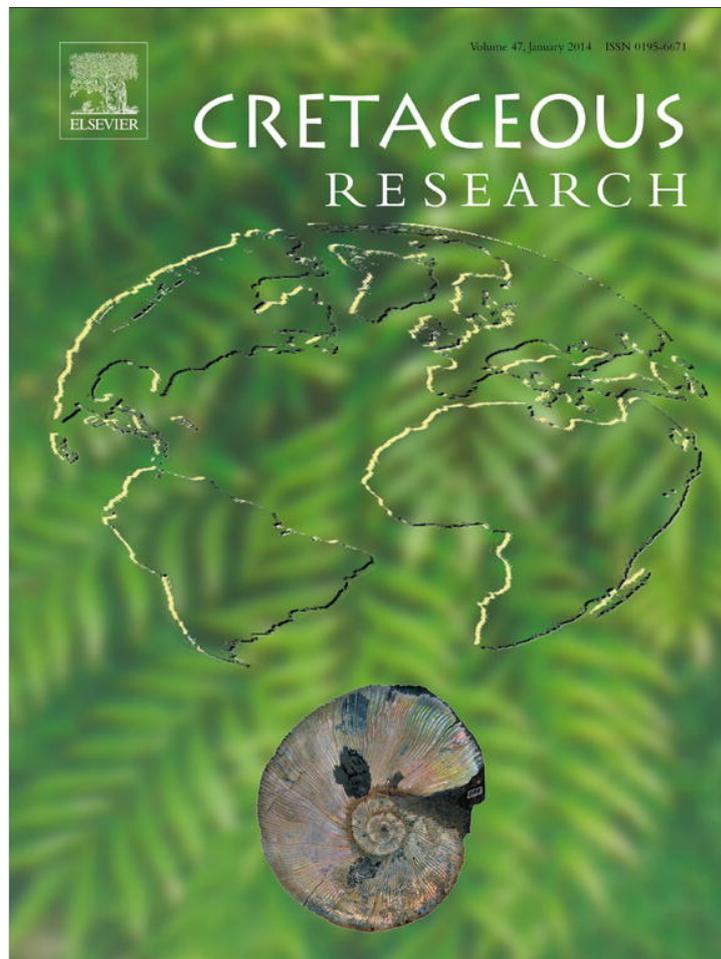


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Late Albian chimaeroid fishes (Holocephali, Chimaeroidei) from Annapol, Poland



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ABSTRACT

Remains of Late Albian chimaeroid fishes (Holocephali, Chimaeroidei) are described from the mid-Cretaceous condensed succession of the Annapol anticline, Poland. The described material consists of dental plates, dorsal-fin spines and a single frontal clasper. These remains are assigned to five genera and seven species of 'edaphodontids', namely *Ischyodus thurmanni*, *Ischyodus* aff. *bifurcatus*, '*Ischyodus incisus*', *Elasmodus* sp., *Elasmodectes* sp., *Lebediodon oskolensis* and *Edaphodon sedgwickii*. Most of these taxa are recorded from Poland for the first time, documenting a much greater regional chimaeroid diversity than previously recognised. In terms of taxonomic composition, the Annapol chimaeroid fauna is intermediate between coeval assemblages from the Cambridge Greensand (England) and from Belgorod Province, Russia, having more taxa in common with the latter.

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1. Introduction

Chimaeroids (suborder Chimaeroidei) constitute a compact group of holocephalian cartilaginous fishes (Holocephali). In Recent faunas, this suborder is represented by three families, six genera and 50 species (Didier, 1995, 2004; Web-project 'Catalogue of Life', www.catalogueoflife.org) that inhabit mainly deep waters (rhinochimaerids, chimaerids) or nearshore environments (callorhynchids).

In fossil chimaeroid material isolated dental plates (two pairs in the upper jaw – vomerine and palatine plates; one pair in the lower jaw – mandibular plates) predominate. Fin spines and frontal claspers are less common, and extremely rare are egg case imprints and (near-)complete skeletons, such as those from the Upper Jurassic of Germany and the Upper Cretaceous of Lebanon and England. Dentitions are the commonest and best preserved remains usually found; these provide the basis for taxonomy and phylogenetic research.

The earliest fossil records of chimaeroids are from the Upper Triassic of northern Eurasia, e.g., egg case imprints from the Carnian of Yakutia, Russian Far East (Vozin, 1968) and dental plates from the Norian of the North Ice Ocean archipelago (Popov et al., 2009).

Sporadic finds are known from the Pliensbachian (Ward and Duffin, 1989) and Toarcian (Duffin, 1995; Stahl, 1999) of western Europe. From the Aalenian onwards, chimaeroids have accounted for stable assemblages, experiencing two acmes, one during the Callovian (up to 11 genera; see Popov, 2011) and another during the mid-Cretaceous (Albian–Cenomanian, up to 14 genera; see Nessov and Averianov, 1996a; Popov and Averianov, 2001). The mid-Cretaceous also is the period with the highest ecological diversity amongst the Chimaeroidei and a wide variety of functional and morphological types of dentition. These ranged from primitive crushing types (*Callorhynchus*), through more advanced ones (*Ischyodus*, *Edaphodon* and allies), up to highly specialised cutting dentitions (*Elasmodectes*, *Stoiodon* and *Lebediodon*).

The most comprehensively studied mid-Cretaceous chimaeroid assemblages are those from western Eurasia. These are faunas from the Albian (Gault and Upper Greensand) of England (Newton, 1878; Woodward, 1891), the Albian–Cenomanian of Belgorod Province, Russia (Nessov and Averianov, 1996a), the Cenomanian of the Volga River basin, Russia (Popov, 2004) and the Cenomanian (Lower Chalk) of England (Newton, 1878; Woodward, 1911). Mid-Cretaceous chimaeroids are also known from Lithuania (Dalinkevicius, 1935) and France (Sauvage, 1867; Leriche, 1902). Additionally, two assemblages have been recorded from the Southern Hemisphere, i.e. from the Aptian and Albian of Queensland, northeast Australia (Lees, 1986; Bartolomai, 2008) and from the Albian–Cenomanian of Western Australia (Popov, 2011). Of the mid-Cretaceous chimaeroid assemblages listed above, two acmes of generic diversity have been

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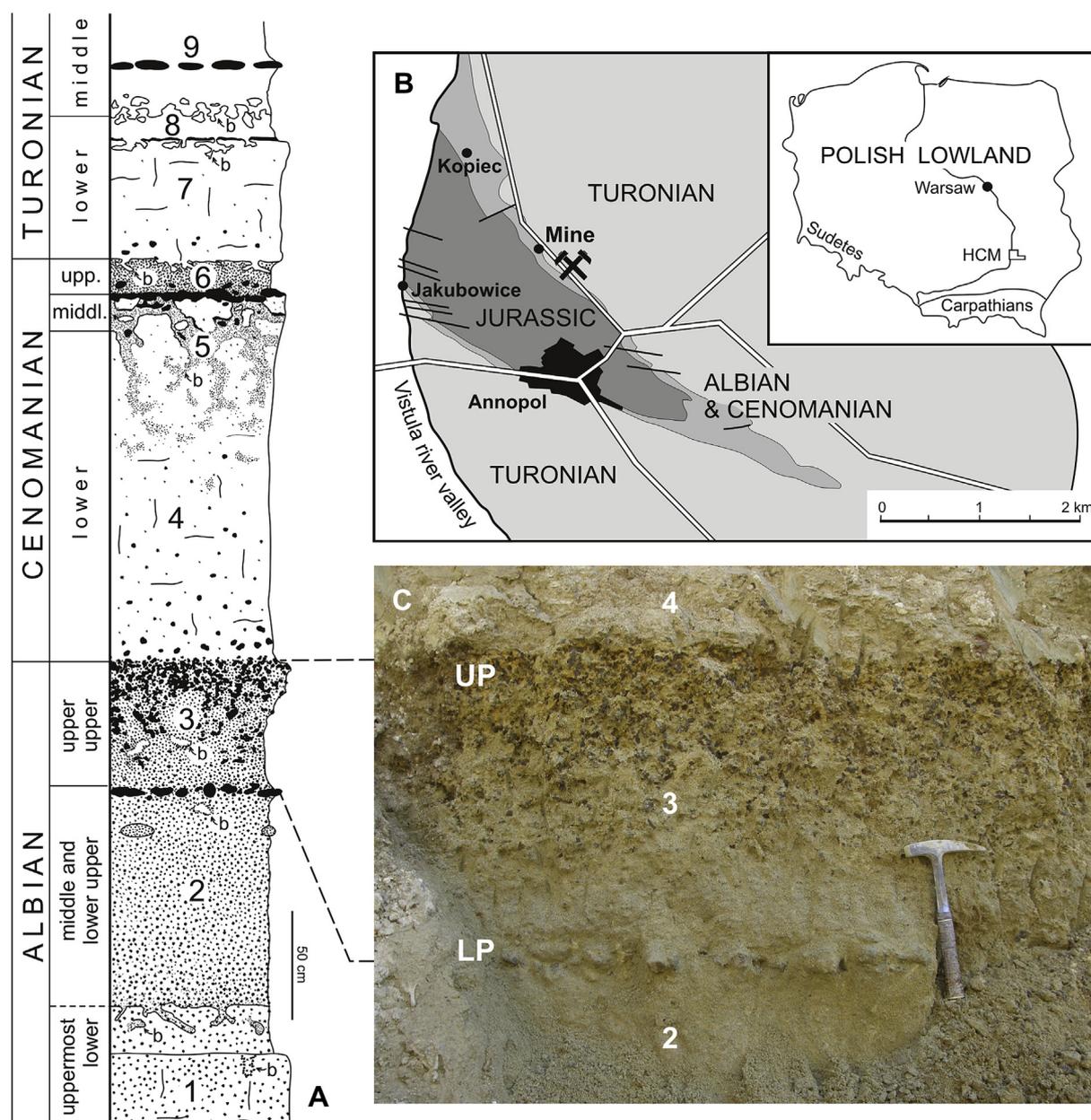


Fig. 1. A. Lithology and stratigraphy of the condensed mid-Cretaceous succession of the Annapol anticline (modified after Walaszczyk, 1984). Units 1–9 are the transgressive–regressive units (Machalski and Olszewska-Nejbert, in prep.). 1. Quartzose sandstone, replaced upwards by quartz sands truncated by a burrowed surface. 2. Quartz sands with glauconite and rare sandstone nodules near the top; unit 2 is capped by a phosphate horizon. 3. Quartz sands with glauconite passing upwards into marly sands with glauconite and phosphates, forming a distinct horizon at the top of the unit. 4. Quartzose marls with glauconite and phosphates in the lower part. 5. Glauconitic marls infilling burrows in the underlying unit, truncated by a hardground with phosphate and glauconite impregnation. 6. Strongly glauconitic marls with burrowed omission surface at the top. 7. Limestone with rare phosphatic nodules and glauconite, capped by a hardground with glauconitic mineralisation. 8. Marls with burrowed omission surface at the top. 9. Marls with black flint; b – burrows. B. Geologic sketch-map of the Annapol anticline (modified after Walaszczyk, 1987) with localities studied (see text for further explanations) and location of the study area within Poland. C. Close-up view of the upper Upper Albian unit 3 at Kopiec. LP – lower part of the Phosphorite Bed, UP – upper part of the Phosphorite Bed.

recognised: an Albian assemblage from England (six or seven genera; see Popov, 2008a) and a Late Albian–Early Cenomanian one from Belgorod Province, Russia (10–11 genera; see Popov and Averianov, 2001).

The first fossil chimaeroids recorded from Poland are ‘jaws’ (i.e., isolated dental plates) of *Edaphodon sedgwickii* (Agassiz, 1843) from Albian phosphorite-bearing deposits of the Annapol (Rachów) anticline, as reported by Samsonowicz (1925, 1934). Subsequently, Radwański (1968) noted some chimaeroid specimens from the Albian of Annapol and the Cenomanian of Skotniki (Zajęcza Góra) and Staniewice (see Marcinowski and Radwański, 1989, figs 1 and 8

for location and stratigraphic logs of these sections, respectively). However, only a single mandibular plate of *Ischyodus thurmanni* Pictet and Campiche, 1858 from Annapol was described in detail and figured by Radwański (1968).

In the present paper we describe new chimaeroid material from the phosphorite-bearing Upper Albian in the Annapol area (Poland), amassed between 2008 and 2012 (Machalski et al., 2009; Machalski and Olszewska-Nejbert, in prep.). This new collection adds to the regional taxonomic chimaeroid diversity up to the mid-Cretaceous standard as recorded earlier from England and Russia (see above).

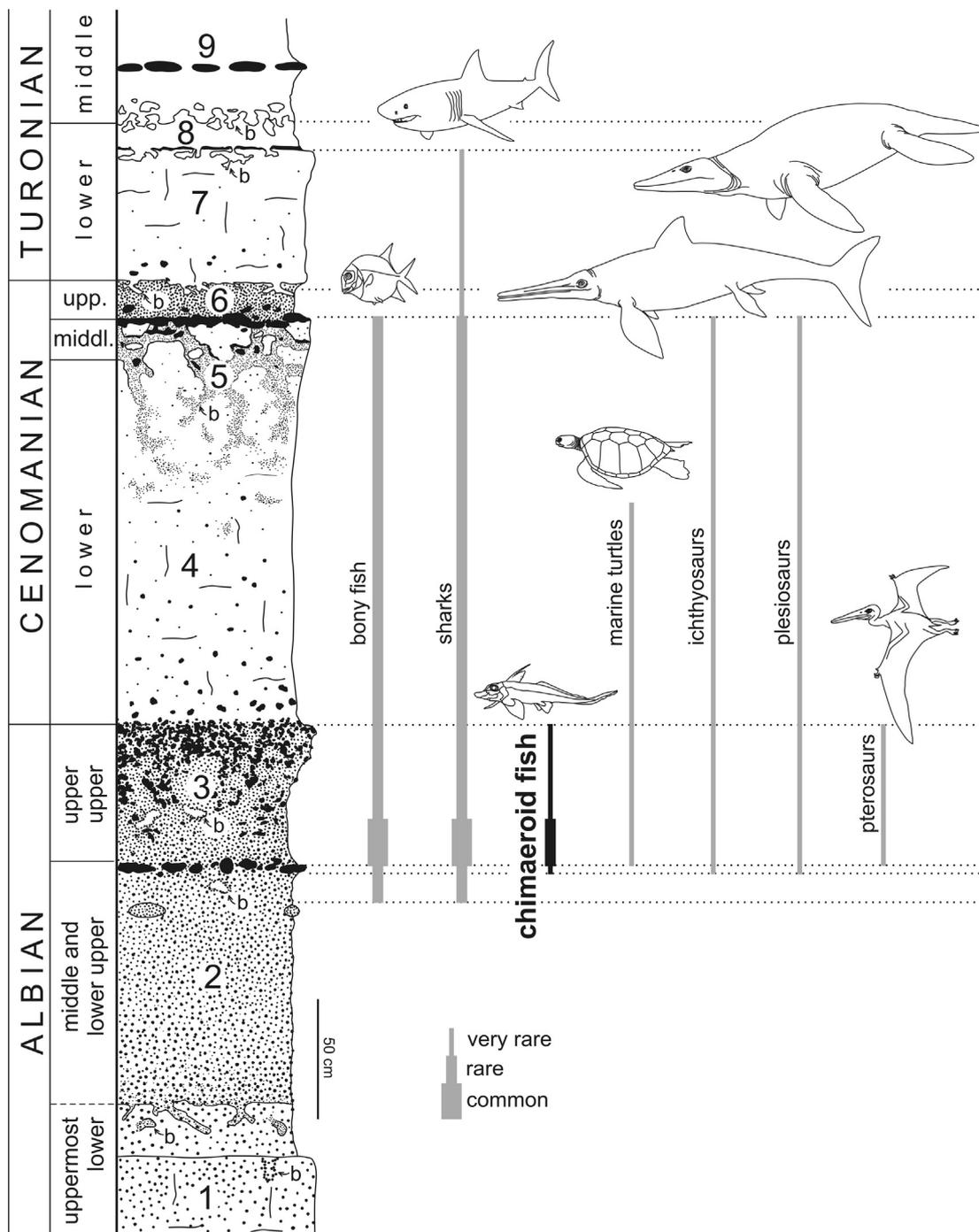


Fig. 2. Vertical ranges of the main vertebrate groups in the Annapol succession (Machalski and Olszewska-Nejbert, in prep.). See caption of Fig. 1 for explanations.

2. Geological background

Mid-Cretaceous (uppermost Lower Albian–Lower Turonian) condensed strata are exposed along the limbs of a small anticline (Annapol anticline, or Rachów anticline in earlier papers; see Samsonowicz, 1925, 1934; Pożaryski, 1947, 1948; Cieśliński, 1959, 1976) situated on the east bank of the Wisła (Vistula) River, Poland (Fig. 1A–C). Geotectonically, the Annapol anticline forms the easternmost part of the so-called Mesozoic Border of the Holy Cross Mountains (Marcinowski and Radwański, 1983).

The mid-Cretaceous strata of the Annapol anticline rest, with a slight angular unconformity, on Upper Jurassic (Kimmeridgian) deposits (Samsonowicz, 1925, 1934; Walaszczyk, 1984). Their lithology was described in detail by Samsonowicz (1925, 1934), Pożaryski (1947), Cieśliński (1959), Uberna (1967) and Walaszczyk (1984, 1987). The stratigraphy is based mainly on ammonites, inoceramid bivalves and foraminifera (Samsonowicz, 1925, 1934; Pożaryski, 1947; Cieśliński, 1959, 1987; Marcinowski, 1980; Marcinowski and Wiedmann, 1985, 1990; Marcinowski and Radwański, 1989; Marcinowski and Walaszczyk, 1985; Walaszczyk, 1987, 1992; Peryt,

1983; Walaszczuk and Peryt, 1998). Upper Albian biostratigraphy has recently been updated by Machalski and Kennedy (in press).

The Annopol succession records the early phases of the great Cretaceous transgression (Marcinowski and Radwański, 1983; Walaszczuk, 1987) and is extremely thin (condensed) in comparison to coeval strata in adjacent areas, due to its location on a submarine swell (Cieśliński, 1976). With reference to the simple transgressive–regressive model proposed by Juignet (1980) and Hancock (1990, 1993, 2004), the Annopol succession is interpreted as a series of thin transgressive units, capped by layers of reworked phosphatic nodules and clasts, hardgrounds and burrowed omission or erosional surfaces, reflecting a series of regression maxima (Fig. 1A; Machalski and Olszewska-Nejbert, in prep.).

3. Localities

Most of the former outcrops in the Annopol area (Samsonowicz, 1925, 1934; Walaszczuk, 1984) are no longer accessible. The material studied comes from two localities along the northern limb of the Annopol anticline (Fig. 1B). These are the abandoned underground phosphorite mine Jan 1 at Annopol (see Makowska and Jędrzejczak, 1975 for a historical overview of phosphorite mining here), and the surface locality of Kopiec, comprising a series of temporary trenches dug near the old sandstone quarry south of the village (Fig. 1B).

4. Material and methods

In the chimaeroid collection described and illustrated herein dental plates or fragments of such predominate. Amongst 76 specimens examined, 23 represent more complete ones, while 53 pertain to fragments. Only 34 plates or fragments of such could be identified at the generic and/or specific level. Other fragments of plates could only be referred to as ‘Chimaeroidei gen. et. sp. indet.’ Additionally, three fragments of dorsal spines and a single frontal clasper are here recorded.

A minor part of the chimaeroid material studied (13 specimens) has been collected *in situ* both in the mine and at Kopiec. The remainder stems from screen washing of sediment from Kopiec. This was done in the field with assistance of local fire fighters. Two screens, 1.0 × 0.8 m in size, with an 8-mm mesh size and a motorised pump were used. The total weight of sediment processed amounted to about 15 tonnes, with c. 5 tonnes of phosphates remaining after removal of the finer fraction. For comparison, the total production of phosphates at the Jan 1 mine was 943 545 tonnes (see Makowska and Jędrzejczak, 1975). Some specimens were broken during extraction or screen washing; these have subsequently been prepared and glued (e.g., Figs. 4A, G–H; 5A, G; 6A–B), although not all fragments could be recovered and reassembled (e.g., Figs. 4A, G–H; 5A, G).

All material is housed at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland (prefix ZPAL V.38); other referred specimens are in the collections of the Natural History Museum, London (prefix: NHMUK), the British Geological Survey at Keyworth, England (BGS) and Saratov State University, Russia (SSU).

5. Vertical distribution of chimaeroids

According to Samsonowicz (1925, 1934), Radwański (1968) and Marcinowski and Radwański (1983), chimaeroids and most other vertebrate remains recorded from the Annopol succession came from the so-called Phosphorite Bed, which was subjected to intensive mining operations for production of agricultural fertilisers. Those authors subdivided the Phosphorite Bed into two parts:

a lower and an upper one (e.g., Marcinowski and Radwański, 1983, fig. 6; see also Fig. 1A, C herein) and noted that vertebrate remains were particularly abundant in the lower part. The present study generally confirms these observations. However, what was referred to as the Phosphorite Bed by previous authors, is better interpreted as two independent phosphorite horizons that terminate two distinct transgressive units, numbered 2 and 3 (Fig. 1A, C; Machalski and Olszewska-Nejbert, in prep.).

The exact provenance of chimaeroid specimens in the section could be recorded only in the case of material collected *in situ* from underground and surface sections. These records demonstrate the following pattern of chimaeroid distribution:

- 1) Chimaeroid remains range from the top of unit 2 to the top of unit 3, i.e., throughout the Phosphorite Bed as understood by previous authors.
- 2) Only four poorly preserved fragments of chimaeroid dental plates have been recorded from the phosphorite layer at the top of unit 2 (i.e., from the lower part of the Phosphorite Bed of former authors). Two of these (ZPAL V.38/947–948) reveal distinctly polished surfaces. These indeterminate specimens are not included in the taxonomic part of the present study.
- 3) Other chimaeroid material collected *in situ* (10 dental plates) comes from unit 3 (Fig. 1A, C). The best-preserved specimens have been collected from a thin interval (the lowermost few centimetres) at the base of that unit.
- 4) No chimaeroid remains have been recovered from other levels in the Annopol succession.

The position of vertebrate remains recovered by means of screen washing of sediment at Kopiec could not be precisely determined. Material for screen washing was amassed by using an excavator and, for technical reasons, this could be subdivided merely into two portions. The lower portion corresponded roughly to the highest 20 cm of unit 2 and the lowest 20 cm of unit 3, and encompassed the lower part of the Phosphorite Bed as understood by previous authors. The upper portion corresponded to the remaining part of the unit 3, being roughly equivalent to the upper part of the Phosphorite Bed of previous authors (Fig. 1A, C). Vertebrate remains, including those of chimaeroids, were commonest (and best preserved) in the lower set of screen-washed samples, which is compatible with data on specimens collected *in situ*. For the sake of simplicity we treat all material described herein as a single chimaeroid assemblage and refer it to unit 3, although it cannot be ruled out that a few specimens may have actually come from the top of unit 2.

6. Lithology of the chimaeroid-bearing interval and associated fossils

The top of unit 2 is composed of phosphate nodules and clasts, up to 20 cm in diameter, set in a quartz sand (Fig. 1A, C). Some of these phosphates contain ammonites, mostly hoplitids, which range in preservation from worn, fragmentarily preserved moulds to (rare) specimens in shell preservation (Marcinowski and Wiedmann, 1985, 1990). Other nodules are spindle-shaped and contain crustacean burrows in their axial zone. Rare sponges, inoceramids and other bivalves, cephalopod mandibles and pieces of conifer wood riddled with bivalve borings also occur in the phosphates. Only a few vertebrate remains were found in nodules, including some tiny vertebrae of bony fish and a large plesiosaur vertebra. Some small shark teeth and bony fish vertebrae were also found between and beneath the phosphatic nodules (Fig. 2). A mix of ammonites that represent various biostratigraphic zones (see below), differences in phosphatisation of particular fossils and nodules, and common

fragmentation and chaotic orientation of the phosphates and fossils clearly are indicative of their being reworked during repeated burial/exhumation cycles (compare Samsonowicz, 1925, 1934; Marcinowski and Radwański, 1983, 1989).

Unit 3 is c. 50 m thick and is composed of highly bioturbated quartz sand with abundant glauconite passing gradually upwards into quartz-glauconitic marl. A distinct horizon of phosphatic clasts and fossils occurs in the upper part of this unit. Its upper boundary usually is sharp, whereas the lower one is diffuse due to intensive burrowing of the sediment (Marcinowski and Walaszczyk, 1985; Walaszczyk, 1987). The phosphatic clasts usually are c. 1 cm in diameter, but in the upper part of the layer they are commonly cemented together, forming larger aggregates, up to 10–12 cm in diameter. These aggregates are composed of up to three generations of clasts showing the same matrix, but differing in intensity of phosphatisation. This indicates multi-phase intraformational and within-habitat reworking and redeposition of phosphatic material (Machalski and Olszewska-Nejbert, in prep.).

Fossils associated with chimaeroid remains in the lower part of unit 3 comprise rhynchonellid brachiopods, wood fragments and relatively common teeth and vertebrae of bony fish and sharks. The latter include *Paraisurus macrorhiza* (Pictet and Campiche, 1858), *Eostratolamia* sp., *Dwardius?* sp., *Gladioserratus aptensis* (Pictet, 1865), *Synechodus?* sp. and *Heterodontus* sp. Associated are teeth, fragments of jaws and vertebrae of ichthyosaurs (inclusive of *Platypterygius* sp.) and pliosaurs (amongst others *Polyptychodon interruptus* Owen, 1841), marine turtle bones and indeterminate remains of pterosaurs (Fig. 2). In the upper part of unit 3, fossils become more numerous and are frequently incorporated into larger phosphorite bodies. The commonest invertebrates are phosphatised fragments of lithistid sponges (Samsonowicz, 1925, 1934), calcitic-shelled bivalves, dominated by *Aucellina gryphaeoides* and *Pycnodonte vesiculosum*, and guards of a small belemnite, *Neohibolites ultimus*. Shells of rhynchonellid and terebratulid brachiopods, serpulid tubes and rare shrimp remains are subsidiary components of the invertebrate assemblage. No remains of the originally aragonitic molluscs have been recorded from unit 3, except for occasional ammonite replicas preserved as attachment scars on some oyster shells (Machalski and Kennedy, in press). Vertebrate remains are less common and less well preserved than in the lower part of the unit, but essentially represent the same taxa. Small vertebrate specimens occur either loose or embedded within the phosphorites, larger ones are commonly fragmented and covered by phosphatic overgrowths (Machalski and Olszewska-Nejbert, in prep.).

7. Biostratigraphic dating of chimaeroid assemblage

The biostratigraphy of the chimaeroid-bearing interval in the Annopol succession is based mainly on ammonites (Samsonowicz, 1925, 1934; Cieśliński, 1959; Marcinowski and Wiedmann, 1985, 1990). The phosphatic concretions and clasts forming the top of unit 2 have yielded a biostratigraphically mixed ammonite assemblage, ranging from the Middle Albian *Hoplites dentatus* Zone to the lower Upper Albian *Mortoniceras inflatum* Zone (Marcinowski and Radwański, 1983, 1989; see Table 1 for the current ammonite zonation of the Albian interval exposed at Annopol). Unit 3 may be dated on the basis of recent finds of *Mortoniceras* (*Subschloenbachia*) sp., preserved as attachment scars on the left valves of some oysters (Machalski and Kennedy, in press). These specimens show the closest affinity with *Mortoniceras* (*Subschloenbachia*) which are characteristic of the upper Upper Albian *Mortoniceras perinflatum* Zone in the subdivision proposed by Kennedy and Latil (2007) (Machalski and Kennedy, in press; Table 1 herein). We take this to be the age of all chimaeroid material

Table 1

Ammonite zonation of the upper Lower to the uppermost Albian, based on Machalski and Kennedy (in press).

Substage	Ammonite zones
Upper Albian	<i>Praeschloenbachia briacensis</i> <i>Mortoniceras perinflatum</i> <i>Mortoniceras rostratum</i> <i>Mortoniceras fallax</i> <i>Mortoniceras inflatum</i> <i>Mortoniceras pricei</i> <i>Dipoloceras cristatum</i>
Middle Albian	<i>Euhoplites lautus</i> <i>Euhoplites loricatus</i> <i>Hoplites dentatus</i>
Lower Albian (upper part)	<i>Otohoplites auritiformis</i>

described in the present paper, although it cannot be ruled out that some of the specimens collected during screen washing of the sediment come from the top of unit 2 and are thus significantly older than the bulk of material.

8. Chimaeroid taphonomy

General characteristics of the vertebrate assemblage from the Phosphorite Bed of the Annopol anticline and a discussion of its taphonomy will be presented elsewhere (Machalski and Olszewska-Nejbert, in prep.). For the purpose of the present paper a brief description of preservational features of the chimaeroid material suffices:

- 1) The material studied is represented exclusively by isolated elements. No associations of dental plates (see e.g., Cicimurri et al., 2008; Ward and McNamara, 1977) have been found at Annopol, although associations of disarticulated skeletal elements (bones, vertebrae and teeth) representing single individuals of bony fish, ichthyosaurs and marine turtles have been documented from unit 3, particularly from its lower part (Machalski and Olszewska-Nejbert, in prep.).
- 2) Of the 42 dental plates and fragments in the present material which could be assigned to a particular plate type, mandibular plates predominate ($n = 25$; 60%); palatine ($n = 10$; 24%) and vomerine plates ($n = 7$; 16%) are less common. This numerical regression is typical of chimaeroid assemblages from Cretaceous concentrate-type sandy deposits with phosphorites across Europe (E.V.P., pers. obs.) and seems to be correlated mainly with regression in size and sturdiness of particular types of plate (mandibulars > palatines > vomerines). Smaller and less solid plates could be preferentially lost as a result of taphonomic and possibly also sampling processes.
- 3) Most of the specimens studied are well preserved; in most cases their fragmentation may be the result of mechanical damage during extraction from the hard rock (in the underground mine) or screen washing of loose sandy sediment at Kopiec. Only a few specimens reveal signs of predepositional abrasion. The most poorly preserved specimen in the collection described is *Ischyodus* aff. *bifurcatus* (Fig. 4F), which has a worn and deeply abraded basal surface with visible pleromin bodies.
- 4) Large specimens (e.g., *Edaphodon sedgwickii*) show superficial traces of post-mortem corrosion as well as bioerosional marks (Fig. 6A2). In the last case a series of short radial scratches around the distal half of a corrosion pit (bite mark?, boring?) are visible. Several similar pits have also been observed at the basal surface of the same specimen (Fig. 6A5). These marks may be analogous to those found on pterosaur bones from the Cambridge Greensand and attributed by Unwin (2001) to the activity

of bone-eating osteopeltid gastropods. However, the latter occur in Recent deep-sea environments (Marshall, 1987) which are incompatible with those of the Annapolis and Cambridge Greensand successions.

In summary, the chimaeroid assemblage studied clearly is biased to some degree due to taphonomic processes and, possibly, also sampling procedures. There are no indications, however, of any significant temporal and habitat mixing of the specimens discussed in the taxonomic part below.

9. Tooth plate terminology

The main contributions to the terminology of chimaeroid tooth plates were those by Newton (1878; tritors), Ørvig (1986; pleromin types), Patterson (1992; orientation of dental plates) and Stahl (1999; summary of terminology). Updated descriptive terms and measurements used here are the same as presented earlier by the first author (Popov, 1999, 2003; Popov and Efimov, 2012). A key to the main descriptive terms is presented in Fig. 3. Some terms may be commented on as follows:

- 1) Tritorial series (Popov, 2003) are a group of small tritors showing a tendency to serial arrangement (N equal to or over 3). This series usually is situated in a specific part of the functional surface, corresponding to the function it performs (cutting or fine grinding) and is well separated from another series or group of tritors. The nomenclature is based on the location of the series: thus there are 'postero-outer tritorial series' (Fig. 4G1; Fig. 7A1, A3), 'symphyseal tritorial series' (Fig. 5F2, G3) and 'outer tritorial series' (Fig. 4I1, I3; Fig. 5C1–2, C4; Fig. 7B1–3).
- 2) 'Reference width', as proposed by Popov and Efimov (2012), refers to a measurement (in mm) used to determine the location of a dental plate in an ontogenetic series of any given taxon (separately for mandibular, palatine or vomerine plates, see Fig. 3). This is the incomplete width of a dental plate, measured perpendicular to the medial termination of this tritor, which is most commonly preserved in fossils – the outer tritor in palatine plates (Kp), the antero-outer tritor in mandibular plates

(Km) and the most lateral tritor of the outer tritorial series in vomerine plates (Kv). This measurement is effectively applied to track growth and individual variability of 'edaphodontid' and rhinochimaerid dental plates; however, it is not applicable for the majority of callorhynchids (*Callorhynchus*, *Brachymylus*, *Pachymylus* and allies). In the past, this measurement was referred to as 'medial width', 'selected width' or 'coefficient of the selected width' of the dental plate (Popov, 1999, 2003). 'Reference width', in addition with 'mesio-distal length of the specimen' (Fig. 3L), characterise dimensions of specimens well.

10. Systematic palaeontology

Higher-level taxonomy (superfamily and up) follows Nelson (2006). The family 'Edaphodontidae' Owen, 1845 is here considered to represent a collective unit that is in need of revision (see also Popov and Beznosov, 2006). Its composition and relationships with other chimaeroid families require phylogenetic analysis, which is beyond the scope of the present paper.

10.1. Dental plates

Class Chondrichthyes Huxley, 1880
 Subclass Holocephali Bonaparte, 1832
 Superorder Holocephalomorpha Nelson, 2006
 Order Chimaeriformes Obrucsev, 1953
 Suborder Chimaeroidei Patterson, 1965
 Superfamily Chimaeroidea Bonaparte, 1832
 Family 'Edaphodontidae' Owen, 1845
 Genus: *Ischyodus* Egerton, 1843

Type species. *Ischyodus townsendi* Buckland, 1835; Upper Jurassic (Tithonian), southern England.

Ischyodus thurmanni Pictet and Campiche, 1858
 Fig. 4A–E

1858 *Ischyodus thurmanni* Pictet and Campiche, p. 76, pl. 9, fig. 8.

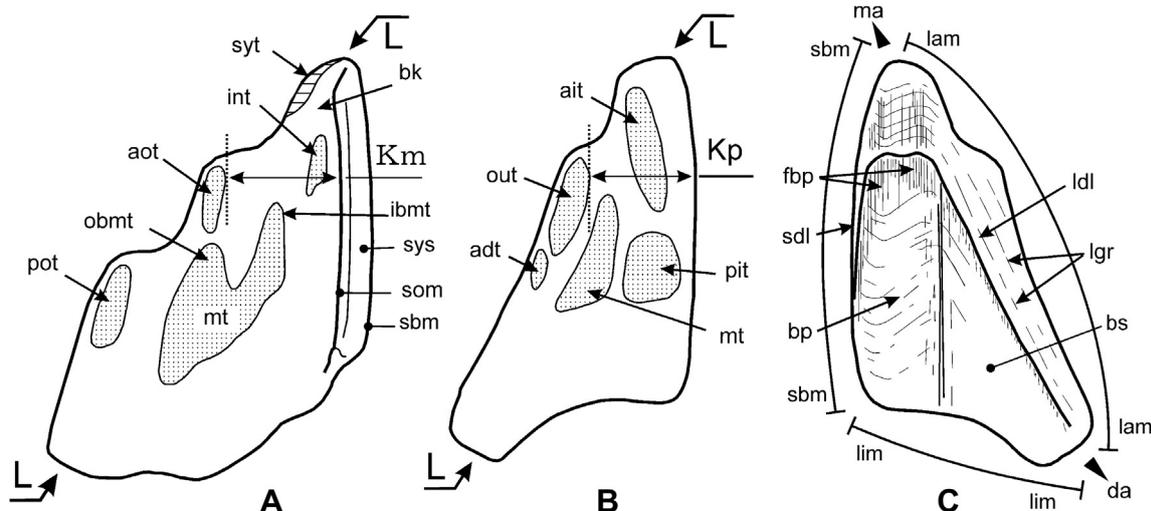


Fig. 3. Chimaeroid dentition terminology and measurements, based on mandibular (A, occlusal view) and palatine (B, occlusal view; C, basal view) dental plates of a generalised mid-Cretaceous species of *Ischyodus*. Abbreviations (also see Figs. 4–7): da – distal angle (direction); ma – mesial angle (direction); adt – additional (inner or outer) tritor; ait – antero-inner tritor; aot – antero-outer tritor; bk – mandibular beak; bp – basal pocket of palatine plate; bs – basal surface; fbp – field of basal perforation; ibmt – inner branch of median tritor; int – inner tritor; Km, Kp, Kv – 'reference width' of mandibular, palatine and vomerine dental plates, respectively; L – mesio-distal length of specimen; lam – labial margin; ldl – lateral descending lamina; lim – lingual margin; lgr – growth lines; mt – median tritor; obmt – outer branch of median tritor; out – outer tritor; pit – postero-inner tritor; pot – postero-outer tritor; sbm – symphyseal-basal margin; sdl – symphyseal descending lamina; som – symphyseal-occlusal margin; sys – symphyseal surface; syt – symphyseal tritor.

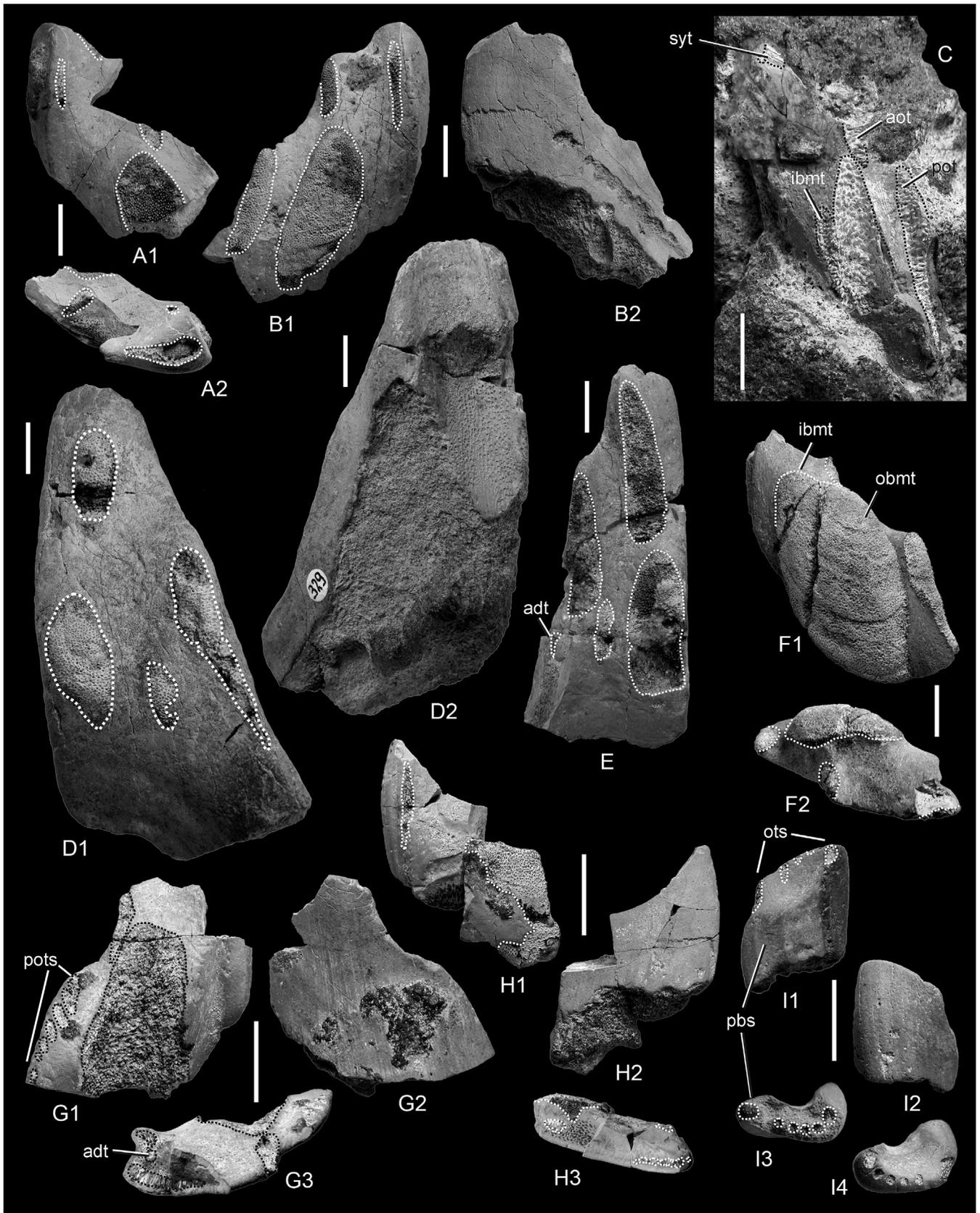


Fig. 4. A–E, *Ischyodus thurmanni* Pictet and Campiche, 1858. A, incomplete right mandibular (Km18, L48) plate (ZPAL V.38/476) in occlusal (A1) and mesial (A2) views. B, left mandibular (Km14, L59) plate (ZPAL V.38/475) in occlusal (B1) and basal (B2) views. C, right mandibular (Km7.5, L28.5) plate of a juvenile (ZPAL V.38/798) embedded in phosphatic nodule, in occlusal view. D, left palatine (Kp24, L87) plate (ZPAL V.38/329) in occlusal (D1) and basal (D2) views. E, right palatine (Kp14.5, L68) plate (ZPAL V.38/435) in occlusal view. F, *Ischyodus* aff. *bifurcatus* Case, 1978, right mandibular (Km15, L62) plate (ZPAL V.38/474) in occlusal (F1) and mesial (F2) views. G–I, '*Ischyodus incisus*' Newton, 1878. G, left mandibular (Km13, L31) plate (ZPAL V.38/330) in occlusal (G1), basal (G2) and mesial (G3) views. H, right mandibular (Km14.5, L38) plate (ZPAL V.38/332; unit 3a) in occlusal (H1), basal (H2) and mesial (H3) views. I, right vomerine (Kv9.3, L30, h6) plate (ZPAL V.38/479) in occlusal (I1), basal (I2), lingual (I3) and mesial (I4) views. Partial outlines of some tritoral structures are highlighted by black/white dotted lines. Scale bars represent 1 cm. Abbreviations (see also Fig. 3): ots – outer tritoral series; pbs – parabasal surface; pots – postero-outer tritoral series.

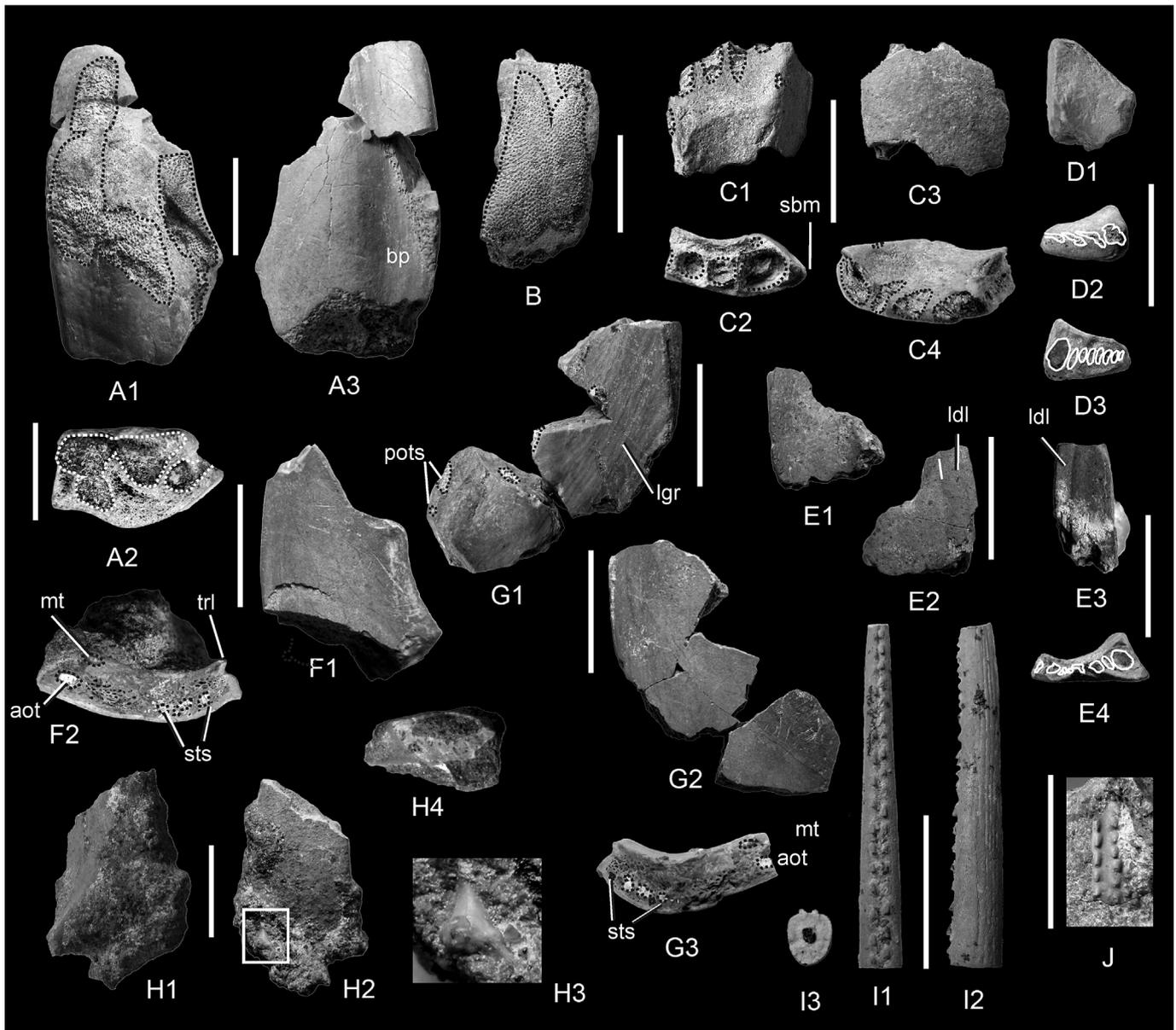


Fig. 5. A–B, *Ischyodus incisus* Newton, 1878. A, left palatine (Kp11.6, L35) plate (ZPAL V.38/497) in occlusal (A1) and basal (A2) views. B, incomplete right palatine (L20.8) plate (ZPAL V.38/498) in occlusal view. C, *Elasmodus* sp., right vomerine (Kv8.6, L13.5, h5.7) plate (ZPAL V.38/314) in occlusal (C1), basal (C2), lingual (C3) and lateral (C4) views. D–E, *Elasmodectes* sp. D, apical fragment of right mandibular (L9.2, h5.2) plate (ZPAL V.38/890) in occlusal (D1), mesial (D2) and lingual (D3) views. E, fragment of right mandibular (L9.8, h4.2) plate (ZPAL V.38/500) in occlusal (E1), basal (E2), symphyseal (E3) and lingual (E4) views. F–G, *Lebediodon oskolensis* Nessov and Averianov, 1996b. F, incomplete left mandibular (Km10, L19.5, h3.5) plate (ZPAL V.38/480) in basal (F1) and lingual (F2) views (occlusal surface phosphate covered). G, incomplete left mandibular (Km10.8, L27, h3) plate (ZPAL V.38/496) in occlusal (G1), basal (G2) and lingual (G3, enlarged, symphyseal part of plate only). H–J, non-dental chimaeroid remains. H, frontal clasper (frontal tenaculum) (ZPAL V.38/801) in ventral (H2) and distal (H4) views; H3 close-up view of elasmobranch tooth (*Protosqualus?* sp.) embedded in phosphate on dorsal part of clasper (H2, white square); I–J, chimaeroid fine spine fragments. I, distal portion of fine spine (ZPAL V.38/704) in posterior (I1) left lateral (I2) views and proximal cross section (I3). J, piece of fine spine (ZPAL V.38/864) embedded in phosphate nodule, posterior view. Partial outlines of some tritoral structures are highlighted by black/white dotted lines. Scale bars represent 1 cm. Abbreviations (see also Fig. 3): sts – symphyseal tritoral series; trl – tritoral ledge.

1878 *Ischyodus brevirostris* Agassiz, 1843: Newton, p. 326, pl. 9, figs. 1–21.
 1891 *Ischyodus thurmanni* Pictet and Campiche, 1858: Woodward, pp. 67–68.
 1911 *Ischyodus thurmanni* Pictet and Campiche, 1858: Woodward, p. 188, text-fig. 56, pl. 40, fig. 7.
 1968 *Ischyodus thurmanni* Pictet and Campiche, 1858: Radwański, p. 316, pl. 1, fig. 1.
 1999 *Ischyodus thurmanni* Pictet and Campiche, 1858: Stahl, p. 137, fig. 139D–F.

Material. Thirteen dental plates (ZPAL V.38/39, 117, 121, 122, 156, 157, 329, 435, 475, 476, (477 + 478), 798 and 799); illustrated are specimens ZPAL V.38/329, 435, 475, 476 and 798.

Description. Dental plates are of medium to large size, moderately robust and flat, with fine descending lamina across the entire basal surface visible.

Mandibular plate with construction typical of the genus, showing a thin and clear lateral descending lamina at the base, inclined on a basal surface. Symphyseal surface of moderate height,

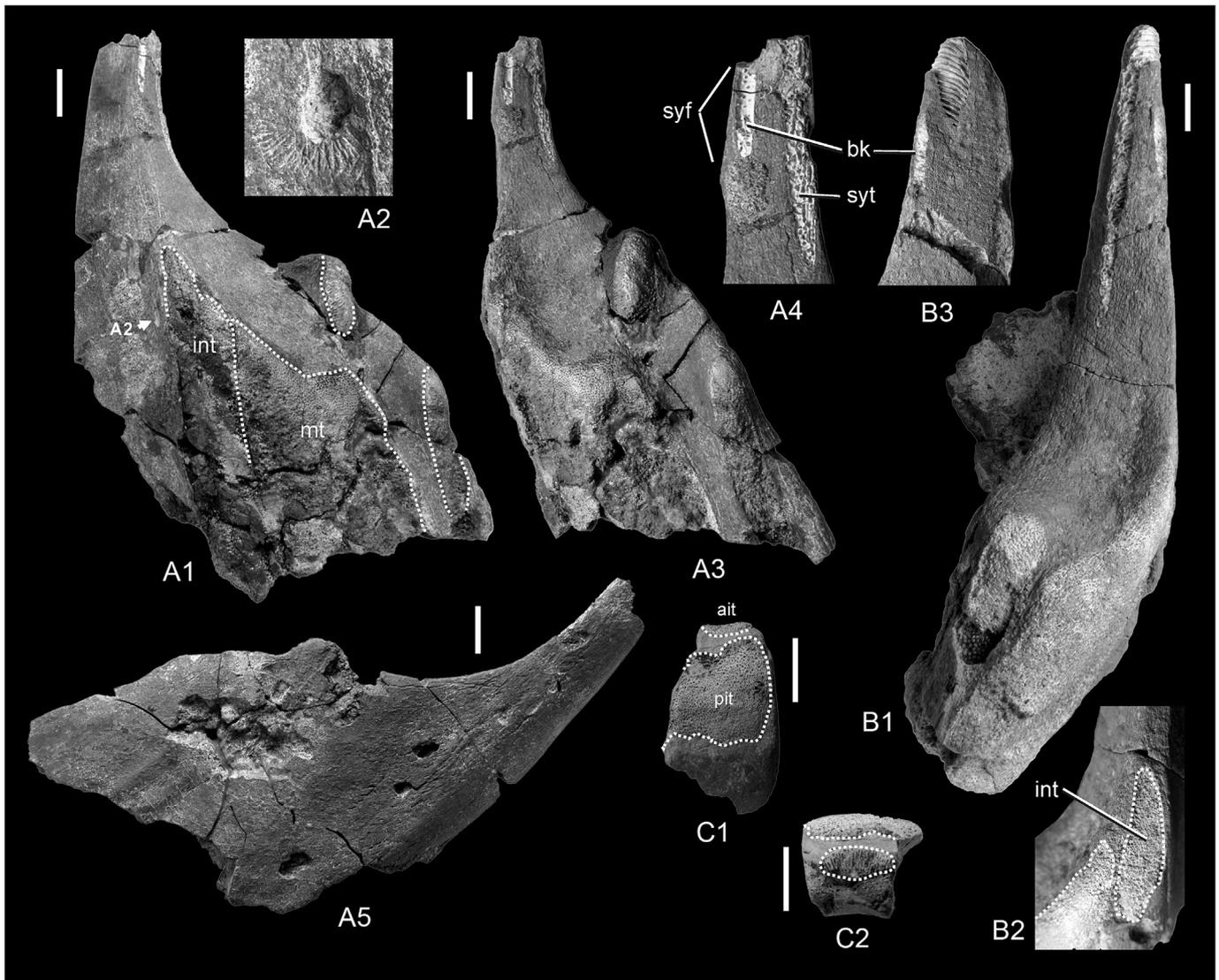


Fig. 6. *Edaphodon sedgwickii* (Agassiz, 1843). A, right mandibular (Km32, L129) plate (ZPAL V.38/428) in symphyseal–occlusal (A1), occlusal (A3; A4, enlarged beak) and basal (A5) view; A2 showing enlargement of bioerosional trace (A1, white rectangle). B, left mandibular (Km21, L125) plate (ZPAL V.38/33) in occlusal (B1) view with enlarged sections: B2, junction of median and inner tritors, B3, enlarged apical portion of beak, in symphyseal view. C, right palatine (L30.5) plate (ZPAL V.38/499) of a young individual in occlusal (C1) and mesial (C2) views. Partial outlines of some tritoral structures are highlighted by white dotted lines. Scale bars represent 1 cm. Abbreviations (see also Fig. 3): bk – beak tritor; syf – symphyseal (?) facet.

sloping occlusally. Mandibular beak short. Occlusal tritors as follows: fine inner tritor (may be absent); both slender antero-outer tritor and postero-outer tritor, the latter being larger in occlusal view and more rounded in cross section, the former being compressed laterally. A superficial median tritor centrally placed, moderately wide and tapering mesially, not compound in cross section, well separated from both postero-outer and inner tritors, further away from the latter. Mesial outline of median tritor almost symmetrical, but can be complex with symphyseal appendix or (in some juvenile individuals) with rudimentary inner branch of median tritor (Fig. 4C).

Mandibular beak reinforced with symphyseal tritor, moderately broad, asymmetrical and falcate in cross section, with rounded symphyseal edge and tapered lateral edge. Tritor consisting of laminated pleromin with lateral inclusion of vascular pleromin (in adults).

Palatine plates with four occlusal tritors of vascular pleromin. Postero-inner tritor largest, median one smallest, measuring 30–50% in width of former and displaced distally. Antero-inner and outer tritors of equal width, the latter with distally tapering branch.

A single specimen (ZPAL V.38/435) has one small additional tritor, placed distally to outer tritor (Fig. 4E).

Remarks. Amongst eight nominal Cretaceous species of the genus *Ischyodus* reviewed by Stahl (1999), only two species show a similar plate morphology: *I. thurmanni* from the Albian of England and Switzerland (Woodward, 1891) and *I. gubkini* Nessov in Nessov et al. (1988) (Nessov et al., 1988; Popov and Ivanov, 1996; Stahl, 1999) from the Upper Albian of European Russia.

By superposition of occlusal tritors, the Annapol material falls within the range of variation of *I. thurmanni* as described and illustrated by Newton (1878, pl. 9, figs. 1–19). The presence of additional outer tritor(s) on palatine plates is not typical of *I. thurmanni* but has been noted in some specimens from the English Albian (BGS 1483 and 112368; NHMUK P.475). Palatine plates of the similar *I. gubkini* have more consistently large one to three additional outer tritors (Nessov et al., 1988, fig. 1 (6); Popov and Ivanov, 1996, fig. 2; Stahl, 1999, fig. 134E, non fig. 134D (misinterpretation of tritoral pattern)). For this reason, it is possible to refer

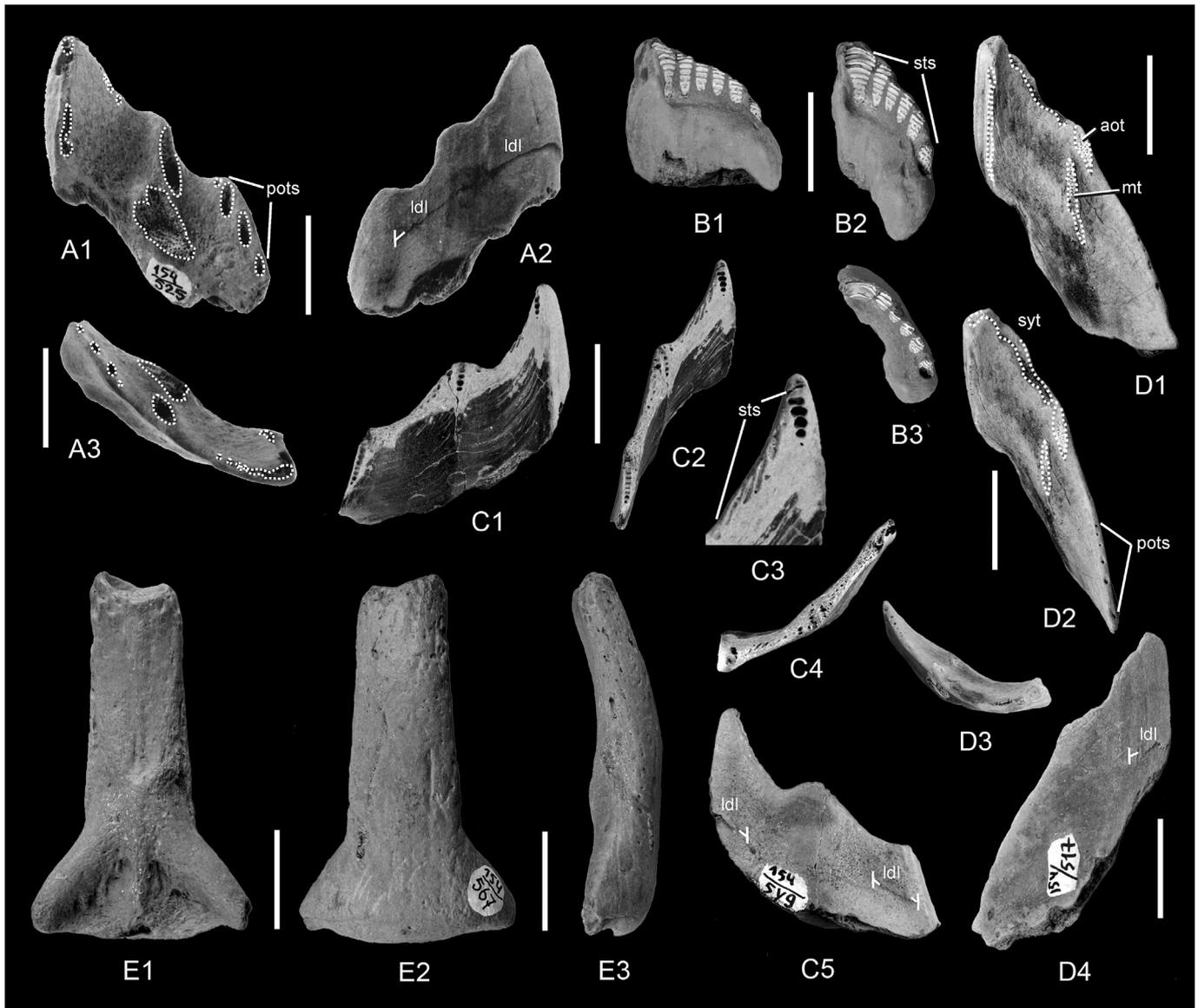


Fig. 7. Comparative chimaeroid material from the Upper Albian of the Stoilenski quarry (Belgorod Province, Russia). A, '*Ischyodus incisus*' Newton, 1878, right mandibular (L34, Km11) plate (SSU 154/525) in occlusal (A1), basal (A2) and mesial (A3) view; B, *Elasmodon rossicus* Averianov in Averianov et al. (1999), left vomerine (L22, Kv11) plate (SSU 154/630) in symphyseal-occlusal (B1), lateral (B2) and mesial (B3) view; C, *Elasmodectes kiprijanoffi* (Nessov et al., 1988), left mandibular (L30, Km8.5) plate (SSU 154/549) in symphyseal-occlusal (C1), lateral (C2), beak enlarged, not to scale (C3) and mesial (C4) view; D, *Lebediodon oskolensis* Nessov and Averianov, 1996b, left mandibular (L35, Km9) plate (SSU 154/517) in symphyseal-occlusal (D1), lateral (D2), mesial (D3) and basal (D4) view; E, frontal clasper of *Ischyodus?* sp. (SSU 154/567; L39, width 23 mm, height 7.6 mm) in ventral (E1), dorsal (E2) and lateral (E3) views. Partial outlines of some tritor structures are highlighted by white dotted lines. Scale bars represent 1 cm. For abbreviations see Fig. 3.

the Annapol specimens to *I. thurmanni*, although the plates (and palatine plates in particular) appear not well enough preserved for firm identification.

Size differences in dental plates of *I. thurmanni* (Km 8–20, Kp 15–24) from Annapol demonstrate the presence of individuals of different age (juveniles, adults) in this assemblage. Large-sized palatine plates show less occlusal occupation by tritors (Fig. 4D1) than smaller ones (Fig. 4E), which reflects a decrease of total area occupied by tritors due to ageing. A similar trend was shown by Ward and Grande (1991) for mandibular plates of *I. dolloi* (Leriche, 1902) from the Eocene of Antarctica.

Ischyodus aff. *bifurcatus* Case, 1978
Fig. 4F

Material. A single right mandibular plate, ZPAL V.38/474.

Description. A medium-sized mandibular plate (Km15, L62), markedly abraded, in particular along basal and symphyseal surfaces, and with broken apical beak. Distribution of tritors typical of *Ischyodus*, one antero-outer and one postero-outer, both with circular cross section, the latter slightly wider and displaced distally.

Centrally placed large median tritor, forming prominent pad, compound in cross section, bifurcated in occlusal view, but with poorly marked and rounded branches. Outer branch of median tritor (Fig. 4F1: ibmt) deeper and moderately separated from inner branch (Fig. 4F1: obmt), the latter not distinctly pronounced in mesial direction and well separated from symphyseal margin. Postero-outer tritor well separated from median one; no traces of

inner tritor seen. Symphyseal tritor narrow and low in cross section, formed by vascular pleromin (mainly), symphyseally flanked by laminated pleromin (up to one-third the width of tritor). Traces of descending lamina missing on account of abraded state of basal surface.

Remarks. Mandibular dental plates of *Ischyodus* with mesially bifurcated median tritors have been recorded on some occasions for Jurassic species (e.g., *I. egertoni*); they become commoner in Late Cretaceous ones (*I. bifurcatus*, *I. rayhaasi*). *Ischyodus bifurcatus* was originally described on the basis of dental plates from the Navesink Formation (Maastrichtian, reworked) of New Jersey, USA (Case, 1978) with referred material from the Santonian and Campanian of Delaware, New Jersey (mostly), Montana, Arkansas, western Georgia, California (all USA) and southern Belgium (Case, 1978, 1979; Case and Schwimmer, 1992). This species was recorded also from the Campanian of the Saratov and Volgograd areas of European Russia (Popov and Ivanov, 1996, fig. 2). Maastrichtian material from North Dakota (USA) that shows a more advanced bifurcation of the mandibular median tritor has recently been named *I. rayhaasi* by Hoganson and Erickson (2005). This form can be recorded, with a query, from the Maastrichtian of the Volgograd region (see Popov and Ivanov, 1996, as *Ischyodus ?bifurcatus*).

A less prominent bifurcation of the mandibular median tritor is visible in some Jurassic species such as *I. egertoni*, *I. emarginatus* and others (Stahl, 1999, fig. 138), suggesting that the 'bifurcatus' mandibular morphotype could have arisen independently on several occasions during the Mesozoic evolution of the genus. Mid-Cretaceous mandibular plates of an unnamed 'bifurcatus' morphotype are known from Upper Albian strata in the Belgorod area of European Russia (Popov and Ivanov, 1996, fig. 2) and from the Cambridge Greensand (basal Cenomanian, with remanié Albian fossils) of England (Popov, 2008a).

Specimen ZPAL V.38/474 differs from the mid-Cretaceous 'bifurcatus' plates of Russia and England in having a less prominent mesial bifurcation with shorter and more swollen branches. Additionally, this shows rounded antero-outer and subrounded postero-outer tritors, both in cross section, which is not typical of mandibulars of *I. thurmanni*. In this case, the bifurcation of the mandibular median tritor cannot be interpreted as a large tritoral aberration of *I. thurmanni* (as in ZPAL V.38/798; see Fig. 4C) and the specimen is referred to a different species, albeit in open nomenclature.

Mandibular plates of *I. bifurcatus* and other related Cretaceous species with clear 'bifurcation' correspond to palatine plates with close-set occlusal tritors and relatively large and forwardly displaced median tritor. Such plates are absent from the Annopol material.

It is obvious that mid-Cretaceous *Ischyodus* with the 'bifurcatus' morphotype of mandibular plates represents a separate species of the genus, with a wide distribution during the Albian of the Northern Hemisphere (see below).

'*Ischyodus incisus*' Newton, 1878
Figs. 4G–I, 5A–B

Material. Nine dental plates and fragments (ZPAL V.38/312, 323, 330, 332, 479, 497, 498, 501 and 800); illustrated are specimens ZPAL V.38/330, 332, 479, 497 and 498.

Description. Mandibular plates compressed in occlusal-basal projection, with more distal compression forming cutting edge along distal part of labial margin. Lateral descending lamina reduced distally, completely absent in distal two-thirds of normal projection and forming laterally reduced tiny band in symphyseal-labial sector of basal surface.

Occlusal tritors well developed, all composed of vascular pleromin and comprising antero-outer tritor, postero-outer tritoral series, median tritor, symphyseal tritor and inner tritor. Median tritor moderately broad and deep, with compound cross section, asymmetrical with deeper lateral part, but with no distinct occlusal bifurcation. Postero-outer tritor with tritoral series composed of 6–7 linked tritoral elements, decreasing in occlusal size and lingual diameter distally. Most mesial 2–4 tritoral elements of series may be fused incompletely. Antero-outer tritor of normal size, semi-circular in cross section. Narrow inner tritor and broad, low symphyseal tritor separated one from another. Occasionally, intermediate additional tritor present (Fig. 4G3: adt).

Palatine plates of *Ischyodus* type, but less robust than those of *Ischyodus* spp., moderately compressed in occlusal-basal projection. Basal pocket weak and asymmetrical. Basal perforation restricted to mesial-symphyseal angle of pocket. Lateral descending lamina absent outside basal pocket; moderately developed symphyseal descending lamina present. Vascular occlusal tritors well developed, joined in part and occupying most part of occlusal surface. Distribution of tritoral bodies in lingual view compact. Antero-inner and postero-inner tritors joined mesially and in cross section, the latter joined laterally with median tritor and both of equal width. Median tritor of triangular shape in cross section and closely approaching outer tritor in mesial part.

Vomerine plate (ZPAL V.38/479) tentatively assigned to this taxon with chisel-like form with subtrapezoid shape in occlusal view. Symphyseal surface sloping well occlusally and with rounded symphyseal-basal margin, lacking typical crest. Basal surface concave with no descending lamina.

Labial margin reinforced by outer tritoral series with six individual tritors, forming asymmetrical series. First (and most mesial) tritor of series slightly larger than others and of equal size to most distal one. Distal (sixth) tritor well separated from remainder of subseries (first to fifth tritors) and open laterally, forming curve of labial margin to parbasal surface. Mesial subseries curved in outline and increasing laterally by intertritoral distances (in particular between third and fifth tritors; see Fig. 5I3–I4). Tiny inner tritor present.

Remarks. Dental plates of this taxon, tentatively lumped into a single dentition, differ significantly from other species of *Ischyodus* in the Annopol assemblage in the following characters: mandibular and palatine plates with moderately compressed outlines in lingual view (not so much compressed as in plates of *Lebediodon*; compare Fig. 7A3 and 7D3), with reduced descending lamina and laminated pleromin in the structure of all tritors absent. Mandibular plates have an unbroken vascular symphyseal tritor and postero-outer tritoral series, whilst palatine plates show fused antero-inner and postero-inner tritors and the latter with the median tritor (Fig. 5A–B). The basic plate design is intermediate between the condition seen in *I. thurmanni* and *L. oskolensis*.

The nominal species *Ischyodus incisus* was described from the Lower Chalk (Cenomanian) of England (Newton, 1878), on the basis of several mandibular plates and a single, incomplete vomerine plate that was tentatively considered conspecific. The mandibular plates of this species (Newton, 1878, pl. 12, figs. 3–6; Woodward, 1911, pl. 41, figs. 5–6; Stahl, 1999, fig. 139A) are similar to the Annopol specimens in having distally reduced descending lamina and developed postero-outer tritoral series. Nevertheless, mandibular plates from Annopol show a less compressed outline in lingual view, more developed postero-outer tritoral series, broader and semi-bifid median tritor and no serial symphyseal tritor (Fig. 4G–H). In some features both mandibular plates from Annopol display a closer resemblance to specimen SSU 154/525 from the Upper Albian of the Belgorod area, Russia (Fig. 7A), yet differ by the

presence of more numerous and closely placed units in the postero-outer tritoral series. All English, Polish and Russian material discussed here possibly represents a distinct genus which is related to *Ischyodus* and *Lebediodon* (Popov, 2008a)

Palatine plates of *I. incisus* from England are unknown. As far as the Annapol material is concerned, mandibular and palatine plates of '*Ischyodus incisus*' have been lumped into a single dentition on the basis of a similar degree of reduction of the descending lamina as well as the comparable stage of moderate compression of the plates; a vomerine plate is also referred here, albeit tentatively, because it differs from vomerine plates of *Ischyodus* spp.

Genus: *Elasmodus* Egerton, 1843

Type species. *Elasmodus hunteri* Egerton, 1843; Lower and Middle Eocene, England.

Elasmodus sp.
Fig. 5C

Material. A single incomplete right vomerine plate, ZPAL V.38/314.

Description. Plate form typical of *Ischyodus*, chisel like, sub-rectangular in occlusal view; symphyseal surface sloping well occlusally, as well as outer tritoral series along labial margin. Outer tritoral series not preserved completely (distally), showing at least four subcylindrical bodies of laminated pleromin. Individual tritoral bodies of series situated closely to each other and with sub-rectangular outlines in cross section. First and second tritors joined together labially, forming single pleromin body lingually; largest within series. Tiny inner tritor situated over 1st outer tritor, at symphyseal-occlusal margin. Basal surface weakly concave and smooth, lacking any traces of descending lamina.

Remarks. Chisel-like, *Ischyodus*-type vomerine plates with a laminated outer tritoral series (3–8 tritoral units) must be attributed to *Elasmodus* (Averianov, 2001). This genus comprises nine species, recorded from the Albian to Upper Eocene and (?)Oligocene of Europe (mainly) and the Upper Cretaceous and Paleocene of North America, but it can be traced back at least to the Callovian (Middle Jurassic; see Popov, 2013). There are three mid-Cretaceous species: *E. rossicus* Averianov in Averianov et al. (1999) from the Upper Albian of Belgorod Province, Russia (Averianov et al., 1999; Averianov, 2001), *E. planus* (Newton, 1878) from the Cambridge Greensand of Cambridge, England (Newton, 1878; Popov, 2008a) and *E. sinzovi* Averianov in Averianov and Glickman (1994) from the Cenomanian of the Volga River Basin, Russia (Averianov and Glickman, 1994). *Elasmodus planus* (= *Ischyodus planus* of Newton, 1878) is based on a single mandibular plate (holotype); both other species have no previously figured vomerine plates. However, these are represented in collections (e.g., SSU 154/630; see Fig. 7B) and show a structure and tritor pattern that is typical for other Late Cretaceous and Paleogene species of *Elasmodus* (Case, 1979, pl. 2, fig. 4; Gurr, 1962, fig. 8B, pl. 26, fig. 4; Stahl, 1999, fig. 157B). Vomerines of *E. rossicus* (SSU 154/630; see Fig. 7B) and *E. sinzovi* (SSU 154/443 and 596, not illustrated here) show no significant differences, reflecting the fact that chimaeroid vomerine plates generally are of very limited diagnostic value for specific identification. In view of the absence of more useful mandibular plates for specific identification in the Annapol collection, the vomerine plate (ZPAL V.38/314) described here is referred to in open nomenclature.

Genus: *Elasmodectes* Newton, 1878

Type species. *Elasmodectes willetti* Newton, 1878; Upper Cretaceous (Turonian), Sussex and Kent, England.

Elasmodectes sp.
Fig. 5D–E

Material. Two right mandibular plate fragments, ZPAL V.38/500 and 890; both are illustrated.

Description. Both triangular beak fragments from right mandibular plates, thin in lingual view and widening in direction of symphyseal surface, the latter sloping occlusally and marking highest point of preserved fragment (Fig. 5D2–3, E4). Symphyseal surface flat, straight.

At base, ZPAL V.38/500 shows fragment of lateral descending lamina of typical *Elasmodectes* type structure (Fig. 5E2), as narrow longitudinal strip tapering laterally but forming small ledge in symphyseal view (Fig. 5E3). Basal surface of other specimen (ZPAL V.38/890) abraded, showing no trace of descending lamina. Labial margin reinforced by cutting symphyseal tritor, of compound structure with laminated and relatively large cylindrical first (mesial) tritoral unit, flanked laterally by series of rounded or curved narrowly packed units forming cutting edge of diagonally laminated pleromin. Occlusal tritors absent in both fragments.

Remarks. Despite the fragmentary nature of these specimens, they do show characters (i.e., thin plate with high symphysis, compound laminated symphyseal tritor of cutting type; reduced, strip-like descending lamina) which are typical of mandibular beaks of the genus *Elasmodectes* which has been recorded from the Middle Jurassic (Bathonian) to uppermost Cretaceous (Maastrichtian). Three Cretaceous species are known: *E. kiprijanoffi* (Nessov et al., 1988; see Fig. 7C) from the Albian and Cenomanian of European Russia (Nessov et al., 1988; Popov, 2004), *E. willetti* from the Turonian of England (Newton, 1878; Woodward, 1911; Stahl, 1999) and *E. zangerli* (Stahl and Chatterjee, 1999) from the Maastrichtian of Seymour Island, Antarctica. The last-named was originally attributed to *Chimaera* Linnaeus, 1758, but palatine plates described and illustrated (Stahl and Chatterjee, 1999, pl. 1, figs. 1–3, 6) show a form and tritoral pattern which is typical of *Elasmodectes* (compare Stahl, 2004). The Annapol specimens can be attributed definitively to this genus and, probably, to *E. kiprijanoffi* (compare Figs. 5D and 7C). However, on account of poor preservation, these fragments are best left in open nomenclature.

Genus: *Lebediodon* Nessov and Averianov, 1996b

Type species. *Lebediodon oskolensis* Nessov and Averianov, 1996b; mid-Cretaceous (Upper Albian), Belgorod Province, central Russia.

Lebediodon oskolensis Nessov and Averianov, 1996b
Fig. 5F–G

- 1988 (?)Rhinochimaeridae: Nessov et al., p. 128, fig. 1 (4).
1996a *Lebediodon oskolensis* Nessov and Averianov, p. 15 (*nomen nudum*).
1996b *Lebediodon oskolensis* Nessov and Averianov, p. 6, fig. 1 (6–7); non fig. 5 (*Elasmodectes kiprijanoffi*).
1999 *Lebediodon oskolensis* Nessov et Averianov, 1996b: Stahl, p. 149, fig. 158A.

Material. Two incomplete mandibular plates, ZPAL V.38/480 and 496; both illustrated here.

Description. Both plates of same size, left plate (ZPAL V.38/496) more complete, but broken with parts missing, thin and equally

compressed in occlusal-basal projection, concave in symphyseal-lateral projection and with low symphyseal surface. Basal surface smooth, with rare tiny longitudinal grooves, weak symphyseal descending lamina along symphyseal margin and without any traces of lateral descending lamina. Occlusal surface thin and in mesial-distal direction just along labial margin. Growth lines of post-occlusal surface oriented in similar way (Fig. 5G1: lgr). All occlusal tritons greatly reduced, consisting of vascular pleromin. Tritors visible mostly labially or in lingual view except for two tiny units of postero-outer tritor which are visible occlusally along labial margin (Fig. 5G1). Equal-sized (1–1.5 mm) antero-outer and median tritons visible in lingual view. More tiny inner tritons and thin symphyseal tritoral series comprising 6–7 tiny (less than 1 mm) pleromin units.

ZPAL V.38/480 lacks distal half of plate (Fig. 5F), showing fragment of symphyseal descending lamina, smoothly turned into rudiment of lateral descending lamina, forming in general tiny subcircular ledge (width c. 5 mm) in symphyseal sector of surface, and disappearing laterally. Symphyseal surface longitudinally concave and showing longitudinal groove joined with tritoral ledge above, the latter forming symphyseal-occlusal margin. Lingual distribution and dimension of tritoral bodies similar to ZPAL V.38/496, showing equal-sized antero-outer and median tritons as well as symphyseal tritoral series with 3–4 pleromin units. Inner tritor absent; postero-outer tritor not preserved.

Remarks. Features diagnostic of mandibular plates of *L. oskolensis* include the thin cutting plate with tritons well reduced in size and showing an *Ischyodus*-type distributional pattern (Fig. 7D; Nessov and Averianov, 1996b, fig. 1 (7); Popov and Efimov, 2012, fig. 3). There are both narrow median and antero-outer tritons as well as two tritoral series armouring the distal and mesial parts of labial margin, respectively: postero-outer tritoral series and symphyseal tritoral series; all occlusal tritons are composed of vascular pleromin. These diagnostic characters are visible on both Annopol specimens illustrated here (Fig. 5F–G), which is why they are listed as *L. oskolensis* (Fig. 7D). Some differences are visible in the development of lateral descending lamina (Fig. 5F1, G2); these can be interpreted to be the result of intraspecific variability of this plate, which became reduced and lost its functional significance in evolution (Popov, 2004).

Plates of *L. oskolensis* represent 7% of the total number of mandibular plates in the Belgorod chimaeroid assemblage (Popov and Averianov, 2001). Previously, this taxon was known exclusively from mandibular and palatine plates (Nessov and Averianov, 1996b); a single vomerine plate that was referred to this species (Nessov and Averianov, 1996b, fig. 1(5)) actually is a misidentified mandibular plate of *Elasmodectes kiprijanoffi* (E.V. Popov, pers. obs.).

Recently, *L. oskolensis* has been recorded from the Albian of France and England (Popov, 2007). The most recent addition is from the Cambridge Greensand chimaeroid assemblage (Popov, 2008a) as well as the Lower Albian Lower Greensand of England (E.V. Popov, pers. obs., 2007). Thus, this taxon may be regarded as a typical Albian chimaeroid for mid-latitude areas in the Northern Hemisphere.

Genus: *Edaphodon* Buckland, 1838

Type species. *Edaphodon bucklandi* Agassiz, 1843; Lower and Middle Eocene, England.

Edaphodon sedgwickii (Agassiz, 1843)
Fig. 6A–C

1843 *Chimaera* (*Psittacodon*) *sedgwickii* Agassiz: p. 349, pl. 40, figs. 17–18.

1878 *Edaphodon sedgwickii* (Agassiz, 1843): Newton, p. 7, pls. 1–2.
1891 *Edaphodon sedgwickii* (Agassiz, 1843): Woodward, p. 73.
1911 *Edaphodon sedgwickii* (Agassiz, 1843): Woodward, p. 184, text-fig. 55.

Material. Seven dental plates and fragments (ZPAL V.38/33, 319, 428, 438, 499, 502 and 803); the best preserved plates, ZPAL V.38/33, 428 and 499, are illustrated.

Description. Mandibular plates illustrated constitute largest (Km 21 and 32) chimaeroid plates in present collection, with construction typical of genus: plates tall and laterally compressed with pronounced, long beaks.

Plates with six occlusal tritons mainly of vascular pleromin (except for symphyseal tritor). Antero-outer and postero-outer tritons of equal width. Large and centrally placed median tritor occupying most part of occlusal surface. Tritor compound in cross section, displaced in symphyseal direction and with weakly defined bifurcation in occlusal view. Inner branch of median tritor extended mesially up to junction with inner tritor, the latter being of variable size and form, from fully developed individual unit (Fig. 6B2) to joined part of extended median tritor (Fig. 6A1).

Apical part of mandibular beak formed with symphyseal tritor, with falciform cross section and compound pleromin filling, forming mandibular apex and enforcing labial margin of beak. Mesial part of symphyseal tritor composed of laminated pleromin, replaced distally by irregular vascular pleromin. In addition, narrow beak tritor with vascular pleromin placed in mesial part of beak, lying along symphyseal margin. Near beak tritor of ZPAL V.38/428, well-defined and aberrant symphyseal protuberance (Fig. 6A3, A4) with flat surface (symphyseal ?facet).

Palatine plate of smaller individual (ZPAL V.38/499; see Fig. 6C) relatively narrow and robust, showing preserved distal part of antero-inner tritor, with broad and oval cross section in lingual view. Most part of visible occlusal surface occupied by compound and asymmetrical postero-inner tritor. Lateral and symphyseal parts of this tritor well visible in both occlusal and lingual views. Latter part more expanded mesially and rounded in occlusal view. Lateral part of plate, usually having outer tritor, missing. Basal surface of plate broken and abraded.

Remarks. Mandibular plates described here do not differ significantly from the corresponding plates of *E. sedgwickii* from the Cambridge Greensand of England (Newton, 1878, pl. 1, fig. 2; pl. 2, figs. 1, 8) showing a tritoral pattern typical of *Edaphodon* with a wide median tritor, which has a close junction with the inner tritor. The type specimen (BGS GSa 1524) of *Chimaera* (*Psittacodon*) *sedgwickii* is an incomplete mandibular plate (with missing mandibular beak) from the Upper Greensand (Albian) of England. The type is similar in size (e.g., Km 22.5) and tritoral topology (compare Agassiz, 1843, pl. 40, figs. 17–18) to the Annopol mandibular plates.

The significant difference in the size of mandibular (Km 21–32, L 125–129) and palatine plates (L 30.5) illustrated here indicates the presence of different chimaeroid ontogenetic stages (juveniles, adults) in the Annopol assemblage.

According to Stahl (1999) and Popov (2008a), *E. sedgwickii* had an extended stratigraphical distribution from the Albian (Lower Greensand) to the Campanian (Upper Chalk) in England. Additionally, the species was recorded from the Albian of Annopol (Samsonowicz, 1925, 1934; Radwański, 1968) and uppermost Cretaceous of New Jersey, USA (Hussakof, 1912). A recent revision of the chimaeroid fauna from the latest Cretaceous–earliest Paleocene Hornerstown Formation of New Jersey has indicated that

E. sedgwickii is missing from that assemblage (Popov, 2010). As far as the English material is concerned, records of the present species from deposits younger than the Lower Chalk (e.g., Middle and Upper Chalk) are doubtful because some specimens illustrated reveal a derived morphology of the mandibular median tritor (Woodward, 1911, pl. 40, fig. 4; Stahl, 1999, fig. 148 I). Well-documented records of the species are restricted to the Aptian–Cenomanian interval (Popov, 2008a). This widely distributed species was the largest in chimaeroid assemblages of this age.

10.2. Frontal clasper (frontal tenaculum)

Fig. 5H

Material. A single incomplete clasper, ZPAL V.38/801.

Description. Bilaterally hollow mineralised structure, 19 mm in total length and 13 mm in maximum width; only central part preserved, showing dorsoventral compression and weak proximal expansion forming triangular base. Low and broad cavity visible in distal cross section (Fig. 5H4).

Remarks. Chimaeroid frontal claspers (frontal tenacula) are rare in the fossil record and have not been described nor illustrated for a long time, while the larger and better-preserved frontal claspers of other Early Mesozoic holocephalians (myriacanthids, squalorajids) had been recorded on several occasions (Stahl, 1999). Chimaeroid frontal claspers are more reduced and uniform in structure and are covered with denticles (Duffin and Reynders, 1995; Herman et al., 2001; Kriwet and Klug, 2011).

Probably the single chimaeroid locality with frequent records of frontal claspers is that of Stoilensky quarry (Albian; Belgorod region, Russia) with more than 200 specimens preserved in collections (SSU 154/567 and others). Two frontal clasper morphotypes have been recognised in this assemblage; the predominant one is illustrated here (Fig. 7E). It has a structure which is unknown in Recent chimaeroids (Herman et al., 2001), being straighter and with a triangular base. It may represent any species of *Ischyodus*, which is the predominant genus in the Stoilensky quarry assemblage (Popov and Averianov, 2001). The Annopol specimen displays some similarity to this morphotype of frontal clasper and may thus also be tentatively attributed to *Ischyodus* spp.

With this frontal clasper, there is a shark tooth crown embedded in the phosphatic nodule (Fig. 5H2). Judging from small size, the distally inclined cutting type of the crown with a broad base, as well as presence of a central protuberance (lingual uvula) in the basal part of the crown, it is possible to refer this tooth to a squalid shark, possibly *Protosqualus* sp.

10.3. Fin spines

Fig. 5I–J

Material. Three fragments; illustrated are ZPAL V.38/704 and 864.

Description. Largest fragment (maximum length 21.8 mm, maximum height 3.3 mm, width 2.6 mm; Fig. 5I), is distal part of small fin spine with broken apex. It is weakly laterally compressed with suboval cross section, with longitudinal tiny striae in anterior halves of both sides, and with double asymmetrical series of distal denticles (Fig. 5I1; for additional specimen, ZPAL V.38/864; see Fig. 5J). Denticles short, tapering distally and decreasing gradually in size in proximal direction.

Remarks. Fin spine fragments are common chimaeroid fossils (e.g., Case and Herman, 1973; Case, 1979). The morphological diversity of

Recent chimaeroid fin spines is low (Herman et al., 2001). In the fossil record, two principal morphotypes occur, namely small-sized, straight spine with two posterior rows of relatively large denticles and irregular lateral ornament (*Elasmodectes*; see Woodward, 1911), and medium- to large-sized, faintly curved fin spines with relatively small and proximally tapering, with two rows of denticles within apical one-third of spine length and with tiny lateral ornament (*Edaphodon* and *Ischyodus*-related types of Newton, 1878). Fin spines, associated with *Edaphodon* (of which other skeletal remains are known), are larger in size and attain lengths of up to 520 mm (Duffin and Reynders, 1995; Cicimurri et al., 2008). Based on size and structure of the Annopol fragments, it is clear that they are attributable to *Ischyodus*, the dental plates which predominate in the local chimaeroid assemblage.

11. Palaeobiogeographic implications

On a global scale, nine mid-Cretaceous chimaeroid assemblages of key palaeobiogeographical importance are known (Fig. 8). Not all of these have been described and illustrated in detail to date, but some preliminary palaeobiogeographic conclusions may be drawn, on the basis of diversity and distribution in space and time.

Seven key assemblages are known from the Northern Hemisphere; the other two are from the Southern Hemisphere. Pre-Aptian chimaeroid history is not adequately known, in view of the fact that the fossil record of that age is composed of incidental records (Popov and Efimov, 2012). The oldest assemblage recorded from the Northern Hemisphere is from the Lower Greensand (Aptian) of England consists of two taxa, *Ischyodus thurmanni* and *Edaphodon sedgwickii* (see Popov, 2008a).

Albian and Cenomanian chimaeroid assemblages stem from the shallow inner continental seas of temperate latitudes (Boreal Realm) of Europe, except for the Asiatic limb (Kolbai, Mangyshlak peninsula), which is situated along the margin of the Tethyan Realm. The most diverse is the Late Albian assemblage from the Belgorod region (central Russia) with up to 11 genera of diverse ecology (Table 2). It consists of primitive callorhynchids (*Callorhynchus*, *Brachymylus*), well-diversified 'edaphodontids', as well as a single rhinochimaerid genus (*Harriotta*). Seven genera in the Belgorod assemblage are of pre-Cretaceous origin (64%), the remaining four (36%) of Cretaceous date. The Albian assemblage from the Cambridge Greensand of England is less diverse taxonomically, comprising four species of *Edaphodon*. It is interesting to note the presence of *Edaphodon crassus* in the Cambridge Greensand assemblage and in the lowermost Cenomanian of Kolbai, western Kazakhstan (Popov, 2008b; Kennedy et al., 2008); this species is absent in the much richer central Russian Belgorod assemblage. This probably is a reflection of unknown ecological factors.

In terms of taxonomic composition, the Annopol chimaeroid assemblage is intermediate between the Cambridge Greensand and Belgorod assemblages. All these sets have the following chimaeroid taxa in common: *Ischyodus* spp., *Elasmodus* sp., *Elasmodectes* sp., *Lebediodon* sp. and *Edaphodon* spp. The absence of callorhynchids, rhinochimaerids and some 'edaphodontid' taxa (e.g., *Stoiodon*) from the Annopol assemblage may be explained by collection bias. A specific identification of *Elasmodectes* and *Elasmodus* in the Annopol material is impossible, but the former might represent *E. kiprijanoffi*, which is the sole known Albian species of *Elasmodectes*.

The presence of *Ischyodus thurmanni* in the English and Polish assemblages and its absence from the central Russian faunas cannot be regarded as a significant difference between these assemblages, in view of the fact that *I. thurmanni* and *I. gubkini* are closely related. Additionally, *Ischyodus latus* known from England, but is missing from the Annopol assemblage and only a single

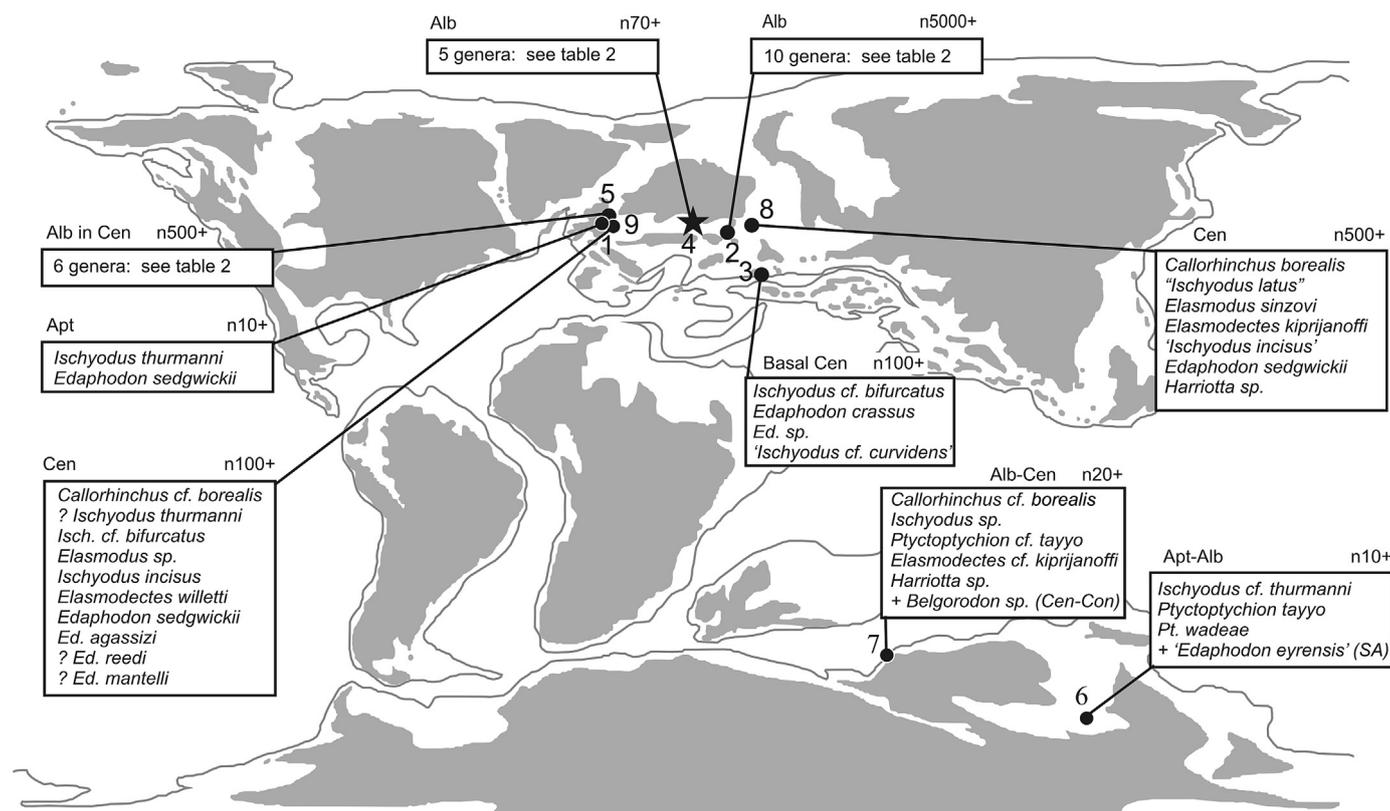


Fig. 8. Simplified palaeogeography during the Albian (105 Ma) (modified from Blakey, 2013) with the main mid-Cretaceous chimaeroid-bearing localities with taxonomic composition and total number of specimens in collections (indexed as nXX+), numbered here: 1 – Lower Greensand (Aptian) of England (Popov, 2008a); 2 – Upper Albian of Belgorod Province, Russia (Popov and Averianov, 2001); 3 – basal Cenomanian of Kolbay, Mangyshlak, Kazakhstan (Popov, 2008b; Kennedy et al., 2008); 4 – Upper Albian of Annapol, Poland (present study); 5 – Albian (Gault, Upper Greensand), England (Popov, 2008a); 6 – Aptian–Albian, Queensland, Australia (Lees, 1986; Bartolomai, 2008; Popov, 2011); 7 – Albian–Cenomanian of Western Australia (Popov, 2011); 8 – Cenomanian of Saratov Province, Russia (Popov, 2004); 9 – Cenomanian (Lower Chalk), England (Popov, 2008a).

Table 2
Taxonomic composition of the most important chimaeroid assemblages from the Aptian–Cenomanian of the Northern Hemisphere, based on literature sources referred to in the table.

Cambridge, UK (Cambridge Greensand: Albian reworked in Cenomanian) Ref.: Popov, 2008a	Annapol, Poland (upper Albian), present study	Belgorod Province, Russia (upper Albian) Ref.: Nesson and Averianov, 1996b; Popov and Averianov, 2001; modified
<i>Cal</i> <i>Callorhynchus cf. borealis</i>	–	<i>Callorhynchus borealis</i>
–	–	<i>Brachymylus</i> sp.
'Ed' <i>Ischyodus thurmanni</i>	<i>Ischyodus thurmanni</i>	<i>Ischyodus gubkini</i>
<i>Ischyodus</i> aff. <i>bifurcatus</i>	<i>Ischyodus</i> aff. <i>bifurcatus</i>	<i>Ischyodus</i> aff. <i>bifurcatus</i>
<i>Ischyodus latus</i>	–	–
' <i>Ischyodus incisus</i> '	' <i>Ischyodus incisus</i> '	' <i>Ischyodus incisus</i> '
<i>Elasmodus planus</i>	<i>Elasmodus</i> sp.	<i>Elasmodus rossicus</i>
<i>Lebediodon oskolensis</i>	<i>Lebediodon oskolensis</i>	<i>Lebediodon oskolensis</i>
<i>Elasmodectes kiprijanoffi</i>	<i>Elasmodectes</i> sp.	<i>Elasmodectes kiprijanoffi</i>
–	–	<i>Stoilodon aenigma</i>
–	–	<i>Belgorodon bogolubovi</i>
<i>Edaphodon sedgwickii</i>	<i>Edaphodon sedgwickii</i>	<i>Edaphodon sedgwickii</i>
<i>Edaphodon crassus</i>	–	–
<i>Edaphodon reedi</i>	–	<i>Edaphodon ? reedi</i>
' <i>Edaphodon</i> ' <i>laminosus</i>	–	–
Har –	–	<i>Harriotta</i> sp.

Abbreviations: Cal – Callorhynchidae; 'Ed' – Edaphodontidae; Har – Harriotinae (Rhinochimaeridae).

species of *Edaphodon* is present (vs four in English assemblages). On the other hand, the central Russian *Belgorodon* and *Stoilodon* are absent at Annapol. All of these taxa are rare and it is possible that they will be found at Annapol in future. The sole exception may be *Edaphodon crassus*, which is easily identified and relatively common both in English and Kazakh assemblages. Its absence from central Russia and Annapol may suggest that these assemblages are more closely related to each other than to the English faunas.

During the Cenomanian, the English and central Russian chimaeroid key assemblages became less diverse taxonomically and more differentiated in terms of ecology. The Russian faunas lost some 'edaphodontid' taxa (*Lebediodon*, *Belgorodon*) and callorhynchids (*Brachymylus*), whilst the English assemblage lost other 'edaphodontid' taxa (*Ischyodus latus*, *Lebediodon oskolensis*, *Edaphodon crassus*, '*Edaphodon*' *laminosus*). At the same time, the English faunas reveal more diverse records of *Edaphodon* spp. and a presence of two evolutionarily advanced taxa (*Ischyodus incisus*, *Elasmodectes willetti*). The appearance of the latter two taxa indicates that during the Cenomanian the chimaeroid speciation centre moved from the Russian Plate to the northeastern sector of the opening Atlantic. In summary, the Northern Hemisphere shows the most significant chimaeroid diversity during the Albian with up to 10 genera (based on a total of 5670+ specimens) with decreasing diversity during the Cenomanian (maximum 7 genera, based on 600+ specimens).

In spite of the limited material from the Southern Hemisphere (30+ specimens), a series of very rare and small-sized taxa

(*Callorhynchus*, *Harriotta*) have recently been recorded (Popov, 2011). This material is assigned to two temporal and regional assemblages, i.e., the Aptian–Albian of eastern Australia and Albian–Cenomanian of western Australia. Pre-Aptian chimaeroid history in the Southern Hemisphere is obscure (López-Arbarello et al., 2008). During the Aptian–Albian a local diversification centre existed in eastern Australia, in the semi-isolated Eromanga Basin; this comprises the endemic genus *Ptyktoptychion* Lees, 1986, plus cosmopolitan *Ischyodus* spp. A similarly mixed cosmopolitan–endemic fauna has recently been recorded from western Australia, albeit of a younger date (Albian–Cenomanian), but illustrating Albian (*Elasmodectes*, *Harriotta*) and Cenomanian (*Belgorodon*) ties amongst Eurasian chimaeroid taxa (Popov, 2011). It is interesting that '*Edaphodon eyrensis*' Long, 1985 from the Cretaceous of Australia is more closely related to *Ptyktoptychion* spp. and *Ischyodus thurmanni* than to any species of *Edaphodon* and, obviously, cannot be assigned to *Edaphodon* (Popov, 2011). If this reinterpretation is correct, *Edaphodon* was completely missing during the Aptian–Cenomanian in the Southern Hemisphere, in contrast to the Northern Hemisphere, where representatives of this genus were numerous and well differentiated.

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