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The first record of *Scheenstia* (Actinopterygii, Holostei) from the Late Cretaceous of Ukraine in the context of European occurrence of Mesozoic lepisosteiform fishes

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The first record of *Scheenstia* (Actinopterygii, Holostei) from the Late Cretaceous of Ukraine in the context of European occurrence of Mesozoic lepisosteiform fishes. — L. S. Kyselevych, O. M. Kovalchuk. — Lepisosteiform fishes are represented in the fossil record of Europe from the Late Jurassic until the Miocene. Most of their remains were found in the western and central parts of the continent. Here we report about a new find of the large and exceptionally well-preserved ganoid scale sharing similar morphological features with those in *Scheenstia*. It comes from the Upper Cretaceous (middle Cenomanian) marine deposits of Nova Ushytsia locality (western Ukraine). The age of these deposits is estimated as ca. 98–95 Ma due to the presence of ammonites *Turrilites costatus*, *T. acutus*, *Acanthoceras* cf. *rhotomagense*, and *Schloenbachia coupei*. The faunal assemblage also includes sharks, gars, reptiles, sponges, corals, bivalves, gastropods, belemnites, brachiopods, and bryozoans. The specimen described here is characterized by the presence of the longitudinal "peg-and-socket" articulation formed by two almost equally well-developed anterior processes and smooth surface lacking the regular structure inherent to lepisosteids. Lithological and paleontological investigation of Nova Ushytsia suggests the presence of an epicontinental, shallow and ramified sea with normal salinity and well-aerated warm water (+17–20 °C), temporary strong bottom currents and deep-water areas up to 150–200 m (10–80 m in average) with soft muddy bottom. Almost complete phosphatization of the early-middle Cenomanian faunal remains indicates an important role of the Carpathian upwelling. Microscopic observation of the studied scale surface and the presence of etched areas and digestion marks suggests that this fish specimen probably was a prey of ichthyosaur *Platypterygius indicus* Lydekker, 1879, which remains were also found in this locality. *Scheenstia* was a nektonic carnivore inhabiting marine coastal areas with normal salinity. The finding of *Scheenstia* in Ukraine is recently the youngest known record of this genus within the former European Archipelago extending its temporal range up to the Late Cretaceous. It allows filling the gap in lepisosteiform occurrences within Eurasia during the Mesozoic.

Key words: Lepisosteiformes, scale, morphology, biogeography, Cenomanian, Eastern Europe.

Introduction

Gars (order Lepisosteiformes) are a relatively small group of primitive neopterygian fishes comprising two families — Lepisosteidae with seven genera (*Atractosteus* Rafinesque, 1820; †*Herreraichthys* Alvarado-Ortega et al., 2016; *Lepisosteus* Lacépède, 1803; †*Masillosteus* Micklich and Klappert, 2001; †*Nhanulepisosteus* Brito et al., 2017; †*Oniichthys* Cavin and Brito, 2001; †*Paralepidosteus* Arambourg, 1943), and †Obaichthyidae including two genera (†*Dentilepisosteus* Grande, 2010; †*Obaichthys* Wenz and Brito, 1992). In addition, seven extinct genera of lepisosteiform fishes are indicated by incertae familiae — †*Araripelepidotes* Santos, 1990; †*Beiduyu* Murray et al., 2015; †*Isanichthys* Cavin and Suteethorn, 2006; †*Lepidotes* Agassiz, 1832; †*Pliodetes* Wenz, 1999; †*Thaiichthys* Cavin et al., 2013, and †*Scheenstia* López-Arbarello and Sferco, 2011. The latter was erected after the re-classification of Late Jurassic–Early Cretaceous species previously referred to *Lepidotes*.

Seven species were assigned to the genus *Scheenstia* — *S. mantelli* (Agassiz, 1833), *S. laevis* (Agassiz, 1837), *S. maximus* (Wagner, 1863), *S. decoratus* (Wagner, 1863), *S. degenhardti* (Branco, 1885), *S. hauchecornei* (Wagner, 1863), and *S. zappi* López-Arbarello and Sferco, 2011. These species

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cover a temporal range from the Late Jurassic to the Early Cretaceous, i.e. 157.3–129.4 Ma (López-Arbarello, 2012). The current distribution of gars is restricted to North America, Central America and the Caribbean islands (Nelson et al., 2016), however it was much wider in the past as evidenced by their fossils in South America, Africa, Europe and Asia (Böhme and Ilg, 2003; López-Arbarello, 2012).

Here we describe an exceptionally well-preserved scale of possible *Scheenstia* from the Cenomanian deposits of Ukraine in a broad biogeographical context.

Geological setting

The specimen described here was collected by one of the authors (L.K.) in 1982 in a small ravine on the left slope of the Kalius River valley (left tributary of the Dniester River) near Nova Ushytsia (Khmelnytskyi Region, western Ukraine); coordinates — N 48°50′, E 27°16′ (Fig. 1). The oldest rocks in the basement of this section are Silurian shales with rare sandstone tiles (visible thickness up to 3 meters). Above them, there is a series of dense green quartz-glauconitic sands with sandstone nodules, bryozoans, mollusc shells and rare bone fragments. It is covered by gray hornstones with light gray, clayey sands filling the cavities.

Fig. 1. Location map of Nova Ushytsia locality.
Рис. 1. Географічне положення місцезнаходження Нова Ушиця.

The most productive sequence is represented by greenish-gray glauconitic sands (up to 2 meters in thickness) yielding numerous macrofaunal remains. The presence of ammonites *Turrilites costatus*, *T. acutus*, *Acanthoceras* cf. *rhotomagense*, and *Schloenbachia coupei* indicates the middle Cenomanian age (ca. 98–95 Ma) of these deposits. The faunal assemblage also includes sharks, gars (represented by the isolated scale described here), reptiles (i.e. vertebrae and teeth of ichthyosaurs *Platypterygius indicus* Lydekker, 1879 and *Platypterygius* sp.), as well as sponges, corals, bivalves (*Cyprimeria faba*, *Cucullaea mailleana*, *C. subglabra*, *Venericardia tenuicosta*, *Eurotrigonia aliformis*, *Myoconcha cretacea*, *Plicatula inflata*, *Plicatula gurgitis*, *Trigonarca orbignyana*, *Chlamys* cf. *hispida*, *Ch.* (*Merklinia*) *aspera*, *Ch.* cf. *fissicosta*, *Amphidonte conicum*, *Grammatodon* (*Nanonavis*) *carinatus*, *Nodosiella* cf. *nodosa*, *Neithea* sp., *Donax* sp.), gastropods (*Avellana cassis*, *Natica lyrata*, *Nairiella* cf. *tenuicosta*, *Pleurotomaria* sp.), brachiopods (*Terebratula striatula*, *Rhynchonella subhercynica*, *Rh. grasiana*),

bryozoans, and numerous belemnite rostra. Phosphatization of the fossils led to their good preservation. The fossil-bearing deposits are covered by black flints and kaolinized sands of Pliocene age.

Material and methods

The examined specimen is stored in the Department of Paleontology, National Museum of Natural History of the National Academy of Sciences of Ukraine (collection PI), Kyiv, Ukraine.

It was identified using diagnostic features based on comparisons with extinct and modern taxa (deposited in Virginia Institute of Marine Science, USA, Hungarian Natural History Museum, and Babeş-Bolyai University Cluj-Napoca, Romania) as well as on data from the literature (Thomson and McCune, 1984; Grande, 2010; Sweetman et al., 2014; Pouech et al., 2015; Haddoumi et al., 2016). The taxonomic hierarchy follows Grande (2010), López-Arbarello (2012), and Nelson et al. (2016). Morphological description is presented here according to Grande (2010), with reference to Kerr (1952), Grande and Bemis (1998), Kumar et al. (2005).

A JEOL JSM-606 OLA scanning electron microscope was used for preparing SEM pictures. The specimen was measured by an electronic caliper with an accuracy of 0.01 mm.

Systematic paleontology

Class Actinopterygii Cope, 1887 *sensu* Rosen et al., 1981

Subclass Neopterygii Regan, 1923

Infraclass Holostei Müller, 1844 *sensu* Grande, 2010

Division Ginglymodi Cope, 1872 *sensu* Grande, 2010

Order Lepisosteiformes Hay, 1929 *sensu* López-Arbarello, 2012

Genus *Scheenstia* López-Arbarello and Sferco, 2011

Scheenstia? sp.

Material: one complete lateral scale, No. PI-1 (Fig. 2 *a-d*).

Description. The scale is exceptionally well preserved, large and massive. Its maximum length is 32.4 mm, width — 17.8 mm, and the depth is 6.9 mm. The scale plate is slightly convex longitudinally, mostly in its central part (see Alvarado-Ortega et al., 2014 for comparison).

Unoverlapped field is clearly rhomboid in shape. Posteroventral angle of the scale is almost equal to the anterodorsal one (110°); posterodorsal and anteroventral angles are acute (75°). Outer surface of the specimen is covered with a ganoin layer, which is thicker along the scale borders. The basal plate is formed by a thick bony case up to 5.7 mm in depth. There is a tiny vertical serration between these layers, which is characteristic for lepisosteiform fishes (see Thomson and McCune, 1984 for details). The posterior edge of the scale is straight and narrow.

There is an elongated (10.4 mm) shaft-like ventral anterior process (*vap*). A dorsal anterior process (*dap*) is also well developed being only slightly shorter than *vap* (7.4 mm) and almost the same in width. Both these processes are narrowed towards the top, slightly curved dorsally, and connected by a convex arc-shaped ridge (ca. 8 mm in length) forming a longitudinal "peg-and-socket" articulation (see Grande and Bemis, 1998; Kumar et al., 2005; Grande, 2010; López-Arbarello, 2011; Lourembam et al., 2017). There is a small invagination near the base of *vap*, and elongated keel (peg) at the dorsal edge of the scale. Ten annual ridges and three small rounded papillae are recognizable at its outer surface. Other ornamentation is absent.

The scale surface looks completely smooth when observed with naked eye only. However, under magnification (×50, ×100), wide etched areas are clearly visible (Fig. 3 *a-b*). The outer surface of the scale is uneven and lacks some regular microstructure (e.g. granular one as those in Lepisosteidae; see Gayet and Meunier, 1986: p. 1260; Szabó et al., 2016).

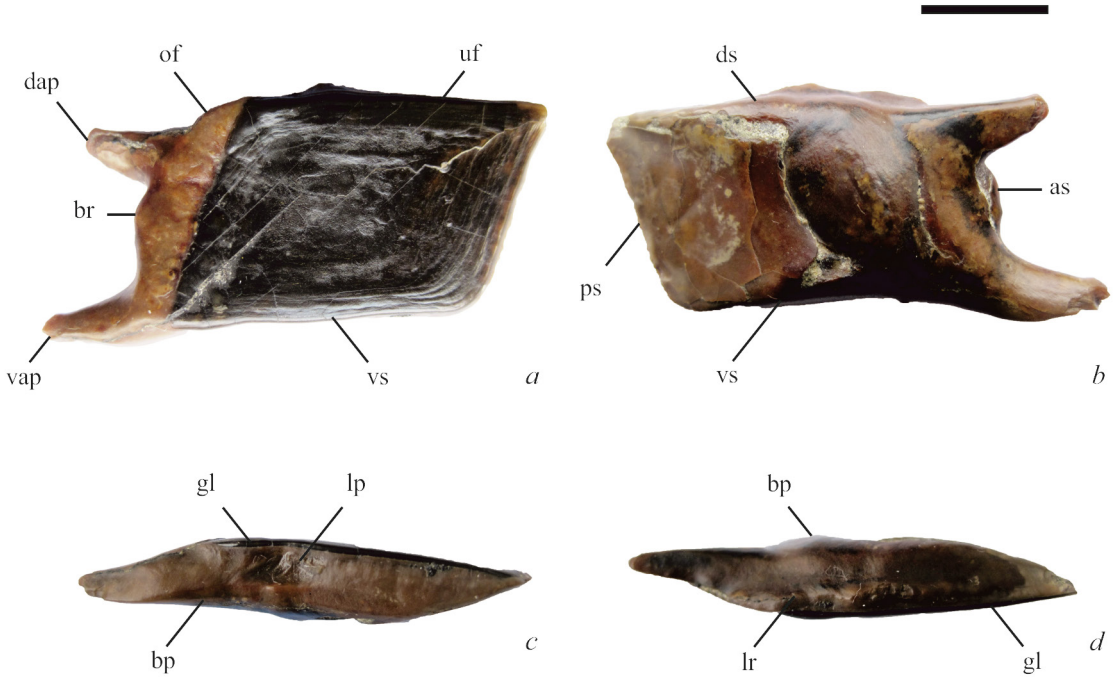

Fig. 2. *Scheenstia*? sp. scale No. PI-1 from Nova Ushytsia: *a* — external view; *b* — internal view; *c* — dorsolateral view; *d* — ventrolateral view. Abbreviations: *as*, anterior surface; *bp*, basal plate; *br*, basal ridge; *dap*, dorsal anterior process; *ds*, dorsal surface; *gl*, ganoin layer; *lp*, lateral pit; *lr*, lateral ridge; *of*, overlapped field; *ps*, posterior surface; *uf*, unoverlapped field; *vap*, ventral anterior process; *vs*, ventral surface. Scale bar equals 1 cm.

Fig. 2. Луска *Scheenstia*? sp. № PI-1 із місцезнаходження Нова Ушиця: *a* — вигляд зовні; *b* — вигляд зсередини; *c* — дорзолатеральна поверхня; *d* — вентролатеральна поверхня. Скорочення: *as*, передня поверхня; *bp*, базальна пластинка; *br*, базальний гребінь; *dap*, дорзальний передній відросток; *ds*, дорзальна поверхня; *gl*, ганоїновий шар; *lp*, бічна ямка; *lr*, бічний гребінь; *of*, перекрите поле; *ps*, задня поверхня; *uf*, неперекрите поле; *vap*, вентральний відросток; *vs*, вентральна поверхня. Масштабний штрих — 1 см.

There are traces of dissolution (Fig. 3 *c*; ×250), single large and deep round cavities with torn edges (Fig. 3 *d*; ×250), as well as small pits of different size (Fig. 3 *e*; ×300). At a higher magnification (Fig. 3 *f*; ×650), flattened tubercles with wide bases and eroded tips are visible.

Remarks. The scale is identical in general morphology and shape to those in Lepisosteiformes. Its basal bony plate is directly covered by ganoin layer without dentine intercalation. The absence of posterior spines differs the examined scale from those in representatives of the family †Obaichthyidae (Grande, 2010). Direct comparison shows its similarity to the lepisosteid scales, e.g. rhomboidal shape, smooth and rounded borders, concave central part of the scale plate, and the presence of variably developed anterior processes. However, there are considerable differences between them. For instance, scales of the extant *Atractosteus spatula* have serrated posterior edge with festoons and only one (dorsal) anterior process.

The scales of *Lepisosteus osseus* are more elongated, and characterized by well-pronounced ganoin ornamentation at their outer surface. Extinct species of the genus *Lepisosteus* have wider and shorter anterior processes, as well as shallower and weakly developed ridge between them. The same is visible on illustrations from the literature (Buffetaut et al., 1996: fig. 2 *l-n*; Cavin et al., 1996: pl. 1, fig. 4; Codrea et al., 2010: fig. 2 *e*). Additionally, both *Atractosteus* and *Lepisosteus* have characteristic "lepisosteid tubules" at the surface of their scales (Gayet and Meunier, 1986; Szabó et al., 2016; Szabó and Ősi, 2017).

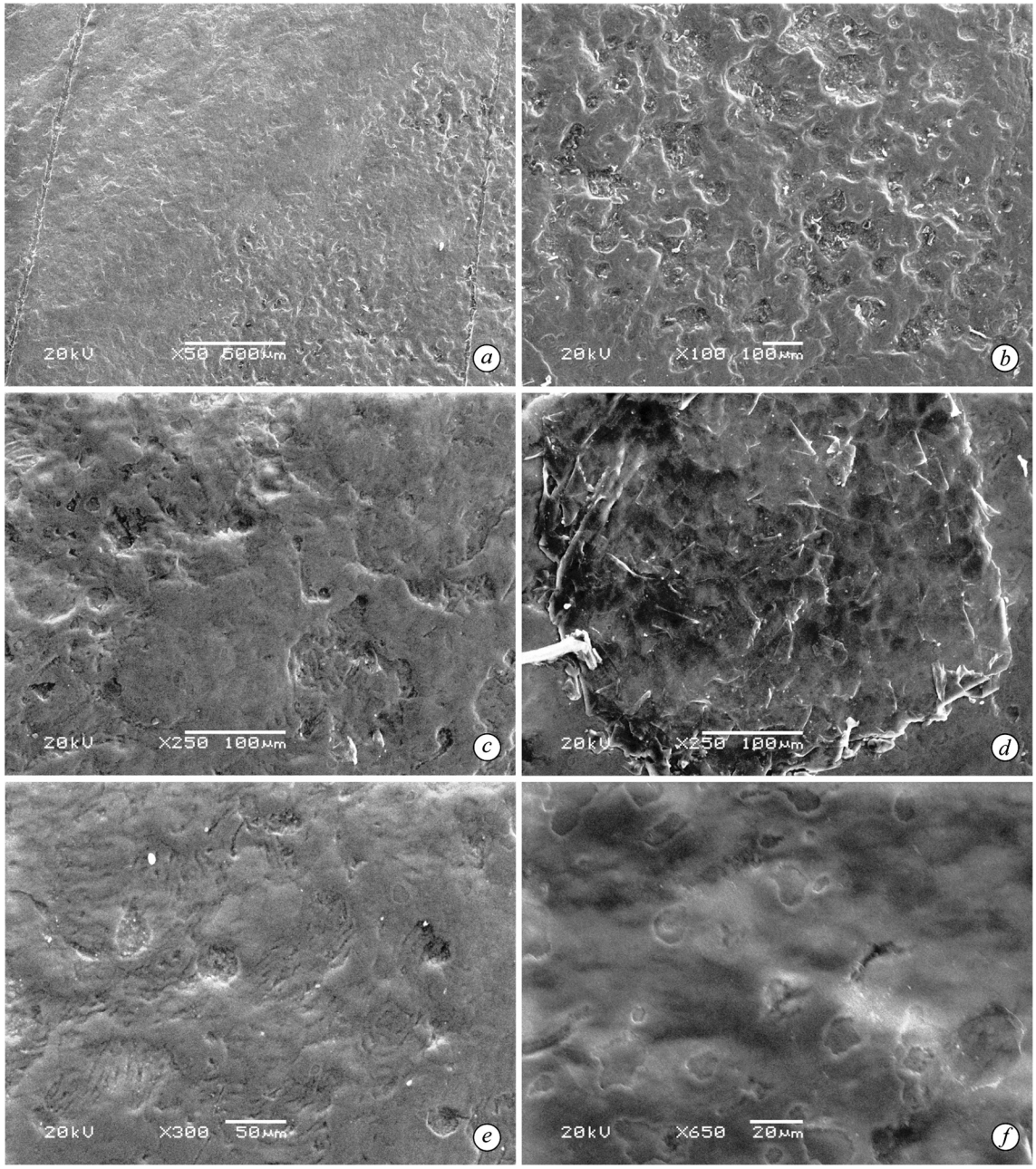

Fig. 3. SEM photos of the scale at various magnification: *a* — ×50; *b* — ×100; *c–d* — ×250; *e* — ×300; *f* — ×650.
Fig. 3. СЕМ фото луски на різному збільшенні: *a* — ×50; *b* — ×100; *c–d* — ×250; *e* — ×300; *f* — ×650.

We tentatively assign the described specimen to *Scheenstia* due to the presence of vertical peg-and-socket articulation formed by two almost equally well-developed anterior processes (López-Arbarello, 2012). The scale is identical to those in *Lepidotes* sp. from the Late Jurassic of Guimarota Coal Mine in Portugal (Kriwet, 1998: pl. 3, fig. 7; Kriwet, 2000: fig. 6.13).

It has the same structure as the scales assigned to *Lepidotes* cf. *mantelli* from the Early Cretaceous of Lobber Ort in Germany (Ansorge, 1990: abb. 16) and the same age as *Scheenstia* sp. from the Isle of Wight, England (Sweetman et al., 2014: fig. 13 *c-d*) and Cherves-de-Cognac in France (Pouech et al., 2015: fig. 3 *m*). However, the specimen described here is larger. Very similar in shape and overall morphology are the isolated scales identified as *Lepidotes* sp. (or *Scheenstia* sp.) from the

Middle Jurassic of Guelb el Ahmar, Morocco (Haddoumi et al., 2016: fig. 10 *a*) and the Late Jurassic *Scheenstia* sp. from Tlaxiaco, Mexico (Alvarado-Ortega et al., 2014: fig. 8.2). At the same time, the scales of *Scheenstia zappi* are smaller and characterized by the presence of slightly serrated posterior borders (López-Arbarello and Sferco, 2011).

As far as we know, the scale surface of the genus *Scheenstia* has not yet been investigated microscopically. Therefore, it is not possible to assign the specimen to a certain species.

Discussion

Paleoenvironmental and taphonomic implications

A study of the lithology, macro- and microfauna, facial distribution, and living conditions of the fossil-bearing Nova Ushytsia locality suggests the presence of an epicontinental, shallow and ramified sea with normal salinity and well-aerated warm water (+17–20 °C), temporary strong bottom currents and deep-water areas up to 150–200 m (10–80 m in average) with soft muddy bottom. Almost complete phosphatization of the early-middle Cenomanian faunal remains indicates an important role of the Carpathian upwelling. Geochemically active phosphorus concentrated on the sea shelf within Volyn-Podillya as a result of changes in salinity, temperature, pH, and CO_2 content. Upwelling is also interpreted as a rise of deep waters enriched with gases, redistribution of exogenous mineralized water masses by sea currents over long distances, and the occurrence of redoxillin zones. Such conditions probably occurred during the phosphatization of remains in the studied area during the early and middle Cenomanian.

Two areas of sedimentation are distinguished for the Cenomanian sea basin within the current Middle Dniester region (Sobetsky, 1961): northwestern shallow (sublittoral) area where the terrigenous deposits were predominantly accumulated (Sobetsky, 1979), and the southeastern deep-water region (pseudoabissal) with carbonate-clayey and carbonate sediments (Sobetsky, 1979). The boundary between these lithofacial zones is fuzzy; lithological interchange occurs there because of sequential-pulsating (transgressive and regressive) "wedging" and cross-linking of marlstones with sands (Vorobiev et al., 1971). It is manifested in the gradual growth of clay content in marlstones, up to their transformation into carbonate clays, and after in dense quartz-glauconitic sands due to the growth of glauconite content.

The scale of *Scheenstia*? sp. was found in the layer yielding ichthyosaur remains. Ganoid scales are sometimes found in coprolites of these reptiles (Segesdi et al., 2017). The slight etching at the surface of the scale described here should be tentatively interpreted as digestion marks caused by the stomach acid. As it was argued by Hone and Rauhut (2010) and Segesdi et al. (2017), theropod dinosaurs, mosasaurs (and ichthyosaurs), unlike crocodiles (Hunt and Lucas, 2010), did not have such acidic stomach environment or long digestion period to completely dissolve the ganoin of lepisosteiform scales. Therefore, *Scheenstia*? from Nova Ushytsia could have been a potential prey of ichthyosaur.

Biogeographical and biostratigraphic significance

Lepisosteiform fishes appeared in the fossil record in the Early Jurassic (López-Arbarello, 2012) and became diverse during the Late Jurassic and Early Cretaceous (Grande, 2010). Gars were much more widely distributed during the Mesozoic and the first half of the Cenozoic compared to their current range. López-Arbarello (2012) presented a thorough review of all known localities bearing ginglymodian fish remains including the representatives of *Scheenstia*. Among them, the oldest are the fossils assigned to *Scheenstia* sp. from the Middle Jurassic of Morocco (Haddoumi et al., 2016) as well as to *S. maximus* and *S. laevis* from the Upper Jurassic deposits of France and Germany (López-Arbarello, 2012).

Other European *Scheenstia* fossils are of Early Cretaceous age and restricted to central and western parts of the continent, being referred to *S. mantelli* and related species (Böhme and Ilg, 2003).

Their distribution is connected with the former European Archipelago. Numerous Late Jurassic–Early Cretaceous remains from Belgium, Denmark, England, France, and Germany, previously assigned to *Lepidotes* using open nomenclature (Sauvage, 1879-80; Buffetaut et al., 1985; Ansorge, 1990; Böhme and Ilg, 2003; Austen et al., 2010; Olive et al., 2017), should be reconsidered and most probably included into the genus *Scheenstia*. The scale of *Scheenstia* from Nova Ushytsia is recently the youngest known record. It allows suggesting the presence of this genus in Europe until the middle Cenomanian. Besides, it is the easternmost European occurrence of lepisosteiform fishes filling the gap in their known past distribution within Eurasia.

Conclusions

Every new find of lepisosteiform remains in Europe is of great interest because it allows presenting the biogeographical history of this group in more detail. The specimen described here is a single scale, however, due to its preservation, it was identified up to the genus level.

This find revealed the presence of *Scheenstia* within the European Archipelago at least until the middle Cenomanian, making it the youngest ever known record of this genus. Besides, it is the easternmost occurrence of lepisosteiform fossil remains for Europe as well, thus providing an opportunity to consider its former distribution within Eurasia more precisely. It was found that the extinction of *Scheenstia* coincides in time with the appearance and wide distribution of lepisosteid fishes and their close relatives (e.g. obaichthyids, etc.).

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