FIRST RECORD OF POSTCRANIAL BONES IN *DEVINOPHOCA EMRYI* (CARNIVORA, PHOCIDAE, DEVINOPHOCINAE)

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First Record of Postcranial Bones in *Devinophoca emryi* (Carnivora, Phocidae, Devinophocinae). Rahmat, S. J., Koretsky, I. — The *Devinophoca emryi* material from the early Badenian, early Middle Miocene (16.26–14.89 Ma) presents mixed cranial and especially postcranial characters with the three extant phocid subfamilies (Cystophorinae, Monachinae and Phocinae), as well as unique postcranial characters not seen in any taxa. These distinguishing characters (i. e. well-outlined, large oval facet on greater tubercle of humerus; broader width between the head and lesser tubercle of humerus; femoral proximal epiphysis larger than distal; thin innominate ilium that is excavated on ventral surface) demonstrate that this material belongs to a recently described species (*D. emryi*). During ecomorphotype analyses, fossil humerus and femur bones were directly associated with their corresponding mandible to reveal associations based on Recent morphological analogues. Strong correlation between ecomorphotypes and postcranial morphology supports placement of this material to *D. emryi* and not its sister taxon, *D. claytoni*. The previously described skull, mandible and teeth and postcranial bones described herein were discovered at the same locality during excavations at the base of the Malé Karpaty Mountains (Slovakia), at the junction of the Morava and Danube rivers. The geological age of *D. emryi* and the presence of mixed characters strongly suggest that this species was an early relative to the ancestor of seals, possibly being a terminal branch of the phocid tree. This material allows for emended diagnoses of the species, updated assessments of geographical distribution and provides further material for clarification of controversial phylogenetic relationships in Phocidae.

K e y w o r d s: Phocidae; early Middle Miocene; Badenian; Vienna Basin; Paratethys.

Introduction

Through the years, there has been significant controversy in subfamilial classification of phocids (Koretsky and Rahmat, 2013). While several researchers (Wyss, 1988; McKenna and Bell, 1997) have divided the Family Phocidae into one subfamily (Phocinae) and others (Burns and Fay, 1970; Muizon, 1992; King, 1983; Wyss, 1994; Berta and Sumich, 1999) have described two subfamilies (Phocinae and Monachinae), some have not separated true seals into any subfamilies at all (Sokolov, 1979; Wozencraft, 1989; Berta et al., 2015). Therefore, this study continues with the traditional (Gray, 1866; Trouessart, 1897; Scheffer, 1958; Chapskii, 1974) classification of true seals in which the Family Phocidae includes semi-aquatic carnivorans divided into three extant subfamilies (Phocinae, Monachinae, and Cystophorinae) and one extinct subfamily (Devinophocinae; Koretsky and Holec, 2002).

The Paleobiology Departments of the Smithsonian Institution (Washington, D.C., USA) and Comenius University collected cranial and multiple mandibular, dental and postcranial bones from the same site at the base of the Malé Karpaty Mountains in Slovakia. This site, named Bonanza, is near the junction of the Morava and Danube rivers (Koretsky and Rahmat, 2015; fig. 1). While numerous vertebrate fossil material from this site has previously been reported (Holec et al., 1987; Holec and Sabol, 1996; Holec et al., 1997; Schultz, 2004; Fejfar and Sabol, 2009), there has been no description of any postcranial material of the subfamily Devinophocinae.

This is our subsequent publication on undescribed Devinophocinae fossil material found at the Bonanza site. Our previous publication (Koretsky and Rahmat, 2015), detailed the description of a new species (*Devinophoca emryi*) of the extinct phocid subfamily Devinophocinae from the early Badenian, early Middle Miocene (16.26–14.89 Ma). The *Devinophoca* material (skull, mandibles and teeth) presents distinguishing characters of the subfamily as well as mixed characters with the three extant phocid (Cystophorinae, Monachinae and Phocinae) subfamilies.

The cranial and postcranial material of *D. emryi* (collected by I. A. Koretsky, R. J. Emry, and team-members from the U.S., Slovakia and Ukraine) was found at the same site as material for its sister taxon, *D. claytoni*. As demonstrated in Koretsky and Rahmat (2015), several isolated mandibles and many individual teeth were found at the same Bonanza locality, with some teeth *in situ* corresponding morphologically and anatomically with the mandible and skull of *D. emryi*, while others associate to teeth *in situ* in the mandible and skull of *D. claytoni*.

Despite the abundance of discovered fossil material worldwide over the past three decades, there remains a significant lack of published phocid cranial remains. The extreme fragility of seal skulls (Koretsky and Rahmat, 2013) is the main reason for the lack of preservation over time. To date, fewer than 15 fossil seal skulls have ever been described. Thus, taxonomic classification of seals has been largely based on the morphology of both complete and fragmentary dissociated postcranial bones, mainly the humerus and femur (Koretsky and Rahmat, 2013). Koretsky (2001) has reported how modern species of seals have specific ecological niches reflected in morphology of postcranial bones (commonly the humerus and femur) and the mandible. Using these osteological characters, modern phocines were separated into morphoecological units, with fossil seal remains placed into analogous ecomorphological groups.

Since our previous publication (Koretsky and Rahmat, 2015) detailed direct associations of discovered mandibles with the skulls of *D. emryi* and *D. claytoni*, we were able to determine that that these postcranial bones do indeed belong to *D. emryi*. More recently, P. Goldin and D. Pilipenko (2012) reported the finding of an almost complete skeleton *in situ* (from Kerch Peninsula, Crimea, Ukraine) of *Monachopsis pontica*. Their examination of the associated postcranial bones with fragments of the skull and mandible strongly supported Koretsky's (2001) ecomorphotype theory. In addition, our current method of associating isolated bones followed those of Muizon (1981), Koretsky and Grigorescu (2002), Koretsky and Ray (2006) and Amson and Muizon (2014), who described more complete associated partial skeletons.

Thus, the strong correlations between ecomorphotypes and cranial/postcranial morphology supports placement of this postcranial material to the same species, *D. emryi*, and not its sister taxon, *D. claytoni*. Furthermore, according to the ecomorphotype hypothesis of Koretsky (2001), the bones of *D. emryi* belong to the same group (ecomorphotype III) on the basis of characters such as:

1) mandible — symphyseal part acute and weakly pronounced; chin prominence weakly outlined and not bent labially, and located beneath posterior alveoli of p2 and p4;

2) humerus — lesser tubercle slightly higher than head; intertubercular groove narrow; maximum width of the deltoid crest located in its middle;

3) femur — greater trochanter slightly higher than head; its proximal part is beveled; intertrochanteric crest shortened and located slightly inferior to trochanteric fossa.

As an example of this methodology, the modern species *Histriophoca fasciata* (Ribbon seal) belongs in ecomorphotype III, along with the extinct taxa *Sarmatonectes sintsovi*, *Praepusa vindobonensis*, *Monachopsis pontica* and *Leptophoca lenis,* each belonging to a different biostratigraphic age (Koretsky, 2001). The feeding behavior/habitat ecology of the modern genus *Histriophoca* includes medium diving depths of usually 50–100 meters and feeding on crabs, shrimp, mollusks and fish near the water floor (Heptner et al., 1976; Ridgway and Harrison, 1981; Riedman, 1990; Adam and Berta, 2002; Boveng et al., 2008). While the ecomorphotype analysis places *D. emryi* into the same group as *H. fasciata* and *Pr. vindobonensis*, the sizes of these seals differ significantly, with *Histriophoca* being the largest (Koretsky, 2001). The total skull length of *H. fasciata* is 184.5 mm, considerably larger than that of *D. emryi* (119.5 mm) and the juvenile *Pr. vindobonensis* (116.0 mm). The overall length of the *D. emryi* skull is even smaller than that of *Pusa sibirica* (173 mm; Heptner and Naumov, 1996), the smallest known living seal. Although *D. emryi* belongs to ecomorphotype III based on bone morphology, the size of this extinct seal (smaller than the smallest known living seal) leads us to hypothesize that its ecology likely correlates more with taxa in ecomorphotype II, such as representatives of *Pusa* (Koretsky, 2001), who dive up to 90 meters (Heptner at al., 1976) and feed on crustaceans and fish (Bigg, 1981; Riedman, 1990; Rahmat and Koretsky, 2015).

Morphologically, the mandible of *D. emryi* is similar to Recent *Halichoerus grypus* (Koretsky and Rahmat, 2014), with a triangular coronoid process that has a posterior edge ending as a vertical slope. The masseteric fossa in both *D. emryi* and *H. grypus* is well defined, implying strong masseter muscle attachment. The mandibular condyloid angle of *D. emryi* was found to be 20°, suggesting a diet of medium-sized prey (Koretsky and Rahmat, 2014). This ecomorphological analysis is applied to the level of alpha systematics.

Additionally, the bones were collected from the same site, all belonging to adult individuals (fused epiphyses). The hindlimb (innominate, femur, tibia and fibula) and forelimb (scapula, humerus, radius and ulna) bones are the first record of postcranial material described for the extinct subfamily Devinophocinae and important for improving overall true seal classification. Morphological examination of these postcranial fossils from the Early Badenian, early Middle Miocene of the Central Paratethys will be compared to taxonomic characters used for the classification of Phocidae (Koretsky, 2001; Koretsky and Ray, 2008). Overall, the *D. emryi* postcranial material shares mixed characters with the three extant phocid subfamilies as well as presents distinguishing traits not previously described (see emended diagnosis and description below), similar to our previously described *D. emryi* skull, mandible and dentition (Koretsky and Rahmat, 2015).

Abbreviations. Specimens from the following institutions were examined for this manuscript: IRSNB — Institut Royal des Sciences Naturelles de Belgique; NMNHU-P — National Museum of Natural History at the National Academy of Science of Ukraine, Kyiv, Ukraine; SNMZ — Department of Paleontology, Slovakian National Museum, Bratislava, Slovak Republic; USNM — National Museum of Natural History, Washington, D.C., USA.

Material and methods

During several years of internationally-collaborative (USA, Slovakia, Ukraine) excavations, postcranial material was collected together with a skull, several mandibles and teeth at the base of the Malé Karpaty Mountains, specifically at the Bonanza site near the junction of the Morava and Danube rivers (Koretsky and Rahmat, 2015). Assemblages of marine and terrestrial vertebrates were discovered from the southern slope of Devínska Kobyla Hill (geographic coordinates of the site are 48°12'34" N and 16°58'22" E). Additionally, the amateur paleontologists Š. Mészároš, who called this location "Bonanza" (dated to the Middle Miocene, early Badenian, lower part of MN 6), and Miroslav Hornacek donated their collected material to the Slovak National Museum and our study.

When examining dissociated fossil material, it is imperative to determine correlation of different parts of the skeleton. Using Koretsky's (2001) methodology, we directly associate fossil bones and compare them to other fossil osteological material. We also incorporate Koretsky's (2001) ecomorphotype analysis by linking fossil postcranial bones (humerus and femur) with their corresponding mandible to demonstrate association based on Recent morphological analogues. As a result, taxonomic classification of phocids can be revised accordingly. The methods of Heptner (1947), Chapskii (1952; 1967), Antoniuk (1979) and Koretsky and Rahmat (2013) were used to resolve diagnostic problems. Anatomical nomenclature and updated morphometric analysis of the bones of the postcranial skeleton was carried out using the methods of Aristov and Barushnikov (2001), Koretsky (2001) and Koretsky and Ray (2008).

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

Type genus. Type and only included genus by monotype, *Devinophoca*, Koretsky and 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 (presents diagnostic combination of incisors that differ from Phocinae, Monachinae and Cystophorinae). Middle of internal crest of humeral trochlea at level of coronoid fossa (similar to Phocinae, but different than in Monachinae, where it is arch-like elevated over the coronoid fossa, and Cystophorinae, where it is wave-like raised over the coronoid fossa).

Devinophoca emryi (fig. 1–6; tables 1–6)

Paratype. Left humerus, SNMZ 25507.

Type locality. From the locality of Stokerau lime plant, Bonanza Hill, Devínska Kobyla, outskirt of Bratislava, Slovak Republic.

Range. Badenian (= Langhian), early Middle Miocene (16.26–14.89 Ma); Central Paratethys, Vienna Basin of Western Slovakia.

Emended diagnosis. Diagnosis for skull (holotype), mandibles and teeth was published by Koretsky and Rahmat (2015). Humeral head rounded, flattened, compressed craniocaudally (similar to Monachinae); ratio of head's width to height is 0.94 (similar to Monachinae); intertubercular groove deep, short, narrow (similar to Monachinae, in contrast to Cystophorinae and Phocinae); greater tubercle oval, well developed, slightly elevated above head; lesser tubercle oval, flattened, almost same level as head (in contrast to Monachinae); proximal part of deltoid crest located slightly higher than head and lesser tubercle; deltoid crest strongly developed, short, terminates near middle of diaphysis; greatest width of deltoid crest located in middle (similar to Cystophorinae, in contrast to Phocinae); deltoid tuberosity small, located in middle of deltoid crest (similar to Cystophorinae); medial epicondyle flattened, extends to middle of coronoid fossa (in

T a b l e 1. **Measurements of humeri, mm**

Characters	*Devinophoca emryi*
Absolute length	128.5; 130.1
Length of deltoid crest	80.5; 82.4
Height of head	27.1; 28.1
Height of trochlea	19.2; 23.8
Width of head	28.3; 29.8
Width of deltoid crest	10.8; 11.6
Width of distal epiphysis	38.4; 40.1
Width of proximal epiphysis	40.3; 40.8
Width of trochlea below	27.5; 27.9
Width of trochlea, frontal view	19.7; 20.4
Transverse width of diaphysis	15.2; 16.4
Thickness of proximal epiphysis	59.4; 60.6
Thickness of medial condyle	26.7; 26.8
Thickness of lateral condyle	21.5; 23.2
Diameter of diaphysis with deltoid crest	35.6; 35.9

contrast to Cystophorinae); coronoid fossa oval, shallow (similar to Cystophorinae); entepicondylar foramen large, oval, with wide bridge over it; middle of humeral trochlear crest located at level of coronoid fossa (similar to Phocinae).

Ulna's olecranon large, curves caudally; olecranon tuberosity prominent; trochlear notch flattened, well developed; radial notch very pronounced, concave in shape; coronoid process round, flat, shallow; anconeal process very large, wide, protrudes; styloid process well developed, oval; distal part of ulna flattened; upper part of trochlear notch wider than lower.

Innominate's ilium thin, excavated on ventral surface (similar to Lobodontini, in contrast to Cystophorinae, Monachinae and especially Phocinae); iliac tuberosity flattened, small, averted; iliac crest thin, well outlined, not averted (similar to Monachinae); iliac spine thin (similar to Monachinae, in contrast to Cystophorinae and Phocinae); acetabulum deep, with pronounced rim.

Femoral head small, round, seated on distinct lip on short and wide neck (similar to Phocinae); greater trochanter extends above head; proximal and distal parts of greater trochanter approximately of equal width (similar to some Phocinae); trochanteric fossa oval, deep, with overhanging lip of medial part of greater trochanter (in contrast to Phocinae); supracondylar fossa shallow, wide, elongated; smallest width of diaphysis shifted towards proximal end of bone (similar to Monachinae and Cystophorinae); lateral condyle
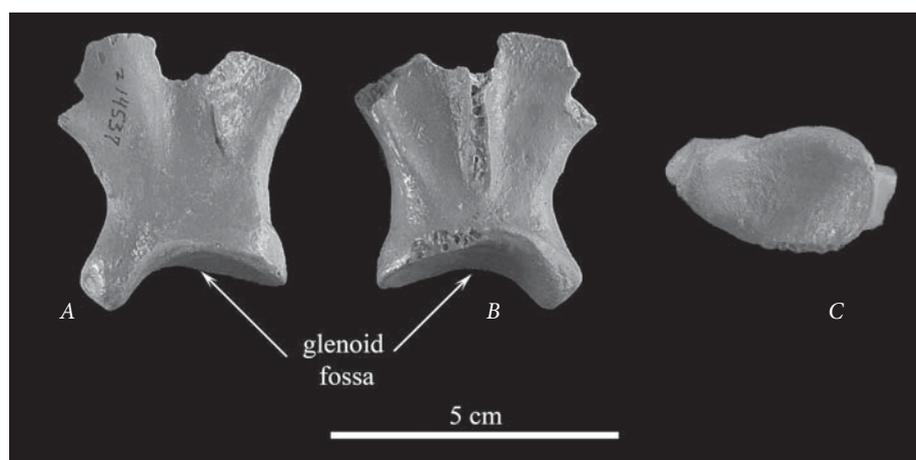

Fig. 1. *D. emryi* scapula, SNMZ 14537 (R., incomplete) in: *A* — anterior; *B* — posterior; *C* — lateral views.

significantly larger than medial (in contrast to Cystophorinae); ratio between proximal and distal epiphyses 1.04 (in contrast to Cystophorinae, Monachinae and Phocinae).

Referred specimens. In addition to the holotype (skull), the following specimens were found: scapula: SNMZ 14537 (R., proximal end); humerus: SNMZ 25507 (L.); radius: SNMZ 25505 (proximal end); ulna: SNMZ 25504 (L.); innominate: SNMZ 14543 (L.); femur: SNMZ 14544 (R.); tibia and fibula: SNMZ 14545 (L., proximal half).

Description. Scapula (fig. 1). The incomplete scapula has a well-developed glenoid fossa that is concavely shaped and has a thin mushroom-like lip. The transverse diameter of the glenoid fossa is 31.5 mm, the anteroposterior diameter of the glenoid fossa is 20.5 mm and the width of the neck is 29.4 mm. The coracoid process, acromion process, spine and other features cannot be described as they are missing.

Humerus (fig. 2, *A*–*D*; table 1). The complete bone is well preserved. The head is well developed, flattened and compressed craniocaudally. The ratio between the length and

Fig. 2. *D. emryi* humerus, SNMZ 25507 (L., paratype) in: *A* — medial; *B* — lateral; *C* — caudal; *D* — cranial views. Cranial views of: *E* — left humerus of *Callophoca obscura* (IRSNB 301, male); *F* — left humerus of *Leptophoca lenis* (USNM 412115); *G* — left humerus of *Pachyphoca chapskii* (NMNHU-P 64-523). The tip of the arrows indicate the shape of the middle of the humeral trochlear crest in: *E* — Monachinae (arch-like, elevated over the coronoid fossa); *F* — Phocinae (at the level of the coronoid fossa (similar to *D. emryi*); *G* — Cystophorinae (rising wave-like over the coronoid fossa).

width of the head is 0.94. The lesser tubercle is well developed, oval, and located almost at the same level as the head. In contrast to *Pontophoca sarmatica* (Monachinae), the lesser tubercle does not parallel the bone's axis, but deviates slightly posteriorly from the bone's axis as in *Cryptophoca maeotica* (Phocinae). The greater tubercle is located above the head, is well developed and flattened on its lateral side as a well-outlined large oval facet, a unique character for the Subfamily Devinophocinae. The width of the anatomical neck between the head and lesser tubercle is significantly broader than the width between the head and greater tubercle (also a unique character for Devinophocinae). The intertubercular groove is deep and narrow. The deltoid crest is strongly developed with the widest portion of the deltoid crest located in its middle, similar to *Pachyphoca ukrainica* (Cystophorinae). The crest extends a little more than half the length of the bone and ends almost as an invisible ridge, reaching the proximal edge of the entepicondylar foramen, but does not reach the coronoid fossa, as in the monachine *Callophoca obscura* (fig. 2*, E*). The deltoid tuberosity is small, markedly convex (as in *Pontophoca sarmatica*) and is located in middle of deltoid crest. The musculospiral groove is absent. The lateral epicondyle is narrow, reaching the distal part of the deltoid crest (as in *Callophoca obscura*) and extends more than twice proximally than the medial. The medial epicondyle is flattened, is located lower than the lateral, and spreads from the middle part of the entepicondylar foramen, extending to the middle of the coronoid fossa. The entepicondylar foramen is large and oval, with a wide bridge over it, like in the phocine *Leptophoca lenis* (fig. 2, *F*) and the cystophorine *Pachyphoca chapskii* (fig. 2*, G*). The coronoid fossa is shallow, oval in shape, and ends at the same level as the tip of the entepicondylar foramen. The middle of the humeral crest of the trochlea (fig. 2, *E–G*) is at the level of the coronoid fossa (similar to Phocinae), unlike Monachinae (arch-like, elevated over the coronoid fossa) and Cystophorinae (rising wave-like over the coronoid fossa). The olecranon fossa is shallow, narrow and oval shaped.

Radius (fig. *3, A–C*). The incomplete radius is missing its distal end. The radius has a well developed, oval-shaped head and a narrow, elongated neck. The fovea of the head is well-outlined, smooth and concave in shape. The circumferential articularis on the lateral aspect of the bone is well-outlined, ridged and does not reach the level of the radial tuberosity, unlike in *Callophoca obscura* (Monachinae) and similar to *Leptophoca lenis* (Phocinae).

Ulna (fig. 3, *D–E*; table 2). The complete bone is long, slender, almost the same length as *Pachyphoca chapskii* (Cystophorinae) and has a significantly large olecranon, in contrast to *Praepusa vindobonensis* (Phocinae) and *P. chapskii*, where the olecranon is short. The medial surface is flat and the most proximal portion of the bone just below the olecranon is concave, unlike in *Pachyphoca ukrainica* and *P. chapskii* (Cystophorinae), where none of the medial surface has any concavity. The well-developed olecranon is unusually long, thin, fan-shaped and curves caudally, with a prominent olecranon tuberosity. The narrow fossa at the level of the trochlear notch for insertion of the *flexor digitorum profundus* (= *communis*) muscle contrasts with the protuberance present at the same position in *P. chapskii*. The presence of this elevated ridge implies that *P. chapskii* seals have a more developed *flexor digitorum profundus* muscle (for flexing the forelimb; Piérard, 1971) than this species of Devinophocinae. Morphology of this character suggests that the condition in *P. chapskii* is more primitive than the geologically older-aged fossil ulna of Devinophocinae, where this character is more advanced. The broad, short and very bulky rugosity for the *brachialis* muscle insertion has a well-developed ridge (unlike in *P. chapskii*), but its location below the trochlear notch is similar to *P. chapskii*. On the lateral surface, a shallow, wide and prominent fossa (in contrast to *P. chapskii*) is present for the *abductor pollicis* muscle. This fossa is absent in *Pr. vindobonensis*. Along the middle of the diaphysis, a long, shallow groove extends from the caudal edge of the articular surface, as a continuation from the *abductor pollicis* muscle fossa, to the well-developed ulnar protuberance (similar to *P. chapskii*, but in contrast to *P. ukrainica*). The ulnar protuberance is significantly thicker and wider in *P. chapskii*. The trochlear notch is flattened and well developed. The radial notch is also

T a b l e 2. Measurements of ulna, mm

Characters	Devinophoca emryi
Width of incisura trochlearis in upper part	17.2
Width of incisura trochlearis in lower part	15.9
Maximal width of middle part of diaphysis	19.9
Maximal width of distal epiphysis	22.4

very pronounced (unlike in *Pr. vindobonensis* and *P. chapskii*) and concave in shape. The radial notch in *Callophoca obscura* and *Pliophoca etrusca* (Monachinae) is absent, replaced by a sharpened ridge. The coronoid process is rounded, flat and very shallow. In contrast to *P. chapskii* and *Pr. vindobonensis*, the coronoid process does not protrude over the radial notch. The anconeal process is very large, wide and protruding, similar to *P. chapskii* and *Cal. obscura*. The head and styloid process are preserved, with the prominent styloid process having an oval shape. The distal part of the ulna of Devinophocinae remains flattened up to the styloid process, in contrast to *P. chapskii* where it becomes enlarged and thicker than the diaphysis.

Innominate (fig. 4; table 3). As in other Monachinae and Cystophorinae, the ilium is fairly thick. The iliopectineal eminence is small and is situated higher than the proximal
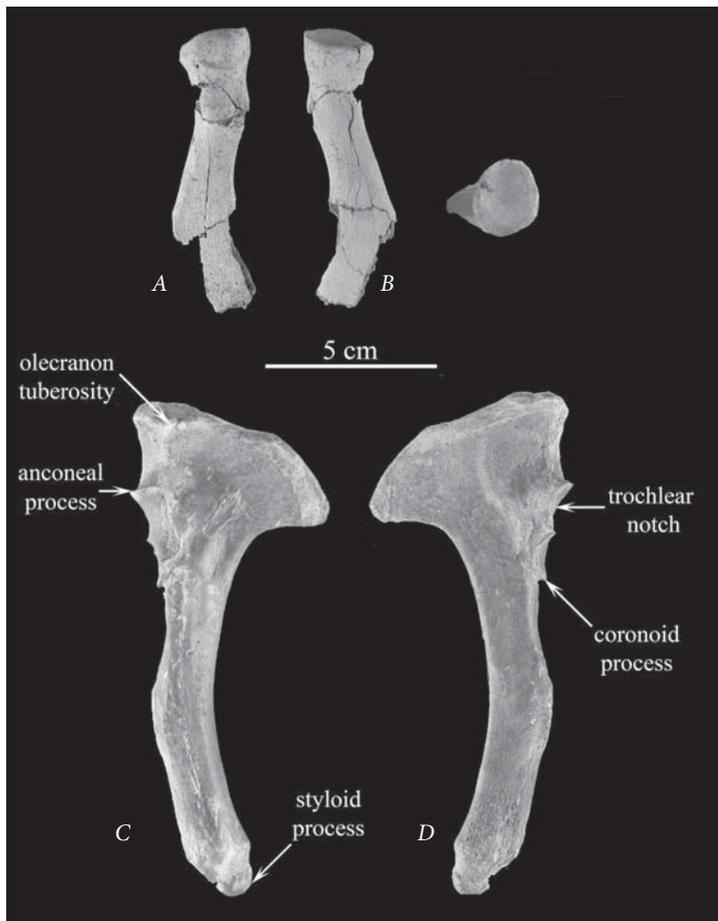

Fig. 3. *D. emryi* radius, SNMZ 25505 (incomplete) in: *A* — dorsal; *B* — ventral; *C* — cranial views and ulna SNMZ 25504 (L.) in: *D* — medial; *E* — lateral views.

T a b l e 3. Measurements of innominate, mm

Characters	*Devinophoca emryi*
Length from center of acetabulum to iliac crest = A	71.9
Width of acetabulum	27.2
Height of acetabulum	26.9
Width of level of iliac crest = O	55.3
Ratio	
O/A	76.9

border of the acetabulum. The greater sciatic notch is almost straight, with a slight concavity (similar to *P. ukrainica*). A shallow depression for the *gluteus medius* muscle is located on the medial aspect of the ilial wing. There is a shallow auricular fossa on the lateral aspect of the ilium for origin of the *psoas major* muscle. The alar spine does not protrude far. The edges of the acetabulum are raised high above the plane of the bone (similar to *P. chapskii*). The acetabulum is conical in shape, a primitive character (similar to *P. chapskii*). Above the acetabulum is a deep and narrow depression for insertion of the *rectus femoris* muscle. The ischium and pubis are not preserved.

Femur (fig. 5, *A–B*; table 4). The femoral head is small in size, round and seated on a distinct lip. The neck is short and wide. The greater trochanter extends proximally above the head, with its proximal part somewhat wider than the distal, similar to the cystophorine *P. ukrainica* (fig. 5, *E*). The greater trochanter is obliquely oriented along the bone's axis, but not as extreme as in *P. chapskii*. The trochanteric fossa is deep, oval in shape and opens proximally, reaching the distal half of the greater trochanter. The lesser trochanter is not
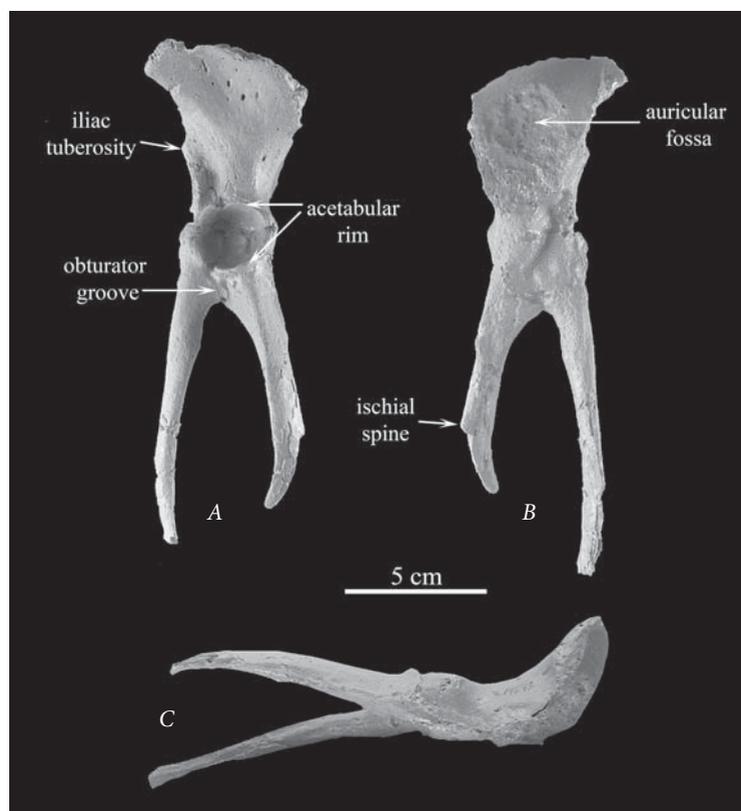

Fig. 4. *D. emryi* innominate, SNMZ 14543 (L., incomplete) in: *A* — lateral; *B* — medial; *C* — posterior views.

T a b l e 4. Measurements of femur, mm

Characters	*Devinophoca emryi*
1. Absolute length	101.9
2. Medial length	97.5
3. Lateral length	95.9
4. Length of medial condyle	19.2
5. Length of lateral condyle	21.9
6. Length of greater trochanter	30.1
7. Intertrochanter length	40.5
8. Height of head	20.6
9. Height of articular area of patella surface	18.9
10 Width of proximal epiphysis	54.7
11. Width of distal epiphysis	52.5
12. Width of condyles	44.7
13. Width of greater trochanter	18.7
14. Width of head	20.8
15. Width of diaphysis	27.9
16. Anteroposterior thickness of diaphysis	15.9
17. Thickness of medial condyle	14.8
18. Thickness of lateral condyle	19.1
19. Distance between condyles	11.5
20. Diameter of neck	16.8

T a b l e 5. Measurements of tibia, mm

Characters	*Devinophoca emryi*
Width of proximal epiphysis	45.5
Height of proximal epiphysis	26.4
Width of distal epiphysis	–

present. The flat, wide intertrochanteric crest reaches the middle of the diaphysis and is where the *adductor cranialis* muscle inserts (Pierard, 1971). The supracondylar fossa is shallow, narrow, and elongated. The smallest width of the diaphysis is shifted more towards the proximal end of the bone. The distance between the condyles is 11.5 mm and the lateral condyle is much larger than the medial. The proximal epiphysis is larger than the distal, in contrast to Cystophorinae, Monachinae and Phocinae (fig. 5, *C–E*).

T a b l e 6. Comparing absolute length of phocid humeri and femora, mm

Subfamily	Humerus	Femur
Devinophocinae		
Devinophoca emryi	129.0	101.9
Phocinae		
Batavipusa neerlandica	64.9	73.5
Praepusa vindobonensis	75.0–101.0	63.0–82.5
Monachopsis pontica	80.5 ♂; 60.0–71.5 ♀	80.5 ♂; 65.0–70.0 ♀
Sarmatonectes sintsovi	91.0	89.5–94.5
Leptophoca lenis	111.0–129.0	119.0–120.0
Leptophoca amphiatlantica	–	96.0–118.3
Monachinae		
Pliophoca etrusca	149.5–166.5	109.5
Cystophorinae		
Pachyphoca ukrainica	85.0–89.0	78.0–82.5

Tibia and fibula (fig. 6, *A–C*; table 5). The two condyles are concave in their centers, with the lateral condyle more concave than the medial. Both medial and lateral condyles are oval in shape. The intercondyloid eminence is well pronounced and only slightly raised above the two pronounced borders of the condyles. On the ventral side of the bone, the tibial tuberosity is flattened, triangular in shape and well developed. The distal portions of the tibia and fibula were destroyed.

Discussion and conclusions

Despite a long history of phocid studies, this is the first record of postcranial bones described for the extinct subfamily Devinophocinae. Overall, the cranial and postcranial bones of *Devinophoca emryi* share mixed characters with the three extant subfamilies
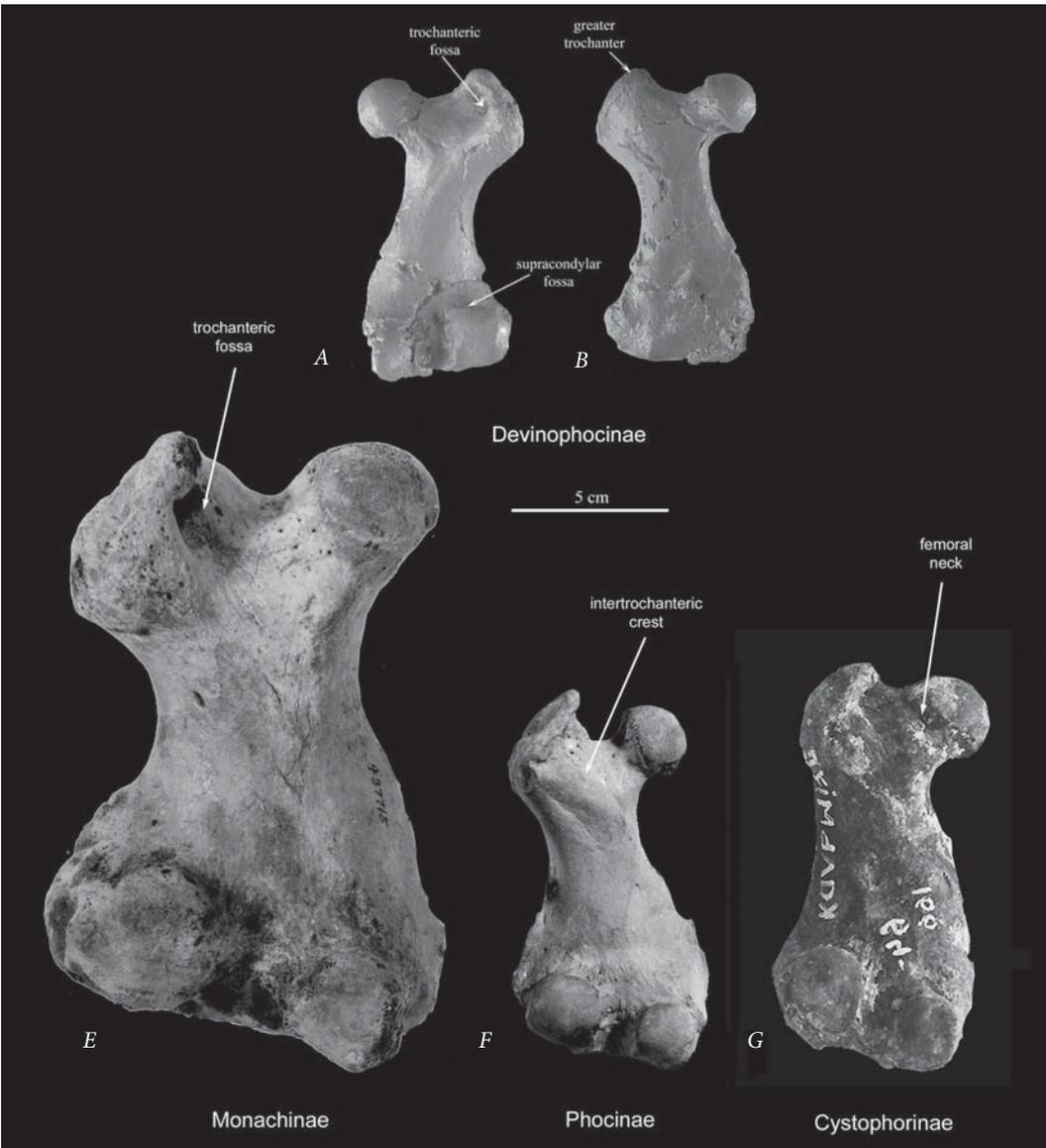
Fig. 5. *D. emryi* femur, SNMZ 14544 (R.) in: *A* — caudal; *B* — cranial views. Caudal views of: *E* —left femur of *Callophoca obscura* (USNM 437715, male); *F* — right femur of *Leptophoca amphiatlantica* (reversed, USNM 263648); *G* — right femur of *Pachyphoca ukrainica* (reversed, NMNHU-P 64-166).
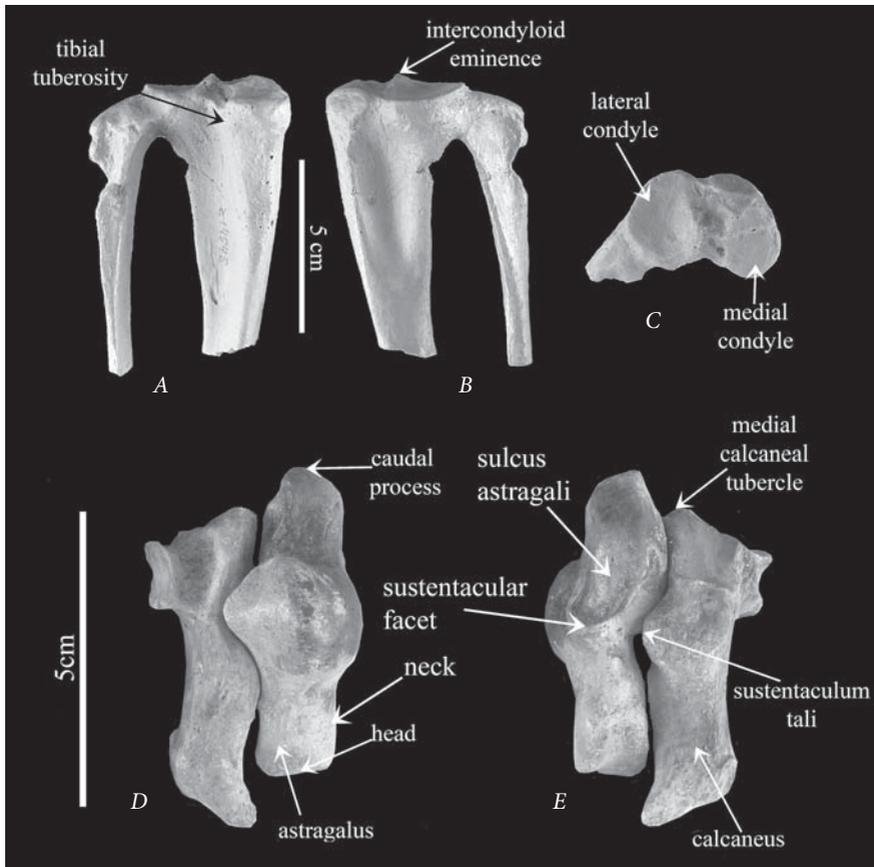
Fig. 6. *D. emryi* tibia and fibula, SNMZ 14545 (L., incomplete) in: *A* — caudal; *B* — cranial; *C* — proximal views. Right calcaneus and astragalus in: *D* — dorsal; *E* — plantar views.

(Cystophorinae, Phocinae and Monachinae), as described above and in our previous publication (Koretsky and Rahmat, 2015). Mandibular morphology of *D. emryi* (condyloid angle of 20°) also demonstrates shared mixed characters as the condyloid angle is the same as that of the phocine *Halichoerus grypus* and the monachine *Lobodon carcinophagus* (Koretsky and Rahmat, 2014; table 1).

However, the presence of several unique postcranial characters not seen in any representatives of the other three subfamilies (such as: well-outlined, large oval facet on greater tubercle of humerus; broader width between the head and lesser tubercle of humerus; femoral proximal epiphysis larger than distal; thin innominate ilium that is excavated on ventral surface) demonstrate that this material belongs to *D. emryi*. The skull, mandibles and teeth (Koretsky and Rahmat, 2015), and postcranial material (scapula; humerus; radius; ulna; innominate; femur; tibia; fibula; and multiple bones of the manus and pedis) were excavated from the same locality as well.

During ecomorphotype analyses, fossil humerus and femur bones were directly associated with their corresponding mandible to reveal associations based on Recent morphological analogues. This strong correlation and the direct association of a mandible with the skull of *D. emryi* (Koretsky and Rahmat, 2015)*,* supports placement of this material to the previously described *D. emryi* and not to its sister taxon, *D. claytoni* (see phylogenetic analysis in Koretsky and Rahmat, 2015; fig. 8, table 4). Koretsky's (2001) ecomorphotype analysis on these *D. emryi* cranial and postcranial bones confirms that the mandible, humerus and femur do indeed belong to the same species. While morphology of cranial and postcranial bones assigns *D. emryi* into ecomorphotype III, we hypothesize that the

feeding behavior and ecology of this extinct seal appears to be closer to representatives of the genus *Pusa*, who belong in ecomorphotype II. The subfamilial mixture of characters in *D. emryi* is clearly evident when assigning this species into an ecomorphotype, as the morphology and size of the *D. emryi* skull and postcranial bones are much larger than *Monachopsis pontica* (ecomorphotype III), yet the skull is significantly smaller than the smallest known living seal *Pusa sibirica* (ecomorphotype II). Thus, the morphology and size of *D. emryi* shows no clear distinction between ecomorphotypes II and III, meaning it likely occupies an intermediate position between these two groups.

When examining the morphology and geological age of *D. emryi*, it appears that this extinct seal demonstrated microcephaly, with a small skull that measures less than the smallest living known seal (*Pusa sibirica*) and with comparatively longer limb bones. This discrepancy is further supported by examining the morphology of the femur and humerus bones of several extinct seal taxa more in detail (table 6).

The *D. emryi* (early Middle Miocene: 14.9–16.3 Ma) femur was larger than the following extinct phocines: the Late Miocene (8.0–11.5 Ma) *Batavipusa neerlandica*; the Middle to Late Miocene (11.2–13.6 Ma) *Praepusa vindobonensis*; the Middle to Late Miocene (8.0–11.2 Ma) *Monachopsis pontica*; the Middle Miocene (9.0–11.5 Ma) *Sarmatonectes sintsovi* and the Middle Miocene (9.6–11.2 Ma) cystophorine *Pachyphoca ukrainica*. The *D. emryi* femur is smaller than the Middle Miocene (11.6–16.0 Ma) *Leptophoca lenis*; the Middle to Late Miocene (15.8–16.0 Ma) *Leptophoca amphiatlantica*; and the Late Pliocene (3.2–4.0 Ma) monachine *Pliophoca etrusca* (see table 6).

The overall length of the *D. emryi* humerus is larger than that of *Praepusa vindobonensis*, *Monachopsis pontica*, *Batavipusa neerlandica* and the cystophorine *Pachyphoca ukrainica*, but smaller than the monachine *Pliophoca etrusca* (Koretsky and Ray, 2008; table 6). Berta et al. (2015) found that the humerus of *Pliophoca* c. f. *P. etrusca* is smaller than *D. emryi*. However, they chose to exclude a large collection of previously described material that included ontogenetic and sexually dimorphic features (Koretsky and Ray, 2008) during their re-evaluation of this extinct genus.

Thus, *D. emryi* had a very small skull that likely correlates with a small body size, despite the presence of long hind- and forelimb bones. While it can be expected in other phocids that long limb bones are generally associated with a larger skull and bigger body size, the cranial evidence of *D. emryi* (Koretsky and Rahmat, 2015) supports the Finarelli and Flynn (2006) finding that the fossil record reveals small-bodied ancestors. Therefore, the geological age of *D. emryi* and the presence of mixed characters from the three extant phocid subfamilies suggests that the early Middle Miocene *D. emryi* could be a basic morphotype and supports the previous claim by Koretsky and Holec (2002) that *Devinophoca* may represent a very primitive relict of the common ancestor of groups of Phocidae, possibly being a terminal branch of the phocid tree. The elongated flippers may have been an unsuccessful evolutionary adaptation that led to survivability difficulties and the ultimate demise of the subfamily Devinophocinae.

Additionally, recent work examining the evolution of the body size of pinnipeds reveals that odobenids and otariids had generally smaller-sized ancestors, while the so-called "limited fossil record" of Phocidae prevents a definitive answer, according to Churchill et al. (2014). Although fossil cranial remains of seals are limited compared to otariids and odobenids, countless recent publications have described small sized fossil seals from both sides of the Atlantic Ocean.

Moreover, studies based only on molecular phylogeny cannot be the sole technique for determining the relationships of extinct phocids, as morphological characters often yield dissimilar, yet critical results. Therefore, future phocid phylogenetic studies comparing extinct and extant taxa need to include a combination of molecular and morphological data.

As the first record of postcranial bones for the extinct subfamily Devinophocinae, this new material allows for emended diagnoses of *D. emryi* based on cranial (Koretsky

and Rahmat, 2015) and postcranial morphology, updated assessments of geographical distribution and provides further material for clarification of controversial phylogenetic relationships in the Family Phocidae.

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