BRANDTOCETUS, A NEW GENUS OF BALEEN WHALES (CETACEA, CETOTHERIIDAE)
FROM THE LATE MIOCENE OF CRIMEA, UKRAINE

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ABSTRACT—A new cetotheriid baleen whale, Brandtocetus chongulek, gen. et sp. nov., is described from the late Miocene of Crimea, Ukraine. The type series is represented by three partial skulls with periotic bones and tympanic bullae, one of the three belonging to a juvenile. Brandtocetus chongulek has transversely expanded squamosals, ‘S’-shaped nuchal crests, an anterior margin of the occipital shield extending anterior to the center of the temporal fossa, and an elongated posterior process of the tympanoperiotic. The tympanoperiotic and postglenoid process of the squamosal are typical of cetotheriines (as opposed to herpetocetes). Comparison of the juvenile specimen with adults shows no differences in tympanoperiotic anatomy, moderate squamosal growth, and significant growth of the neurocranium after the age of at least 1 year. The phylogenetic analysis including 13 cetotheriids supports the monophyly of Cetotheriidae sensu stricto and suggests the monophyly of whales from the Eastern Paratethys (Brandtocetus, Cetotherium, Kuralagonus, and possibly Eucetotherium). Brandtocetus and other cetotheriids from the Black Sea region possess cranial features hypothesized to be adaptations to a generalized filter feeding strategy combining different modes of suction feeding.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION
Baleen whales of the extinct family Cetotheriidae (sensu Boulet and Muizon, 2006; Steeman, 2007; Whitmore and Barnes, 2008; Kimura and Hasegawa, 2010; Steeman, 2010; Fordyce and Marx, 2012; Gol’din et al., in press) were widely distributed in the late Neogene. Their range included the eastern Paratethys, the area of present-day Black and Caspian Seas: Cetotherium Brandt 1843, the nominative genus with the type species Cetotherium rathkii Brandt, 1843, was described from this region. For decades, all late Miocene baleen whales found near the Black Sea have been referred to as Cetotherium. A number of species have been described from the late middle and early late Miocene (middle and late Sarmatian age sensu lato) of the northern Black Sea region (Fig. 1): Cetotherium incertum Brandt, 1873; Cetotherium klinderi Brandt, 1871; Cetotherium maicopicum Spassky, 1951; Cetotherium mayeri Brandt, 1871; Cetotherium prisum Eichwald, 1840; Cetotherium pusillum Nordmann, 1860; Cetotherium riabinini Hofstein, 1948; and a few unnamed cetaceans (Riabinin, 1931, 1934; Spassky, 1951, 1954; Mchedlidze, 1964). Of them, only Cetotherium riabinini is identified as a member of the genus Cetotherium (Gol’din et al., in press). Tarasenko and Lopatin (2012a) described a new genus Kuralagonus with two new species and included Cetotherium maicopicum into it. Kellogg (1931) identified Eucetotherium helmerseni (Brandt, 1871) as the type species for genus Eucetotherium. Tarasenko and Lopatin (2012b) described a new species named Vampalus sayasanicus and argued it to be congeneric with Eucetotherium helmerseni; in this case Vampalus would be a junior synonym for Eucetotherium. Two other genera of middle Miocene baleen whales from Caucasus were earlier described by Gurami Mchedlidze: Imerocetus Mchedlidze, 1964, from the Karagayan (= Badenian) and Otradnocetus Mchedlidze, 1984, from the middle Miocene. However, described taxa do not represent the total diversity of cetotheriids and other Neogene baleen whales of the eastern Paratethys. Here we describe a new genus of Cetotheriidae based on newly discovered material from the late Miocene of Kerch Peninsula in Crimea (Ukraine).

Institutional Abbreviations—MNHN, Muséum National d’Histoire Naturelle, Paris, France; NMNH-P, Academician V. A. Topachevsky Paleontological Museum of the National Museum of Natural History of the National Academy of Sciences of Ukraine, Kiev, Ukraine; NMRA, National Museum of the Republic of Adygeya, Maikop, Russia; NUMMRU, National University of Mineral Resources ‘Mining University,’ St. Petersburg, Russia; TNU, Department of Zoology, Taurida National University, Simferopol, Ukraine.

Measurements and Terminology—Skull measurements are provided in Table 1. The measurements of paired or bilaterally symmetrical structures were taken from the left side. Anatomical terminology generally follows Mead and Fordyce (2009). For the tympanoperiotic region, we also included terms from Geisler and Luo (1996), Mead and Fordyce (2009), Steeman (2010), and Ekdale et al. (2011). Body length estimates were calculated from the regression proposed by Lambert et al. (2010:suppl. fig. 9): y = 8.209x + 66.69, where x is bizygomatic width of the skull and y is body length.

SYSTEMATIC PALEONTOLOGY
CETACEA Brisson, 1762
MYSTICETI Flower, 1864
CETOTHERIIDAE Brandt, 1872

Remarks—Included genera (following the emended diagnosis of the family and related discussion in Gol’din et al., in press): Cetotherium Brandt, 1843; Cephalottrops Cope, 1896; Eucetotherium Kellogg, 1931; Herpetocetus Van Beneden, 1872; Joumocetus Kimura and Hasegawa, 2010; Kuralagonus Tarasenko and Lopatin, 2012a; Metopocetus Cope, 1896; Mixocetus Kellogg, 1934; Nannocetus Kellogg, 1929; Piscobalaena

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fers from all cetotheriids except
exposed as an oval surface on the posterolateral skull wall. Dif- fers from all cetotheriids (in which the diagnostic traits have
progressed and double-bladed, as in
Kurdalagonus
Van Beneden, 1859, with cetotheriids cannot currently be
demonstrated, because the holotype is unavailable for study (see
Steeman, 2010). The status of the genus
Vampalus, as well as taxo-
mony and phylogenetic relationships of
Vampalus sayasanicus,
requires further study. A possible relationship of neobalenids to
ceto"heriids (Fordyce and Marx, 2012) is under debate (Bisconti
et al., 2013).

BRANDTOCETUS CHONGULEK, gen. et sp. nov.

(Figs. 2–9)

Holotype—TNU Skull A, partial skull with peri"otic bones and
partly preserved tympanic bullae, lacking rostrum.
Paratypes—TNU Skull 2, partial skull (basicranium with
squamosal and peri"otic bones) and tympanic bullae; TNU Skull 4,
skull fragments of a juvenile specimen including tympanic bullae
and right peri"otic bone.

Diagnosis—A cetotheriid whale approximately 4–5 m long dif- fering from all cetotheriids (in which the diagnostic traits have
been preserved) by having a transversely expanded lateral portion
of the squamosal; a rhomboid temporal fossa; an occipital
shield extending anterior to the center of the temporal fossa;
and an elongated posterior process of the tympanoperiotic with
a proximodistally extended, and distally expanded, distal portion
process of the squamosal bone. TNU Skull 2 and TNU Skull 4
were found in a block of calcareous siltstone with
preserved posterior portions of the rostral bones. TNU Skull
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FIGURE 1. Main records of Miocene baleen whales from the northern Black Sea region. A, type localities. 1, Kishinev, Moldova, middle Sar- matian s.l. (Cetotherium pusillum, Cetotherium klinkeri); 2, Nikolaev, Ukraine, late Sarmatian s.l. (Cetotherium rhabditis); 3, Kerch Peninsula, Ukraine, late Sarmatian s.l. (Cetotherium mayeri, Brandtocetus chongulek); 4, Pekla (Pekly) Cape, Russia, middle Sarmatian s.l. (Eucetotherium helmersenii); 5, Zhelezny Roq Cape, Russia, late Sarmatian s.l. (Cetotherium rathkii); 6, Malkop, Russia, middle Sarmatian s.l. (Cetotherium maicop- icus, Kuralagonus mchedlidz’e) and late Sarmatian s.l. (Kuralagonus adygeicus); 7, Otradnaya, Russia, middle Miocene (Otradnocetus virodovi); 8, Djla"urtu, Georgia, Karaganian (Imerocetus karanagicus); B, records of Brandtocetus chongulek, gen. et sp. nov. +, TNU Skull A; *, TNU Skull 2 and TNU Skull 4.
TABLE 1. Measurements (mm) of *Brandtocetus chongulek*, TNU Skull A, TNU Skull 2, and TNU Skull 4; *Kurdalagonus mchedlidzei*, NMRA 10476/1; and *Cetotherium riabinini*, NMNH-P 668/1.

| Measurement                                                                 | TNU Skull A | TNU Skull 2 | TNU Skull 4 | Kurdalagonus mchedlidzei | Cetotherium riabinini |
|----------------------------------------------------------------------------|-------------|-------------|-------------|-------------------------|----------------------|
| Body length                                                                | 409 cm*     | 393 cm*     | 312 cm*     | 308 cm*                 | 297 cm               |
| Zygomatic width                                                            | 490 cm*     | 470 cm*     | 372 cm*     | 367 cm                   | 326 cm               |
| Length of neurocranium (measured from the transverse line joining the      | 295 cm      | 295 cm      | 295 cm      | 295 cm                   | 295 cm               |
| antorbital notches to the occipital condyle)                               |             |             |             |                         |                      |
| Length of nasal                                                            | 84          | 50+         | 72          |                         |                      |
| Distal width of nasal                                                     | 18          | 18          | 18          | 10                      | 10                   |
| Greatest width of nares                                                   | 360 cm      | 360 cm      | 360 cm      | 360 cm                   | 360 cm               |
| Distance between the posterior margin of nasal and anterior-most point of | 42          | 30          | 37          |                         |                      |
| occipital shield                                                          |             |             |             |                         |                      |
| Anteroposterior length of parietal exposure on skull vertex                | 15          | 15          | 15          | 19                      | 19                   |
| Skull width across preorbital processes of the frontals                   | 265         | 265         | 265         | 246                     | 246                 |
| Skull width across postorbital processes of the frontals                  | 321         | 321         | 321         | 294                     | 294                 |
| Anteroposterior length of orbit                                           | 130         | 130         | 130         | 130                     | 130                 |
| Minimum intertemporal width                                               | 114         | 114         | 114         | 105                     | 105                 |
| Greatest length of temporal fossa                                         | 118 cm      | 81         | 81          | 81                      | 81                  |
| Greatest width of temporal fossa                                          | 147 cm      | 120 cm     | 120 cm      | 120 cm                   | 120 cm              |
| Distance between tip of zygomatic process and tip of postglenoid process  | 233         | 233         | 233         | 233                     | 233                 |
| Width between posterior-most points of paroccipital processes             | 216         | 216         | 216         | 216                     | 216                 |
| Distance between the dorsal margin of foramen magnum and anterior-most    | 142         | 129         | 115 cm      | 115 cm                   | 115 cm              |
| point of occipital shield                                                 |             |             |             |                         |                      |
| Distance between outer posterior margins of nuchal crests                  | 234         | 215 cm     | 240         | 240                     | 240                 |
| Width of foramen magnum                                                   | 42          | 40 cm      | 54 cm       | 54 cm                    | 54 cm               |
| Height of foramen magnum                                                  | 56          | 56         | 44          | 44                      | 44                  |
| Bicondylar width                                                          | 116         | 95 cm      | 145 cm      | 145 cm                   | 145 cm              |
| Condylar height                                                           | 79          | 70 cm      | 67          | 67                      | 67                  |
| Distance between medial margins of foramina pseudovale                    | 139         | 140        | 72 cm       | 100                     | 100                 |
| Distance between lateral margins of basioccipital crests                  | 106         | 101        | 74          | 74                      | 74                  |
| Width between posterior-most points of postglenoid processes              | 270 cm      | 262        | 222 cm      | 243                     | 243                 |
| Greatest height of neurocranium                                           | 140         | 140 cm     | 138         | 138                     | 138                 |
| Greatest inner length of brain cavity                                     | 140 cm      | 140 cm     | 150 cm      | 150 cm                   | 150 cm              |
| Length of pars cochlearis                                                 | 29          | 29         | 29          | 23                      | 23                  |
| Height of pars cochlearis                                                 | 19          | 20         | 19          | 19                      | 19                  |
| Length of anterior process of periatic                                     | 29          | 30         | 28          | 28                      | 28                  |
| Length of posterior process of tympanoperiotic                            | 86          | 71         | 57          | 57                      | 57                  |
| Length of tympanic bulla                                                  | 59          | 65         | 51          | 51                      | 51                  |
| Maximum width of tympanic bulla                                           | 43          | 46         | 37          | 37                      | 37                  |
| Posterior width of tympanic bulla in medial view                          | 32          | 35         | 25          | 25                      | 25                  |

* e, estimated value; +, minimum value, measured as preserved; *, calculated following Lambert et al. (2010).

2 is a basicranium with associated tympanic bullae. Both skulls belong to adult individuals: many sutures between the bones are completely fused. However, many sutures are also obscured because both skulls are covered with hard sediment. TNU Skull 4 belongs to a juvenile animal; its squamosal sutures are unfused. It is represented by fragments: a right squamosal with a broken zygomatic process, a left glenoid portion of the squamosal, a right pterygoid, both incomplete pterygoids, a basioccipital with a basisphenoid and both alisphenoids, an incomplete presphenoid, incomplete frontals, both tympanic bullae, and unidentified fragments.

**Premaxilla**—Posterior portions of the premaxillae were badly eroded, thus their shape is unknown. The premaxilla terminates at the same level as the posterior margin of nasal.

**Maxilla**—In dorsal view, the ascending process tapers towards its apex. Its lateral margin is concave posterolaterally. Its medial margin cannot be traced, so it is unclear whether the ascending process overlapped the posterior portion of the premaxilla. The apices of the processes approximated each other posterior to the nasals or even possibly converged over a short distance. The angle between the lateral margins of the ascending processes is at least 120° (Fig. 2).

**Nasal**—The nasal is a long and high triangular bone gradually narrowing posteriorly, and is not overlapped by the ascending process of the maxilla. Its posterior margin is at the same level as the anterior edge of the temporal fossa. The nasals are not sagittally keeled and not medially pointed: their anterior margins form a straight line.
FIGURE 2. Dorsal views of the skulls of *Brandtocetus chongulek*, gen. et sp. nov. **A**, holotype, TNU Skull A; **B**, paratype, TNU Skull 2; **C**, line drawing. Scale bar equals 10 cm.
Frontal—The frontal is narrowly exposed on the skull vertex posterior to the ascending process of the maxilla (Fig. 2). In dorsal and ventral views, the anterior margin of the supraorbital process (as preserved) is directed anterolaterally (Figs. 2, 3). In anterior or posterior view, the supraorbital process is dorsally concave; it gradually slopes down at the angle of 15°. There are two transverse crests at the dorsal surface of the supraorbital process: the anterior one, an anterolaterally directed low crest, is possibly an orbitotemporal crest sensu Mead and Fordyce (2009). Posterior to it, there is another well-developed crest, located near the posterior border of the supraorbital process. The posterior surface of the process is nearly vertical; it forms an approximately right angle with its dorsal surface in lateral view (Fig. 4A). A vertical frontal-parietal suture is partly seen in the temporal fossa in dorsal view; it runs anteroventrally from the vertex.

Parietal—In dorsal view, the borders of the parietal bone are barely visible on the vertex owing to excessive development of the nuchal crest, which occupies much of the vertex. The intertemporal region is anteroposteriorly short. In dorsal view, the temporal fossa is rhomboid and transversely extended; it is more than one and a half times as wide transversely as it is long anteroposteriorly. The parietal and the squamosal bulge into the temporal fossa laterally, forming a domelike structure. The parietal—squamosal suture, generally oblique in lateral view, is keeled.

Palatine—Posterior portions of the palatines have been preserved in TNU Skull A and TNU Skull 2 (Fig. 3). The palatine extends posteriorly to the level of the foramen pseudovale. The palatine is posterolaterally notched: this portion surrounds and overlaps the anterior portion of the pterygoid.

Pterygoid—The pterygoid is widely exposed on the ventral side of the skull between the squamosal and the palatine (Fig. 3). Anteriorly, the pterygoid sinus fossa reaches the level of the foramen pseudovale. The medial lamina borders the vomer medially; its posterior margin borders the basioccipital crest. The thick dorsal lamina forms the roof of the pterygoid sinus fossa. The lateral lamina is anterolaterally elongated; in ventral view, it forms a round bulb anterior to the pterygoid hamulus. Its postero-lateral margin borders the squamosal and forms the anterior margin of the foramen pseudovale. The ventral lamina forms the bottom of the pterygoid sinus fossa and borders the palatine anteriorly. The pterygoid hamulus (as preserved) is short and robust; however, it is unclear if it is entirely preserved.

Vomer—The posterior margin of the vomer extends to the anterior portions of the basioccipital crests and wedges between the palatine and the pterygoid. The anterior portion of the vomerine crest is high in TNU Skull A and low in TNU Skull 2. In the holotype, it extends further posteriorly, to the transverse line joining the anterior processes of the pterygoid bones.

Basisphenoid—The rectangular basisphenoid is seen in the disarticulated TNU Skull 4 (Fig. 5). The suture with the basioccipital is completely fused without a trace. There is a low crest dividing the basisphenoid and the basioccipital on the dorsal (inner) surface, a plesiomorphic trait.

Alisphenoid—The alisphenoid is well observed in the TNU Skull 4 (Fig. 5). In dorsal view, the alisphenoid is roughly quadran-gular, dorsoventrally flat, articulated with the basisphenoid through a narrow short neck. It is elongated in an anteromedial to posterolateral direction. In ventral view, it is mostly overlapped by the squamosal and pterygoid. Surfaces for articulation with the parietal and squamosal are seen in dorsal and ventral views. The anterolateral margin is exposed in the ventral part of the medial wall of the temporal fossa. It is partly seen in TNU Skull A (Fig. 4A); the sutures at its borders are almost completely fused with adjoining bones. An oval foramen rotundum is seen at the lateral surface in TNU Skull A and TNU Skull 2 anterior to the alisphenoid margin.

Presphenoid—In ventrolateral view, a metopic process is seen as the area dividing the foramen rotundum and the optic canal in the temporal fossa.

Orbitosphenoid—In ventral view, a relatively small triangular orbitosphenoid is seen anterior to the optic canal, ventral to the supraorbital process (Fig. 3).

Ethmoid—A large cribriform plate with an ethmoid labyrinth is located dorsal to the vomer and palatines (Fig. 3). In ventral or anterior view, tubular ethmoturbinals with large round olfactory foramina are located medial to the frontal at the level of the posterior portions of the nasals.

Squamosal—The squamosal (especially its lateral portion) is transversely wide. The portion bearing zygomatic and postglenoid processes (a glenoid process sensu Mead and Fordyce, 2009) is posterolaterally directed, oblique to the longitudinal axis at the level of the skull, so the postglenoid and zygomatic processes are laterally expanded (Figs. 2, 3). There is a bulge at the posterolateral surface of the squamosal, above the base of the postglenoid process (Fig. 4A, B). The shallow glenoid fossa faces anteromedially. The zygomatic process (partly preserved in TNU Skull 2 and fully preserved in TNU Skull 4) is robust and dorsoventrally high. In the juvenile TNU Skull 4, it is anteroposteriorly short, with a rounded apex. The zygomatic process is directed anterolaterally. Dorsally, there is a high and thick supramastoid crest of irregular shape, which joins the nuchal crest anterior to the paroccipital process at an acute angle (Fig. 2). In lateral view, there is a sternomastoid fossa (Bouetel and Muizon, 2006) between the supramastoid crest dorsally and the posteri- rior process of the periotic ventrally (Fig. 4A). The postglenoid process is directed ventrally to posteroventrally. It is widened transversely and not twisted. In lateral view, its posterior-dorsal surface is concave and the anteroventral surface is convex; the distal margin is dorsoventrally constricted. The distal margin is transversely wide and squared in postero-dorsal view (Fig. 4B). The falciform process is robust, roughly rectangular, antero-posteriorly elongated, with a rectangular anteromedial margin and a notched posterolateral margin (Fig. 3). Lateral and dorsal to it, separated by the foramen pseudovale, there is an antero-lateral part of the bone extending anterior and covering the alisphenoid.

Exoccipital—The exoccipital is completely fused with the supraoccipital (Fig. 4B). The dorsal condylid fossa is well pronounced, and a transverse furrow extends laterally from it. The paroccipital process is large and robust, and directed postero-medially. It extends far posterior to the occipital condyle (Figs. 2, 3). The foramen magnum is oval and dorsoventrally high. In TNU Skull A, occipital condyles are large and widen ventrally; the condyles come close to each other ventrally to the foramen magnum.

Supraoccipital—The anterior-most point of the occipital shield is slightly anterior to the center of the temporal fossa (Fig. 2). In dorsal view, the occipital shield is narrow and transversely constricted, particularly in comparison with transversely expanded squamosals. It is subtriangular, with a sharp apex, strongly S-curved nuchal crests, and a concave posterior margin. The nuchal crests are high, forming a shallow supraoccipital basin-like depression. The external occipital crest is high, especially in the anterior portion, but it is lower than the nuchal crests. The occiput is slightly asymmetrical: the left side with the nuchal crest and the occipital condyle extends posteriorly further than the right side, and the external occipital crest is rotated 5° clockwise to the longitudinal axis of the cranium. No signs of distortion are seen, so this seems to be a natural condition.

Basioccipital—The basioccipital is fused with the basisphenoid and exoccipitals (Figs. 3, 5, 6). Basioccipital crests are wide and extremely high in adult specimens. They grow substantially
FIGURE 3. Ventral views of the skulls of Brandtocetus chongulek, gen. et sp. nov. A, holotype, TNU Skull A; B, paratype, TNU Skull 2; C, line drawing. Scale bar equals 10 cm.
through ontogeny: in TNU Skull 4, the crests are low and occupy a small area. The ventral surface of the basioccipital is smooth, without any crests or fossae.

**Periotic**—Periotic bones have been preserved in all of the specimens; in TNU Skull 4, the right periotic is isolated but lacking the posterior process (Fig. 7). The periotic body is large in comparison with the pars cochlearis, roughly as long as it is high. In ventral view, the anterior process is short, blunt, and moderately transversely compressed; in medial view, it is quadrangular (Fig. 7B). A shallow groove divides it into two portions, of which the ventral one is slightly shifted laterally; there is no gulf or notch between them. The dorsal portion is subtriangular, with the long side converging with the pars cochlearis; it is covered with thin longitudinal grooves. The ventral portion is dorsoventrally compressed and relatively smooth. The shape of the ventral portion varies individually: it is short, anteromedially directed, medially curved, and laterally rounded in TNU Skull A; enlarged, anterolaterally extended, and elongated, with a shallow depression, in TNU Skull 2; broken, in TNU Skull 4. The hiatus Fallopii is small; the groove for tensor tympani is narrow. The tympanic opening of the facial canal is slit-like; its anterior margin is anterior to the adjacent anteroposteriorly short fenestra ovalis.

In dorsomedial view, the spiral cribriform tract (opening for the CN VIII) is subcircular; it is ventrally notched in TNU Skull 4. The endocranial opening of the facial canal (CN VII) is anteroposteriorly elongated. The crista transversa is deeply recessed, so CN VIII and CN VII form an internal acoustic meatus of oval to subtriangular shape (Fig. 7A). The aperture for the cochlear aqueduct (perilymphatic foramen) is positioned in line with the internal acoustic meatus and the fenestra rotunda, so the aperture for the cochlear aqueduct, the internal opening of the facial canal, and the spiral cribiform tract are aligned anteroposteriorly (see also Steeman, 2007). The aperture for the vestibular aqueduct (endolymphatic foramen) is small and slit-shaped; it is located anterodorsally from the aperture for the cochlear aqueduct, so the foramina are closely dorsoventrally aligned and they form a common recess. A thin plate dividing them is oblique to the anteroposterior axis of the periotic. The pyramidal process is small and narrow. In dorsal view, a broad suprameatal fossa is seen (Fig. 7A).

In lateral view, the squamosal fossa is shallow and almost indistinct. The ventral and dorsal lateral ridges are broad and low.
The recessus meatus (external auditory meatus s.l.) is shallow and curved.

In posterior view, the fenestra rotunda is large and circular. The posterior cochlear crest (caudal tympanic process) is short, robust, and rounded. It reaches the base of the posterior process as a narrow high crest with a broad flange extending dorsomedially. The stylomastoid fossa is broad and shallow.

The compound posterior process of periotic and tympanic bulla is long in comparison with other cetotheriids. It is distally widened with an oblique posterior surface. The ventral and posterior surfaces form a blunt angle of approximately 110°. The facial sulcus is deep but open, not tube-like. The distal surface of the process wedges between the exoccipital and the squamosal. It is exposed at the lateral skull wall as an oval-shaped area with a wide dorsal portion.

**Tympanic Bulla**—The description of the tympanic bulla is based on TNU Skull 2 and TNU Skull 4 (Fig. 8). In ventral view, the tympanic bulla is box-shaped, with the prominent narrow main ridge and oblique anterolateral corner. In ventrolateral view, the bulla is close to an oval, with a rounded posterior contour and angular anterior portion. The main ridge is straight and parallel to the longitudinal axis of the bulla. The sigmoid process is transversely straight, short, robust, equally thickened...
FIGURE 7. Right periotic bone of the paratype of Brandtocetus chongulek, gen. et sp. nov., TNU Skull 4. A, dorsomedial view; B, ventral view; C, ventrolateral view; D, posterior view. Abbreviations: aca, aperture for the cochlear aqueduct; ap, anterior process; ap (d), dorsal portion of the anterior process; ap (v), ventral portion of the anterior process; ava, aperture for the vestibular aqueduct; CN VII; CN VIII; ct, crista transversa; dlr, dorsal lateral ridge; fo, fenestra ovalis; fpcc, flange of the posterior cochlear crest; fr, fenestra rotunda; fs, facial sulcus; gtt, groove for tensor tympani; hp, hiatus Fallopii; ipap, lateral projection of the anterior process; maf, malleolar fossa; mpg, median promontorial groove; pcc, posterior cochlear crest; pm, promontorium; pp, compound posterior process of the tympanoperiotic; pyp, pyramid process; smf, supramastoid fossa; sta, stapedia fossa; stl, stylo-mastoid fossa; tofc, tympanic opening of the facial canal; vlr, ventral lateral ridge. Scale bar equals 1 cm.

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The estimated body size (following Lambert et al., 2010) of the juvenile specimen TNU Skull 4 is 312 cm: it could be even larger, given that the formula underestimates the body length of 300 cm long Cetotherium riabinini by 25 cm (Gol’din et al., in press). Thus, the juvenile Brandtocetus chongulek attained 80% of the length of the adult specimen found near it (TNU Skull 2). This suggests rapid postnatal growth, as documented in living mysticetes: 76% of adult length in northern right whales (Fortune et al., 2012), 70% in blue and fin whales (Lockyer, 1981), and 60–70% in minke whales (Christensen, 1981) by the age of 12 months. The basioccipital-basisphenoid suture fuses, as it is in TNU Skull 4, in living baleen whales by the same age (Walsh and Berta, 2011). Thus, we estimate the age of the juvenile specimen as at least 1 year.

The holotype, TNU Skull A, and the paratype, TNU Skull 2, are close in size and identical in bone outlines. This is clearly seen when comparing the shapes of squamosals, pterygoids, and basioccipital crests (Figs. 2, 3). The specimens differ in their occipital condyle size; however, the latter is difficult to estimate due to its damage in TNU Skull 2. All specimens slightly differ in the shape and structure of the anterior process of the petrosal bone.

INDIVIDUAL VARIATION

The estimated body size (following Lambert et al., 2010) of the juvenile specimen TNU Skull 4 is 312 cm: it could be even larger, given that the formula underestimates the body length of 300 cm long Cetotherium riabinini by 25 cm (Gol’din et al., in press). Thus, the juvenile Brandtocetus chongulek attained 80% of the length of the adult specimen found near it (TNU Skull 2). This suggests rapid postnatal growth, as documented in living mysticetes: 76% of adult length in northern right whales (Fortune et al., 2012), 70% in blue and fin whales (Lockyer, 1981), and 60–70% in minke whales (Christensen, 1981) by the age of 12 months. The basioccipital-basisphenoid suture fuses, as it is in TNU Skull 4, in living baleen whales by the same age (Walsh and Berta, 2011). Thus, we estimate the age of the juvenile specimen as at least 1 year.

TNU Skull 4 differs from adult specimens in the following traits: small basioccipital size with a particularly narrow medial part (the distance between the foramina pseudovale is twice as narrow as in adults; Table 1); unfused cranial sutures (only the basioccipital-basisphenoid suture is fused); small pterygoids; low supramastoid crest; extremely low basioccipital crest occupying a small area; and a tympanic bulla with less pronounced ridges and grooves. The squamosals of TNU Skull 4 are somewhat smaller than in adult Brandtocetus chongulek but they are otherwise well developed: if compared with other species, the dimensions of the anteroposteriorly, and directed perpendicular to the main ridge (Fig. 8A). Its base is located at the level of the center of the bulla. The shape of the process is slightly inflated. The median furrow is shallow (Fig. 8E). The conchal process is short and rounded (Fig. 8A, D). In lateral view, the bulla appears box-shaped, narrowing anteriorly. In dorsal view, the bulla is box-shaped, and the involucrum is long and wide, with an angular lateral surface and bulbous dorsal posterior prominence. It is covered by sparse thin grooves, more numerous in the anterior portion. The Eustachian outlet is relatively narrow, quadrangular, and oblique to the longitudinal axis of the bulla. In medial view, the bulla is subtriangular. It gradually tapers anteriorly. Both main and involucral ridges are well developed but narrow; they join together at the anterior-most point of the bulla where they meet the anterodorsal crest (Fig. 8C). Ventrally, the main ridge is slightly convex; it is higher and thicker than the involucral ridge. There is a prominence in the posterior part of the involucral ridge. The median furrow is shallow and elongated; it is laterally curved along its longitudinal axis. The lateral lobe of the bulla extends slightly more posteriorly than the medial one. The involucrum is dorsoventrally flattened. In posterior view, the bulla is roughly hexagonal; the ventral part is slightly transversely wider than the dorsal part (Fig. 8E).

Malleus—The left malleus from TNU Skull A remains unpreserved in the matrix containing the natural mold of the sigmoid process and adjoining area of the bulla. The description of the right malleus is based on TNU Skull 2 (Fig. 9). The anterior process is short and relatively thin. The head is large, bearing the articular facet for the incus divided into two facets (dorsal and ventral), of which the dorsal one is larger. There are large tubercles at the dorsal and medial surfaces of the head, which articulate with the periotic. The manubrium is very small, and the muscular process is short and robust.
squamosal expansion and temporal fossa of TNU Skull 4 are roughly equal to those of an adult *Kurdalagonus mchedlidzei* and exceed those of *Cetotherium rathkii* and *Cetotherium riabinini*, whereas the basicranium is far smaller (Table 1; see also Gol’din et al., in press). Further, the glenoid fossa is more clearly defined in TNU Skull 4, although it is still shallow, as in adults. The comparable parts of the periotic in the specimens of *Brandtocetus chongulek* do not significantly differ in shape and size: the pars cochlearis, periotic body, and dorsal portion of the anterior process are roughly equal in size. No ontogenetic variation is seen in the size and shape of the anterior process or its lateral projection, unlike in living balaenids and balaenopterids (Bisconti, 2001; Ekdale et al., 2011; Pavel Gol’din, pers. data). The tympanic bulla is even slightly larger in TNU Skull 4 than in TNU Skull 2 (Fig. 10). So growth and ontogenetic changes in *Brandtocetus chongulek* after the age of 1 year are limited in the periotic (including its processes), moderate in the squamosal, and significant in the neurocranium. This growth pattern seems to be unusual for mysticetes (e.g., Nakamura et al., 2012). Kemper and Leppard (1999) reported significant elongation of the supraoccipital shield in *Caperea marginata* Gray, 1846, after body length reached its asymptote, and it could be also the case for *Brandtocetus chongulek*, which is distinguished from other cetotheriids by its long neurocranium (Table 1).

**COMPARISONS**

*Brandtocetus chongulek* is assigned to Cetotheriidae on the basis of the following combination of characters (Gol’din et al., in press): strongly telescoped facial bones with the posterior edges of the nasal, premaxilla, and maxilla wedge-shaped and extending almost to the tip of the occipital shield (‘X’-shaped vertex); in dorsal view, the ascending processes of the maxillae have concave lateral margins and approximate each other at their posterior edges; a shallow glenoid fossa; in dorsal view, a paroccipital process extending posterior to the posterior edge of the
Brandtocetus chongulek has cranial morphology typical for subfamily Cetotheriinae, as opposed to Herpetocetinae sensu Whitmore and Barnes (2008): a transversely wide squamosal occipital condyle; a transversely short sigmoid process of the tympanic bulla lacking an inflated base; a well-developed anterior process and lateral tuberosity of the periotic; and a relatively short posterior process of the tympanoperiotic with a flattened distal surface broadly exposed on the posterolateral wall of the skull (Gol’din et al., in press).

Brandtocetus chongulek is similar to other cetotheriids from the Eastern Paratethys (Cetotherium, Kurdalagonus, and Eucetotherium) in a robust and dorsoventrally high zygomatic process of the squamosal and wide cranium. Brandtocetus chongulek is a member of a group including Cetotherium, Kurdalagonus, and related whales from the eastern Paratethys (Fig. 11). These whales lack derived herpetocetine rostral and squamosal characters and have primitive anatomy of the compound posterior process of the tympanoperiotic (except Eucetotherium). A synapomorphy of this group is a high zygomatic process.

Brandtocetus chongulek differs from all cetotheriids (including Cetotherium and Kurdalagonus) by having a transversely expanded lateral portion of the squamosal with anterolaterally directed zygomatic processes: zygomatic width is 4.3–4.9 times greater than condylar width, whereas this ratio is 3.8 in Cetotherium riabinini, 2.8 in Kurdalagonus mchedlidzei (Table 1), and 2.8–3.4 in Piscobalaena nana (Bouetel and Muizon, 2006). Also, it differs from all cetotheriids in its rhomboid temporal fossa; occipital shield extending anterior to the level of the center of the temporal fossa; and particularly elongated posterior process of the tympanoperiotic, with the distal portion exposed as a large oval surface on the skull wall (not triangular, as in Cetotherium, nor roughly rhomboid, as in Kurdalagonus mchedlidzei) (Fig. 12). Another unusual feature of Brandtocetus is its widely exposed pterygoid; however, this trait is unknown or poorly seen in many cetotheres.
Brandtocetus chongulek further differs from Kurdalagonus mchedlidzei in a quadrangular, moderately transversely compressed anterior process of the periotic (not an extremely compressed double-bladed process, as in Kurdalagonus mchedlidzei) (plesiomorphic). Brandtocetus is distinguished by its narrow, transversely constricted occipital region (not particularly wide, as in Kurdalagonus mchedlidzei) (Table 1). It differs from Kurdalagonus mchedlidzei by having a paroccipital process that extends far posterior to the level of the occipital condyles, and forms a semicircular contour in dorsal view; a vertical nuchal crest that does not overhang the temporal fossa; and a foramen magnum that is higher than wide. A synapomorphy of Brandtocetus chongulek and Kurdalagonus mchedlidzei, unique to these taxa among cetotheriids but also present in Piscobalaena, Cetotherium, and Eucetotherium helmersenii, is a strongly curved ‘S’-shaped nuchal crest. Brandtocetus chongulek differs from Cetotherium mayeri and Kurdalagonus adygeicus (both taxa known from incomplete crania), in squared (not tapering distally and contact with the metopoid lobe), in the posterior portion of the outer lip is not swollen, so the bulla in posterior view is roughly hexagonal (not roughly globular with a middle constriction); in dorsal view, the involucrum is as high anteriorly as posteriorly. Brandtocetus chongulek differs also from Kurdalagonus (Cetotherium) maicopicus by having a posteriorly projecting paroccipital process, an apomorphic trait within cetotheriids.

**Phylogenetic Analysis**

**Methods**

Phylogenetic analysis was performed with 59 ingroup taxa of mysticetes, 13 of which were hypothetical Cetotheriidae or Cetotheroidea sensu Steeman, 2007, and two odontocete taxa. Zygorhiza kochii (Reichenbach in Carus et al., 1847) was chosen as the outgroup taxon. The data matrix with 150 characters was adopted from Marx (2011), excluding Aloucetus latus Kellogg, 1940, and Cephalotropis nectus Kellogg, 1940, with five new characters added to it (Supplementary Data 1, Appendix S1). This matrix was used as one of the most recent published studies and the largest matrices containing data for many cetotheriid operational taxonomic units. The character codings for Jousmocetus shimizu Kimura and Hasegawa 2010, Cetotherium rathkii, and Cetotherium riabinini were adopted from Gol’din et al. (in press). Eucetotherium helmersenii and Kurdalagonus mchedlidzei, as well as Brandtocetus chongulek, were added to the analysis with new codings (Supplementary Data 1, Appendix S2). Heuristic parsimony analysis of the matrix was performed in TNT version 1.1 (Goloboff et al., 2003). The ‘traditional search’ option was used. The resulting most parsimonious trees were summarized using strict consensus trees with zero-length branches collapsed (Goloboff et al., 2003). The topologies generated by the parsimony analysis were evaluated by bootstrap resampling, compiled from 1000 replicates.

**Results and Discussion**

A strict consensus tree of 13 equally most parsimonious trees with the length of 433 steps (consistency index [CI] = 0.51, retention index [RI] = 0.83) is presented in Figure 13. Cetotheriidae are confirmed to be a monophyletic family, a sister clade to the clade including families Neobalaenidae, Eschrichtiidae, and Balaenopteridae. The basal-most member of Cetotheriidae is Mixocetus elysius; followed by Jousmocetus shimizu. Derived cetotheriids are tentatively grouped in three clusters, all poorly supported by bootstrap resampling (Fig. 13). The cetotheriids from the eastern Paratethys form a clade: Brandtocetus chongulek, genus Cetotherium with two species (C. rathkii and C. riabinini), Kurdalagonus mchedlidzei and Eucetotherium helmersenii. This clade is supported by a single synapomorphy: a blunt
dorsoventrally high zygomatic process. Another clade includes oceanic cetotheriids: ‘Metopocetus’ (Cetotherium) vandelli Van Beneden and Gervais, 1868, (the basal-most member), Metopocetus durinus, Piscobalaena nana, Nannocetus eremus Kellogg, 1929, and Herpetocetus transatlanticus Whitmore and Barnes, 2008. This clade is characterized by strong development of rostral telescoping: ascending processes of the maxillae extend posterior to the level of the postorbital processes of the frontals. The derived members of this clade have ascending processes of the maxillae overlapping or constricting the posterior portions of the premaxillae and nasals. This trait is absent in ‘Metopocetus’ (Cetotherium) vandelli, which Whitmore and Barnes (2008) did not consider to be a species of Metopocetus. We share this view, but at the same time we do not consider it to be a species of Cetotherium (Gol’din et al., in press). A third clade is represented by ‘Cetotherium’ megalophysum.

Within the Eastern Paratethyan clade, the genus Cetotherium (the monophyly of which is relatively well supported by bootstrap resampling) is characterized by a narrow rostrum, twisted postglenoid processes, an anteriorly rounded tympanic bulla, and a triangular distal surface of the posterior process of the tympanoperiotic. Among Paratethyan genera, Brandoctetus chongulek has two autapomorphies: transverse expansion of the squamosals and an oval distal surface of the posterior process of the tympanoperiotic. Eucetotherium helmersenii has a single autapomorphy: the anteroposteriorly elongated temporal fossa, which is a rare trait among mysticetes (a similar specimen was also reported by Spassky [1954]).

Kurdalagonus mchedlidzei has a posterior process of the tympanoperiotic with a small rhomboid distal surface, similar to Joumocetus shinisui or Piscobalaena nana (Fig. 12); it is likely a plesiomorphic shape for derived cetotheriids, and both the triangular surface of Cetotherium and the large oval surface of Brandoctetus may be derived from it. In the same manner, the small triangular occipital shield of Cetotherium and the anteriorly extended occipital shield with ‘S’-shaped nuchal crests of Brandoctetus may be derived from the small occipital shield with ‘S’-shaped nuchal crests of Kurdalagonus mchedlidzei. Thus, Kurdalagonus mchedlidzei from the late middle Miocene may possess ancestral morphology for features seen in the early late Miocene genera Cetotherium and Brandoctetus. However, this hypothesis is not corroborated by the cladistic analysis.

The proposed phylogeny should be treated as provisional, given a number of poorly known and undescribed cetotheriid taxa. Nevertheless, our attempt to reconstruct the phylogeny of cetotheriids can serve as a basis for further studies. The difficulties in resolving the phylogeny of Cetotheriidae, as demonstrated by contradictions between recent published schemes (Bouetel and Muizon, 2006; Steeman, 2007; Bisconti, 2008; Marx, 2011; Bisconti et al., 2013; Fordyce and Marx, 2013), are perhaps explained by multiple parallelisms in anatomy across genera. For example, Brandoctetus chongulek and Herpetocetus spp. have a similar box-shaped tympanic bulla gradually narrowing anteriorly in medial view, with an anteriorly high involu- crum (Whitmore and Barnes, 2008); Kurdalagonus mchedlidzei and Herpetocetus spp. have a transversely extremely compressed double-bladed anterior process of the periotic (Whitmore and Barnes, 2008); and Eucetotherium helmersenii has a ‘herpetoce- tine’ plug-like posterior process of the tympanoperiotic and a laterally compressed and twisted postglenoid process. However, the Paratethyan whales differ significantly from Herpetocetus spp. in cranial anatomy, and none of them shares the overall herpetocetine pattern of tympanoperiotic anatomy, so a close phylogenetic relationship is questionable and not confirmed by the analysis presented here.

Anatomical differences within the cetotheriid family partly result from variation in feeding strategies. A suction feeding strategy is hypothesized for cetotheriids (Kimura, 2002, 2005;
El Adli and Boessenecker, 2011; Gol'din et al., in press), and possibly it involves a kind of continuous suction feeding, similar to that of filter-feeding ducks (Anatidae) (Kimura, 2008; Gol'din et al., in press). A cetotheriid cranial trait clearly hindering effective gulp feeding is the shallow glenoid fossa, which suggests limited rotation of the mandibles (Lambertsen, 1983). In Herpetocetinae sensu Whitmore and Barnes, 2008, the transverse compression, twisting and vertical orientation of postglenoid processes further limits mandible movements; however, in other cetotheriids it does not, so their generalized feeding strategy could combine the anatine-like herpetocetine feeding and other feeding modes like intermittent suction feeding in living gray whales (Ray and Schevill, 1974; Sanderson and Wassersug, 1993; Gol'din et al., in press). We suggest anatine-like feeding was effective at a small body size; a generalized feeding strategy was necessary with an increase in body size. Transversely expanded squamosals, enlarged pterygoids, and thick nuchal crests, indicating simultaneous strengthening of temporal, external pterygoid, and internal pterygoid muscles, suggest this generalized feeding strategy, and are observed in various forms in large and medium-sized cetotheriids: *Brandtocietus chongulek*, Eucetoerthium helmersnii and possibly *Metopocetus durinus*, and ‘*Cetotherium* megalophysym’ (as preserved in the fragmentary holotype skulls). Among them, *Brandtocietus chongulek* is characterized by extreme transverse widening of the cranium and anteriorly directed telecoping of the occipital shield, traits approaching the typical cranial morphology of balaenopteroids. After the analysis by Bouetel and Muizon (2006), the family Cetotheriidae, now defined as Cetotheriidae s.s., was restricted to six or seven described genera. However, a great diversity of cetotheriids with varying morphology and ecology discovered in recent studies, including this work, demonstrates the necessity for further research into the taxonomy and phylogeny of this family.

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