the paroccipital (= jugular) processes are broken away, but found separate from the skull, and the supraoccipital part of the occipital shield is mostly present, in contrast to the *D. claytoni* skull.

As in *D. claytoni*, the infraorbital foramen in *D. emryi* (Fig. 2E) is located above the posterior P4 - anterior M1; but instead of being small and circular (as in *D. claytoni*), it is oval and large in *D. emryi*.

In contrast to Phocinae (Chapskii 1974), but similar to Devinophocinae, the diameter of the alveolus of the upper canine is 13.4 mm (in *D. claytoni* 13.2 mm), which is greater than the diameter of the infraorbital foramen (= 10.7 mm).

The palatine process of the maxilla (Fig. 2B) is partially broken, and flattened. Similar to *D. claytoni*, the anterior palatal foramina (= *fissurae palatinae*) are located between the canines and are oval and deep, with a big groove directed towards the incisors, in contrast to the condition stated by Wozencraft (1989) for other phocids. Between the canines, the palate becomes wider (21.5 mm), opposite to *D. claytoni* where it is narrow (18.5 mm). The lingual alveolar margins of the canines and incisors are at the same level as those of the cheek teeth. From the anterior palatal foramina to the level of P2, the palate is flat. Posterior to P2 is a shallow antero-posteriorly-aligned groove (= *sulcus palatinus*) that is characterized as a primitive condition among phocids by Wyss and Flynn (1993). 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 missing.

On the ventral surface of the skull, the basioccipital bone is rectangularly shaped between the tympanic bullae (Figs. 2B, 3A) and is continuous with the basisphenoid, in contrast to *Hadrokirus martini* (Amson & Muizon 2014), which has a slight transverse ridge separating these bones. There exists a vertical ridge located approximately in the middle of the basioccipital and basisphenoid between the bullae.

The general structure of the tympanic bulla appears the same in both species. The anteroposterior length of the tympanic bulla in *D. emryi* is 1.30 (in *D. claytoni* - 1.38) times greater than the distance between the bullae (27.4 mm), similar to that of Cystophorinae and Phocinae. The length of the *D. emryi* auditory bulla is 35.7 mm (in *D. claytoni* - 37.5 mm), which is 2.7 times greater than the anteroposterior width of the glenoid fossa (13.0 mm; in *D. claytoni* - 11 mm), similar to phocines where it is 2.5-3.0 times larger. The long axes of the bullae are parallel to the sagittal plane (in contrast to *D. claytoni*, where they are slightly oblique).

The tympanic bulla of *D. emryi* appears triangular on both sides in ventral view, with a smooth, convex ventral surface. The right side displays inflation of both the ectotympanic and entotympanic portions of the bulla (Fig. 3A), also observed in *Lobodon carcinophagus* and *Phoca vitulina* (Amson & Muizon 2014). However, the left bulla has an inflated ectotympanic and caudally flattened entotympanic, a condition similar to what has been described in *Leptophoca lenis* (Fig. 3B; Koretsky 2001) and *Puijila darwini* (Rybczynski et al. 2009). The flatter entotympanic in *D. emryi* is in contrast to the more inflated condition of Mustelinae and other Phocidae described by Wozencraft (1989). Overall, this skull shows a mixture of characters from the three extant subfamilies (Cystophorinae, Monachinae and Phocinae), likely explaining the slight osteological differences between right and left sides of the basicranium.

Similar to *D. claytoni* (Koretsky & Holec 2002), the lateral portion of the tympanic bulla extends as a long tube, with a prominent ventral lip forming the ventral margin of the external auditory meatus on both sides. The opening of the external auditory meatus is oval on the left side and round on the right. The rim of the external auditory meatus is separated from the mastoid process by a deep notch on both sides (similar to other carnivores). In contrast to other phocids studied by Mitchell and Tedford (1973), this notch is separated from the well-defined groove, extending anterolaterally from the stylomastoid foramen along the side of the external auditory meatus, by a wide and prominent lip. Similar to *D. claytoni*, this groove has a different prolongation on either side of the skull, but starts from the *vagina processus hyoidei* (for this terminology see Mitchell 1966 and Burns & Fay 1970). On the right side of the skull, this groove is shorter and disappears at about 1/3 the length of the meatal tube (in *D. claytoni* at the middle), while on the left side (Fig. 3), the groove continues almost to the edge of the meatal tube (in contrast to *D. claytoni*, where it disappears at the lateral 1/3 of the tube). This groove is present in all phocids and absent in all otarioids, including enaliarctines (Koretsky & Holec 2002). Another observed primitive character is that the pit for the tympanohyal ligament is medial to and separated from the stylomastoid foramen.

The musculotubular canal (= *canalis musculotubaris*, cma) is located in the anteromedial corner of the bulla. Caudo-lateral to the pterygoid hamulus is a single opening, the foramen ovale. This contrasts with other fossil seals such as *L. lenis* (Fig. 3B; Koretsky 2001) and enaliarctines (Barnes 1979) which have paired openings (foramen ovale and petrotympanic fissure) and canines which also have paired openings, the foramen ovale and posterior alar foramen (Miller 1964). Modern seals possess dual openings as well, suggesting that a single opening may be the primitive condition.

The carotid foramen (Fig. 3) is separated from the posterior lacerate foramen by a thick wall, similar to *L. lenis* (Koretsky 2001), and in contrast to *D. claytoni* (Koretsky & Holec 2002), where only a tiny lip separates these openings. The posteromedial position of the carotid foramen in *D. emryi* is similar to the Recent *Mirounga angustirostris* and contrasts with the position in *Puijila darwini* (Rybczynski et al. 2009), where it is located at the caudal end of the bulla and in *Enhydra lutris*, where it is located in the middle of the medial side of the bulla. The carotid canal is concealed in the posteromedial wall of the bulla, anterior to the posterior lacerate foramen, similar to both *L. lenis* (Koretsky 2001) and *D. claytoni* (Koretsky & Holec 2002). In contrast to phocines (Berta & Wyss 1994), in *D. claytoni* and *D. emryi*, the posterior opening and the posteromedial process of the carotid canal are visible in ventral view. In both *Devinophoca* species, the posterior aperture of the carotid canal is in the same horizontal plane as (=lateral to) the basioccipital, opens in a posteromedial direction, and has a fully formed margin on both bullae at its medial side. This appears to be the primitive condition in seals, in contrast to that of later phocids in which the posterior opening of the carotid canal is directed ventrally.

The structure of the mastoid process is similar in both *Devinophoca* species (see description in Koretsky & Holec 2002: 171). Posteriorly, the bulla is separated from the base of the paroccipital process by a distance of 14.6 mm (in *D. claytoni* by 10 mm) and contacts both the mastoid and exoccipital bones. In contrast to *D. claytoni*, the base of the paroccipital (= jugular) process is large, but the tip of the process is broken away. The *D. emryi* mastoid is narrow and forms a pronounced prominence anterolateral to the bulla (also seen in *L. lenis*; Koretsky 2001). The mastoids of *E. lutris* and *P. darwini* appear to be shaped like a hook ventrally. Similar to *L. lenis*, the mastoid of *D. emryi* is not so inflated that it obscures the bulla in lateral view, which contrasts with the condition seen in most phocines (Chapskii 1974; Ray 1976; King 1983). The hypoglossal foramen is located caudal to the posterior lacerate foramen in the exoccipital and is clearly visible on one side, but partially destroyed on the other.

Similar to *D. claytoni*, the posterior lacerate foramen in *D. emryi* does not reach the base of the paroccipital process as in other phocids (Mitchell & Tedford 1973). At the posteromedial corner of the bulla, the left posterior lacerate foramen is transversely bilobed and formed of two fenestrae through which a septum is visible. The right posterior lacerate foramen is not bilobed, but is a single large opening, the likely primitive

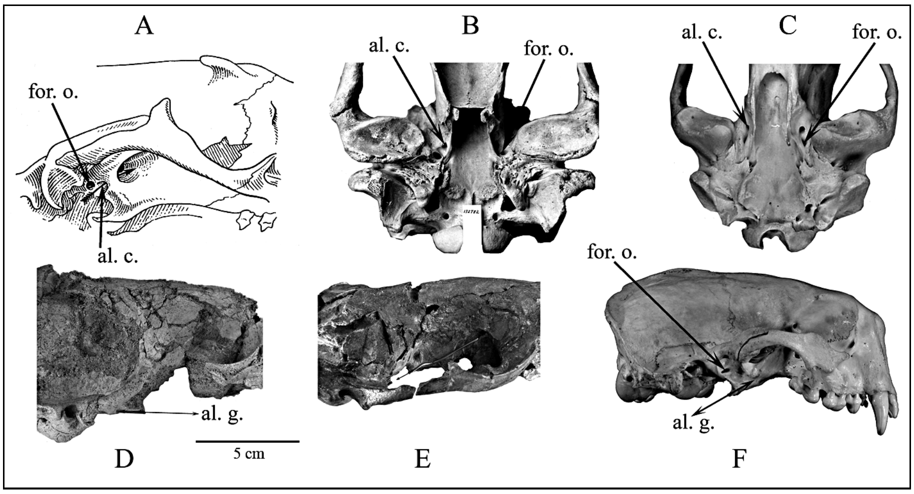

Fig. 4 - Carnivoran skulls showing location of the alisphenoid canal (indicated by arrows) and alisphenoid groove (indicated by double-headed arrows) in: A) generalized otariid representative; B) Southern sea lion (*Otaria byronia*); C) Brown bear (*Ursus arctos*); D) *Devinophoca emryi* sp. n. (Early-Middle Miocene; ~16 Ma; Badenian, Vienna Basin, Slovakia; holotype, USNM 553684); E) *Leptophoca lenis* (Late-Early Miocene; ~18 Ma; Calvert Formation, MD, USA; CMM-V 2021) and F) Sea otter (*Enhydra lutris*). Abbreviations: al. c. = alisphenoid canal; al. g. = alisphenoid groove; for. o. = foramen ovale.

(= ancestral) condition seen also in *E. lutris*, *Desmatophoca brachycephala* (Family Otariidae, Subfamily Desmatophocinae), and *Phoca groenlandica*. In *M. angustirostris*, this septum is incomplete, as the posterior lacerate foramen is not fully bilobed. This contrasts with *D. claytoni*, where both posterior lacerate foramina are bilobed. The carotid foramen does not open into a common fossa with the posterior lacerate foramen (fpl, Fig. 3A), as seen in ursids, otariids, and primitive musteloids (see Mitchell & Tedford 1973; Tedford 1977; Wolsan 1993), but is separated via a thick semicircular ridge (also seen in *L. lenis*). There also are differences in the shape of the posterior lacerate foramen in both devinophocine seals, as the anterior part of the left posterior lacerate foramen is expanded anteromedially in *D. emryi* and anteroposteriorly in *D. claytoni*, while its posterior part extends posteriorly in *D. emryi* and mediolaterally (= transversely) in *D. claytoni*. On the left side, the posterior extremity of the petrosal is visible inside the posterior lacerate foramen, behind the bulla (King 1964; Burns & Fay 1970; Ray 1976; Berta & Wyss 1994). On the lateral margin of the basioccipital, a groove for the inferior petrosal sinus is present that is deeper and wider on the left side.

In contrast to the opinion of Wyss and Flynn (1993), Koretsky (2001) stated the presence of a postglenoid foramen is likely a primitive condition in Phocinae. Examination of this 16 million-year-old skull reveals the presence of a postglenoid foramen, which has also been described in *L. lenis* (Koretsky 2001), *D. claytoni* (Koretsky & Holec 2002) and *P. darwini* (Rybczynski et al. 2009).

The glenoid fossa (g) measures 13 mm anteroposteriorly and 18 mm transversely (11 mm x 23.5 mm in *D. claytoni*). The postglenoid process itself is located about 11.4 mm anteriorly of the meatal tube (in *D. claytoni* - 4 mm). The jugal process (jg) of the squamosal ascends anteriorly, as a long tapered process; the length of this process in front of the glenoid fossa is greater in *D. emryi* (42.3 mm) than in *D. claytoni* (36 mm). The jugal is extremely low and thin, with its dorsal edge forming a sharp crest on the ventral border of the orbit. Its anterodorsal margin reaches the posterior edges of the infraorbital foramen, but well ventral to the small preorbital process of the maxilla.

The sagittal crest is poorly developed, indicating a weak origin for the temporalis muscle. The occipital shield is partially broken away (Fig. 2D), but reconstructions of the supraoccipital and lambdoidal crests appear similar in both species. The occipital condyles are 26 mm apart in the superior part of the foramen magnum and are 16.1 mm apart inferior to the foramen (in *D. claytoni* 27 mm and 18 mm respectively).

According to Mitchell and Tedford (1973), a unique phocid feature, especially well-developed in Phocinae and clearly visible in *D. claytoni* and *D. emryi*, is the inflation of the lateral side of the squamosal between the paroccipital and mastoid processes, joining the two in a crest. Overall, *D. emryi* has some of the most primitive cranial characters seen in seals and differs significantly from modern seals.

The alisphenoid canal is a tube in the pterygoid strut between the palate and basicranium that transmits the internal maxillary artery (= maxillary artery), a branch from the external carotid artery, deep to the neck of the mandible (Fig. 4). Fossil phocids (Fig. 4D, E) and recent mustelids (Fig. 4F) share a derived character by lacking an alisphenoid canal. However, in primitive *Leptophoca* and *Devinophoca* there exists a very shallow groove instead of a proper alisphenoid canal. A completely formed alisphenoid canal is present in Otarioidea (Fig. 4A, B), Ursidae (Fig. 4C), Canidae, and most Procyonidae (Chapskii 1955; McLaren 1960; Heptner et al. 1976; Barnes & Hirota 1994). In one specimen of one species of *Allodesmus* (Barnes 1972), the alisphenoid

Tab. 1 - Cranial measurements (in mm) of the skull of *Devinophoca*.

Characters	*Devinophoca*	
	claytoni	*emryi* sp.n
1. Total length	119.9	119.5
2. Condylobasal length	119.3	118.0
3. Length of palatine process	71.0	81.0
4. Length of rostral part. measured from antero-upper corner of orbit	63.5	60.0
5. Length of braincase. measured from posterior corner of orbit	69.0	70.0
6. Length of tympanic bulla	38.5	33.6
7. Length of tooth-row, P1 to M1	49.0 (L.); 53.2 (R.)	46.9
8. Length of tooth-row, P2 to P4	32.5 (L.); 34.5 (R.)	28.9
9. Maximum diameter of infraorbital foramen	7.5 (L.); 11.2 (R.)	12.1 (L.); 11.2 (R.)
10. Length of temporal fossa	61.5	61.5
11. Width of rostrum across canines	40.0	47.7
12. Maximal infraorbital width	25.5	22.0
13. Minimal infraorbital width	14.0	19.4
14. Width of skull across of zygomatic process of squamosal	124.0	127.7
15. Width of braincase	88.0	78.3
16. Mastoid width	113.0	102.3
17. Width of palatine process between P1's	19.1	20.8
18. Maximum width of palatine process	55.5	40.9
19. Maximum width of infraorbital foramen	9.0 (L.);10.0 (R.)	7.2 (L.. R.)
20. Width of tympanic bulla	49.3	35.7
21. Width of rostrum	37.0	45.8
22. Height of skull in region of tympanic bulla	80.0	81.7
23. Distance from center of stylomastoid foramen to center of postglenoid foramen	15.1	19.2
Ratios of measurements		
meas. 14/ meas. 1	1.03	1.07
meas. 4/ meas. 5	0.92	0.86
meas. 18/ meas. 9	6.17	3.56
meas. 10/ meas. 21	1.66	1.34
meas. 8/ meas. 18	0.59	0.71

canal is not fully formed, but the track of the internal maxillary artery is clearly displayed on the bone. The canal is fully formed in other Allodesminae, such as *Brachyallodesmus packardi* and other species of *Allodesmus* (Barnes 1972).

Enaliarctos, recovered from the western coast of North America, is considered to be the most primitive otariid pinniped (from Late Oligocene - Early Miocene, ca. 24–22 Ma.) by some (Mitchell & Tedford 1973; Berta 1991) and has a fully developed alisphenoid canal. Another semi-aquatic carnivore (from the Arctic Circle) that may represent a morphological link in early pinnipedimorph evolution is *Puijila darwini* (from the Early Miocene, 21 to 24 Ma, Aquitanian, European mammal zones MN1-3), which also has an alisphenoid canal and small postglenoid foramen. *Puijila* is hypothesized to belong to some group of "otterlike protopinnipeds" or aquatic carnivores (Rybczynski et al. 2009).

Recent works (Deméré et al. 2003; Amson & Muizon 2014) acknowledge the importance of the alisphenoid canal as a morphological character. The absence of a proper alisphenoid canal in *D. emryi* and *D. claytoni* supports Tedford's (1976) suggestion that lack of this character relates phocids to the early members of mustelids rather than to ursids (Fig. 4), or at least supports a paraphyletic origin of Pinnipedia.

Detailed descriptions of the morphology of the middle and inner ear regions of *D. emryi* and comparative analyses of these regions in other pinnipeds will be presented in a separate study using modern imaging techniques.

Ontogenetic changes. As previously mentioned by Koretsky (1987, 2001), many cranial and postcranial features are significantly related to individual, ontogenetic, and sexual variability. Despite similar condylobasal and total lengths in both devinophocine skulls, the general proportions of the skulls are different. To eliminate any uncertainties about description of a new species, ontogenetic changes of seal skulls were examined.

According to a described set of characters (Koretsky 2001: 25), subadult individuals have swollen tym-

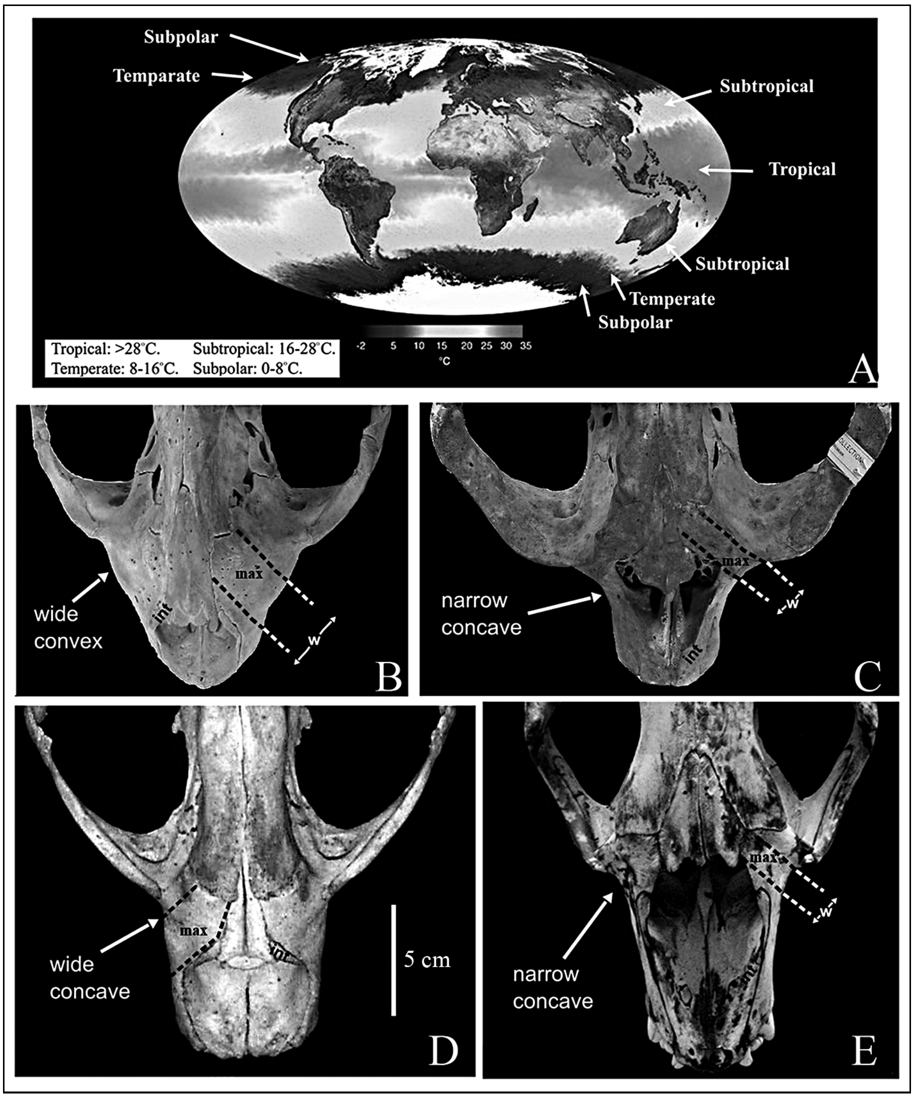

Fig. 5 - A) World map showing oceanic climate zones, for discussion of typical feeding distribution of modern true seals (adapted and modified from NASA/ GSFC, MODIS Land Rapid Response Team data).
Dorsal view of rostral part of the skull with enlargement of the maxilla in: B) Phocinae, Harbour seal (*Phoca vitulina*), deep benthic feeders in Temperate zone; C) Cystophorinae, Hooded seal (*Cystophora cristata*), bottom feeders in more shallow waters in Temperate zone; D) Monachinae, Caribbean monk seal (*Monachus tropicalis*), feeders on planktonic crustaceans in shallow water in Subtropical belt; and E) Lobodontinii, Crab-eater seal (*Lobodon carcinophagus*), feeders on large fish and warm blooded animals in Subpolar zone.
Abbreviations: int = nasal process of intermaxilla; max = maxilla; w = width of exposed portion of maxillary bone.

panic bullae and the rostral portion of the skull is relatively short compared with those of older animals. In the *D. emryi* skull, the rostral part of the skull is not shortened and the tympanic bullae are less swollen (see Tab. 1), suggesting this fossil was an adult. An additional characteristic of subadult individuals is the arrangement of incisors in the form of a half-circle, located at the alveolar margin of the premaxillae. In adult animals, this arrangement generally changes into a straight row with a bony prominence in front of the incisors. Both *Devinophoca* skulls have this adult arrangement.

The overall length of the skull increases as the rostral part grows, significantly influencing ratios of lengths of facial and cerebral parts of the skull in young and adult individuals. The total length and condylobasal length are the same in both species, but the length of the palatine process and braincase is longer in *D. emryi*, while the rostral part of skull is shorter in *D. emryi* (Tab. 1).

In accordance with the development of the facial part of the skull and with strengthening of the musculature during ontogeny, relative increases occur in: zygomatic (= jugal) width; width of the rostrum at the level of the upper canines; width of the palate at P1; greatest width of the palatine bone; and numerous other measurements. All of these measurements are larger in *D. emryi* than in *D. claytoni*.

Lastly, based on obliterated cranial sutures and evaluation of the mentioned ontogenetic characters, the skull of *D. emryi* belongs to an adult individual. Consequently, the proportions of this skull do not correspond to the set of ontogenetic characters.

Enlargement of maxilla. In the devinophocine skulls, the preorbital parts of the maxillae (Fig. 2A) between the nasal aperture and the orbits are wide and concave, similar to Monachinae (Chapskii 1974; Koretsky & Rahmat 2013; Fig. 5). While Wyss (1987) and Berta and Sumich (1999) demonstrated that the contribution of an enlarged maxilla to the orbital region is a feature common to all "pinnipeds" and used this character to support monophyly, it must be noted that the enlargement of the maxilla is a multistate character

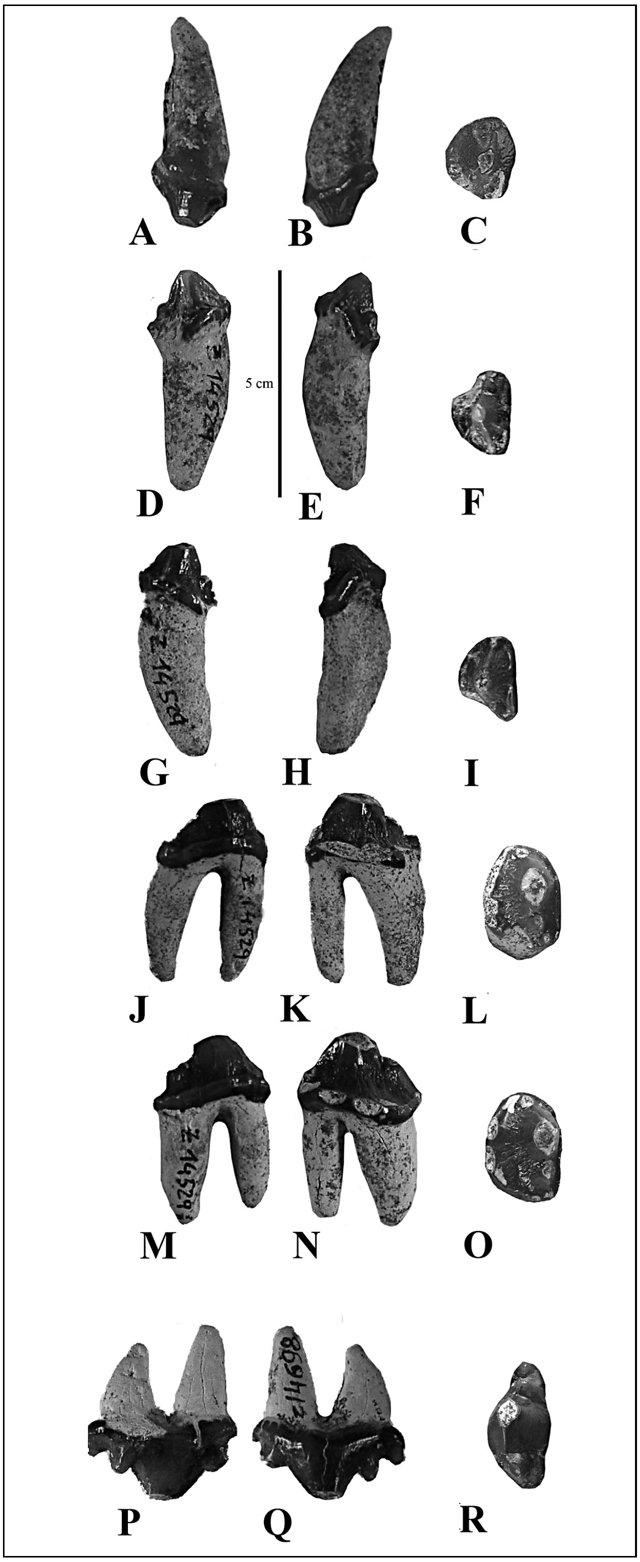

Fig. 6 - *Devinophoca emryi*, sp. n., referred cheek teeth. Right upper P1 (SNMZ 14529) in A) labial, B) lingual and C) occlusal views. Right lower p1 (SNMZ 14529) in D) lingual E) labial and F) occlusal views. Left lower p1 (SNMZ 14529) in G) lingual, H) labial and I) occlusal views. Left upper P3 (SNMZ 14529) in J) lingual, K) labial and L) occlusal views. Left upper P4 (SNMZ 14529) in M) lingual N) labial and O) occlusal views. Lower left p4 (SNMZ 14698) in P) lingual Q) labial and R) occlusal views.

Teeth	*D. claytoni*		*D. emryi* sp. n.	
	length	width	length	width
I1		3.0		3.6
I2		3.0		3.7
I3		5.7		
C	13.2	10.5	11.8	11.5
P1	6.5	5.6	6.2	5.2
P2	10.0	6.5	5.2	7.2
P3	10.0	8.0	9.6	7.0
P4	10.6	8.2	11.0 - 11.1	5.7 - 7.1
M1	9.3	7.5	8.0	4.7

Tab. 2 - Measurements (in mm) of the upper dentition of *Devinophoca.*

(compare the matrices by Berta & Wyss 1994: 37 and Koretsky 2001).

The generally pronounced convex (Fig. 5B) nature of the maxillary enlargement has been noted to be typical only for phocines (Burns & Fay 1970). In cystophorines, the maxilla has a narrow concave shape (Fig. 5C); while in monachines (Fig. 5D) it has a widely concave shape (Chapskii 1974; Koretsky & Rahmat 2013). In Devinophocinae, the maxilla is similar in shape to that of Monachinae (Koretsky & Holec 2002). Ursids and lutrines do not show maxillary enlargements, and are thus similar to other terrestrial mammals. Moreover, some authors state that the phocid condition is not a phylogenetically useful character, but can be attributed to a lateral expansion of the maxilloturbinals, considered to be an adaptation to efficiency in warming of inspired air (Muizon & Hendey 1980; Bininda-Emonds & Russell 1996).

From the same locality, we found isolated mandibles and numerous individual teeth, with some corresponding morphologically and anatomically with teeth *in situ* in the mandible and skull of *D. emryi*, while others associate perfectly to teeth *in situ* in the mandible and skull of *D. claytoni*. We plan to describe the mandible, teeth and some postcranial elements of *D. claytoni* in the near future.

Upper teeth. The skull, several hemi-mandibles, and three isolated upper teeth (Fig. 6A-C, J-O) mentioned in this paper were found near the same locality, and because the upper postcanines have root morphology that corresponds to the shape and size of the alveoli on the maxilla, all of them are identified as belonging to *D. emryi*. The upper dental formula, shape, position of the cingulum and arrangements of incisor alveoli and

Tab. 3 - Means (X) and range for measurements (mm) of number in sample (n) of the mandibles and lower dentition of *Devinophoca emryi* sp. n.

Characters	n	X	Range
Total length	1		131.5
Length of toothrow i1 - m1	1		53.4
Length of toothrow p1 - p4	3	34.7	33.3 - 36.7
Length of toothrow p1 - m1	3	45.3	44.4 - 46.8
Depth under m1	3	19.3	18.8 - 20.0
Depth under p2	2	20.2	20.0 - 20.4
Depth behind m1	3	16.4	15.9 - 16.7
Depth between p3 - p4	3	17.5	16.7 - 17.9
Thickness of mandible under m1	3	8.5	8.3 - 8.7
Height of ramus	2	48.4	44.9 - 51.8
Length of condyle	3	21.7	20.5 - 23.8
Length of retromandibular space	3	12.6	9.7 - 14.2
Length of symphysis	1		23.0
Condylar height	3	29.0	21.7 - 36.0
i1 length	1		4.6
width	1		3.8
c length			
width	1		8.9
p1 length	4	6.2	4.8 - 6.9
width	4	5.0	4.8 - 5.1
p2 length	3	9.4	9.0 - 9.6
width	3	5.4	4.8 - 5.9
p3 length	3	11.0	10.0 - 13.0
width	3	5.7	5.2 - 6.3
p4 length	4	10.8	9.6 - 12.7
width	4	5.2	4.2 - 6.1
m1 length	3	11.3	10.5 - 12.3
width	3	4.0	3.5 - 4.4

canine alveoli in *D. emryi* is the same as in *D. claytoni* (see Koretsky & Holec 2002: 172).

The crown of an isolated right P1 (SNMZ 14529) has a single root (Fig. 6A-C; Tab. 2), oval in cross section and with a central cusp which is slightly worn. The crown of this tooth is 6.8 mm long, has a conical central cusp and a cuspidate lingual cingulum bearing diminutive anterior and slightly larger posterior cusps. The gum line (on P1, P3, and P4), parallel to the lower margin of the enamel, was oblique to the long axis of the root. However, when the tooth is correctly inserted into the alveolus of the holotype maxilla, the gum line is parallel to the margin of the dentary. The complete crown is irregularly shaped in occlusal view, with a flattened labial side, and is inflated distolingually on its lingual side. The cingulum, bearing minute cuspules, encircles the crown and is much smaller on the labial side, whereas, on the lingual side of the crown the cingulum is more prominent, and wrinkled.

All upper cheek teeth show slight wear and both of the other isolated upper cheek teeth are double-rooted (except P1, single-rooted), with posterior roots much larger than anterior (Fig. 6J-O). While the anterior roots are round in cross section, the posterior roots are expanded transversely, but not bilobed as in *D. claytoni*. The crowns of the P3 (SNMZ 14529; Fig. 6J-L) and P4 (SNMZ 14529; Fig. 6M-O) are semi-oval in occlusal view, slightly worn as in the P1 (Fig. 6A-C), and inflated distolingually on its labial side as in P1, but also flattened.

The crown of a left P3 (SNMZ 14529; Fig. 6J-L) has a very prominent lingual cingulum, with only a minute anterior cingular cusp (the parastyle) and slightly larger two posterior cusps. The cingulum on a labial side extends at its mid-length, but without any carina as observed in Monachinae (Amson and Muizon 2014).

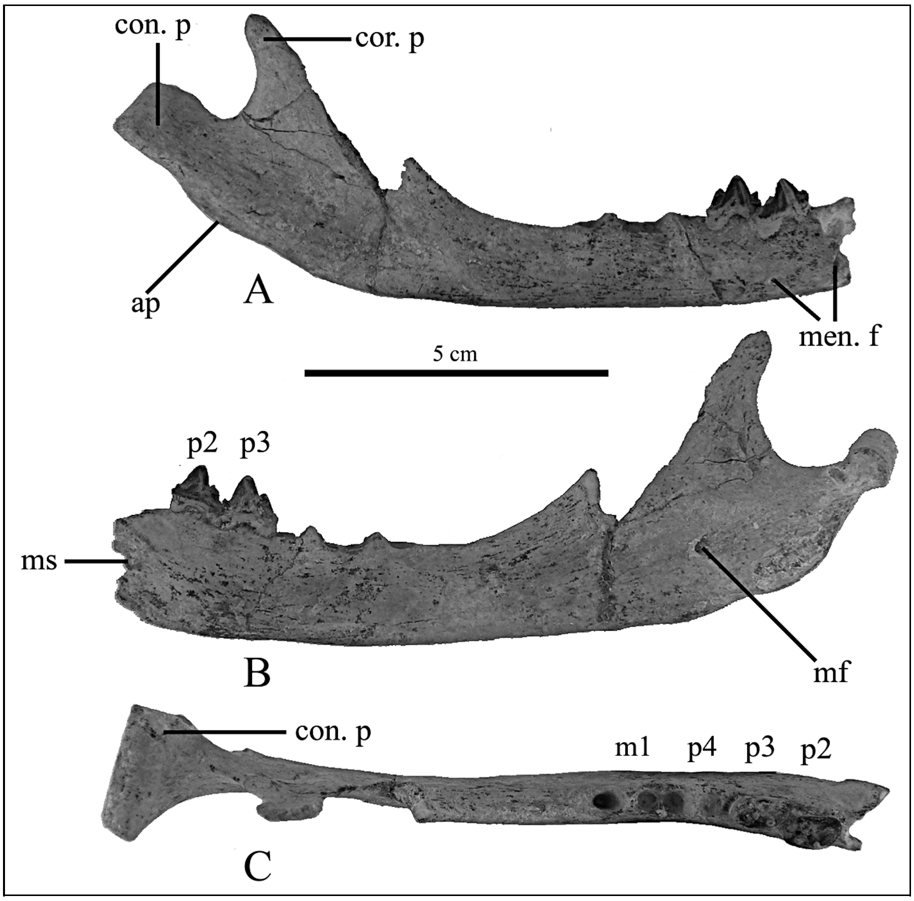

Fig. 7 - Mandible of *Devinophoca emryi* sp. n. (Early-Middle Miocene; ~16 Ma; Badenian, Vienna Basin, Slovakia; USNM 553687), in A) labial, B) lingual, and C) occlusal views.
Abbreviations: ap = angular process; con. p. = condyloid process; cor. p. = coronoid process; men. f = mental foramen; m = molar; mf = mandibular foramen; ms = mandibular symphysis; p = premolar.

The crown of the left P4 (SNMZ 14529; Fig. 6M-O) is even more inflated than in P3 and has one anterior accessory cusp and one slightly larger posterior additional cusp. A likely cuspidate lingual cingulum was present, but showed some wear.

D. emryi, in contrast to *D. claytoni*, does not have two fused posterior roots or a carnassial notch on the metastyle blade of P4. Also, M1 has a regular double root according to the alveoli, not triangular with three cusps and three roots as seen in *D. claytoni*. As previously mentioned (Koretsky & Holec 2002), no other phocid has teeth with three cusps and three roots in a triangular arrangement.

Mandible. The body of several mandibles of *D. emryi* (Fig. 7; Tab. 3) are flattened, thin, and low (varying from 42.8-52.2 mm high), the retromolar space is elongated and the condyloid process is especially short and narrow (21.1 x 8.2 mm; 24.0 x 8.6 mm). The condyloid process is elevated, slightly above the level of the tooth row.

The coronoid process (cor. p.) is very thin and long, with its anterior edge strongly sharpened toward the apex of the process and its posterior edge slightly concave. The masseteric fossa is shallow and narrow (almost indistinct), but very well outlined, which indicates a sizeable insertion for the masseter muscle (Piérard 1971; Amson & Muizon 2014), especially on its ventral edge. The size, width and depth of the fossa resemble those of *Leptophoca lenis* (Koretsky 2001; Koretsky et al. 2012) and differ from the deep and wide masseteric fossa described in *Monachus* and *Cystophora* (Koretsky & Rahmat 2013).

On the medial surface of the ramus, the mandibular foramen is located anterior to the apex of the coronoid process. The foramen and canal are both very well developed, similar to *L. lenis* (Phocinae), but in contrast to *Hadrokirus martini* (Monachinae) from the Early Pliocene (Amson & Muizon 2014).

The symphyseal part of the mandible is partially broken off, but reaches the middle of the alveoli of p2; the chin prominence and diastemata are absent.

Lower teeth. The alveoli of the lower canines are significantly smaller than the upper canines (9 mm: 15 mm respectively), and oval in cross section, but partially destroyed. The cheek tooth row is oriented parallel to the axis of the symphyseal part of the mandible (except p2, where the anterior alveoli is oriented more labial than the posterior). The alveoli are round with the posterior being larger than the anterior.

The crowns of the cheek teeth are wide and swollen. The p2-p4 are multicusped, double-rooted, and have one or two additional cusps on a basal cingulum. The posterior alveoli of the postcanines are slightly larger than the anterior. The m1 is double-rooted as well.

The basal cingulum of m1 is very well developed, especially on the lingual side. The length of the m1 alveoli is shorter than p4.

Two isolated lower cheek teeth, a right (SNMZ14529; Fig. 6D-F) and a left (SNMZ14529; Fig. 6G-I), were identified as p1 of *D. emryi* due to the presence of a single root that is slightly curved, which corresponds to the shape and size of the alveoli on both mandibles. The crown of a right p1 tooth is 16.7 mm long with a conical main cusp (protoconid) and a cuspidate lingual cingulum bearing a small posterior cusp (hypoconid). The gum line, parallel to the lower margin of the enamel, was oblique to the long (= mesiodistal) axis of the root, but when the tooth is correctly inserted into the p1 alveolus of the mandible, the gum line is parallel to the dorsal margin of the dentary. The outline of the crown of p1 is triangular in occlusal view (Figs 6F, I), with a slightly flattened labial side; the tooth has a single root, which is oval in cross section as well. The cingulum encircles the complete tooth, widening on the lingual side. Near the base of the crown, there are very small additional posterior and anterior cusps.

The crown of p2 (*in situ*) is oval in occlusal view (Fig. 7C), the tooth is double-rooted, and the labial side of the crown is convex. A cingulum is located on the lingual side. The main cusp (protoconid) is slightly turned caudally. The two small cusps are located on the posterior side of the major cusp, and one small cusp is located anterior to the main cusp. In addition to the prominent metaconid, are a less prominent posterior cingular cusp (hypoconid) and tiny anterior cingular cusp (paraconid). All cusps are entirely preserved. The crown is 10 mm long, 7.5 mm high, and has the same types of derived characters as the p1 described above: prominent and cuspidate lingual cingulum and less prominent basal cingulum (Barnes 1988). The p2 tooth is situated oblique to the axis of the tooth-row, with the posterior root larger than the anterior.

The overall morphology of p3 (*in situ*) is comparable to p2 (Fig. 7). Despite the similar size of p2 and p3 (p3 has a crown 10 mm long, 8.3 mm high), both secondary cusps are larger and more prominent, especially the metaconid, and the main cusp is not turned caudally. The tooth is positioned parallel to the axis of the tooth-row. The posterior root is larger than the anterior.

One isolated left tooth (SNMZ14698; Fig. 6P-R) has a root morphology that corresponds to the alveolus of p4 in the paratype mandible. The crown of p4 is oval in occlusal view, and the buccal side is convex. A very short cingulum is located on the lingual side, restricted to the level of the main cusp. The basal cingulum is not developed at all. The main cusp (protoconid) is directed dorsally, inflated, and conical. Two additional small cusps (metaconids), located on both sides of the major cusp, are intact. The presence of four cusps in a row on this tooth of *D. emryi* strongly suggests that it is p4. The two roots of the tooth are wide and oval in cross-section, with the posterior root wider than the anterior.

The double-rooted m1 alveoli were much smaller than those of p4. In contrast to other postcanines, the posterior alveoli are smaller than the anterior, and oval.

Discussion and conclusions

As previously noted, the skulls of *Devinophoca* present distinguishing, taxon-specific characters as well as mixed characters with the other three extant subfamilies (see Koretsky & Holec 2002), such as: a thin and low mandibular body (as in Phocinae) and a total of 8 incisors (as in Monachinae, but with different incisors formula). Thus, the two different species of the Subfamily Devinophocinae have three upper incisors (similar to Phocinae, primitive condition) and one lower incisor (similar to Cystophorinae, derived condition).

Studies of Miocene Phocidae over the last century (i.e. from Alekseev 1924 up to Koretsky & Rahmat 2013), as well as the new material described here from early Middle Miocene sediments, further support previous views on dental morphology (Ognev 1935; Chapskii 1955, 1974; Scheffer 1958; Heptner et al. 1976). Detailed descriptions of dentition conclude that true seals ranging from 16 million years ago up to the present have generally uniform incisor formulae within each subfamily, based on total number of the incisors: Phocinae (10 incisors; 3/2), Cystophorinae (6 incisors; 2/1); Monachinae (8 incisors 2/2); and Devinophocinae (also 8 incisors as Monachinae, but in different combination: 3/1).

Although the skull of the newly described *Devinophoca emryi* is incomplete, certain derived characters in pinnipeds were clearly noticeable on it, such as: reduced upper first molar, loss of the fovea between the upper fourth premolar and first molar, closely spaced mastoid and paroccipital processes, and a reduced nasolabial fossa.

Only phocines (with a convex maxilla) have a circumpolar distribution in Arctic regions (latitude 30°-80°N) and in the temperate zones of the Northern Hemisphere (Fig. 5A). Cystophorines (excluding *Mirounga*), which have a narrow, concave maxilla, are distributed similarly to phocines (latitude 45°-80°N). Monachines (wide, concave maxilla) are primarily thermophilic seals, distributed in the subtropical belt (20°-40°), and Lobodontini (narrow, concave maxilla; Fig. 5E) and *Mirounga* (long, concave maxilla) are circumpolar in the Southern Hemisphere above latitude 30°S (King 1964; Heptner et al. 1976; Berta & Sumich 1999). Based on this distribution pattern, seals that adapted to cold and moderately cold waters, in which the surface tempera-

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	33	34	35	36	37	38	39	40
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	0	1	0	1	0	0	0	0	1	0	0	1	1
Lontra canadensis	1	0	1	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	0	0	1	1	0	0	1	1
Puijila darwini †	0	1	0	1	1	0	1	0	0	0	1	2	1	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	0	0	0	0	1	1	1	1	0	2	1	1
Devinophoca claytoni †	0	0	1	0	0	0	0	0	0	0	1	2	1	0	0	?	1	1	0	0	0	?	1	0	0	1	0	0	0	0	0	0	?	?	?	?	?	?	?	?
Devinophoca emryi †	0	0	1	0	1	0	0	0	0	?	?	2	0	0	0	1	0	0	1	0	0	3	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	2	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	0	1	1	0	2	1	1	0
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	2	0	1	2	2	2	2	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	1	2	1	1	2	2	2	1
Monachus schauinslandi	0	0	1	0	1	1	0	1	0	1	1	2	2	0	1	0	0	0	0	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	1	1	2	2	1
Callophoca obscura †	1	0	0	0	0	0	1	1	1	1	1	2	2	0	0	0	1	0	1	0	0	1	1	1	0	0	1	0	0	1	0	2	0	1	1	1	0	2	1	0
Phoca vitulina	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	2	1	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	1
Erignathus barbatus	1	1	1	1	0	1	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	0	0	1	1	1	1	1	2	0
Leptophoca lenis †	0	0	?	0	0	0	1	1	1	0	0	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	0	0	0	0
Pliophoca etrusca †	1	0	?	1	0	0	1	0	1	1	1	2	2	0	0	0	2	1	1	1	1	1	1	1	0	0	1	0	0	1	0	1	1	2	0	0	0	1	0	0
Homiphoca capensis †	0	0	1	0	0	0	0	0	0	1	1	2	2	0	0	1	2	0	1	1	1	1	1	0	1	0	1	0	?	1	1	0	0	1	1	0	1	1	0	1
Phoca largha	0	1	0	0	0	1	0	0	0	1	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	2	1	0	0	0	0	0	0	1
Pusa hispida	1	1	1	0	0	1	0	0	0	1	0	0	2	1	0	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	1	0	0	0	0	0	2	0	2	0
Halichoerus grypus	0	0	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	0	0	1	0	0	1	1	0	1	1	2	0
Pagophilus groenlandica	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	0	0	2	0	0	1	0	0	1	1	1	0	0	0	0	1	1	0	1	1	1	2	0
Hadrokirus martini †	0	0	0	1	1	0	1	0	0	1	0	2	1	1	1	0	0	1	1	1	0	?	1	1	0	1	0	0	0	1	1	2	2	0	1	2	2	1	2	1

Tab. 4 - Matrix for cranial character-state data for Phocidae taxa.

ture does not exceed 20°C, have both types of maxillae (concave and convex).

Therefore, the enlargement of the maxilla, and consequently the choanae, as an adaptation for breathing cold air is not well supported by the pattern of geographical distribution. We suggest another theory, which may better explain the differences in size and shape of the maxilla.

Different types of diet are reflected in the general organization of seals (Riedman 1990). Some species of Phocinae are mainly benthic feeders, while others prey on fish and cephalopods and can dive in deep water up to 300 meters (Heptner et al. 1976; Bigg 1981; Riedman 1990; Koretsky 2001; Berta & Adam, 2001). Cystophorines primarily rely on bottom feeding in deep water, but not as deep as phocines. *Mirounga*, the deepest diver among seals (up to 1,000 m; Le Boeuf & Laws 1994), has a disproportionately elongated maxilla. Monachine seals feed chiefly in shallower water, eating planktonic crustaceans (*Lobodon*), or large fish, warm-blooded animals including birds (penguins), and krill like the leopard seal (*Hydrurga*).

The biomechanical and ecological significance of the traits defining each group give us at least some correlation to morphology. However, it can be suggested that the shape of the maxilla is an adaptive character for diving (providing increased flow rate, not air storage) and should not be involved in discussions of phylogenetic relationships at higher taxonomic levels (Bechly 2000).

Based on the stratigraphy of the site (Shultz 2004; Hohenegger et al. 2008; Domning & Pervesler 2012), the Paratethyan seals from the Vienna Basin, specifically from the Bonanza locality (*Devinophoca claytoni* and *D. emryi*), occupied transitional shallow marine waters with coral-reef zones. Moreover, previous studies by Hohenegger et al. (2008) and Domning & Pervesler (2012), as well as examinations of diagnostic marine and terrestrial faunas of the region (Holec & Sabol 1996; Holec et al. 1997; Shultz 2004; Fejfar & Sabol 2009), support a transition from a humid, tropical shallow shore zone in the early Badenian (16.26 - 14.89 Ma) to a subtropical climate in the middle Badenian (14.89 - 13.82 Ma) and a warm temperate climate during late Badenian (13.82 -12.73Ma).

Phylogenetic analysis

The data matrix for the 40 included characters is shown in Tab. 4. Cranial, mandibular and dental characters and character-states for Phocidae: 0, designates the most primitive state among the taxa studied; 1-2, derived states; ?, unknown or missing data. Some characters have the opposite polarity to that of Berta and Wyss (1994) and Burns and Fay (1970), while some characters have the same polarity as that of Chapskii (1974). Some characters were updated and modified from Koretsky (2001), Koretsky and Grigorescu (2002), Koretsky and Rahmat (2013).

The analysis was done with NONA from Goloboff (1999) and Winclada from Nixon (1999) using a heuristic search of the phocid taxa of 40 unweighted characters. This is the resulting single Wagner most parsimonious tree generated by Winclada with 179 steps long, having Consistency Index of 0.57, and Retention Index 0.64.

The matrix of character-state data for 20 species of fossil and modern phocids is given in Tab. 4; in addition, the following taxa were used as outgroups: fossil representatives, such as *Allodesmus* and *Puijila*, and Recent mustelid *Lontra*.

Skull

1. Tympanic bulla: (0) small; (1) large.

2. External auditory meatus: (0) inframeatal lip is 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 is not directed ventrally; (1) directed ventrally.

5. Mastoid process: (0) not strongly pronounced prominence lateral to auditory bullae; (1) pronounced.

6. Mastoid process: (0) narrow (width of the process is less than the length of the process itself); (1) wide (Chapskii 1974: 301; in contrast to Berta and Wyss 1994: 48).

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 the mastoid process; (2) directed sharply downward behind the mastoid process.

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) has very pronounced convexity anterior to the orbits; (1) has short concavity; (2) has long concavity (Chapskii 1974: 299; in contrast to Berta and Wyss 1994: 46).

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

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

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

16. Oval foramen: (0) hidden under hamular process of pterygoid bones; (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: 370; Chapskii 1974: 299).

18. Jugular process: (0) well developed, large hook shape; (1) poorly developed (as a small conical projection) or absent.

19. Rostrum: (0) short, relative to skull; (1) elongated (Chapskii 1974: 299).

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

21. Anteroposterior length of auditory bullae: (0) equal to or greater than distance between them; (1) less than distance between them (Burns and Fay 1970: 382; Chapskii 1974: 300).

Teeth

22. Number of incisors: (0) 3/2; (1) 2/2; (2) 2/1 (Chapskii 1974: 289; in contrast to Burns and Fay 1970: 380); (3) 3/1.

23. Roots of postcanine teeth (P,p 2 – P,p 3): (0) one (fused); (1) two (Berta and Wyss 1994: 51).

24. Roots of P,p 4: (0) three; (1) two; (2) one.

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

26. Dimensions of postcanine teeth relative to longitudinal diameter of alveolus of upper canine: (0) more than 60.0%; (1) less than 60.0 % or sub-equal.

27. Longitudinal diameter of alveolus of upper canine compared with maximal width of infraorbital foramen: (0) sub-equal 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: (0) aligned parallel to axis of tooth-row; (1) seated obliquely.

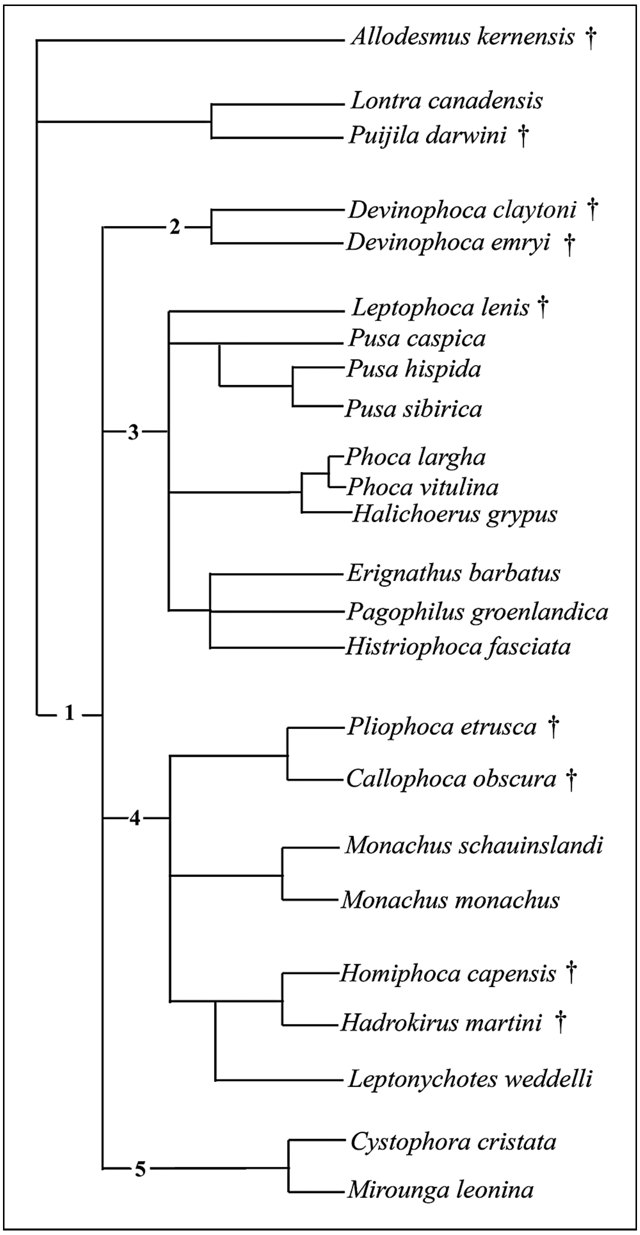

Fig. 8 - The single, most parsimonious Wagner tree generated by Winclada with 179 steps long, CI = 0.57, and RI = 0.64.

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 equal in size.

Mandible

33. Mandibular symphysis: (0) continues at least to the middle of the alveolus of p3; (1) reaches only to the alveolus of p2; (2) reaches only to the alveolus of p1.

34. Lateral outline of symphyseal region: (0) square, symphysis thin; (1) rounded, symphysis thick; (2) straight, symphysis thick.

35. Chin prominence: (0) pronounced; (1) absent or weakly developed.

36. Chin prominence: (0) extends from the anterior or posterior alveolus of p2 to the posterior or anterior alveolus of p4; (1) extends from the anterior alveolus of p2 to the anterior alveolus of p3; (2) extends from the anterior alveolus of p2 to the posterior alveolus of m1.

37. Maximum height of mandibular body: (0) between p2 and p3; (1) in the middle of or at the posterior portion of p2; (2) situated between alveoli p4 and m1 or posterior to alveolus of m1.

38. Diastemata and tooth alveoli: (0) alveoli small with equal diastemata; (1) alveoli round and large, with equal diastemata between them; (2) alveoli shallow, and diastemata unequal.

39. Alveoli of p4 and m1: (0) alveoli similar in size; (1) alveoli of p4 smaller than alveoli of m1; (2) alveoli of p4 larger than alveoli of m1 (unordered character).

40. Retromandibular space: (0) long; (1) short.

Points where the nodes of the present tree (Fig. 8) correspond to traditionally recognized phocid taxa are indicated. Only one new name is introduced here: inclusion of *Devinophoca emryi* within the subfamily Devinophocinae requires recognition of new species.

The nodes of the cladogram shown in Fig. 8 are supported by the following character transformations:

Node 1 (Family Phocidae): 25(0). This paraphyletic group with an ancestral or primitive character (multicuspate crowns of postcanine teeth) is treated as plesiomorphic for the family. Also, unordered character 39(2): the alveoli of p4 larger than alveoli of m1, is shared with other members of the subfamilies Monachinae and Phocinae.

Node 2 (subfamily Devinophocinae, possibly paraphyletic): 13(0); 22(3); 24(0). The anterior palatal foramina are round and deep; number of incisors. Paraphyly of *D. claytoni*: three fused roots of the postcanine teeth.

Node 3 (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 maxillary canine; the length of auditory bulla is less than the distance between them. Also, character 20(1) is homoplasious in *Monachus schauinslandi* and *Leptophoca lenis.*

Node 4 (subfamily Monachinae): 11(1); 12(2); 13(2); 22(1); 31(1). The relative dimensions of the frontal and maxillary parts of the nasal bones; shape of the anterior palatine foramina; maxilla forms a long concavity; reduced number of incisors.

Node 5 (subfamily Cystophorinae): 9(2); 12(1); 22(2); 29(1); 32(1). The mastoid convexity directed sharply downward behind the mastoid process. Maxilla forms a short concavity; advance reduced number of incisors; no additional cusps on premolars. Second incisor is larger than third.

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REFERENCES

Alekseev A.K. (1924) - Seals in the Sarmatian deposits of Southern Russia. *J. Nauch.-Issle. kaf. v Odesse*, 1: 26-34 [in Russian].

Amson E. & Muizon C. de. (2014) - A new durophagous phocid (Mammalia: Carnivora) from the late Neogene of Peru and considerations on monachine seals phylogeny. *J. Syst. Palaeontol.,* 12: 523-548.

Barnes L.G. (1972) - Miocene Desmatophocinae (Mammalia: Carnivora) from California. *Univ. Calif. Publ. Geol. Sci.,* 89: 1-68.

Barnes L.G. (1979) - Fossil enaliarctine pinnipeds (Mammalia: Otariidae) from Pyramid Hill, Kern County, California. *Contrib. Sci. Nat. Hist. Mus. L.A. County* 318: 1-41.

Barnes L.G. (1988) - A new fossil pinniped (Mammalia: Otariidae) from the Middle Miocene Sharktooth Hill Bonebed, California. *Contrib. Sci, Nat. Hist. Mus. L.A. County,* 396: 1-11.

Barnes L.G. & Hirota K. (1994) - Miocene pinnipeds of the otariid subfamily Allodesminae in the North Pacific Ocean: systematics and relationships. In: Barnes L.G., Hasegawa Y. & Inuzuka N. (Eds) -The Island Arc, Special Issue, Evolution and Biogeography of Fossil Marine Vertebrates in the Pacific Realm, Collected Papers from a Symposium Dedicated to the Memory of Arthur Remington Kellogg in the Year of the 100th Anniversary of his Birth. *Proc. 29th Intern. Geol. Congress, Kyoto, Japan,* 3: 329-360, 1992.

Bechly G. (2000) - Mainstream Cladistics versus Hennigian Phylogenetic Systematics. *Stutt. Beitr. Naturk., Serie A (Biologie)*, 613, 11 pp.

Berta A. (1991) - New *Enaliarctos* (Pinnipedimorpha) from the Miocene of Oregon and the role of "Enaliarctids" in Pinniped Phylogeny. *Smithsonian Contrib. Paleobiol.*, 69: 1-33.

Berta A. (1994) - New specimens of the pinnipediform *Pteronarctos* from the Miocene of Oregon. *Smithsonian Contrib. Paleobiol.*, 78: 1-30.

Berta A. & Wyss A.R. (1994) - Pinniped Phylogeny. In: Berta A. & Deméré T.A. (Eds) - Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr. *Proc. San Diego Soc. Nat. Hist.*, 29: 33-56.

Berta A. &. Sumich J.L. (1999) - Marine Mammals: Evolutionary Biology. Academic Press, San Diego, 494 pp.

Berta A. & Adam P.J. (2001) - Evolutionary Biology of Pinnipeds. In: Mazin J.M. & de Buffrénil V. (Eds) - Secondary Adaptation of Tetrapods to Life in Water: 235-260. Verlag Dr. Friedrich Pfeil, München, Germany.

Bigg M. A. (1981) - Harbour seal - *Phoca vitulina* and *P. largha*. In: Ridgway S.H. & Harrison R.J. (Eds) - Handbook of marine mammals. 2 - Seals: 1-27. Academic Press, Inc., London.

Bininda-Emonds O.R.P. & Russell A.P. (1996) - A morphological perspective on the phylogenetic relationships of the extant phocid seals (Mammalia: Carnivora: Phocidae). *Bonner Zool. Monogr.*, 41: 1-256.

Burns J.J. & Fay F.H. (1970) - Comparative morphology of the skull of the Ribbon seal, *Histriophoca fasciata*, with remarks on systematics of Phocidae. *J. Zool.* (London), 161: 363-394.

Chapskii K.K. (1955) - An attempt at revision of the systematics and diagnostics of seals of the subfamily Phocinae. *Trudy Zool. Inst. Akad. Nauk SSSR*, 17: 160-199 [in Russian]. (English translation by Jeletzky, T.F. - *Fish. Res. Board Can.*, *Transl. Ser*, 114, 57 pp., 1957).

Chapskii K.K. (1974) - In defense of classical taxonomy of the seals of the family Phocidae. *Trudy Zool. Inst. Acad. Sci. USSR*. 53: 282-334 [in Russian].

Deméré T.A., Berta A. & Adam P.J. (2003) - Pinnipedimorph evolutionary biogeography. In: Flynn L.J. (Ed.) - Vertebrate Fossils and their Context, Contributions in Honor of Richard H. Tedford, *Bull. Amer. Mus. Nat. Hist.*, 279: 32-76.

Domning D.P. & Pervesler P. (2012) - The sirenian *Metaxytherium* (Mammalia: Dugongidae) in the Badenian (Middle Miocene) of Central Europe. *Austrian J. Earth Sci.*, 105: 125-160.

Fejfar O. & Sabol M. (2009) - Middle Miocene *Plesiodimylus* from the Devínska Nová Ves-Fissures site (western Slovakia). *Bull. Geosci.* 84(4): 611-624.

Flynn J., Finarelli J., Zehr S., Hsu J. & Nedbal M. (2005) - Molecular phylogeny of the Carnivora (Mammalia): assessing the impact of increased sampling on resolving enigmatic relationships. *System. Biol.* 54(2): 317-337.

Heptner V.G, Chapskii K.K. & Arseniev B.A. (1976) - Mammalia of the Soviet Union. Pinnipeds and Cetacea, Moscow, 2(3): 1-717 [in Russian].

Hohenegger J., Coric S., Khatun M., Pervessler P., Rogl F., Rupp Ch., Selge A., Uchman A. & Wagreich M. (2008) - Cyclostratigraphic dating in the Lower Badenian (Middle Miocene) of the Vienna Basin (Austria): the Beden-Sooss core. *Intern. J. Earth Sci.* 98: 915-930.

Holec P., Klembara J. & Meszároš S. (1987) - Discovery of new fauna of marine and terrestrial vertebrates in Devínska Nová Ves. *Geol. Carpath.*, 38: 349-356.

Holec P. & Sabol M. (1996) - The Tertiary vertebrates from Devínska Kobyla. *Miner. Slov.,* 28: 519-522 [in Slovak].

Holec P., Klembara J. & Meszároš S. (1997) - Fossils of the Dévinska Kobyla hill. In: Feráková V. (Ed) - Flora of the Dévinska Kobyla hill, APOP-Edition, Bratislava, 639 pp. [in Slovak].

Howell A.B. (1928) - Contribution to the Comparative Anatomy of the Eared and Earless Seals (Genera *Zalophus* and *Phoca*). *Proc. U.S. Nat. Mus.*, 73: 1-142.

King J.E. (1964) - Seals of the World. Brit. Mus. (Nat. Hist.), London, 154 pp.

King J.E. (1983) - Seals of the World. Second Edition, Brit. Mus. (Nat. Hist.), Comstock Publishing Associates, Ithaca, New York, 240 pp.

Koretsky I.A. (1987) - Sexual dimorphism in the structure of the humerus and femur of *Monachopsis pontica* (Pinnipedia: Phocinae). *Vest. Zool.*, 4: 77-82 [in Russian].

Koretsky I.A. & Ray C.E. (1994) - *Cryptophoca*, new genus for *Phoca maeotica* (Mammalia: Pinnipedia: Phocinae) from Upper Miocene deposits in the Northern Black Sea region. *Proc. Biol. Soc. Wash.*, 107: 17-26.

Koretsky I.A. (2001) - Morphology and Systematics of Miocene Phocinae (Mammalia: Carnivora) from Paratethys and the North Atlantic Region. *Geol. Hung.*, 54, 109 pp.

Koretsky I.A. & Grigorescu D. (2002) - The Fossil Monk Seal *Pontophoca sarmatica* (Alekseev) (Mammalia: Phocidae: Monachinae) from the Miocene of Eastern Europe. *Smith. Contr. Paleobiol.*, 93: 149-162.

Koretsky I.A. & Holec P. (2002) - A primitive seal (Mammalia: Phocidae) from the Early Middle Miocene of Central Paratethys. *Smithsonian Contr. Paleobiol.*, 93: 163-178.

Koretsky I.A., Ray C.E. & Peters N. (2012) - A new species of *Leptophoca* (Carnivora, Phocidae, Phocinae) from both sides of the North Atlantic Ocean (Miocene seals of the Netherlands, part I). *Deinsea Ann. Nat. Hist. Mus. Rotterdam,* 15: 1-12.

Koretsky I.A. & Rahmat S. (2013) - First Record of fossil Cystophorinae (Carnivora, Phocidae): Middle Miocene seals from the Northern Paratethys. *Riv. It. Paleontol. Strat.,* 119(3): 325-350.

Le Boeuf B.J. & Laws R.H. (1994) - Elephant seals: an introduction to the genus. In: Le Boeuf B.J. & Laws R.M. - Elephant seals. Population ecology, behavior and physiology: 1-26, Univ. California Press, Berkeley (CA).

McLaren I.A. (1960) - Are the Pinnipedia biphyletic? *System. Zool.,* 9: 18-28.

Miller M.E., Christensen G.C. & Evans H.E. (1964) - Anatomy of the dog. W.B. Saunders Company, Philadelphia, London, 941 pp.

Mitchell E.D. (1966) - The Miocene pinniped *Allodesmus*. *Univ. Calif. Publ. Geol. Sci.* 61: 1-105.

Mitchell E.D. & Tedford R.H. (1973) - The Enaliarctinae a New Group of Extinct Aquatic Carnivora and a consideration of the Origin of the Otariidae. *Bull. Amer. Mus. Nat. Hist.*, 151(3): 201-284.

Muizon C. de & Hendey Q.B. (1980) - Late Tertiary seals of the South Atlantic Ocean. *Ann. South African Mus.,* 2: 91-128.

Muizon C. de (1981) - Premier signalement de Monachinae (Phocidae: Mammalia) dans le Sahèlien (Miocène Supérieue) d'Oran (Algérie). *Palaeovertebrata*, 11: 181-194.

Muizon C. de. (l982) - Les relations phylogenetiques des Lutrinae (Mustelidae, Mammalia). *Geobios*, *mem. sp.*, 6: 259-272.

Muizon C. de. (1992) - Paläontologie. In: Duguy R. & Robineau D. (Eds) - Handbuch der Säugetiere Europas, Band 6: Meeressäuger. Teil II: Robben - Pinnipedia: 34-41. In: Niethammer J. & Krapp F. (Eds) - AULA-Verlag, Wiesbaden.

Ognev S.I. (1935) - Mammals of the USSR and adjacent countries. Carnivora. Glavpushnina, Moscow-Leningrad, 3, 752 pp. [in Russian] (English translations by Birron A. & Coles Z.S. for Israel Program for Scientific Translations, 1962).

Piérard J. (1971) - Osteology and myology of the Weddell seal *Leptophoca weddelli* (Lesson, 1826). In: Burt W.H (Ed.) - Antarctic Pinnipedia. *Antarct. Res. Ser. Nat. Acad. Sci.-Nat. Res. Cen.* 18, 53-108.

Ray C.E. (1976) - *Phoca wymani* and other Tertiary seals (Mammalia: Phocidae) described from the eastern seaboard of North America. *Smithsonian Cont. Paleobiol.*, 28: 1-36.

Riedman M. (1990) - The Pinnipeds: Seals, Sea Lions, and Walruses. University of California Press, Berkeley, Los Angeles, Oxford, 439 pp.

Rybczynski N., Dawson M.R., & Tedford R.H. (2009) - A semi-aquatic Arctic mammalian carnivore from the Miocene epoch and origin of Pinnipedia. *Nature,* 458 (7241): 1021-24.

Scheffer V.B. (1958) - Seals, Sea Lions, and Walruses. A Review of the Pinnipedia. Stanford University Press, Stanford, California, 179 pp.

Schultz O. (2004) - A Triggerfish (Osteichthyes: Balistidae: *Balistes*) from the Badenian (Middle Miocene) of the Vienna and the Styrian Basin (Central Paratethys). *Ann. Naturhist. Mus. Wien,* 106A: 345-369.

Simpson G.G. (1945). The Principles of Classification and a Classification of Mammals. *Bull. Amer. Mus. Nat. Hist.* 85: 1-350.

Tedford R.H. (1976) - Relationship of pinnipeds to other carnivores (Mammalia). *System. Zool.*, 25(4): 363-374.

Wolsan M. (1993) - Phylogeny and classification of early European Mustelidae (Mammalia: Carnivora). *Acta Theriologica,* 38(4): 345-384.

Wozencraft C. (1989) - The phylogeny of the Recent Carnivora. In: Gittleman J.L. (Ed.) - Carnivore behavior, ecology, and evolution: 495-535.

Wyss A.R. (1987) - The walrus auditory region and monophyly of pinnipeds. *Am. Mus. Novitates* 2871, 31 pp.

Wyss A.R. & Flynn J.J. (1993) - A phylogenetic analysis and definition of the Carnivora. In: Szalay F. S., Novacek M. J. & McKenna M. C. (Eds) - Mammal phylogeny: Placentals: 32-52, Springer-Verlag, New York.

Wyss A.R. (1994) - The evolution of body size in phocids: some ontogenetic and phylogenetic observations. In: Berta A. & Deméré T.A. (Eds) - Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr. *Proc. San Diego Soc. Nat. Hist.*, 29: 69-77.