Polar Records of Chimaeroid Fishes (Holocephali, Chimaeroidei) from the Upper Cretaceous of Eastern Siberia

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Abstract—We describe the discovery of five fragments of chimaeroid tooth plates from the Lower Coniacian deposits (*Volviceramus subinvolutus* Zone) of the Yangoda River, Krasnoyarsk Krai (Eastern Siberia). The material is identified as the 'edaphodontid' *Edaphodon* sp. and the long-nosed chimaera *Harriotta* sp. This is the northernmost known locality for Cretaceous chimaeroids in the world (70.5 degrees north), the palaeo-geographic position of which in the Coniacian is calculated as 71 degrees north. The new findings show that chimaeroid associations including 'edaphodontids' and rhinochimaerids existed in the Late Cretaceous in the polar latitudes of Eastern Siberia as well as in Chukotka (Russian Far East). Moreover, chimaeroid fishes in the terminal Jurassic in Eastern Siberia were already spawning in the polar environment. In the Southern hemisphere, findings of polar chimaeroids are known as early as the Early Cretaceous (Aptian age), and the diversity of polar chimaeroid associations from the Campanian–Maastrichtian of Antarctica (3–4 genera) allow us to expect a greater diversity of polar chimaeroid assemblages in the Northern hemisphere as well.

INTRODUCTION

The nature of "fossil beaks" (=tooth plates of fossil chimaeroid fishes) was discovered by the English geologist William Buckland at the dawn of geology and paleontology (Buckland, 1835). The rapid development of these branches of science in the 19th century in Western Europe and then in North America led to the description of many taxa of Jurassic, Cretaceous and Paleogene chimaeroid fishes and their assemblages—primarily from the Cretaceous deposits of England (Agassiz, 1833–1843; Newton, 1878; Woodward, 1891; Popov, 2008). In Eastern Europe, isolated finds from the end of the 19th century (Rogovich, 1860; Sintzov, 1872) were compensated by the numerous and diverse material accumulated by the end of the 20th century thanks to the research of Soviet and Russian geologists and paleontologists (Nessov and Averyanov, 1996). Known European Cretaceous localities are grouped between 48°–56° N latitude. In Asia, chimaeroid records are very scare and are known mainly from the badlands of western and northern Kazakhstan, localized at latitudes of 43°–53° N (Nessov and Averyanov, 1996). In most of Asia, Cretaceous finds of fossil chimaeroids were previously unknown (Nessov and Averyanov, 1996).

In recent years, new records of Arctic terrestrial and marine vertebrate assemblages were reported from the Cretaceous period in northeastern Eurasia (Kurzanov et al., 2003; Lopatin et al., 2008; Kolosov et al., 2009; Averianov et al., 2020; Bapinaev et al., 2023; Kolosov et al., 2023). These are mainly terrestrial or semiaquatic tetrapods (amphibians, dinosaurs, mammals), but there are also representatives of the aquatic ecosystems of the marginal seas of mainland Asia—plesiosaurs, mosasaurs and sea turtles (Rogov et al., 2019; Grigoriev and Grabovskiy, 2020; Zverkov et al., 2023). The associated remains of chondrichthyan fish have frequently been recorded (Zakharov et al., 1980; Grigoriev and Grabovskiy, 2020), but they have not previously been described or illustrated. Therefore, the discovery by one of the authors (M.A. Rogov) in 2021, of five incomplete chimaeroid tooth plates from the Upper Cretaceous deposits on the Yangoda River in northwestern Eastern Siberia, is of interest. The locality is in the Russian Arctic, 170 km north of Norilsk (Krasnoyarsk Krai) and at a 70.5° N, which makes it the northernmost known Cretaceous chimaeroid locality in Eurasia and in the world (Nessov and Averyanov, 1996; Popov, 2004; Johnson-Ransom et al., 2018).

Despite the fragmentary nature of the material, it can be identified in an open nomenclature and some conclusions can be made about the diversity of polar associations of chimaeroid fish in the Northern Hemisphere in the Late Cretaceous.

The figured tooth plates are housed in the Earth History Museum, Saratov State University (SGU collection no. 155).

GEOLOGICAL BACKGROUND

The described tooth plates of chimaeroid fish were collected in the Lower Coniacian deposits of the Yangoda Uplands, in the western part of the Yenisei-Khatanga Trough, Eastern Siberia (Figs. 1a–1b). Here, during geological surveys in the 1950s, outcrops of Upper Cretaceous deposits were discovered (Saks and Ronkina, 1957). Later, Turonian and Lower Coniacian bivalves of the genus *Inoceramus* were illustrated and described from these sections (Efremova, 1978). The sections and stratigraphic subdivision of the Turonian-Coniacian deposits were later examined and described by Zakharov et al. (1989). The subdivision and correlation of the sections was carried out on the basis of the index macrofauna of ammonites (for the upper Turonian), bivalves (inoceramids) and dinocysts (Zakharov et al., 1989; Lebedeva, 2008), but figures and descriptions of fossils from here remained unpublished, except for the upper Turonian inoceramids, which are not associated to specific sections. The description of individual outcrops also remains unpublished. The paper by Zakharov et al. (1989) contains only a description of members in a composite section, while the outcrops are illustrated as lithological logs, but not described individually.

The Upper Cretaceous deposits of the Yangoda Upland are exposed in the middle reaches of the Yangoda (Dzhangoda) River. The sections of the so-called "upstream site" (according to Zakharov et al., 1989, text-fig. 2) are located along the left tributaries of the Yangoda River (the Turonka and Konyachnaya rivers). Here the Cretaceous beds are strongly influenced by glacial dislocations—they often contain folds, faults, and in some cases the same intervals are repeated within a single section (Zakharov et al., 1989). In general, the sequence of Turonian-Coniacian deposits demonstrates a gradual increase of the sand contents up the section, with a predominance of coastal-marine shallow-water sandy facies in the Coniacian interval. Erosion horizons and bioturbation are common in the section. Inoceramid mollusks dominate among the Coniacian fossils. At some stratigraphic levels, shark teeth and marine reptile bones are also common here (Zakharov et al., 1989; Rogov et al., 2019; Zverkov et al., 2023).

The most frequent finds of chondrichthyan fish remains come from the heavily bioturbated deposits of the Lower Coniacian Member XIV, which, in addition to the shark teeth and chimaeroid tooth plates, also contain bony fish vertebrae and elasmosaurid teeth and bones (Zverkov et al., 2023). In 2021, in Bed 9 of Outcrop no. 2 (coordinates 70°53′40.15″ N, 88°14′03.54″ E; Figs. 1c–1d; numbers of Members, beds and outcrops follow Zakharov et al., 1989), a small collection of elasmobranch teeth was collected, in which the following taxa were identified: (?) *Meristodonoides* sp., *Polyacrodus* sp., *Dwardius* sp., *Archaeolamna* sp. (identifications by E.V. Popov). In addition to fragments of chimaeroid tooth plates and shark teeth, shark vertebrae (including those in sandstone concretions), teeth and vertebrae of bony fish Enchodontidae, and small accumulations of crustacean coprolites were also found. Outcrop 2 was not described during the 2021 fieldwork. This stratigraphic interval was studied in detail in Outcrop 14, but there Member XIV is not so well exposed and no remains of chondrichthyan fish were found in it.

All specimens were collected on the weathered surface of the formation in places where it flattens out on the crest of the section (Fig. 1d). The host rock is yellow medium-grained sand with rare inclusions of phosphatized sandstone, fragments of which massively cover the weathering surfaces (Fig. 1e). In some places, the Member contains levels with ichnofossils of the *Skolithos* ichnofacies, characteristic of a coastal shallow-water environment.

In Member XIV, vertebrate remains are accompanied by inoceramid bivalve mollusks, indicating the Lower Coniacian *Volviceramus subinvolutus* Zone. In addition to the index species, the species *Inoceramus (Inoceramus) schulginae* Efremova, 1978 and *I. (I.) jangodaensis* Efremova, 1978 are quite common here. There are also rare findings of the species *I. (I.) lamarcki* Parkinson, 1819, *I. (I.) monopterus* Efremova, 1978 and *Inoceramus (Cremnoceramus) inconstans* Woods, 1912 (Zakharov et al., 1989). At the same time, it is noteworthy that all inoceramid finds in Member XIV apparently come from other sections (M.A. Rogov, pers. obs.). The age of Member XIV, in which the chimaeroid tooth plates were found at Outcrop no. 2, is substantiated by correlation with other sections, as well as by the finds of Lower Coniacian *Inoceramus* in the underlying and overlying members.

In other localities on the Yangoda River (outcrops nos. 1, 7a, 14, 15a), teeth and bones of Upper Turonian and Lower Coniacian plesiosaurs were collected (Zverkov et al., 2023).

MATERIAL

The five fragmented tooth plates described here were collected using the surface collection technique (walking, crawling sensu Welton and Farrish, 1993). Based on the growths of small spherical crustose lichens, the plates were on the exposed surface for a long time (more than one season). At the same time,
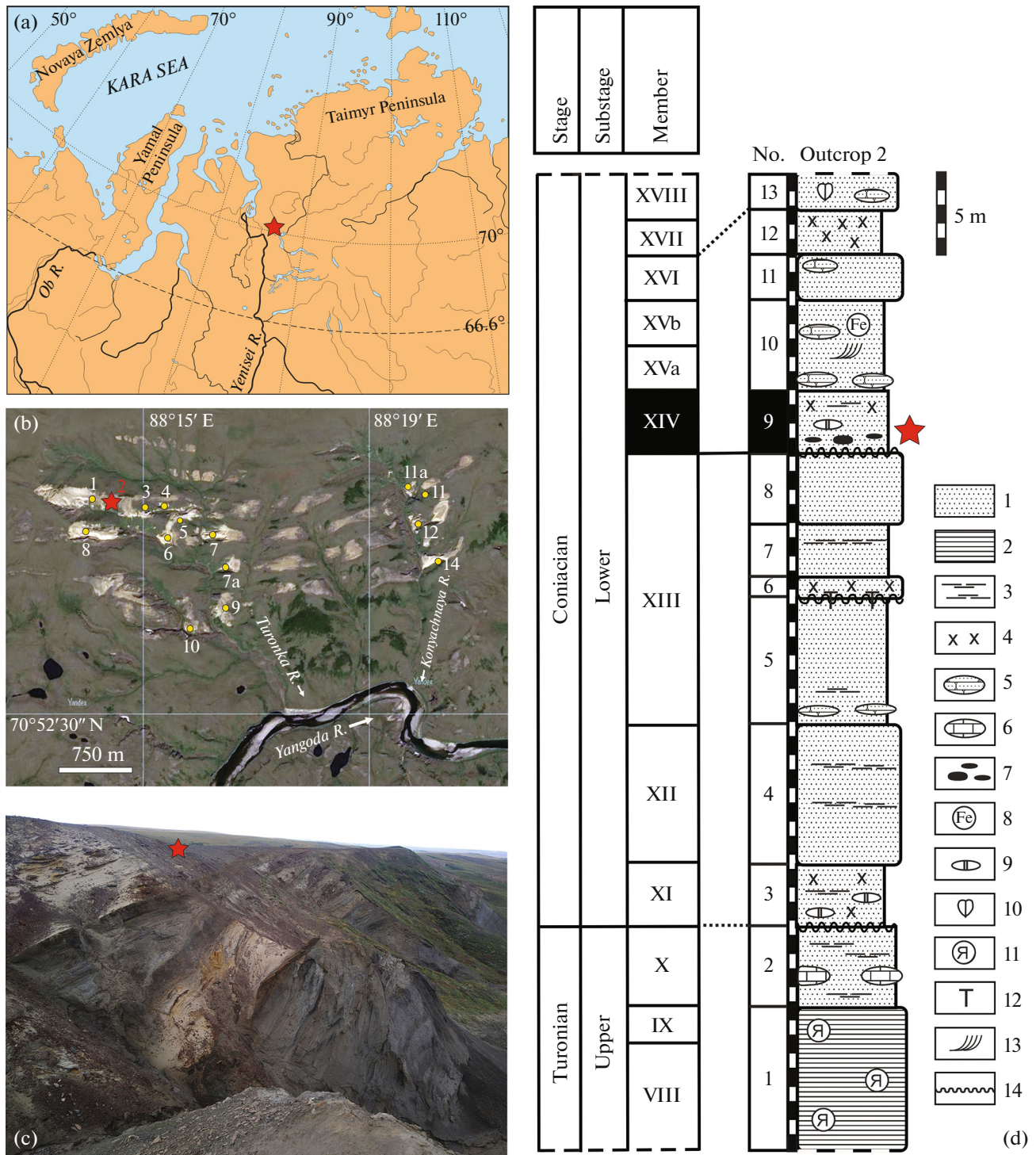
Fig. 1. Geographical and stratigraphic position of the section on the Yangoda River with remains of Arctic Upper Cretaceous chimaeroid fishes: (a) overview map; (b) satellite image (map © Yandex) of the Yangoda Uplands with the position of known Turonian−Coniacian sections of the "upstream site" along the Yangoda River (marked with yellow dots; after: Zakharov et al., 1989) and Outcrop no. 2 (red star) with remains of chimaeroid fishes; (c) general view of Outcrop no. 2 with sand outcrops of Member XIV, where remains of chondrichthyan fishes and marine reptiles were collected on the subhorizontal erosional surface (marked with a red star). Photo by M.A. Rogov, 2021; (d) stratigraphic position and lithology of Outcrop no. 2 with remains of chimaeroid fishes (the level of the find is marked with a red star). Stratigraphy, correlation, numbering of Members of the composite section, lithology and numbering of beds of Outcrop no. 2 are given according to Zakharov et al. (1989). Legend: (1) sand; (2) silty clay; (3) clay bands in sandy beds; (4) leptochlorite; (5−10) concretions: (5) sandstone; (6) limestone; (7) phosphate; (8) ferruginous; (9) siderite; (10) "bull's heart" morphotype; (11) jarosite (after sulfides); (12) ichnofossils; (13) cross bedding; (14) erosion.

the hypermineralized tissue (whitlockin) is dense, white, and very well preserved. Large plates are fragmented, smaller ones have rounded, smoothed edges and bear traces of primary rounding—the whitlockin bodies are well exposed on the basal surfaces (sample SGU, no. 155/373-375). The surfaces of the plates are covered with iron oxides and dendrites of manganese oxides, the latter are also developed along cracks, forming a characteristic spotting of the plates of a dark blue (gray) color. The only vomerine tooth plate (specimen SGU. no. 155/375) differs from the others in color—it may come from a different, less condensed bed within Member XIV or may have been in the weathering zone for a shorter period of time.

TOOTH PLATE TERMINOLOGY

The descriptive terminology and measurements here follow the first author (Popov, 1999, 2003; Popov and Beznosov, 2006; Popov and Shapovalov, 2007, 2021; Popov and Machalski, 2014; Popov et al., 2019, 2020). Some descriptive terms are shown in Fig. 2. Taking into account the poor preservation of the plates, only one control measurement was used—the maximum mesiodistal length of the specimen (L). For hypermineralized tissue (pleromin, according to Ørvig, 1986), which forms crushing areas (tritors), the term "whitlockin" was used, following Smith et al. (2019). Morphological differences in the structure of whitlockin allow recognition of several types in its structure: vascular, laminated and solid (Popov et al., 2020). The laminated whitlockin is considered to be composed of two morphotypes: transversally laminated (present in the structure of the plates described here, specimens SGU, nos. 155/371, 373−375) and diagonally laminated (for example, in the structure of the symphyseal tritor of the mandibular plates of *Elasmodus* spp.) (Popov, 2004; Popov and Efimov, 2012).

The authors follow the system of chimaeroid fishes according to Didier (1995); the fossil family 'Edaphodontidae' Owen, 1846 is considered as a composite (Popov and Beznosov, 2006).

DESCRIPTION OF TOOTH PLATES

Specimen SGU no. 155/371 (Figs. 2a−2e) is a fragment of the beak of the right mandibular plate, 12.1 mm in mesio-distal length. About half of the fragment's volume is occupied by the body of the symphyseal tritor, composed of a transversely laminated whitlockin. The whitlockin body is narrow, weakly falcate occlusally, with a maximum thickness of 3.8 mm. The whitlockin units are well defined, curved, and of uniform thickness. Parallel to the symphysial surface is the body of the "beak tritor", rounded in profile, about 0.8 mm in diameter, composed of an undeveloped vascular whitlockin—poor development of septa and vascular tubules brings the tissue closer to the solid whitlockin (sensu Popov et al., 2020). The whitlockin

of the "beak tritor" is located close to the whitlockin of the symphysial tritor near the symphysial margin of the latter.

The combination of a closely spaced short and falcate symphyseal tritor and a "beak tritor" is unique to the mesial part of the mandibular plate of Cretaceous and Paleogene chimaeroids of the genus *Edaphodon* Buckland, 1835 (Newton, 1878, pl. 2, figs. 1, 10; pl. 6, fig. 1; pl. 7, fig. 2, figs; Woodward, 1911, pl. 40, figs. 4a−4b, pl. 41, figs. 1−1a; Stahl, 1999, figs. 143C, 148G, I; Stahl and Parris, 2004, figs. 1−3, 2−1; Popov and Machalski, 2014, figs. 6 A1, A3, A4, B1, B3; Popov, 2021, figs. 3D, 3E). This fragment can be classified as *Edaphodon* sp.

Another fragment of the plate (SGU, no. 155/372, mesio-distal length 26.9 mm) can be attributed to the same taxon; it is the body of a vascular whitlockin, up to 5.5 mm thick (Figs. 2f−2j). The body is slightly narrowed laterally, the preserved symphyseal margin is rounded, and a bevel of the surface is observed in the mesial area—apparently, the place of the distal border of the tritor functional region. Judging by the shape, the body of the whitlockin is the posterior-inner tritor of the right palatine plate of *Edaphodon* sp. The species *Edaphodon mantelli*, *E. sedgwicki*, *E. agassizi*, and *E. crassus* are known from the Turonian−Coniacian deposits of England (the Middle Chalk Formation and the lower part of the Upper Chalk Formation) (Woodward, 1891, 1911), however, *Edaphodon* species from these deposits require revision (Popov, 2008).

Three other, smaller plates (SGU, no. 155/373−375) represent a single taxon, judging by their similar sizes and the presence of a transversally laminated whitlockin in the tritors, and the shape and combination of preserved tritors.

Specimen SGU, no. 155/373 (Figs. 2k−2o) is an incomplete, relatively small left mandibular plate, with a mesio-distal length of 15.4 mm. The plate has a thin symphyseal part and, apparently, a narrow symphyseal tritor (traces of its whitlockin are absent in the mesial part of the fragment). Most of the occlusal surface is occupied by a suboval in profile median tritor composed of vascular whitlockin, 5 mm wide, with a maximum thickness of 2.2 mm. The anterior-outer tritor composed of transversaly laminated whitlockin, 2.7 mm wide, is pressed mesio-laterally to the median tritor. The lateral half of the median tritor is composed of a loosely organized vascular whitlockin, whereas in the symphysial half of the tritor and in its mesial third the vascular tubules are united to varying degrees, forming an undeveloped laminated whitlockin (Fig. 2k). The other tritors have not been preserved.

Specimen SGU, no. 155/374 (Figs. 2p−2t) is a similar fragment of the right mandibular plate, but in a worse state of preservation. The mesio-distal length of the specimen is 10.6 mm. Most of it is composed predominantly of the vascular mesan tritor, rounded in profile, with an undeveloped laminated whitlockin
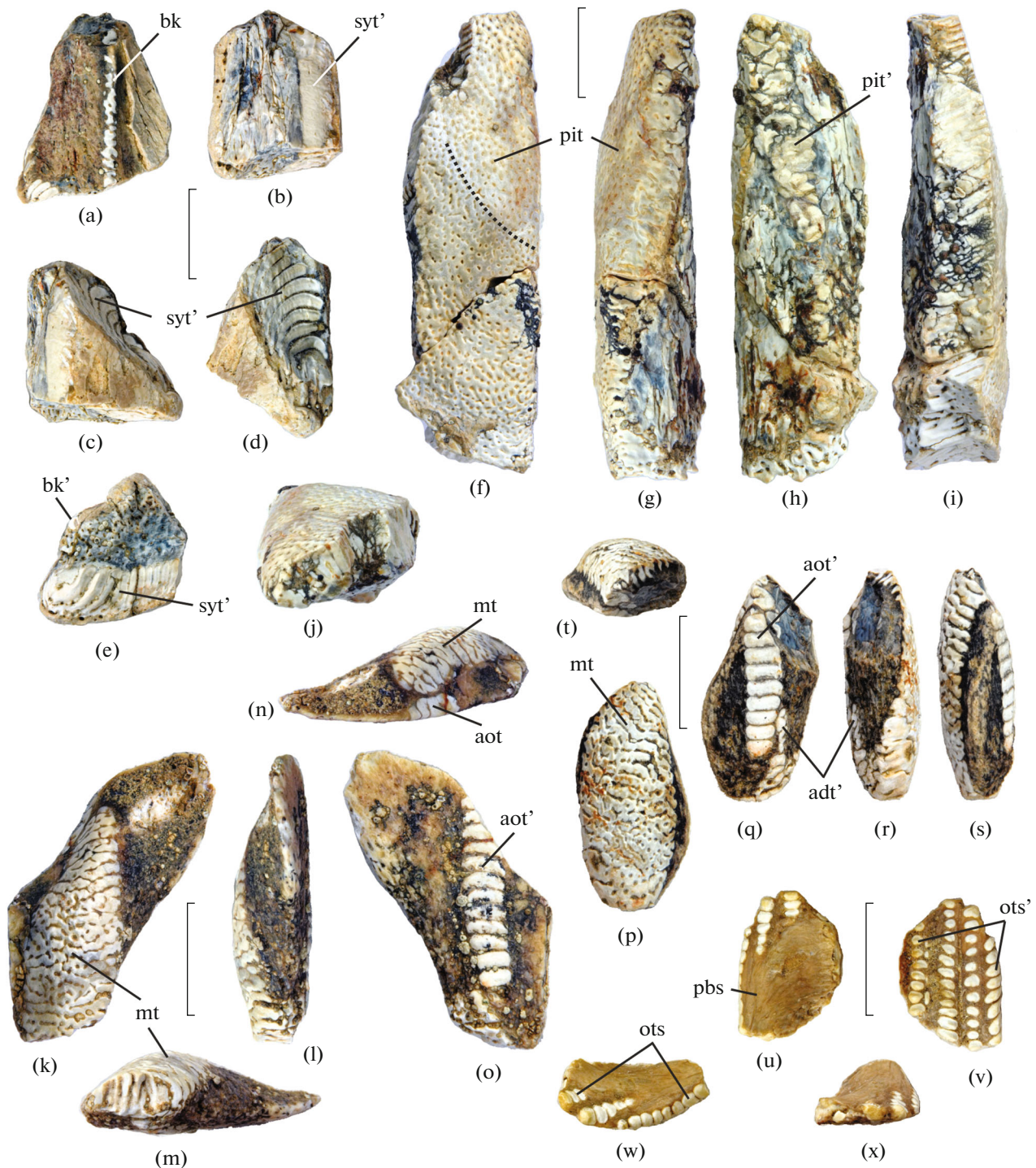
Fig. 2. Tooth plates of chimaeroid fishes from the Lower Coniacian deposits along the Yangoda River (Outcrop no. 2, Member XIV, Bed 9); Krasnoyarsk Krai, Eastern Siberia: (a–e) specimen SGU, no. 155/371, fragment of the beak of the right mandibular (L = 12.1 mm) plate of *Edaphodon* sp.: (a) symphyseal view; (b) lateral view; (c) basal view; (d) symphyseal-basal view; (e) lingual view; (f–j) specimen SGU, no. 155/372, fragment (?) of the palatine plate (L = 26.9 mm) plate of *Edaphodon* sp.: (f) occlusal view (the boundary of the functional wear surface of the tritor shown by a dotted line); (g) symphyseal view; (h) basal view; (i) lateral view; (j) mesial view; (k–o) specimen SGU, no. 155/373, incomplete left mandibular (L = 15.4 mm) plate of *Harriotta* sp.: (k) occlusal view; (l) symphyseal view; (m) lingual view; (n) mesial view; (o) basal view; (p–t) specimen SGU, no. 155/374, fragment of left mandibular (L = 10.6 mm) plate of *Harriotta* sp.: (p) occlusal view; (q) basal view; (r) symphyseal view; (s) lateral view; (t) mesial view; (u–x) specimen SGU, no. 155/375, incomplete right vomerine tooth plate (L = 7.1 mm) of *Harriotta* sp.: (u) occlusal view; (v) basal view; (w) lateral view; (x) mesial view. Scale bar 5 mm. Legend: adt—accessory tritor; aot—anterior-outer tritor; bk—beak tritor; mt—median tritor; ots—outer tritor series; pbs—parabasal surface; pit—posterior-inner tritor; syt—symphyseal tritor; bk', syt' etc.—the apostrophe (') marks the whitlockin bodies extending to the corresponding tritors, secondarily exposed on the surface as a result of weathering or observed in the profile of the plate (mesially, lingually).

in the mesal part. The body of transversally laminated whitlockin of the anterior-outer tritor, as well as the body of a small additional tritor (Fig. 2q) adjoin the body of the median tritor basally.

The fragment of the right vomerine plate (specimen SGU, no. 155/375) is the smallest tooth plate in size, with a mesio-distal length of 7.1 mm (Figs. 2u−2x). The distal half of the plate is preserved, with a low parabasal surface (contact with the corresponding palatine tooth plate) and four most distal tritors of the outer tritor series. The whitlockin of the series is transversaly laminated, of uniform width, 0.7−1 mm, well expressed. The three most distal lines have uniform inter-tritoral diastemas, while the fourth line (counting from the most distal) is slightly more distant and is associated with the lateral intrusion of the additional whitlockin body (Fig. 2v).

The combination of a vascular median tritor and a small anterior-outer tritor of laminated whitlockin on the mandibular plates of SGU no. 155/373−374, as well as an outer tritor series of laminated whitlockin on the vomerine plate of SGU no. 155/375, brings the studied material closer to the tooth plates of the extant long-nosed chimaera *Harriotta raleighana* Goode et Bean, 1895 (Herman et al., 2001, pls. 12−13; Smith et al., 2019, figs. 1B−1D, 16A−16L, 17A−17E; Popov et al., 2020, text-fig. 3H). The absence of traces of whitlockin in the mesial direction from the median tritor in specimen SGU no. 155/373 (Fig. 2k, 2n) suggests a shorter symphyseal tritor series, as in the mandibular plates of *Harriotta gosseleti* (Winkler, 1880) from the Oligocene of Belgium (Popov et al., 2020, text-fig. 3G). A holomorphic small (with a body length of about 20 cm) chimaeroid *Harriotta lehmani* Werdelin, 1986 is recorded from the Santonian Lagerstätte Sahel Aalma in Lebanon (Werdelin, 1986; Stahl, 1999; George et al., 2024). This skeletal imprint clearly shows the structure of the left palatine tooth plate (L = 10 mm), and partially—the right palatine and left mandibular plates (L = 10 mm); the latter, like the Yangoda specimens SGU, no. 155/373−374, is characterized by a vascular median tritor and a transversally laminated anterior-outer tritor (Werdelin, 1986, text-fig. 2, Pl. 1, fig. A). The *Harriotta lehmani* imprint bears an elongated unpaired nasal cartilage, a typical Rhinochimaeridae skull structure (Didier et al., 2012), and the structure of the palatine plate is close to that of modern Harriottinae[1]. Isolated tooth plates of similar structure are common in the Cenomanian, Campanian, and Danian deposits of the Volga region (Popov,

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[1] The subfamily Harriottinae Gill, 1898 (sensu Didier, 1995) includes two genera: *Harriotta* Goode et Bean, 1895 (three extant species) and the genus *Neoharriotta* Bigelow et Schroeder, 1950 also with three recent species. The genera differ in the presence of an anal fin in *Neoharriotta*. The structure of the dental system of both genera is almost identical, although some authors recognize generic differences (Herman et al., 2001). *Neoharriotta* is not known in the fossil record (Stahl, 1999).
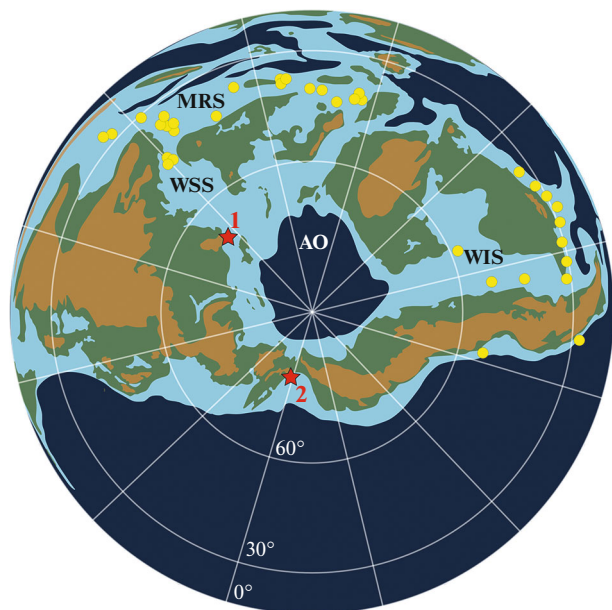
2004). Based on the totality of data, specimens SGU, nos. 155/373−375 can be classified as *Harriotta* sp.

The laminated whitlockin is also developed in the dentition of chimaeroid fishes of the genus *Elasmodus* Egerton, 1846, which are common in the Upper Cretaceous (Averianov, 2001). However, mandibular plates of Cretaceous *Elasmodus* possess a wide symphyseal tritor composed of a diagonally laminated whitlockin or of its combination with a transversally laminated whitlockin, and small and separate lamellar "pearl" tritors are usually present along the labial margin, mesial and distal to the anterior-outer tritor (Averianov and Glickman, 1994, fig. 1; Averianov, 2001, text-fig. 1c, text-fig fig. 2c, pl. 10, figs. 2a, 7b, pl. 11, fig. 3b). The vomerine plates of the Albian-Santonian species of *Elasmodus* (*E. rossicus, E. sinzovi*) have an outer tritor series of a combined structure—transversally laminated in the medial part and vascular in the extreme distal units (Popov and Machalski, 2014, text-figs. 7 B1−B3), while the Campanian representatives of *Elasmodus* (*E. avirostris*) lack vascular whitlockin in the structure of the outer tritor series, but the serial units are asymmetrical, more oval in profile and larger (Averianov, 2001, text-fig. 2b).

This is not observed on the vomerine plate SGU, no. 155/375, the preserved distal part of which has a well-defined transversally laminated structure, and the tritors of the series have a similar diameter and are distributed evenly (Fig. 2u−2x). In addition, the plates of *Elasmodus* are on average significantly larger.

DISCUSSION

Polar records of Chimaeroids in the Northern Hemisphere

The paleolatitude of the sections on the Yangoda River discussed here was previously calculated as 70.9° N (for the group of localities: Rogov et al., 2019) or as 71° N for Outcrop no. 2 (Zverkov et al., 2023). Thus, in the Coniacian age, this part of the water basin was also located beyond the Arctic Circle, like the modern localities. The limited material does not allow the chimaeroid fish association to be characterized in full, but even such fragmented material shows that it included two genera of two families—'Edaphodontidae' (*Edaphodon* sp.) and Rhinochimaeridae (*Harriotta* sp.).

Polar chimaeroid fishes are also found in Chukotka. Here, a palatine tooth plate of the "edaphodontid" *Ischyodus* sp. was found in the deposits of the Ginterovskaya Formation (Cenomanian-Lower Turonian) of the "Zolotaya Vtoraya" section (determination by E.V. Popov in the paper: Grigoriev and Grabovskiy, 2020). In addition to a chimaeroid tooth plate, teeth of elasmobranchs were also found in the bed, including the taxa: *Cretoxyrhina* sp., *Palaeoanacorax* sp., *Archaeolamna* sp., *Synechodus* sp., *Eostria-*

Fig. 3. Paleogeographic map of the Northern Hemisphere in the Late Cretaceous (Turonian), modified after Scotese, 2021. The main groups of Upper Cretaceous chimaeroid fish localities in northern Eurasia and North America are shown as yellow circles (Nessov and Averianov, 1996; Averianov, 2001; Popov, 2004; Johnson-Ransom et al., 2018), the polar localities discussed in the discussion are shown as red stars (Grigoriev and Grabovskiy, 2020; this work): (1) Yangoda, Outcrop no. 2; (2) Zolotaya Vtoraya. Abbreviations: AO, Arctic Ocean; WIS, Western Interior Seaway; WSS; West Siberian Sea; MRS; Middle Russian Sea.

tolamia subulata*, *Polyacrodus* sp. and *Squatina* sp. The species *Eostriatolamia subulata* is characteristic of the Cenomanian of Europe, and a certain part of the assemblage is typical of the Cenomanian of the Russian Plate (Biryukov, 2018, 2024).

The Zolotaya Vtoraya locality is located at 65° N, while the paleolatitude for the Turonian is calculated as 76° N (Grigoriev and Grabovskiy, 2020). Thus, the two localities in the Asian part of Russia are paleopolar, they are located significantly north of the known localities with chimaeroid remains in Eurasia and North America (Fig. 3). Summarizing the data for these two localities shows that in the Late Cretaceous, associations of chimaeroid fishes existed at polar latitudes of Asia, consisting of at least 2−3 taxa, including relatively more diverse "edaphodontids" (*Ischyodus, Edaphodon*), as well as rhinochimaerids (*Harriotta*).

Unlike marine reptiles (mosasaurs, plesiosaurs) with presumed seasonal latitudinal migrations for their Arctic representatives (Rogov et al., 2019; Grigoriev and Grabovskiy, 2020; Zverkov et al., 2023), significant latitudinal migrations are not known for extant chimaeroids, as all callorhinchid species are locally seasonally migratory and make inshore migrations for breeding and spawning, to shallower waters and river

mouths (Didier et al., 2012). Hence, modern callorhinchids are commercially traded. Large individuals of another species of commercially traded chimaerids (*Hydrolagus colliei*) also make seasonal migrations to shallow waters; moreover, this feature of their biology is more often recorded with increasing latitude (Mathews, 1975; Quinn et al., 1980). Such a strategy could have existed in the Cretaceous "edaphodontids", as the closest group to extant callorhinchids (Popov, 2004)[2]. At the same time, it can be assumed that chimaeroids lived in polar conditions of seasonally alternating continual day and night, but may have migrated to shores or rivers during the polar day for spawning, like extant elephant chimaeras (*Callorhinchus* spp.) do in the southern temperate latitudes (Gorman, 1963; Last and Stevens, 1994; López et al., 2000).

In Eastern Siberia, near the settlement of Zhigansk (Lena River), three localities are known (Nuorda River, Chonoko Cape and Porog Cape: Nessov and Averyanov, 1996) with numerous imprints of egg cases of elephant fish *Callorhinchus rossicus* Voronetz (=*Chimaerotheca rossica*). The capsules come from the Upper Jurassic (Middle Volgian, *Dorsoplanites maximus* Zone) sandstones of the "*Aucella* horizon" of the Chonoko Formation (Voronets, 1952; Test et al., 1962; Obruchev, 1966; Zinchenko et al., 1978). An abundant occurrence is confirmed by additional collections by one of the authors (MAR) at the Porog locality in 2013 (SGU, coll. no. 155). All this may indicate the existence of spawning conditions for chimaeroid fish here in ancient times, in the conditions of coastal shallow waters. The paleolatitude of the area of finds for the end of the Jurassic period (143 million years ago) is calculated as 73°−77° N[3], which also characterizes the paleoaquatic area near the settlement of Zhigansk as paleopolar. This indicates that at the end of the Jurassic period in Eastern Siberia, chimaeroid fish already spawned in polar conditions and, perhaps, this ability was preserved until the Late Cretaceous epoch and is indirectly reflected in polar localities with tooth plates (Yangoda, Zolotaya Vtoraya).

The presence of chimaeroid remains in the Middle Volgian and Cenomanian−Coniacian deposits that accumulated in polar latitudes is consistent with the climate of these time intervals. The Volgian time is one of the warmest in the Jurassic, which is confirmed by both isotopic and paleontological data (Vakhrameev, 1982; Dzyuba et al., 2018; Rogov et al., 2019). The

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[2] This is also indirectly indicated by the large number of locations of Cretaceous chimaeroid fishes in the shallow epicontinental seas and straits of Northern Eurasia (Fig. 3), in many of which callorhinchids (*Callorhinchus*) are found in association with the dominant "edaphodontids" (Nessov and Averianov, 1996; Popov, 2004, 2008).

[3] The paleolatitude was calculated using the Paleolatitude.org online calculator (van Hinsbergen, 2015), based on the standard paleomagnetic grid (Torsvik et al., 2012).

Late Cretaceous, especially the Cenomanian−Coniacian interval, is also considered the warmest in the Cretaceous period. Although most of the available information on the climate of the Late Cretaceous is based on the interpretation of data from middle and low latitudes (Burgener et al., 2023; Price and Sheng, 2025), the available paleontological and isotopic indicators of climate in high-latitude sections are consistent with the idea of a warm climate during this epoch (Jenkyns et al., 2004; Spicer et al., 2008). The recently obtained data on the composition of high-latitude floras, the fauna of marine vertebrates, as well as preliminary determinations of the isotopic composition of oxygen in the rostra of Turonian−Coniacian belemnites in Siberia (Herman et al., 2019; Rogov et al., 2019; Zverkov et al., 2023) also confirm a warm climate at high latitudes at this time.

Polar Records of Chimaeroids in the Southern Hemisphere

The oldest record of chimaeroids in polar paleoenvironments dates back to the Aptian of southern Australia, where a tooth plate of *Edaphodon eyrensis* Long, 1985 was described from the Bulldog Shale. This single find was recently assigned to the Australian endemic genus and species *Ptyktoptychion eyrensis* (Long, 1985) (Popov, 2021). Calculation of the locality position indicates a polar latitude (66°−69°S) for the Aptian (Popov, 2021), and finds of growth-banded wood, glendonites, and glacial erratics in the host deposits suggest a paleoenvironment with seasonally cool/cold conditions and possible winter freezing (Dettmann et al., 1992; Kear, 2006; Alley et al., 2019).

Another polar association of the western Gondwana shelf is known from the Campanian-Maastrichtian (Santa Marta, Snow Hill Island and López de Bertodano Formations) of the islands near the Antarctic Peninsula (Seymour, James Ross, and Vega Islands) and includes 3−4 genera (for different formations) of "edaphodontids", callorhinchids and ?rhinochimaerids (Otero et al., 2013, 2014; Gouiric-Cavalli et al., 2015). This association is comparable in diversity with the associations of the temperate latitudes of the Northern Hemisphere, for example, five genera are known from the Campanian of the Trans-Urals (Popov et al., 2021), and four genera and five species of chimaeroids are known from the terminal Maastrichtian−Danian of New Jersey, USA (Popov, 2010). This suggests that targeted collections of chimaeroid fish remains in the Arctic latitudes of northern Eurasia may yield new material, while the diversity of Arctic chimaeroid fish associations may be comparable to that of already known associations in both the temperate latitudes of the Northern Hemisphere and the polar latitudes of the Southern Hemisphere.

ETHICS APPROVAL AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

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