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# A “preglacial” giant salamander from Europe: new record from the Late Pliocene of Caucasus

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## KEY WORDS

*Andrias*,  
Cryptobranchidae,  
giant salamander,  
Northern Caucasus,  
Pliocene.

## ABSTRACT

Disarticulated cranial and postcranial bones of a giant salamander (Cryptobranchidae: *Andrias* sp.) were found in the Upper Pliocene deposits of the Belorechensk locality in the Northern Caucasus. These remains probably belonged to one individual that died during a stage of rapid growth and had a total length of about 90-100 cm. The giant salamander from Belorechensk is among the geologically youngest and the easternmost known in Europe.

## RÉSUMÉ

*Une salamandre géante « préglaciaire » d'Europe : nouveau signalement du Pliocène supérieur du Caucase.* Des os crâniens et post-crâniens désarticulés d'une salamandre géante (Cryptobranchidae : *Andrias* sp.) ont été trouvés dans les dépôts du Pliocène supérieur de la localité de Belorechensk dans le Caucase du Nord. Ces restes appartenaient probablement à un individu décédé au cours de la phase de croissance rapide et d'une longueur totale d'environ 90 à 100 cm. La salamandre géante de Belorechensk est l'une des plus récentes et des plus connues d'Europe.

## MOTS CLÉS

*Andrias*,  
Cryptobranchidae,  
salamandre géante,  
Caucase du Nord,  
Pliocène.

## INTRODUCTION

Cryptobranchidae Fitzinger, 1826 are a family of large to giant (up to 180 cm total length), strictly aquatic, and obligatory neotenic salamanders. It is a morphologically uniform group with few modern representatives and a relatively poor fossil record. Two recent genera are recognized: the Asian *Andrias* von Tschudi, 1837 with four living species, *A. japonicus* (Temminck, 1836), Japan, *A. davidianus* (Blanchard, 1871), eastern China, *A. jiangxiensis* Lu, Wang, Chai, Yi, Peng, Murphy, Zhang & Che, 2022, eastern China, and *A. sligoi* (Boulenger, 1924), southern China, and the North American *Cryptobranchus* Leuckart, 1821 with a single living species *C. alleganiensis* Daudin, 1803, eastern United States (Turvey *et al.* 2019; Chai *et al.* 2022; Dubois *et al.* 2022; Frost 2023). Based on molecular data, Yan *et al.* (2018) recognized at least five species of Chinese giant salamanders.

The oldest known cryptobranchids were reported from the Late Mesozoic of Asia, i.e., *Chunerpeton tianyiensis* Gao & Shubin, 2003, *Eoscapherpeton asiaticum* Nesov, 1981, and *Eoscapherpeton gracilis* Nesov, 1981 (Skutschas 2009, 2013). Recent phylogenetic analyses recovered *Chunerpeton* Gao & Shubin, 2003, previously hypothesized to be a basal (stem) member of the Cryptobranchidae, as instead belonging in the stem-group Caudata (Rong *et al.* 2021; Jones *et al.* 2022). The position of *Eoscapherpeton* Nesov, 1981 as a basal Cryptobranchidae is supported by several features (midline contact of the dorsal [alary] processes of the premaxillae, frontal-maxillary contact, parietals strongly overlapped by the frontals, absence of a distinct medial process of the pterygoid and presence of pterygoid-parasphenoid contact; see Skutschas 2013), but its assignment to cryptobranchids has never been tested by a formal phylogenetic analysis.

The Asian Cenozoic cryptobranchids are represented by *Aviturus exsecratus* Gubin, 1991 and *Ulanurus fractus* Gubin, 1991, both from the latest Paleocene of Mongolia (Gubin 1991), *Zaissanurus beliajevae* Chernov, 1959 from the late Eocene-Oligocene of Kazakhstan (Chkhikvadze 1982), and *Andrias karelcapeki* Chkhikvadze, 1982 from the Early Miocene of Kazakhstan (Chkhikvadze 1982). However, *U. fractus* has been suggested to be a junior synonym of *Aviturus exsecratus* (Vasilyan *et al.* 2013) and the taxonomic validity of *Andrias karelcapeki* also requires clarification (see Vasilyan *et al.* 2017).

The North American cryptobranchids are represented by *Andrias matthewi* (Cook, 1917) from the Miocene of the United States and *Andrias* (orig. *Cryptobranchus*) *saskatchewanensis* Naylor, 1981 from the late Paleocene of Canada and the early Eocene of United States (Meszoely 1966; Naylor 1981; Holman 2006). The taxonomic status and generic allocation of both species are unresolved because of the fragmentary nature of the fossil material (Dubois *et al.* 2022). Other cryptobranchid fossils come from the Pleistocene and are assigned to the modern hellbender, *C. alleganiensis* (Holman 2006). *Cryptobranchus guildayi* Holman, 1977, from the Pleistocene of the United States is considered conspecific with *C. alleganiensis* (Bredehoeft & Schubert 2015).

The European cryptobranchids include the widely distributed *Andrias scheuchzeri* (Holl, 1831), ranging from the late Oligocene to the Late Pliocene of Central Europe (Estes 1981), and the stem cryptobranchid *Ukrainurus hypsognathus* Vasilyan, Böhme, Chkhikvadze, Semenov, Joyce, 2013, described from the Late Miocene of Ukraine (Vasilyan *et al.* 2013). Additional records of the family (not identified below the family or genus levels) have been reported from several Cenozoic European and Asian localities (e.g. Shikama & Hasegawa 1962; Chkhikvadze 1982, 1984; Vasilyan *et al.* 2017; Georgalis *et al.* 2019). The geologically youngest and easternmost European records came from Ruscinian (MN 14) of the Kuchurgan locality in Moldova and the Antipovka locality in Russia (Chkhikvadze 1981; Averianov 2001). These remains are important for documenting the distribution of cryptobranchids in Eastern Europe, but they are still undescribed. Recently, fossil bones of a giant salamander were discovered at Belorechensk, a new Eastern European locality yielding Late Pliocene vertebrates that are younger than those from the Kuchurgan and the Antipovka localities. Here we describe remains of the giant salamander from the Belorechensk locality, infer the individual age of this salamander, and discuss its paleoecological context.

## MATERIAL AND METHODS

The cryptobranchid remains described below come from the Belorechensk locality, on the left bank of the Belaya River near the town of Belorechensk, Krasnodar Region of Russia (Fig. 1). The Belorechensk locality was discovered in 2021 by a joint expedition of the Geological Institute of RAS (Moscow, Russia) and the Southern Scientific Centre of RAS (Rostov-on-Don, Russia). The cryptobranchid remains were recovered during the field seasons of 2021 and 2022 from the bone-bearing clay layer of the Belorechensk Formation. The Belorechensk Formation overlays the Upper Miocene Gaverdovsky Formation along the Belaya River. The Belorechensk Formation is represented by pebbly deposits with interbedded layers of clays and sands and has a total thickness up to 100 m (Beluzhenko 2006). Apart from the cryptobranchid remains, the recovered vertebrate material includes remains of teleosts (cf. *Tinca*, *Rutilus* sp., *Silurus* sp., *Esox* sp.), amphibians (*Mioproteus* sp., cf. *Pelophylax*), turtles (Emydidae indet.), birds (*Heteroscelus* spp.), and mammals (*Hypolagus* cf. *brachygnathus*, *Talpa* sp., *Eutamias* ex gr. *orlovi*, *Trogontherium* cf. *minus*, Spalacidae indet., cf. *Neocricetodon*, *Miomys* cf. *stehlini*, *Pliomys jalpugensis* Nesin, 1983, *Apodemus* sp., *Nyctereutes* sp., *Ursus minimus* Devèze & Bouillet, 1827, *Archidiskodon meridionalis* cf. *rumanus*, *Stephanorhinus* sp., *Arvernoceros* cf. *ardei*, *Sus* cf. *arvernensis*, and *Procacpreolus* sp.) (modified and updated after Titov *et al.* 2023). The presence of brachyodont smaller *Miomys* Forsyth Major, 1902 and *Pliomys jalpugensis* indicates the correlation of the Belorechensk fauna to the Late Pliocene, Early Villafranchian/Early Villanyian ELMA and the MN 16a zone of the European Neogene Mammal biochronological system, dated to about 3.5–3.2 Ma. The fauna of this time interval corresponds to the Uryvian faunal complex of Eastern Europe.



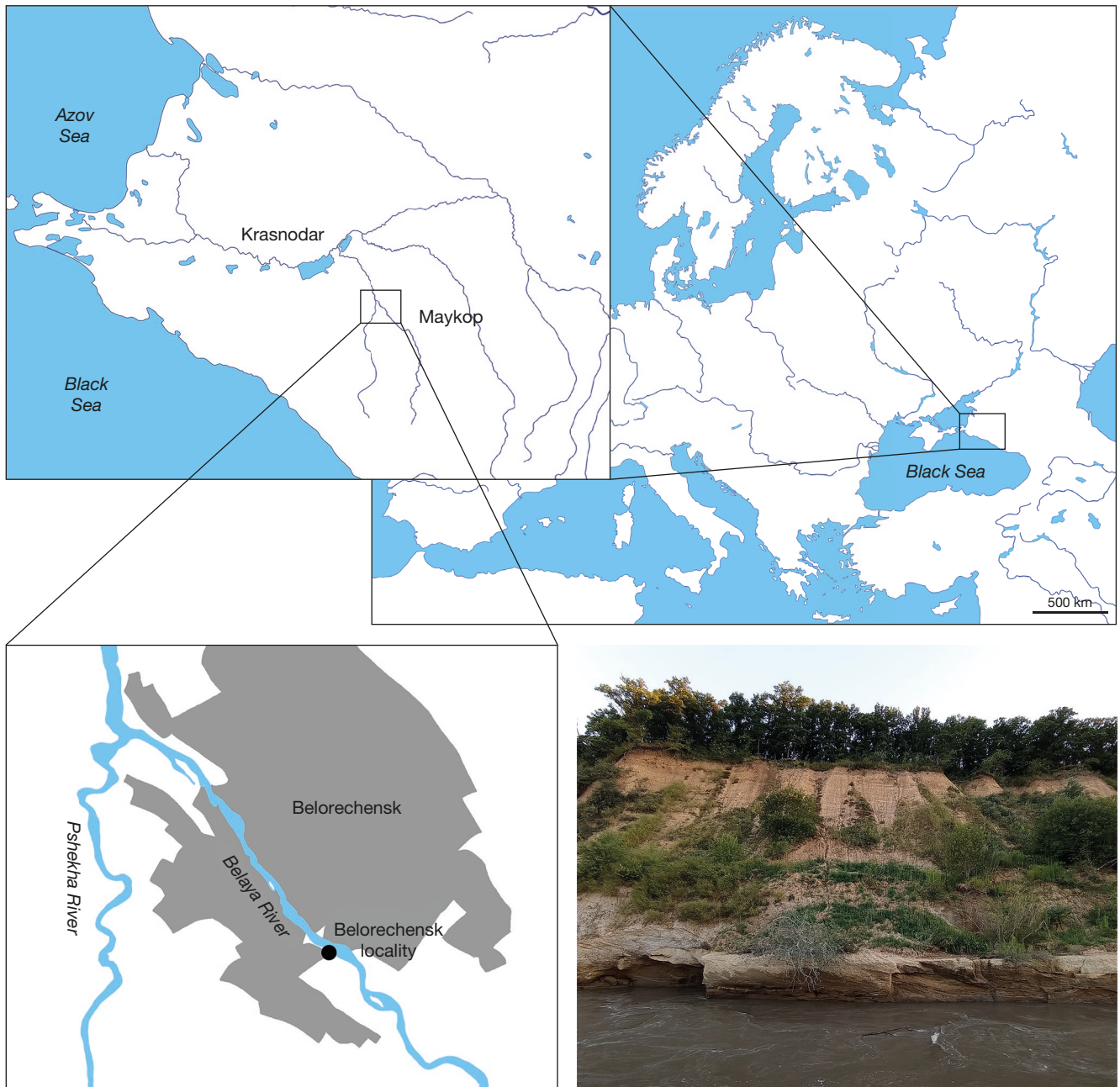


FIG. 1. — Maps showing geographic location of the Belorechensk locality and a photo of the Upper Pliocene deposits of the Belorechensk Formation.

The  $\mu$ CT-scans (computed microtomography) were performed in order to better visualize external morphological details and reveal internal morphology of the fossil cryptobranchid remains. The  $\mu$ CT-scans were obtained on a NEOSCAN N80 (Belgium) X-ray scanner at the Paleontological Institute of the Russian Academy of Sciences (PIN hereinafter). The scanning parameters were as follows: source voltage 101 kV (frontal PIN 5882/1), 92 kV (rib PIN 5882/12), and 84 kV (other bones); current 40  $\mu$ A (frontal PIN 5882/1), 44  $\mu$ A (rib PIN 5882/12), and 191  $\mu$ A (other bones); image resolution 27  $\mu$ m (dentaries PIN 5882/3 and 4), 17  $\mu$ m (prearticular PIN 5882/5), 15  $\mu$ m (femur PIN 5882/11), 26  $\mu$ m and 23  $\mu$ m (frontals PIN 5882/1 and 2), and 7.5  $\mu$ m (rib

PIN 5882/12) per pixel; frame averaging 2 (rib PIN 5882/12) and 3 (other bones); rotation step 0.2°; filters 0.5 mm Cu (frontals PIN 5882/1 and 2), 0.25 mm Cu (rib PIN 5882/12), and 0.1 mm Cu (other bones). A skull of the extant *Andrias japonicus* (PIN H 107) was used for comparative purposes. The scanning parameters were as follows: source voltage 92 kV; current 173  $\mu$ A (skull) and 44  $\mu$ A (dentary); image resolution 37.3  $\mu$ m (skull) and 26.7  $\mu$ m (dentary) per pixel; frame averaging 2, rotation step 0.2°, and a 0.25 mm Cu filter. Cross-sections were reconstructed using Neoscan (Belgium) software. 3D models were built with Avizo v.8.

Morphological terminology follows Vasilyan *et al.* (2013). Until recently, *Andrias jiangxiensis* and *A. sligoi* were con-

sidered within *A. davidianus* (Turvey *et al.* 2019; Chai *et al.* 2022). These three species are differentiated by soft features and molecular data, but no osteological data was provided. Because our study relies entirely on osteological features, in this paper we consider *A. jiangxiensis* and *A. sligoi* within *A. davidianus*. The fossil cryptobranchid material from Belorechensk is curated in the paleoherpetological collection of the Palaeontological Institute of the Russian Academy of Sciences (PIN) under collection no. 5882.

#### ABBREVIATIONS

ELMA	European Land Mammal Ages;
MN	biochronological zones (units) of Neogene Mammals;
PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow;
RAS	Russian Academy of Sciences.

#### SYSTEMATIC PALAEOLOGY

Class AMPHIBIA Linnaeus, 1758  
 Order CAUDATA Scopoli, 1777  
 Family CRYPTOBRANCHIDAE Fitzinger, 1826  
 Genus *Andrias* von Tschudi, 1837

*Andrias* sp.  
 (Figs 2-6; 7A, D)

**MATERIAL.** — Two frontals, PIN 5882/1 and 5882/2; two dentaries, PIN 5882/3 and 5882/4; one prearticular, PIN 5882/5; five trunk vertebrae, PIN 5882/6-10; one femur, PIN 5882/11; one rib, PIN 5882/12; all from the Belorechensk locality, Northern Caucasus, Late Pliocene, and interpreted as belonging to a single individual.

#### DESCRIPTION

##### *Frontal*

Both left and right frontals are almost completely preserved (Fig. 2). They match each other along the medial suture, which indicates they came from the same individual. The length of the complete specimen is 54.5 mm. The medial suture is markedly thickened dorsoventrally and interdigitated. The frontal is widest anteriorly and becomes narrower posteriorly, without a lateral constriction in the olfactory region. The dorsal surface is shallowly convex and smooth. The antero-medial portion of the bone is broad and forms a triangular facet for a nasal; the anterolateral portion is extended anteriorly and forms a narrow facet for a maxilla; and the lateral portion forms a facet for a prefrontal. Judging by the size of the facet on the frontals, the nasals overlapped the frontals for the anterior 30% of the length of the frontals. The ventral surface of the frontal is shallowly concave. The ventral surface bears the anterior portion of the roof of the cranial cavity and, posteriorly, an elongate facet for a parietal (Fig. 2E, H). The anterior portion of the cranial cavity is elongate and subtriangular in outline, narrowing posteriorly. Its anterior margin is straight and indistinctly bordered, whereas the lateral and posterior margins have sharp edges; the anterolateral margin has a bump. A shallow olfactory tract is visible in the olfactory region of the left frontal (Fig. 2E).

##### *Dentary*

The dentaries are represented by a complete right ramus and the anterior part of the left ramus (Fig. 3). They are long, slender, and slightly compressed labiolingually. The length of the complete specimen is 109.5 mm in straight line distance between its posterior and anterior tips and 120.2 mm along the curvature of its labial surface. The height of the dentary is 9.2 mm at the symphysis and 14.4 mm at the middle part of the tooth row. The symphysis is wide, convex, and roughly rhomboid in outline. The symphyseal surface is slightly rugose, mostly in its medial part, which suggests high mobility of the mandibular symphysis (Cundall *et al.* 1987). In lingual view, the dental lamina is of the same height throughout its length. The subdental lamina is half as high as the dental lamina or lower. The sulcus dentalis (subdental shelf) is wide and slightly concave along its anterior portion, but flat and narrow along its middle and posterior portions. It bears several small foramina. The margin of the sulcus dentalis is clear and rounded in PIN 5882/3, but acute along its anterior part in PIN 5882/4. The Meckelian groove is deep and extends anteriorly to a point below the 26-28 tooth positions (as counted from the anterior end). The corpus dentalis is smooth and flattened anterior to the Meckelian groove. Ventrally, it becomes thinner and ends with a ventral keel. In labial view, the surface of the dentary is only slightly rugose. The eminentia longitudinalis is clearly developed throughout the bone. A few small neurovascular foramina extend below the eminentia longitudinalis. The tooth row contains 80 small and closely spaced pleurodont teeth. The tooth crowns are completely missing, but the pedicellar portions show that the teeth were narrow, as in other cryptobranchids. Internally, the dentary is compact and encloses a few small and medium-sized neurovascular cavities and canals (Fig. 3D). In the region containing the anterior part of the tooth row, the cavities are mostly located below the subdental shelf. In the regions containing the middle and the posterior parts of the tooth row, the cavities are located above and below the Meckelian groove. There are no cavities in the area of the Meckelian groove and the ventral keel.

##### *Preatticular*

The prearticular is represented by the right element lacking its anterior and posterior tips (Fig. 4). It is low anteriorly and posteriorly and highest in the area of the coronoid process. The coronoid process is large, but short anteroposteriorly, nearly triangular, and tilted posterolingually. The articular facet is narrow and smooth. The dental facet widens posteriorly and has a sharp dorsal border that forms the lingual border of the coronoid process. It occupies about half of the length of the coronoid process.

##### *Vertebrae*

The vertebrae are represented by five nearly complete specimens from the trunk region (Fig. 5). The centrum is deeply amphicoelous, antero-posteriorly short and hourglass-shaped in lateral view, and circular in anterior and posterior views.



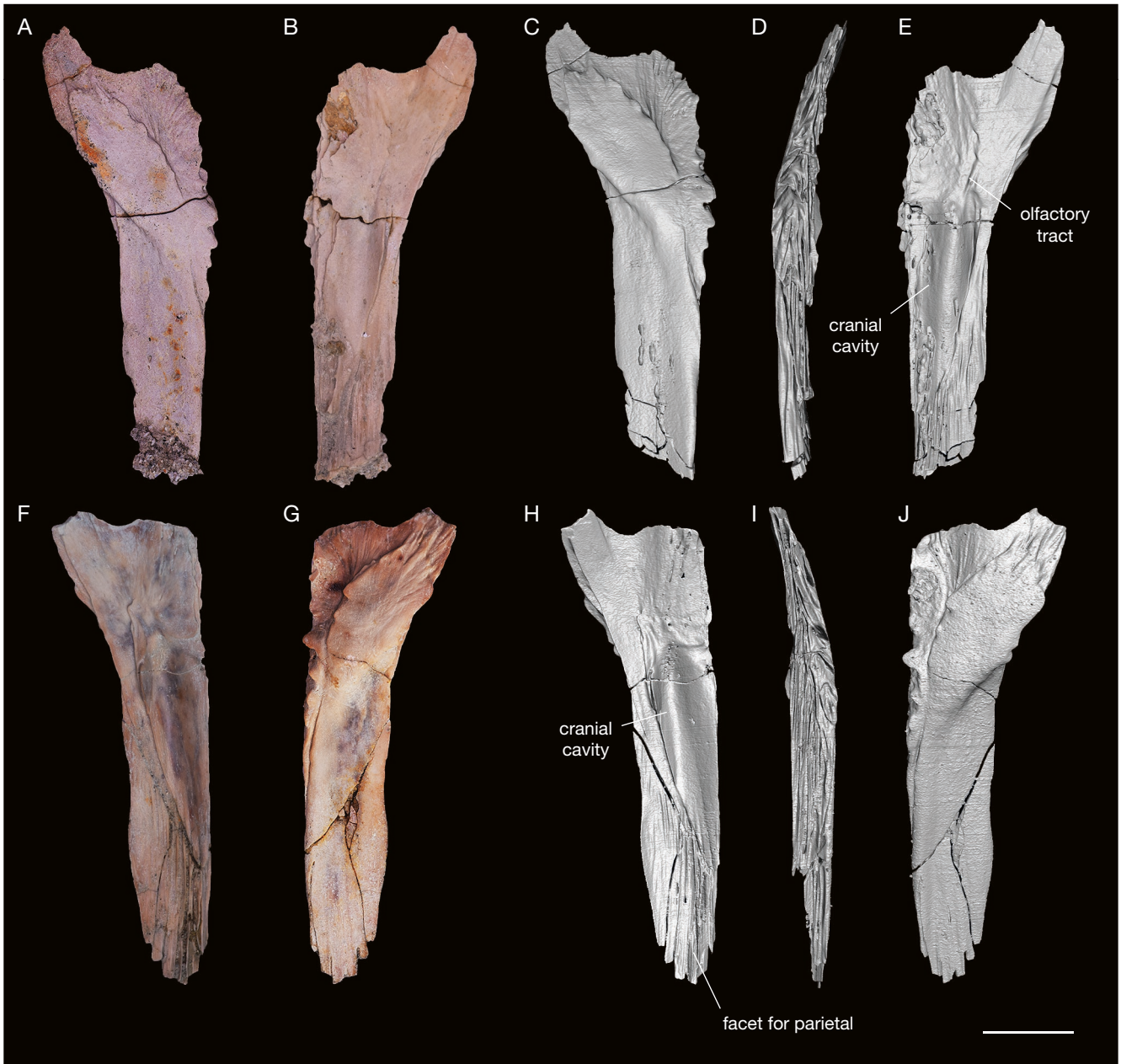


FIG. 2. — Frontals of *Andrias* sp. from the Belorechensk locality, Late Pliocene: **A–E**, PIN 5882/1, left frontal in dorsal (**A**, **C**), medial (**D**), and ventral (**B**, **E**) views; **F–J**, PIN 5882/2, right frontal in ventral (**F**, **H**), medial (**I**), and dorsal (**G**, **J**) views. **A**, **B**, **F**, **G**, photographs; **C**, **D**, **E**, **H**, **I**, **J**, 3D models. Scale bar: 1 cm.

Its length varies between 19–21 mm. Both cotyles have a notochordal pit. Lateral and ventral surfaces of the centrum are densely porous. The cotylar rim is robust and ventrally forms a larger anterior and a smaller posterior knob. Ventrally, the centrum is perforated by a large central foramen in all vertebrae. One or two subcentral foramina are situated at the bases of the transverse process in PIN 5882/8 and 5882/9. The transverse processes (rib-bearers) are completely preserved only in two specimens. The transverse processes are unicipital and expanded distally, and articular surface for the rib heads is dumbbell-shaped. On its posterior surface it bears a wide depression that is surrounded by distinct ridges. The base of the transverse process is perforated by a large vertebral arterial

canal. The neural arch is inverted V-shaped in anterior view and deeply concave in dorsal view; it is markedly vaulted posteriorly. Its posterior surface bears a pair of depressions spanning between the neural spine and the postzygapophyses. The spinal nerve foramina are absent. The neural canal is depressed and widened, with small internal projections (spinal cord supports; see Skutschas & Baleeva 2012) on its sides. The neural spine is posteriorly high and ends in a facet for a cartilaginous tip. The angle formed by the neural spine with the centrum is about 40 degrees. The pre- and postzygapophyses vary from round to elongate (Fig. 5K, L). Their articular surfaces are slightly inclined medially. The articular surfaces of the zygapophyseal processes show growth ridges,

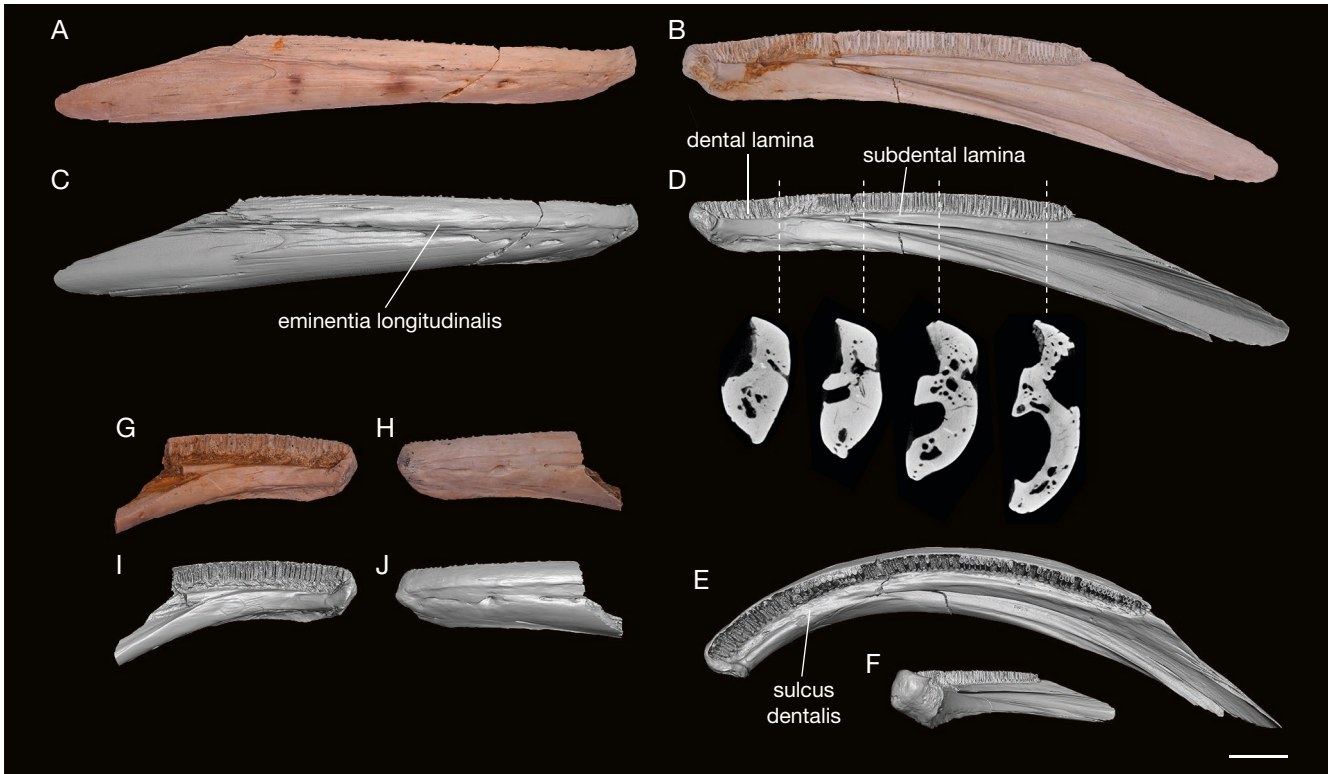


FIG. 3. — Dentaries of *Andrias* sp. from the Belorechensk locality, Late Pliocene: **A-F**, PIN 5882/3, right dentary in labial (**A, C**), lingual (**B, D**) with latter showing cross-sections along the tooth-bearing portion of the dentary, dorsal (**E**), and symphyseal (**F**) views; **G-J**, anterior portion of left dentary, PIN 5882/4, in lingual (**G, I**) and labial (**H, J**) views. **A, B, G, H**, photographs, **C-F, I, J**, 3D models. Scale bar: 1 cm.

which are most visible across the distal portions (Fig. 5M). Most of the observed articular zygapophyseal surfaces have six or seven growth ridges. The interzygapophyseal ridges are not developed.

#### Femur

The femur is represented by its distal portion only (Fig. 6A-G). It is asymmetrically rounded, being convex dorsally and concave ventrally. Cross-sections of the femur (Fig. 6E) show a thick cortex with a few vascular canals and/or erosion cavities in the proximal part of the preserved fragment, i.e., near the diaphyseal region, and a dense vascular network of canals in its distal part. The vascular canals open into grooves on the bone surface.

#### Rib

The rib is represented by a single proximal fragment (Fig. 6H-L). It is anteroposteriorly flattened and medially slightly concave. The articulation surface is hourglass-shaped with narrow upper and wide lower portions. Ridges extend along the upper and lower margins of the rib.

#### COMPARISON AND REMARKS

We suggest that all listed bones come from a single individual because they were found close to each other, correspond well to each other in size and type of preservation, and there is no duplication of elements.

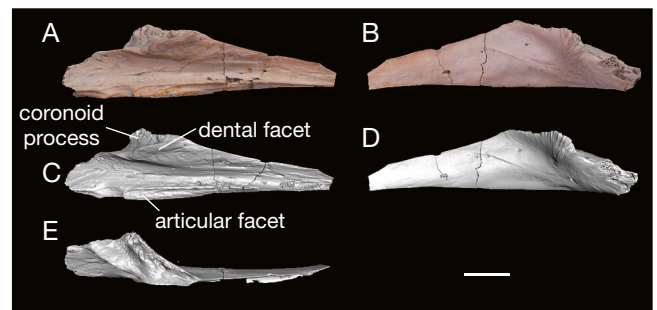


FIG. 4. — Right prearticular of *Andrias* sp. from the Belorechensk locality, Late Pliocene, PIN 5882/5, in: **A, C**, labial; **B, D**, lingual; **E**, dorsal views. **A, B**, photographs, **C-E**, 3D models. Scale bar: 1 cm.

The giant salamander from Belorechensk can be assigned to Cryptobranchoidea and Cryptobranchidae (e.g. Gao & Shubin 2012) in having large body size, frontals strongly overlapped onto parietals, anterolateral extension of frontal, absence of the spinal nerve foramina, and unicapitate trunk ribs.

According to the criteria of Gubin (1991), the giant salamander from Belorechensk can be assigned to Cryptobranchinae based on its relatively small size, tooth bases situated directly above sulcus dentalis, and prezygapophyses situated above the base of the neural spine. However, 80 teeth in the dentary are too many for Cryptobranchinae, which are supposed to have 60-75 teeth (Gubin 1991). On the other hand,



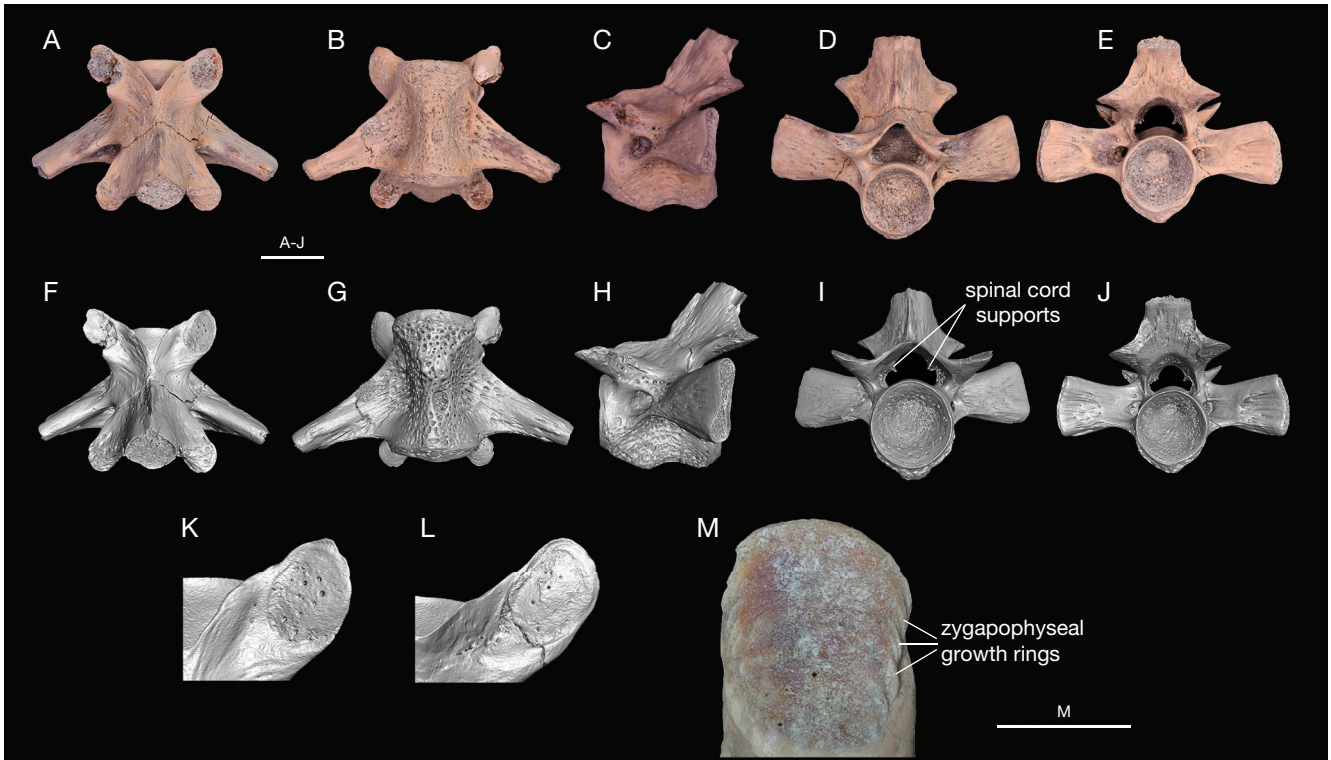


FIG. 5. — Trunk vertebrae of *Andrias* sp. from the Belorechensk locality, Late Pliocene: **A–J**, trunk vertebra, PIN 5882/6, in dorsal (**A, F**), ventral (**B, G**), lateral (**C, H**), anterior (**D, I**) and posterior (**E, J**) views; **K, L**, close ups of right prezygapophyses, PIN 5882/6 and PIN 5882/7; **M**, close up of right prezygapophyseal articular surface showing growth rings, PIN 5882/7. **A–E, M**, photographs; **F–L**, 3D models. Scale bars: **A–J, M**, 1 cm; **K, L**, not to scale.

the cryptobranchine *Andrias scheuchzeri* has been reported to have as many as 82 teeth (Böttcher 1987). Therefore, it seems that the distinction between Cryptobranchinae and Aviturinae (sensu Gubin 1991) has to be revised with respect to this, and possibly to other, characters. The lack of consistent differences in other characters has been mentioned earlier (Vasilyan *et al.* 2013).

The cryptobranchid from Belorechensk clearly differs from the Paleogene species *Aviturus exsecratus* (Gubin 1991; Vasilyan & Böhme 2012) in a number of characters, i.e., its smaller overall size, markedly slender bones, different shapes of the frontals and the cranial cavity, a narrower and deeper sulcus dentalis of the dentary, a lower subdentual lamina, absence of developed presymphyseal sulcus, fewer teeth, a markedly vaulted neural arch of the vertebrae, the absence of interzygapophyseal ridges, a poorly developed accessory alar process, and the presence of a depression on the posterior surface of the transverse process. It differs from another Paleogene cryptobranchid, *Zaissanurus beliajevae* (Chkhikvadze 1982), in having lower subdentual laminae.

The cryptobranchid from Belorechensk differs from the Mio-Pliocene *Andrias scheuchzeri* (Westphal 1958, 1970; Estes 1981; Böttcher 1987) in a greater overlap between the nasals and the frontals, a slender and lower dentary, and a shallower sulcus dentalis. Additionally, it differs from individuals of *A. scheuchzeri* from the Late Miocene of Pécs-Danitzpuszta (Hungary) in its dental symphysis being rhomboid (Fig. 3F) rather than triangular (Szentesi *et al.* 2020: fig 3c).

The cryptobranchid from Belorechensk differs from *Ukrainurus hypsognathus* from the Late Miocene of Ukraine in having its dentary slender and lower, the corpus dentalis and the subdentual lamina both lower, the subdentual shelf anteriorly concave, the lingual crista absent, the neurovascular foramina smaller, the labial side of the dentary nearly smooth, and the dentary facet of the prearticular situated more posteriorly (Vasilyan *et al.* 2013). It shares with *U. hypsognathus* the short and broad shape of the coronoid process of the prearticular and may have extremely elongated, elliptical prezygapophyseal articulation surfaces (Fig. 5L).

Among the Recent genera, the cryptobranchid from Belorechensk can be assigned to *Andrias* based on the frontals excluded from the narial opening (not excluded in *Cryptobranchus*) and a larger angle (about 40 degrees) between the neural spine and the axis of the vertebral centrum (19–37 degrees in *Andrias* vs 15–20 degrees in *Cryptobranchus*) (Estes 1981). Westphal (1958) could not diagnose modern *Andrias* species based solely on osteology. Some relevant characters were mentioned by Meszoely (1966): the shape of the orbit and the separation between the pterygoid and the maxilla. Unfortunately, neither of these features can be observed in the cryptobranchid from Belorechensk. Finally, Estes (1981) could not find any differences between *A. scheuchzeri* and *A. davidianus*, and he placed the latter within *A. scheuchzeri*. Comparisons between the cryptobranchid from Belorechensk with *Andrias japonicus* and *Andrias davidianus* are difficult, because we are not aware of any publications listing osteological characters diagnostic

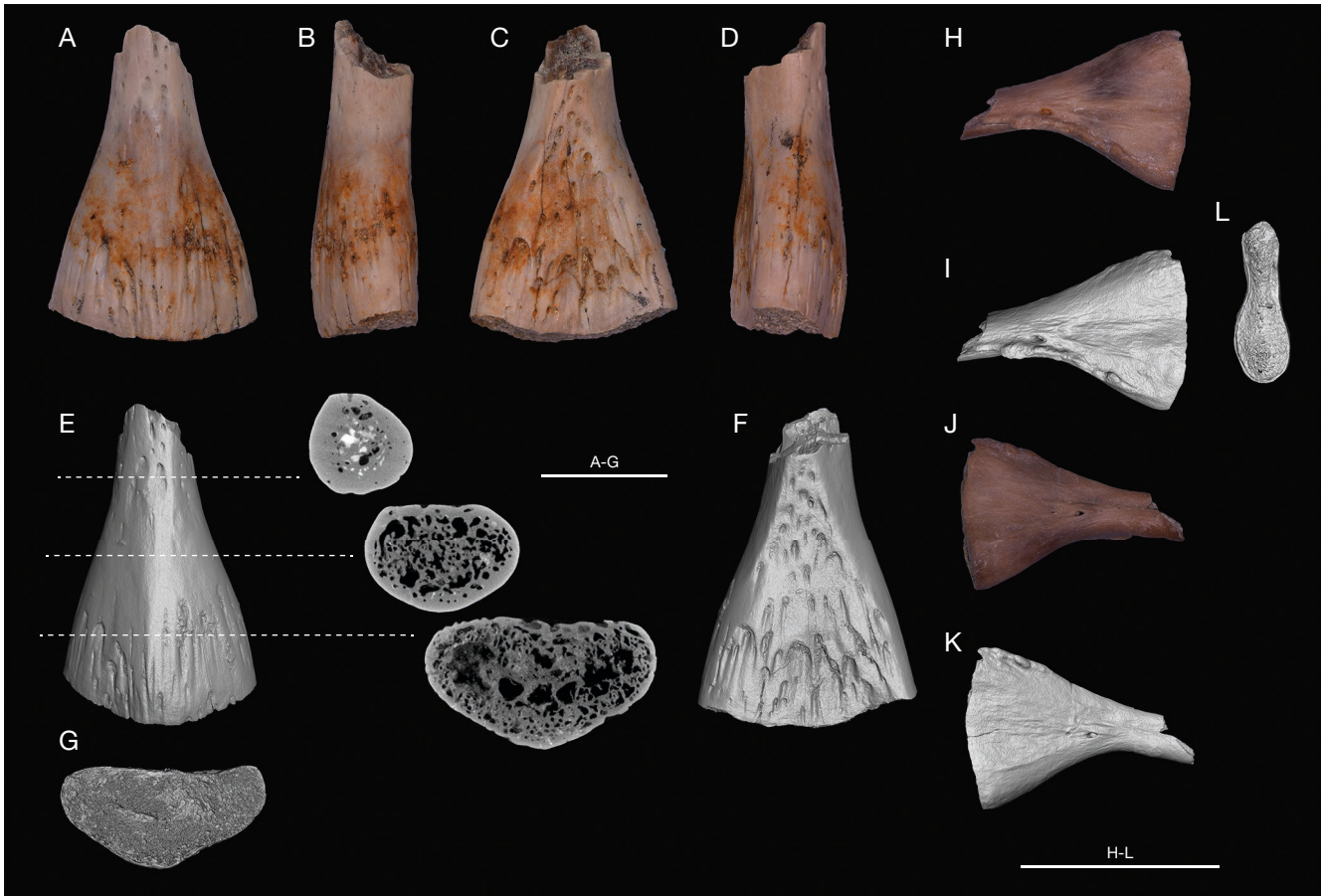


FIG. 6. — Femur and rib of *Andrias* sp. from the Belorechensk locality, Late Pliocene: **A-G**, distal end of left femur, PIN 5882/11, in dorsal (**A**, **E**) with latter showing cross-sections along the femur, anterior (**B**), ventral (**C**, **F**), posterior (**D**), and distal (**G**) views; **H-L**, proximal portion of rib PIN 5882/12 in anterior (**H**, **I**) and posterior (**J**, **K**) views, surface of articulation with vertebra (**L**). **A-D**, **H**, **J**, photographs; **E-G**, **I**, **K**, **L**, 3D models. Scale bars: 1 cm.

of these modern species. Nevertheless, it seems possible to differentiate the cryptobranchid from Belorechensk from modern species of *Andrias* by its frontal not being laterally constricted in the olfactory region and having a longer contact with the nasals (Fig. 7A-C) and by the coronoid process of its prearticular being broad and long (Fig. 4). The cryptobranchid from Belorechensk seems closer to *A. davidianus* in having the cranial cavity of the frontals subtriangular, widest anteriorly and narrowing posteriorly (Fig. 7D, E), whereas in *A. japonicus* it is rhomboid (Fig. 7F). However, until reliable data on the comparative osteology of the modern species of *Andrias* become available and/or new material on the cryptobranchid from Belorechensk appears, we provisionally can assign the latter only to *Andrias* sp.

## DISCUSSION

**INDIVIDUAL AGE OF THE BELORECHENSK GIANT SALAMANDER**  
The *Andrias* from Belorechensk has an internally compact dentary with a few small to middle-size cavities and canals (Fig. 3D), in contrast to the large cavities and canals observed inside the dentaries of most other cryptobranchids (i.e., *Andrias scheuchzeri*, *Ukrainurus hypsognathus*, *Andrias davidianus*, and

*Zaissanurus beliajevae*; Vasilyan *et al.* 2013: fig. 3). Although the amount of internal compactness of the dentary seems to be of taxonomic value (Vasilyan *et al.* 2013), its variation among the studied cryptobranchids can probably be explained by differences in the individual age. However, this hypothesis has to be tested with specimens of different ontogenetic stages. Poor development of cavities and canals in the dentaries from Belorechensk may be a consequence of a younger age of this individual, in comparison to other studied cryptobranchids (Canoville *et al.* 2018; Skutschas *et al.* 2019).

Counting growth rings on the articular surfaces of the vertebral zygapophyseal processes is one of the methods for estimating the individual age of living and extinct tetrapods. It was recently applied to *Aviturus* (Skutschas *et al.* 2020; Grigoriev *et al.* 2022). The *Andrias* from Belorechensk shows six or seven zygapophyseal growth rings on most of its zygapophyseal articular surfaces, suggesting that the animal died approximately during its seventh year of life. Its zygapophyseal growth rings are still widely spaced, which indicates that it died during a stage of rapid growth. Meanwhile, the estimated (based on the length of the dentary) total length of the *Andrias* from Belorechensk is about 90-100 cm. Both modern species of *Andrias* undergo a rapid initial growth until reaching about 60% of their final total length at which point the growth rate



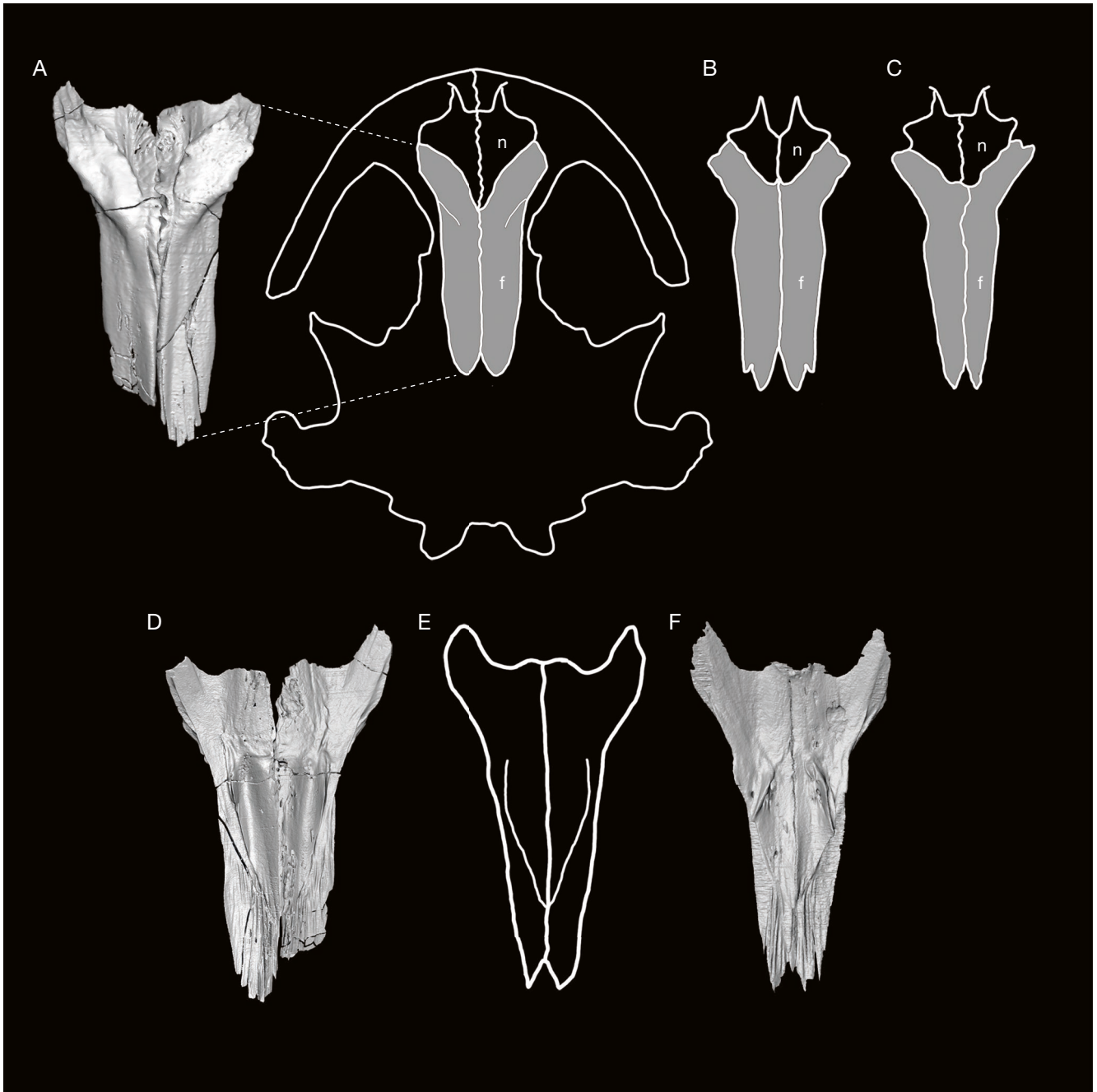


FIG. 7. — Frontals of selected species of *Andrias*: **A, D**, *Andrias* sp. from the Belorechensk locality, dorsal (**A**) view with outline schematic drawing of skull showing proportions of frontals and nasals, and ventral (**D**) view (PIN 5882/1 and 5882/2); **B, E**, *Andrias davidianus* (Blanchard, 1871), recent, dorsal (**B**) and ventral (**E**) views (modified from Vasilyan & Böhme 2012); **C, F**, *Andrias japonicus* (Temminck, 1836), recent, dorsal (**C**) and ventral (**F**) views (PIN H 107). Abbreviations: f, frontal; n, nasal. Images not to scale.

declines (Browne *et al.* 2014). *Andrias davidianus* reaches the total length of 100 cm in eight years, whereas *Andrias japonicus* is usually half as long at the same age (Browne *et al.* 2014). These data suggest that the *Andrias* from Belorechensk had a growth rate more similar to *A. davidianus* than to *A. japonicus*.

**PALAEOECOLOGY OF THE BELORECHENSK GIANT SALAMANDER**  
The Belorechensk vertebrate assemblage includes predominantly inhabitants of forest and coastal biotopes (e.g. the mammals *Apodemus* sp., *Nyctereutes* sp., and *Ursus minimus*),

with a few representatives of steppe and forest-steppe habitats (e.g. southern elephant *Archidiskodon meridionalis* cf. *rumanus*). The bone-bearing layer is lithologically characterized by silty deposits with a number of fossil bones preserved in a position close to an anatomical one (i.e., bones articulated in their natural positions and partial skeletons); e.g. vertebral columns of the salamander *Mioproteus* sp. The remains of freshwater teleost fishes (cf. *Tinca*, *Rutilus* sp., *Silurus* sp., *Esox* sp.; determination by S.V. Kurshakov), amphibians (*Mioproteus* sp. and cf. *Pelophylax*) and turtles (Emydidae indet.), as well as



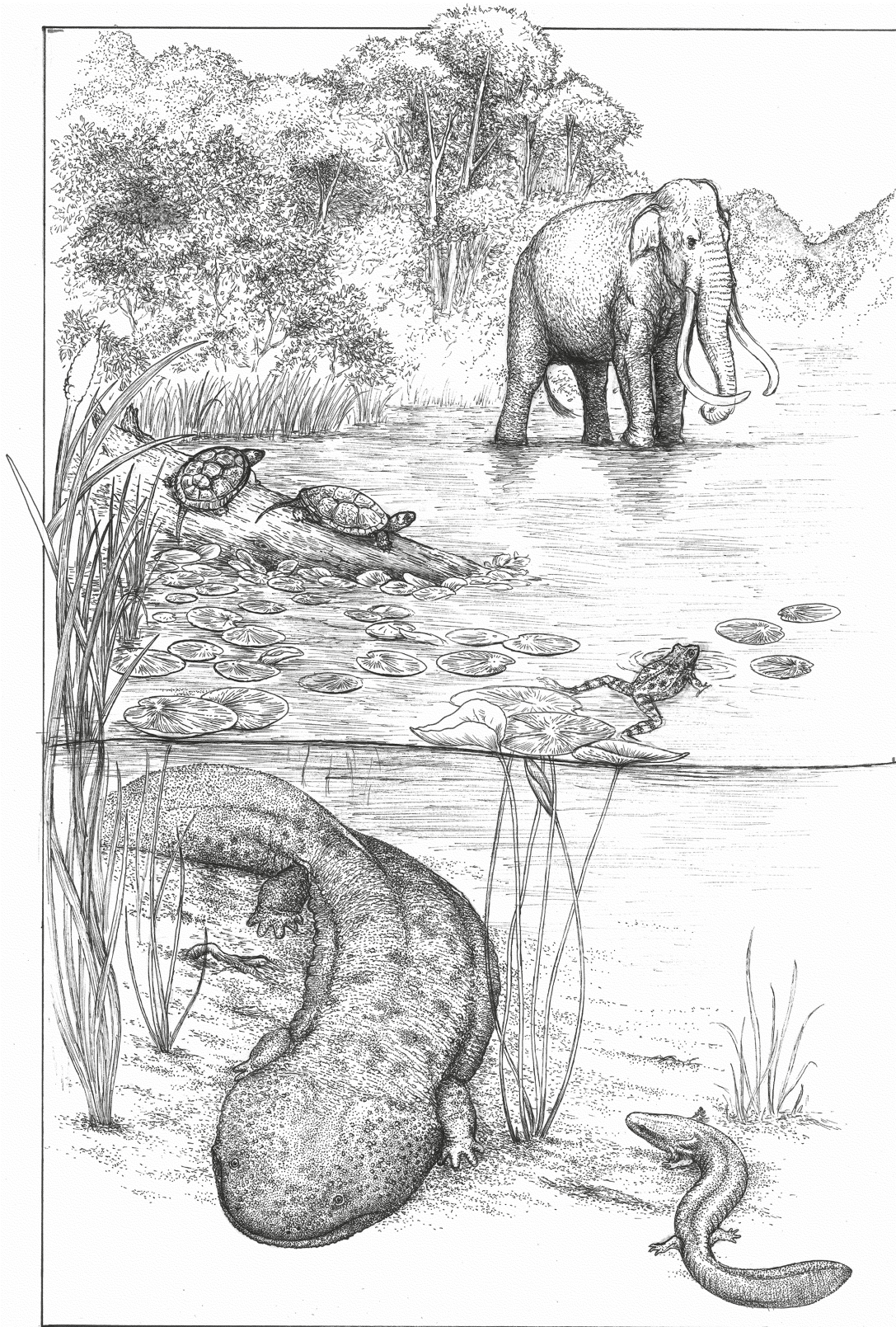


FIG. 8. — Reconstructions of the landscape and herpetofaunal community of the Belorechensk locality. Credits: drawing by A. Ostroshabov.



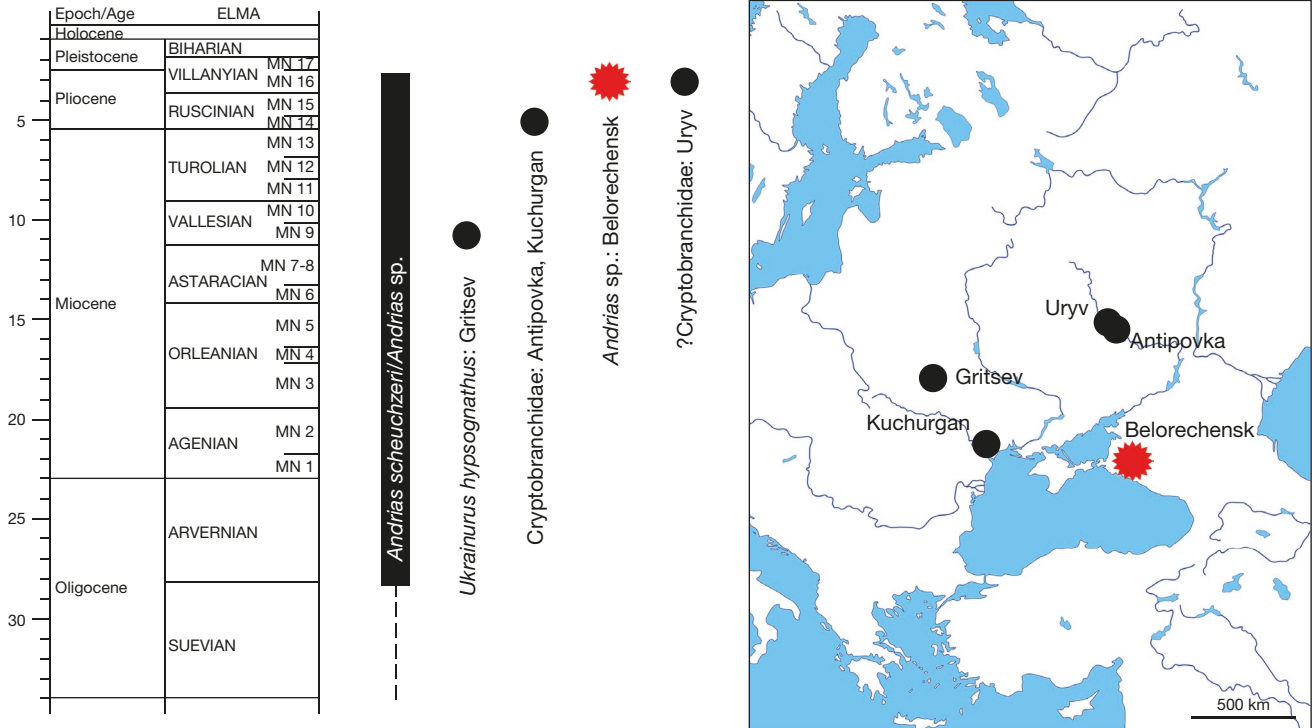


FIG. 9. — Stratigraphic distribution of cryptobranchids for all of Europe and a map showing cryptobranchid occurrences in Eastern Europe discussed in the text.

freshwater stagnophilous mollusks, together with ferruginous plant remains, suggest the Belorechensk salamander inhabited a freshwater and slow-flowing reservoir, the banks of which were covered with forest and shrub vegetation (Fig. 8).

#### THE EAST EUROPEAN GIANT SALAMANDERS

The *Andrias* from Belorechensk greatly extends the known geographic range of giant salamanders in Europe. The most widespread species, *A. scheuchzeri*, is known from a number of Oligo-Miocene localities in Central Europe (Böhme *et al.* 2012). The geologically youngest locality for this species is Willershausen in Germany (Westphal 1967) and is dated to the Late Pliocene, Villanyian, MN 16 (Rietschel & Storch 1974; Manning *et al.* 2019). In Eastern Europe, an undescribed dentary fragment of a cryptobranchid salamander has been listed from the Antipovka locality (MN 14), Voronezh Region of Russia (Averianov 2001). A cryptobranchid record has been mentioned from the Kuchurgan locality (MN 14) in Moldova (Chkhikvadze 1981). A possible cryptobranchid fragment comes from the Uryv locality of Russia (Agadzhanian pers. comm., 2022). The Uryv locality belongs to the Uryvian faunal complex, which is the same age (MN 16a) as the Belorechensk locality. Given that modern cryptobranchid salamanders occur in humid subtropical or temperate areas with temperatures of 8–25°C, their fossils can be useful palaeoclimatic and palaeoenvironmental indicators (Böhme *et al.* 2012). The cryptobranchid records of the Uryvian faunal complex suggest favorable conditions for these animals in Eastern Europe up to the Late Pliocene, i.e., warm humid to very humid climates with mean annual precipitation exceeding 900 mm (Böhme *et al.* 2012). This hypothesis is

corroborated by the presence in the Eastern European localities of the Uryvian faunal complex of other “archaic” taxa, i.e., the amphibians *Latonia*, *Palaeobatrachus*, and *Mioproteus* at the Uryv locality and *Mioproteus* at the Veselovka and the Plevaka localities (Ratnikov 2009; Syromyatnikova 2022). A climatic cooling at the Pliocene–Early Pleistocene transition (MN 16/MN 17) at *c.* 2.6 Ma, certainly disrupted the faunal assemblages of Europe and particularly affected the herpetofaunal communities (Delfino *et al.* 2003). Both the Belorechensk and possible Uryv cryptobranchid specimens are among the geologically youngest and easternmost records of giant salamanders in Europe, from where they disappeared because of the Late Pliocene climatic deterioration (Fig. 9).

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