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## *Basilotritus* (Cetacea: Pelagiceti) from the Eocene of Nagornoye (Ukraine): New data on anatomy, ontogeny and feeding of early basilosaurids



### *Basilotritus* (Cetacea : Pelagiceti) de l'Éocène du Nagornoye (Ukraine) : nouvelles données sur l'anatomie, l'ontogénèse et l'alimentation des basilosauridés précoces

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## ABSTRACT

A new specimen of early basilosaurid, now identified as *Basilotritus* sp., comes from the late Middle Eocene of Ukraine. It has basilosaurid-type cheek teeth with cinguli, similar to those of *Zygorhiza*, and roots resembling those of *Georgiacetus vogtlensis* and early Neoceti; an unusual feature of these teeth is the presence of accessory denticles of the second order located on the crown denticles. The postcranial anatomy shows a mixture of primitive and advanced basilosaurid traits. The phylogenetic position of the genus *Basilotritus* is confirmed to be near the base of Basilosauridae, between *Supayacetus* and *Zygorhiza*. The ontogeny of the specimen from Nagornoye is characterized by large body size, slow skeletal maturation and intensive pachyosteosclerosis that are interpreted as neotenic development. Rapid tooth wear with strong apical abrasion is the result of specialized diet, possibly feeding on sharks.

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## R É S U M É

Un nouveau spécimen de basilosauridé précoce, actuellement identifié comme *Basilotritus* sp., provient de l'Éocène moyen tardif d'Ukraine. Il a des dents jugales de type basilosauridé, avec des cinguli semblables à ceux de *Zygorhiza* et des racines ressemblant à celles de *Georgiacetus vogtlensis* et des Néocètes précoces; un trait inhabituel de ces dents est la présence de denticules accessoires de second ordre, localisés sur les denticules de la couronne. L'anatomie post-craniale présente un mélange de traits de basilosauridés, à la fois primitifs et perfectionnés. La position phylogénétique du genre *Basilotritus* est confirmée comme

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étant proche de la base des Basilosauridae, entre *Supayacetus* et *Zygorhiza*. L'ontogénie du spécimen de Nagornoye se caractérise par une grande taille du corps, une maturation lente du squelette et une pachyostéose intensive, qui est interprétée comme un développement néoténique. L'usure rapide de la dent, avec une abrasion apicale intense, est le résultat d'un régime alimentaire spécialisé, éventuellement une nourriture de requins.

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## 1. Introduction

All the known records of archaeocetes from the central and East Europe, from Rohrdorf (Germany) to Tsimlyansk area (Russia), were dated as the late Middle Eocene (Bartonian) and are now referred to as early basilosaurids with moderately elongated posterior thoracic and lumbar vertebrae (Gol'din and Zvonok, 2013; Gol'din et al., 2012; Gritsenko, 2001; Tesakov et al., 2012; Uhen and Berndt, 2008). Some of them were described as *Basilotritus uheni* Gol'din and Zvonok (2013). Other specimens also possibly belong to this genus or species or to closely related genera (Gol'din and Zvonok, 2013). Earlier, a cetacean from Nagornoye (Nagirne) locality (Svetlovodsk District, Kirovograd Region, Ukraine; N 49°05', E 33°08') was described as Basilosauridae indet. (Zvonok, 2012). We were not able to compare it with other cetaceans from this region due to the lack of common elements. Now we obtained new material from this specimen (see [Material and methods](#)), which makes it possible to specify its taxonomic position and significantly contribute to the anatomical description of early basilosaurids.

Here, we redescribe the cetacean from Nagornoye with the newly found skeletal elements and reinterpret those found before.

## 2. Material and methods

The fossil remains were taken by L.R. in 2004 and 2006 and by A.K. in 2010: this portion of the material is housed in NMNH-P and includes three teeth (NMNH-P Ngr-2, 3, 4), three vertebrae (NMNH-P Ngr-7, 8, 12), a sternal element (NMNH-P Ngr-14), a rib (NMNH-P Ngr-15), scapula fragments (NMNH-P Ngr-17) and a digit phalange (NMNH-P Ngr-18). Another portion was taken by E.Z. in 2010 and N.I. Udovichenko in 2011; it is housed in GMTSNUK and was described by Zvonok (2012): it includes seven teeth (GMTSNUK 15/1-7), a sternal element (GMTSNUK 15/8) and a rib (GMTSNUK 15/9); fragments from this portion, which have not been described before and were identified in the course of this study, are housed in NMNH-P and include a sternal element NMNH-P Ngr-13. The third portion was taken in 2012 by E.Z. and P.G.: it includes a tooth, mandible fragments, four vertebral centra, fragments of scapula and ribs and unidentified fragments (NMNH-P Ngr-1, 5, 6, 9, 10, 11, 16, 17). In total, the material includes mandible fragments, eleven teeth, seven vertebrae, three sternal elements, fragments of at least three ribs, scapular fragments and unidentified fragments. All the material was identified as belonging to the same individual, based on the following arguments: close arrangement of bones; their compatibility in size, ontogenetic age and bone suture fusion; no

visible traces of abrasion; and no duplicate elements. Nevertheless, there is a small probability that the bones belong to a few individuals.

We used the same taxa and characters for the phylogenetic analysis as in the original description of genus *Basilotritus* (Gol'din and Zvonok, 2013). We added the examined specimen to the matrix as GMTSNUK 15 (the character codings are provided in [Supplementary data](#)).

Heuristic parsimony analysis of the matrix was performed in TNT v. 1.1 (Goloboff et al., 2003). The “traditional search” option was used. Five most parsimonious trees with the length of 231 steps were generated. They were summarized using strict consensus trees with zero-length branches collapsed (Goloboff et al., 2003).

**Institutional abbreviations.** GMTSNUK, Geological Museum of Taras Shevchenko National University of Kiev, Ukraine; OU, Geology Museum, University of Otago, Dunedin, New Zealand; NMNH-P, Palaeontological Museum, National Museum of Natural History of the National Academy of Sciences of Ukraine, Kiev, Ukraine; USNM—United States National Museum, Washington DC, USA.

### 2.1. Geological setting

The site is located at a bank slope of the Kremenchug water reservoir (49°05'N, 33°08'E). Gray clays of the Kiev Formation (Upper Lutetian to Bartonian, after Zosimovich et al., 2005) are exposed above a bed of Precambrian crystalline rocks. Above gray clays, yellowish-green (the Munsell Color System value of the hue is 1GY–10GY) aleuritic sands or sandy aleurites probably representing the upper part of the Kiev Formation, are exposed with a well-defined boundary: their thickness is 2 m (visibly increasing to 10 m in southern direction), the roof is eroded. Boulders of crystalline rock are embedded in the layer. In the lower portion of this layer, there is dark-green highly glauconitic rock with high sand content and with numerous fish teeth and bones. On 0.8–1.2 m above the base of the layer, the content of glauconitic rock and sand falls, the rock colour becomes lighter, and the concentration of fish remains decreases: here, the cetacean bones were located. Above those, fish remains occur only rarely. A west-east oriented bulge of Precambrian crystalline rock extends 3 m north from this point. Vertebrate remains end up at the distance of 5 m from this bulge (Fig. 1). Udovichenko (2011) identified 35 shark species from this locality: the dominant taxa were *Scyliorhinus* sp., *Hemiscyllium bruxelliensis* Herman and Crochard, 1977, *Carcharias acutissimus* (Agassiz, 1844), *Clerolamna umovae* Zhelezko and Kozlov, 1999; based on the shark complex, he identified the geological age of the layer as Bartonian.

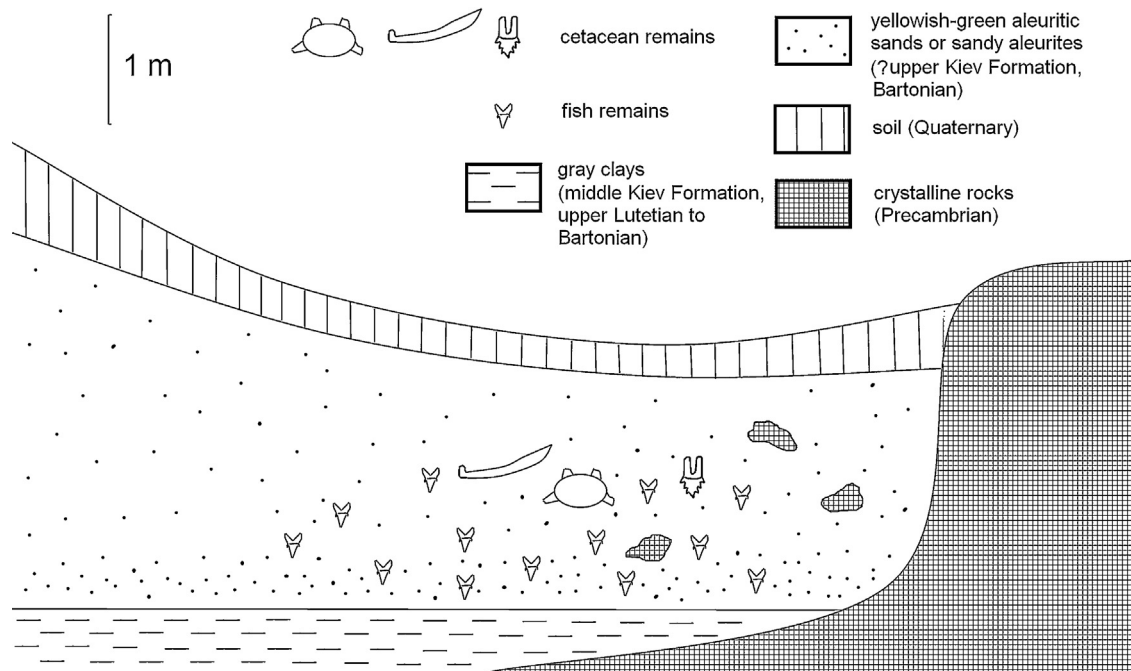


Fig. 1. Geological setting of Nagornoye site.

Fig. 1. Le site géologique de Nagornoye.

### 3. Systematic palaeontology

Cetacea [Brisson, 1762](#)

Pelagiceti [Uhen, 2008](#)

Family BASILOSAURIDAE [Cope, 1868](#)

Genus *Basilotritus* [Gol'din and Zvonok, 2013](#)

Type species: *Basilotritus uheni* [Gol'din and Zvonok, 2013](#).

*Basilotritus* sp.

Age and horizon: late Middle Eocene (Bartonian), upper Kiev Formation

[Figs. 2–6](#)

#### 3.1. Description

##### 3.1.1. Mandible

Preserved fragments of the ramus have a thick wall; layered compact tissue with 4 or 5 growth layers is seen in the periosteal zone at the cross-sections. A fragment identified as a condyle (NMNH-P Ngr-5) has been preserved. In posterior view, it is oval and has a thin neck.

##### 3.1.2. Teeth

Isolated upper and lower permanent teeth including incisors, canines, premolars and molars have been preserved ([Figs. 2 and 3](#)). The teeth are heavily worn. The enamel is finely striated longitudinally. All teeth positions in the tooth rows are identified tentatively. Some of the teeth were partly described by [Zvonok \(2012\)](#); here, we add to this description. Teeth measurements are provided in the [Supplementary data](#).

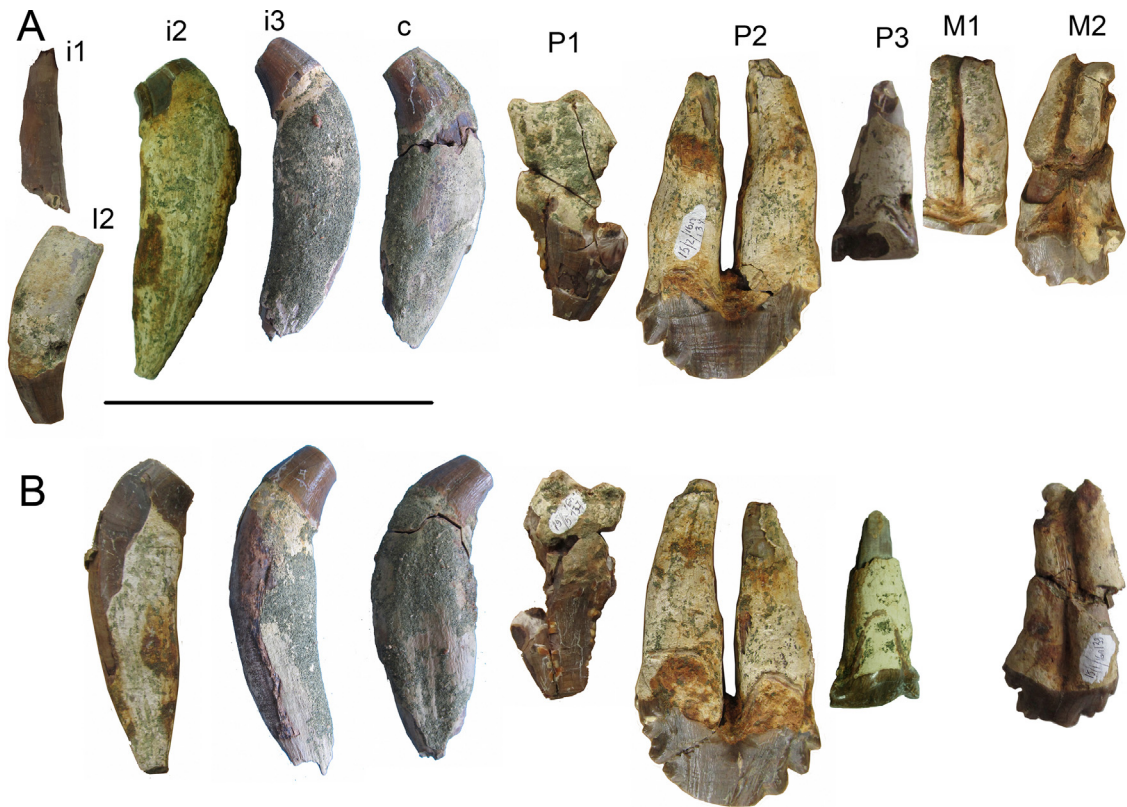
**Incisors.** Four incisors have been partly preserved. All preserved crowns are severely worn.

i2? (GMTSNUK 15/6): a root fragment and a worn crown, nearly ground off. The tooth is slightly curved: the angle between the longitudinal axes of the root and the crown is ca. 140°. There are no carinae on the crown. The root is straight, slightly transversely compressed and basally narrowing.

All the lower incisors are transversely compressed and bear carinae at the crowns. i1? (NMNH-P Ngr-1): a basally narrowing straight root, round at the cross-section. The pulp cavity is open; growth layers are seen at the cross-section. Right i2 (GMTSNUK 15/7): a crown and an incomplete root; there is a low carina at the anterior surface of the crown. Right i3 (NMNH-P Ngr-2): a long root with the greatest anteroposterior diameter (26 mm) in the distal portion. The angle between longitudinal axes of the root and the crown is ca. 130°. There is a low anterior carina at the crown.

**Lower canines** (NMNH-P Ngr-3, left, and NMNH-P Ngr-4, right) are substantially anteroposteriorly enlarged in comparison to the incisors (32 mm); there are longitudinal shallow grooves on the medial and lateral sides; anterior and posterior carinae are well developed; enamel is clearly longitudinally striated.

**Premolars.** P1? (GMTSNUK 15/5). A crown with a root fragment, transversely compressed. The crown has a worn apex. Anterior and posterior carinae are well developed; there are six tiny denticles in the basal portion of the posterior carina. The single root is lacking a vertical groove. The tooth is similar to a canine (e.g., an upper deciduous canine of *Dorudon atrox* [Andrews, 1906](#) [[Uhen, 2004](#): fig. 10]), and first, it was identified as such ([Zvonok, 2012](#)). However,



**Fig. 2.** Teeth of *Basilotritus* sp., NMNH-P Ngr 1-18 and GMTSNUK 15. A. Labial view. B. Lingual view. Scale bar equals 10 cm.  
**Fig. 2.** Dents de *Basilotritus* sp. NMNH-P Ngr 1-18 et GMTSNUK 15. A. Vue labiale. B. Vue linguale. Barre d'échelle = 10 cm.

it differs from other basilosaurid canines in its transverse flattened (rather than conical) shape and in the presence of accessory denticles on its distal carina.

P2 (GMTSNUK 15/2): two roots, the apex of the crown slightly worn. The tooth is strongly transversely compressed. Accessory denticles are wide and high (their width is 10–15% of the crown width, and the height is up to 25% of the crown height). Three denticles have been preserved on the anterior keel (one of them heavily worn); the principal denticle distal to them is totally worn. There are accessory tubercles, the denticles of the second order, on their anterior margins. Three denticles have been preserved on the posterior keel. They also bear faint tubercles. The cingulum is weakly developed in the middle portion of the tooth and well developed on the anterior and posterior margins where large prominent denticle-like tubercles are formed; their size is comparable with the basal accessory denticles of the crown keel. No protocone remnant is developed. The roots are robust; they approximate each other but are neither fused nor joint with an isthmus. Their basal ends narrow. The anterior root is longer than the posterior one. There is no rudiment of the third root.

P3 or P4? (GMTSNUK 15/4): one of two roots and a half-worn crown have been preserved. There is a large accessory denticle near the crown base. A cingulum with a small cusp-like prominence basal to the accessory denticle is developed.

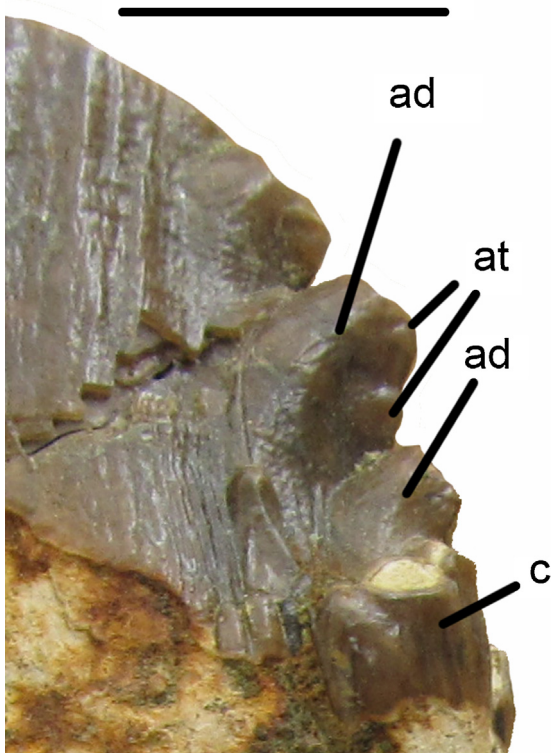
**Molars.** Two upper molars have been preserved. M1 (GMTSNUK 15/3): the crown is almost grounded off. A short and robust cingulum has been preserved near its base. Straight roots come close to each other but do not fuse. The anterior root is slightly thicker than the posterior one. M2 (GMTSNUK 15/1): the principal denticle of the crown has been worn. The lateral crown profile is round. Two denticles are situated on both anterior and posterior crown margins. The low cingulum is equally developed around the crown. There is no protocone. The roots (with a lifetime trauma trace) are fused; there is no remnant of the third root.

### 3.1.3. Vertebrae

**Cervical vertebrae.** Three cervicals have been partially preserved, two of them represented by centra, and one by centrum and partial transverse processes. They were identified as C4, C5 and C7 (Fig. 4). Epiphyseal plates are not fused with the centra except for C4, in which the anterior epiphysis nearly completed its fusion. Measurements of vertebrae are listed in the [Supplementary data](#).

C4 (NMNH-P Ngr-6): the centrum is oval (in anterior view, sub-rectangular), transversely widened, slightly flattened at the dorsal surface. The base of the diapophysis is 1.2–1.3 times higher than that of the parapophysis; there is a medium-sized vertebral foramen between them (the maximum width is 11 mm), and the anterior portion of the foramen is situated higher than the posterior one. The foramen contacts the centrum and forms a canal on its





**Fig. 3.** Premolar of *Basilotritus* sp., GMTSNUK 15/2, details of the crown anatomy. Abbreviations: ad, accessory denticle; at, accessory tubercles (denticles of the second order); c, cingulum.

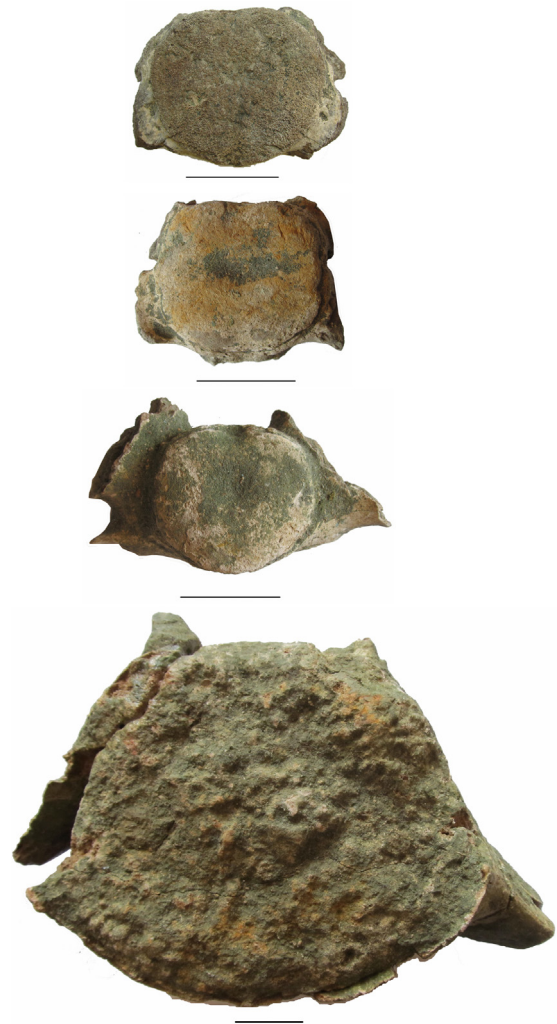
**Fig. 3.** Prémolaire de *Basilotritus* sp., GMTSNUK 15/2, détail de l'anatomie de la couronne. Abréviations : ad, denticules accessoires; at, tubercules accessoires (denticules de second ordre); c; cingulum.

lateral surface. There is a low ridge on the dorsal side and a low ridge with a pair of vascular foramina and two fossae lateral to it on the ventral side.

C5 (NMNH-P Ngr-7): in anterior view, the centrum is rounded with the flattened dorsal surface. Parapophyses are 1.5 times higher at the bases than diapophyses; they are ventrolaterally directed. Vertebral arterial foramina are the same as in C4.

C7 (NMNH-P Ngr-8): in anterior view, the centrum is round. The transverse processes are anteroposteriorly thin; the bases of diapophyses and parapophyses are fused lateral to the centrum, thus, vertebral arterial foramina are separated from the centrum. The bases of the transverse processes are anteriorly bent. The bases of the diapophyses are twice as high as those of the parapophyses. The dorsal ridge on the centrum is wide, the ventral one is low, with deep vascular foramina.

**Thoracic vertebrae.** TA (NMNH-P Ngr-9) is an anterior (possibly, T4 or T5) thoracic vertebra. In dorsal view, the centrum is rectangular; in lateral view, it is dumbbell-shaped. The surface is covered by numerous small vascular foramina, typical for *Basilotritus* (Gol'din and Zvonok, 2013). TB (NMNH-P Ngr-10) is a middle thoracic vertebra (possibly, T8 or T9); in anterior view, the centrum is rounded and angular; bases of the transverse processes are robust. TC (NMNH-P Ngr-11) (tentatively, T10 or T11): in



**Fig. 4.** Vertebrae of *Basilotritus* sp., NMNH-P Ngr 1-18, anterior view: C4, C5, C7, LA. Scale bars equal 5 cm.

**Fig. 4.** Vertèbres de *Basilotritus* sp., NMNH-P Ngr 1-18, vue antérieure: C4, C5, C7, LA. Barre d'échelle = 5 cm.

dorsal view, the centrum is trapezium-shaped; the posterior surface is far wider than the anterior one. In addition, fragments of centra and processes of a few small-sized anterior thoracic vertebrae were found.

**Lumbar vertebra** (NMNH-P Ngr-12). In dorsal view, the centrum is trapezium-shaped; in lateral view, it is dumbbell-shaped, and in anterior view, it is rounded. The ridge on the dorsal side of the centrum is weakly developed. Transverse processes are ventrolaterally directed; in anterior view, their bases are located just ventrally from the level of the middle of the centrum. The processes are pachyosteosclerotic. Layered tissue is clearly seen at the cross-sections of neural arches and transverse processes: five layers are counted in the periosteal zone. Separate fragments of large metapophyses and transverse processes of a few lumbar vertebrae have also been preserved.



**Fig. 5.** Sternum of *Basilotritus* sp., NMNH-P Ngr 1-18 and GMTSNUK 15, ventral view. Scale bars equal 5 cm.

**Fig. 5.** Sternum de *Basilotritus* sp., NMNH-P Ngr 1-18 et GMTSNUK 15, vue ventrale. Barre d'échelle = 5 cm.

### 3.1.4. Sternum

**Mesosternal element 1** (NMNH-P Ngr-13) is dorsoventrally flattened (minimum thickness is 15 mm, and the length, as preserved, is 80 mm); only its right half has been preserved. In ventral view, it is nearly oval, with a flat anterior side, as reconstructed. The anterior end is straight, without a trace of cartilaginous articulation. In lateral view, the bone is equally slightly concave on the dorsal side. There are notches for rib attachment at the lateral surfaces of the anterior end. This element is similar in shape to a manubrium of basilosaurids and neocetes; its smooth anterior surface indicates the lack of cartilaginous articulation with another anteriorly located element. However, this bone differs from all basilosaurid (including *Basilotritus wardii*), neocete and protocetid manubria in the lack of dorsal concavity of the anterior portion, which usually forms a 30° angle in lateral view. In addition, sternal elements of crown basilosaurids (*Basilosaurus*, *Dorudon*) were similarly loosely joined. Finally, a narrow element fits an intermediate position between a narrow manubrium (like in *Basilotritus wardii*) and a wide mesosternal element 2. Based on this, we identify this fragment as the mesosternal element 1 (Fig. 5).

**Mesosternal element 2** (GMTSNUK 15/8) is a dorsoventrally flattened bone. The rectangular anterior portion is transversely wider than the posterior one. The anterior and posterior margins are straight; their surfaces are rugose. There are notches for rib attachment on lateral surfaces, nearly at the anterior third of the bone.

**Xiphisternum** (NMNH-P Ngr-14) is anteroposteriorly elongated, slightly dorsally concave, and distally narrowing. In ventral view, it is dumbbell-shaped. The anterior margin is straight; its surface is rugose (indicating a cartilaginous articulation). The posterior end is bifurcated (the margin is broken).

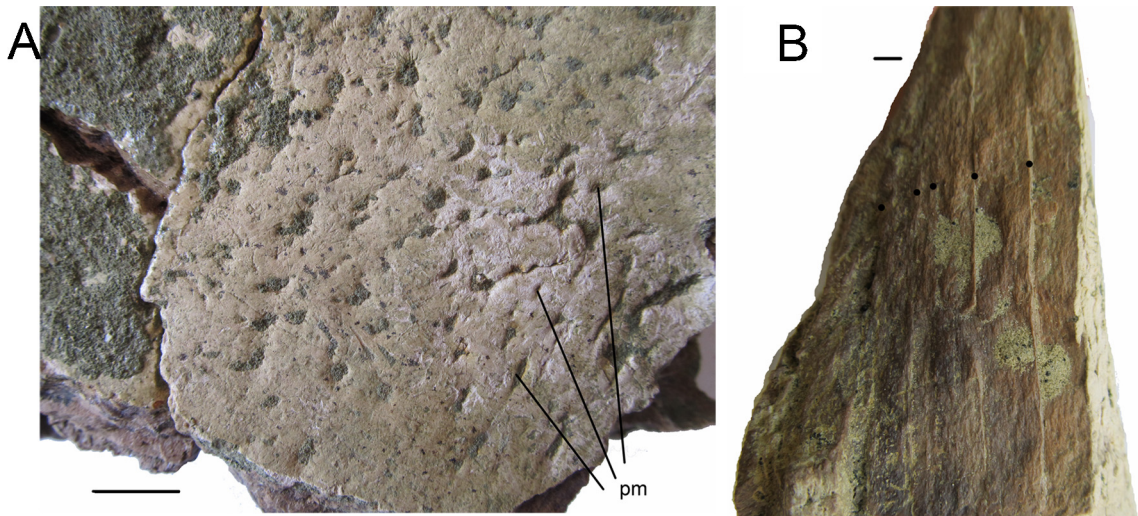
### 3.1.5. Ribs

The ribs were identified based on similarity with *Zygorhiza kochii* Reichenbach in Carus et al., 1847 (Kellogg, 1936: Plate 17). The 2nd rib (NMNH-P Ngr-15) is represented by the head and the fragment of the sternal rib. The distance between capitulum and tubercle is 52 mm. The 4th rib (GMTSNUK 15/9; Zvonok, 2012: Plate 2, Fig. 2) is 56 cm long. The capitulum is 90° directed to the longitudinal rib axis. The distance between capitulum and tubercle is 20 mm. There is a distal expansion giving the rib a paddle-like shape. The 6th rib (NMNH-P Ngr-16) is represented by at least three fragments, 46 cm the longest; it differs from the anterior ribs in round (rather than angular) cross-sections. More than 20 fragments of other ribs were found as well. Layered compact tissue is seen at oval or round cross-sections; it occupies the most part of the rib. The layering patterns differ depending on rib and area: spongy tissue can be found in the centre of the rib, as well as off-centre shifted.

### 3.1.6. Forelimb

**Scapula** (NMNH-P Ngr-17) preserved as numerous fragments. The bone is fan-shaped, relatively thick in the middle portion, with a vast thin outer margin.





**Fig. 6.** Details of the vertebral anatomy of *Basilotritus* sp., NMNH-P Ngr-12. A. Pock-marked surface of a lumbar vertebra. B. Growth layers in a vertebral neural arch (right is the lateral margin). Scale bars equal 1 cm. Abbreviations: pm, pock marks.

**Fig. 6.** Détail de l'anatomie vertébrale de *Basilotritus* sp. NMNH-P Ngr-12. A. Surface grêlée sur une vertèbre lombaire. B. Feuillet de croissance sur un arc neural vertébral (à droite, la marge latérale). Barre d'échelle = 1 cm. Abréviations : pm, marques.

**Proximal phalanx** II-1, III-1 or IV-1 (NMNH-P Ngr-18): the proximal portion has been preserved; it is thickened at the end, oval at the cross-section. The palmar surface is flat with a longitudinal groove.

#### 4. Discussion

##### 4.1. Geological age

The cetacean from Nagornoye is suggested to be of the same age as two specimens of *Basilotritus uheni* from Beloskelevatoye and Kurenevka, both originating from the Kiev Formation (Bartonian), and also possibly as old as the specimen from the “Kharkov stage” of Tsimlyansk, the Late Bartonian (Kalmlykov, 2012; Tesakov et al., 2012). Records from Vlasovka and Velykaya Andrusovka can be dated as the same age (Gol'din and Zvonok, 2013). Thus, all recent Ukrainian and Russian records of genus *Basilotritus* and cetaceans related to it are tentatively dated as Bartonian. The age of these records is older than of the most of the basilosaurids from the North America and Egypt (Uhen, 2013). However, it is somewhat younger than vertebrae of *Basilotritus* sp. from the Lower Bartonian of Egypt (Uhen, 1999) and it is close to the age of *Basilotritus wardii* from USA (Uhen, 2013; Weems et al., 2011), *Supayacetus* Uhen et al., 2011 and *Ocucajea* Uhen et al., 2011 from Peru and *Zygorhiza* sp. (OU 22100, 22221, 22222, 22242) from Waihaio, New Zealand (Köhler and Fordyce, 1997).

##### 4.2. Comparison and phylogeny

The cetacean from Nagornoye is a member of Pelagiceti (the clade including Basilosauridae and Neoceti), because it has premolars and molars with additional cusps, relatively short cervical vertebrae and a fan-shaped scapula. It is a member of the genus *Basilotritus* or closely related to it

because it has anteroposteriorly elongated pachyosteosclerotic transverse processes and neural spines of vertebrae, which contain layered compact tissue; anteroposteriorly elongated centra of lumbar vertebrae; and a pock-marked surface of the vertebrae with numerous small vascular foramina (Fig. 6A). No genera closely related to *Basilotritus* have been described by now, except *Platyosphys* Kellogg, 1936, but the type specimen of its type species, *Platyosphys paulsonii* Brandt, 1873, was not described sufficiently and now it is lost; thus, its identification is impossible, and we consider its name as nomen dubium (see Gol'din and Zvonok, 2013). The relation of the cetacean from Nagornoye to *Basilotritus uheni* is unclear, because no complete neural arches, necessary for species identification, are preserved; however, the body sizes of the cetacean from Nagornoye and *Basilotritus uheni* are quite similar and far larger than *B. wardii*. Thus, we classify the cetacean from Nagornoye as *Basilotritus* sp., Basilosauridae. The record of the specimen of *Basilotritus* with evident Pelagiceti traits (first of all, teeth with accessory cusps) confirms the identification of this genus as a member of early basilosaurids rather than protocetids (Gol'din and Zvonok, 2013), which was previously based on anatomy of the tympanic bulla.

**Teeth** as a whole are characterized by advanced basilosaurid features: differentiated incisors (small first incisors and long-rooted posterior lower incisors); a large number of moderately wide (not palmate) and relatively high accessory cusps (denticles) on premolars and molars; lack of protocones on cheek teeth. The accessory cusps of the second order on the denticles of anterior keel of P2 (Fig. 3) are an advanced autopomorphy, whereas the inflated cheek teeth roots approximating each other are a primitive feature shared by *Georgiacetus vogtlenis* Hulbert et al., 1998 and early neocetes, but lost in advanced basilosaurids. Crenelated cingulum with cusps near the crown base, close to the basal crown accessory denticles,

is the trait shared by *Zygorhiza kochii*, *Zygorhiza* sp. from Waihao and, for some extent, by *Chrysocetus healyorum* Uhen and Gingerich, 2001; i.e., it is common for a small basilosaurid group and possibly inherited from a primitive common ancestor.

**Cervical vertebrae** present the combination of plesiomorphic and apomorphic basilosaurid traits. Advanced traits are: loss of hexagonal shape of C4 (in comparison with *Georgiacetus vogtlensis* and *Zygorhiza* sp. from Hulbert, 1998; Köhler and Fordyce, 1997); extension of bases of parapophyses on lower portions of their centra and their thinness; somewhat enlarged vertebralarterial foramina (a trait shared by *Basilosaurus*, *Cynthiacetus* and *Saghacetus*). The primitive trait is the transverse elongation of centra (the most developed in a rectangular C4). In general, the cervicals are most similar to *Zygorhiza kochii* (e.g., USNM 4678 and USNM 4680). The thoracic and lumbar vertebrae have the autapomorphous features of *Basilotritus* and the related taxa, and they resemble *B. uheni* in shape and size, but differ in proportions from other basilosaurid records from Ukraine.

**Sternum.** The manubrium was not found: it could be T-shaped, like in *B. wardii* (Uhen, 2001: Fig. 7A–B) and *Supayacetus muizoni* (Uhen et al., 2011: Fig. 7–7,8). The mesosternum is presented by at least two elements, one of which is nearly identical to that of *B. wardii* (Uhen, 2001: Fig. 7); the mesosternum is similar to other basilosaurids in its dorsoventral flatness. However, it differs from most basilosaurids in plesiomorphic traits: its elements are narrow and long, and there is an extension with the surfaces for the rib attachment in the anterior portion of each. The xiphisternum is identical to that of *Dorudon atrox* (Uhen, 2004: fig. 73), and differs from the wider, flatter and not bifurcated xiphisternum of *Cynthiacetus maxwelli* (Uhen, 2005: Fig. 6D–E) and from the wider and anteriorly angular bone of *B. isis* Andrews, 1904 (Stromer, 1908: pl. 6, Fig. 4) and anteriorly angular bone of *Saghacetus osiris* Dames, 1894 (Stromer, 1908: pl. 5, fig. 23).

Thus, the cetacean from Nagornoye shows a mixture of primitive and advanced basilosaurid features implying its intermediate position between the Bartonian early pelagicetes, which are now referred to as basilosaurids (*Ocucajea*, *Zygorhiza* sp. from Waihao, *Supayacetus*) and the basilosaurids sensu stricto (first of all, *Zygorhiza*).

The results of the phylogenetic analysis (Fig. 7) demonstrate that the cetacean from Nagornoye falls within the same clade as the previously reported specimens of *Basilotritus* and MUSM 1443 from Peru (Uhen et al., 2011), which is close to the base of basilosaurid phylogeny, between *Supayacetus* and *Zygorhiza* (see also Gol'din and Zvonok, 2013). This confirms the identification of this specimen as a representative of *Basilotritus* or a closely related genus.

#### 4.3. Age, growth and tooth wear

Age identification using growth layers in the compact bone tissue of the periosteal zone is a widespread method applied for many tetrapods. Normally, the number of complete layers (growth layer groups, GLG) corresponds to age in years. In extant cetaceans, growth layers in mandible and

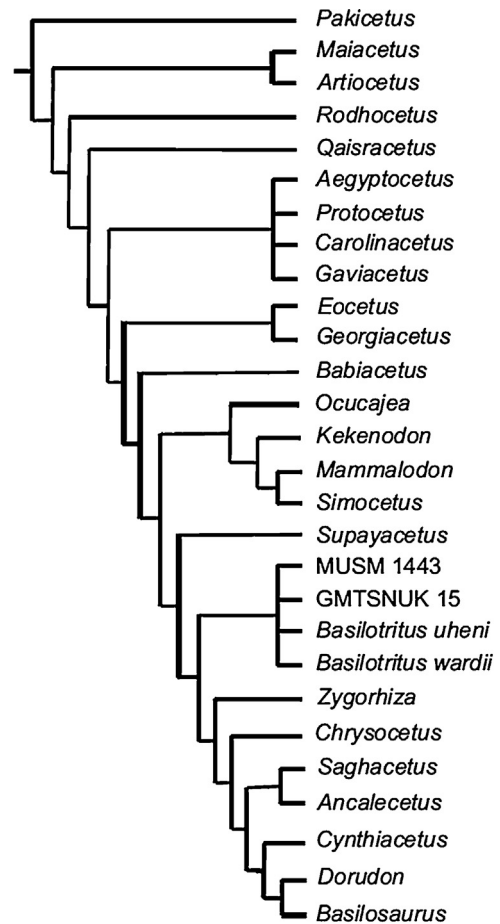
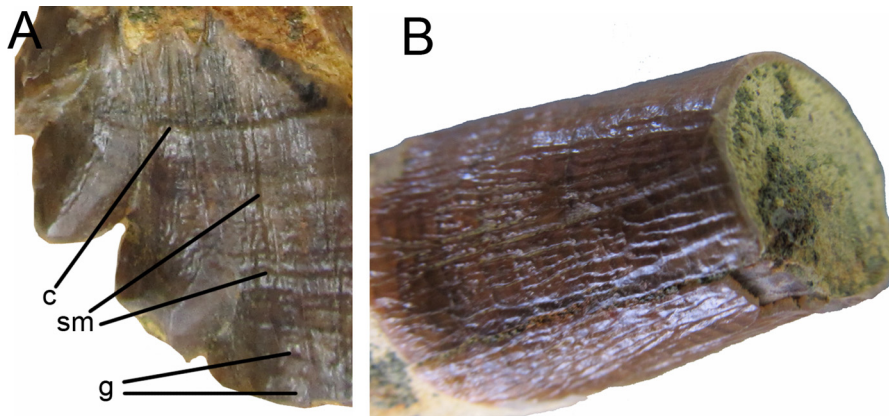


Fig. 7. Phylogeny of Basilosauridae, strict consensus tree arising from the phylogenetic analysis.

Fig. 7. Phylogénie des Basilosauridae, arbre de strict consensus issu de l'analyse phylogénétique.

tympenic bulla were used for age determination (Buffrénil et al., 2004; Christensen, 1981; Gol'din, 2001; Klevezal and Kleinenberg, 1962); similar layers were found in pachyosteosclerotic ribs of basilosaurids (Buffrénil et al., 1990). Based on a large number of representative fragments with layered compact tissue (mandible, processes of vertebrae, ribs) found in Nagornoye, one could identify its individual age as 5 years (Fig. 6B). However, it has the unfused epiphyses of the vertebral centra not only in the thoracic and lumbar but also in the cervical vertebrae, which show that it was far from physical maturity. Thus, the rate of the vertebral ossification in the cetacean from Nagornoye was substantially slower than in extant cetaceans (both baleen and toothed whales), in which the cervical epiphyses normally fuse first of all, in early postnatal ontogenesis (Galatius and Kinze, 2003; Ohsumi et al., 1958). Combined with the large body size and pachyosteosis in many bones, this trait is the evidence for an ontogenetic trajectory following paedomorphosis, namely neoteny (Alberch et al., 1979; Ricqlès and Buffrénil, 2001). In addition, the cetacean from Nagornoye has heavily worn permanent teeth; however, as Loch and Simões-Lopes (2013) note, this trait





**Fig. 8.** Tooth wear marks in *Basilotritus* sp., NMNH-P Ngr 1-18 and GMTSNUK 15. A. P2. B. i2. Scale bars equal 1 cm. Abbreviations: c, cingulum; g, gouges; sm, scratch marks

**Fig. 8.** Marques d'usure dentaire chez *Basilotritus* sp. NMNH-P Ngr 1-18 et GMTSNUK 15. A. P2. B. 12. Barres d'échelle = 1 cm. Abréviations : c, cingulum ; g, creux ; sm, marques de rayure.

weakly correlates with body size or age in extant whales. Thus, neither epiphyseal fusion, nor teeth wear can be a reliable indicator of individual age in this case. Definitive body size of the cetacean from Nagornoye depends on the pattern of development of its growth curve: it could be similar to that of extant baleen whales, in which the body size attains its asymptotic values at early age (far before physical maturity), or alternatively, it could resemble that of killer whales, in which the growth lasts until 15–20 years (Best et al., 2010).

The tooth wear pattern in the cetacean from Nagornoye provides a clue to its diet. Thewissen et al. (2011) found three types of the tooth wear in archaeocetes: abrasion leading to apical wear, wear after the Phase I of jaws contact (longitudinal scratches on the buccal side of the upper teeth and on the lingual side of the lower teeth), wear after the Phase II of jaws contact (scratches on the lingual side of the upper teeth and on the buccal side of the lower teeth). They showed that *Babiacetus* was lacking the traces of the Phase II and demonstrated strong apical abrasion that can be explained by its suggested carnivorous diet. Fahlke et al. (2013) noted that carnivorous cetaceans *B. isis* and the killer whale have a distinctly coarse pattern of tooth wear: not only scratches, but also numerous gouges are seen in enamel microwear. Extant piscivorous toothed whales have longitudinal and cross-oriented marks.

The cetacean from Nagornoye shows abrasion marks owing to both Phases I and II (Fig. 8A), presented by longitudinal and cross-oriented scratches and few gouges. The gouges make it similar to *Basilosaurus*, and the absence of Phase II traces resembles *Zygorhiza*. However, the main specific feature of these teeth is their unusually strong apical abrasion affecting all teeth, from incisors to molars. The canine is the least abraded tooth. This apical abrasion is characterized by uniform wear, smooth margins of wear surface and strict perpendicularity of wear plane to the long axis of the crown (Fig. 8B). Such an unusually rapid apical teeth abrasion in killer whales is a result of feeding on objects with hard covers, for example, sharks with placoid scales (Ford et al., 2011). In this connection,

it is notable that the cetacean from Nagornoye was found together with exceptionally abundant shark teeth (Udovichenko, 2011). We consider the specific pattern of tooth wear in this cetacean to be an indicator of its specialized feeding on sharks.

## 5. Conclusions

*Basilotritus* from Nagornoye is an early basilosaurid combining primitive and advanced traits of the family. Its closest relatives are *Supayacetus* and *Zygorhiza*. *Basilotritus* is characterized by neotenic trajectory of development, with a large body size and slow skeletal maturation. Its distinct pattern of tooth wear is hypothesized to indicate specialized feeding on sharks.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.crpv.2013.11.002>.

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