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RESEARCH PAPER

Late Pennsylvanian fishes from the Finis Shales of North-Central Texas (USA)

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Abstract
A diverse assemblage of fish microremains is reported from the Virgilian (Gzhelian), Upper Pennsylvanian Finis Shale outcrop at Lost Creek Lake near Jacksboro (Texas, USA). The assemblage contains diverse remains of chondrichthyans, rare acanthodians and actinopterygians. The chondrichthyans are represented by a xenacanthimorph, ctenacanthiforms, symmoriiforms, an euselachian, a neoselachian, a petalodontiform, eugeneodontiforms, a helodontiform and euchondrocephalian taxa. The teeth of *Bransonella* dominate the chondrichthyan microremains. The occurrence of *Bransonella lingulata* in the Gzhelian Finis Shales of Texas is the youngest in the world. The assemblage includes widely distributed taxa of chondrichthyans. The chondrichthyan fauna from the Finis Shale outcrop differs from the rich faunas of the Kasimovian–Gzhelian from other regions such as New Mexico and Nebraska in the USA, Moscow, Samara and Volgograd regions of Russia, Spain, Germany and the Czech Republic by the dominance of bransonelliform remains and the set of diverse ctenacanthiforms and euchondrocephalians. The new assemblage of fishes demonstrates the presence of chondrichthyan taxa with different food specialisation in the Virgilian faunal community.

Keywords Pennsylvanian · Fishes · Chondrichthyes · Texas · USA

Introduction

The Finis Shale outcrop (TXV-200, "Spillway Section") at Lost Creek Lake near Jacksboro (Texas, USA) is famous for its rich assemblage of well-preserved and taxonomically diverse fossils (e.g. Roden et al. 2019) including vertebrates, invertebrates and plants. Macroremains of fishes are known from this locality. The incomplete fin spine of *Physonemus mirabilis* St. John and Worthen, 1875 was reported from this Finis Shale outcrop (Dalquest et al. 1993). McKinzie and McLeod (2003, 2015) described and illustrated the following remains: teeth and jaw fragment of the ctenacanthiform *Glikmanius occidentalis* (Leidy 1859) (determined as *Symmorium reniforme* Cope 1893); neurocranium fragments of cladodontomorphs (determined as *Glikmanius occidentalis* or cladodont shark); fragments of fin spines determined as *Physonemus mirabilis* St. John and Worthen, 1875 or *Ctenacanthus* sp.; fragment of eugeneodontiform tooth whorl (determined as *Edestus* sp.); eugeneodontiform teeth including an *Arpagodus* tooth (determined as *Orodus variabilis* Newberry 1875); petalodontiform tooth determined as *Peripristis semicircularis* Newberry and Worthen 1866; tooth plates of cochliodontiform *Deltodus* sp.; denticles of *Petrodus* type; scapulocoracoid of an undetermined chondrichthyan; braincases of undetermined palaeoniscids. The petalodontiform *Petalodus ohioensis* Safford 1853 was mentioned also from that locality (McKinzie and McLeod 2003). Neurocranium occipital regions of the gigantic ctenacanthiform sharks were described from the Finis Shale outcrop (Maisey et al. 2017). Itano and Lucas (2018) redescribed tooth whorls of *Edestus* from this locality as *Campyloprion*

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sp. In this study, we present so far unstudied microremains of fishes collected in two sections at the TXV-200 site.

Finis Shale geography and geology

The vertebrate remains investigated in this study derive from the Finis Shale outcrop at Lost Creek Lake near Jacksboro, Texas, USA (Fig. 1a). This outcrop (Figs. 1b–e, 2b–e) is also known as TXV-200 or "Spillway Section" (AMNH locality #5562) and an excellent site for sampling the Upper Pennsylvanian as it contains a rich and well-preserved fauna (Ernst et al. 2023). Roden et al. (2019) characterised the fossil locality as Liberation Lagerstätte; this type of Lagerstätte is defined by fossils that are extremely well preserved and easily freed from the surrounding sediment.

Whilst the Finis Shale is famous for the quality and diversity of the fossil assemblage and for being widely distributed in Northern Texas (Barnes et al. 1987), it has so far only been partially studied. Conodonts and foraminifers,

Fig. 1 **a** Geographic position of Jacksboro, the next town to TXV-200, approximately 80 km NW of Forth Worth, Texas, USA. **b** View from above (googlemaps; July 2023) onto the horseshoe-shaped outcrop of TXV-200 ("Spillway Section) with the bedding plane and lake. Three sections were prepared, the fossil remains derive from sections B and C (compare Fig. 1B, D, E, Fig. 2B–F). **c** Panoramic view onto the outcrop, arrow in the left indicates section B, right one section C (compare Fig. 2B–F). **d** Freshly prepared section B with the yellowish shale. **e** Weathered greyish shale and view into the horseshoe

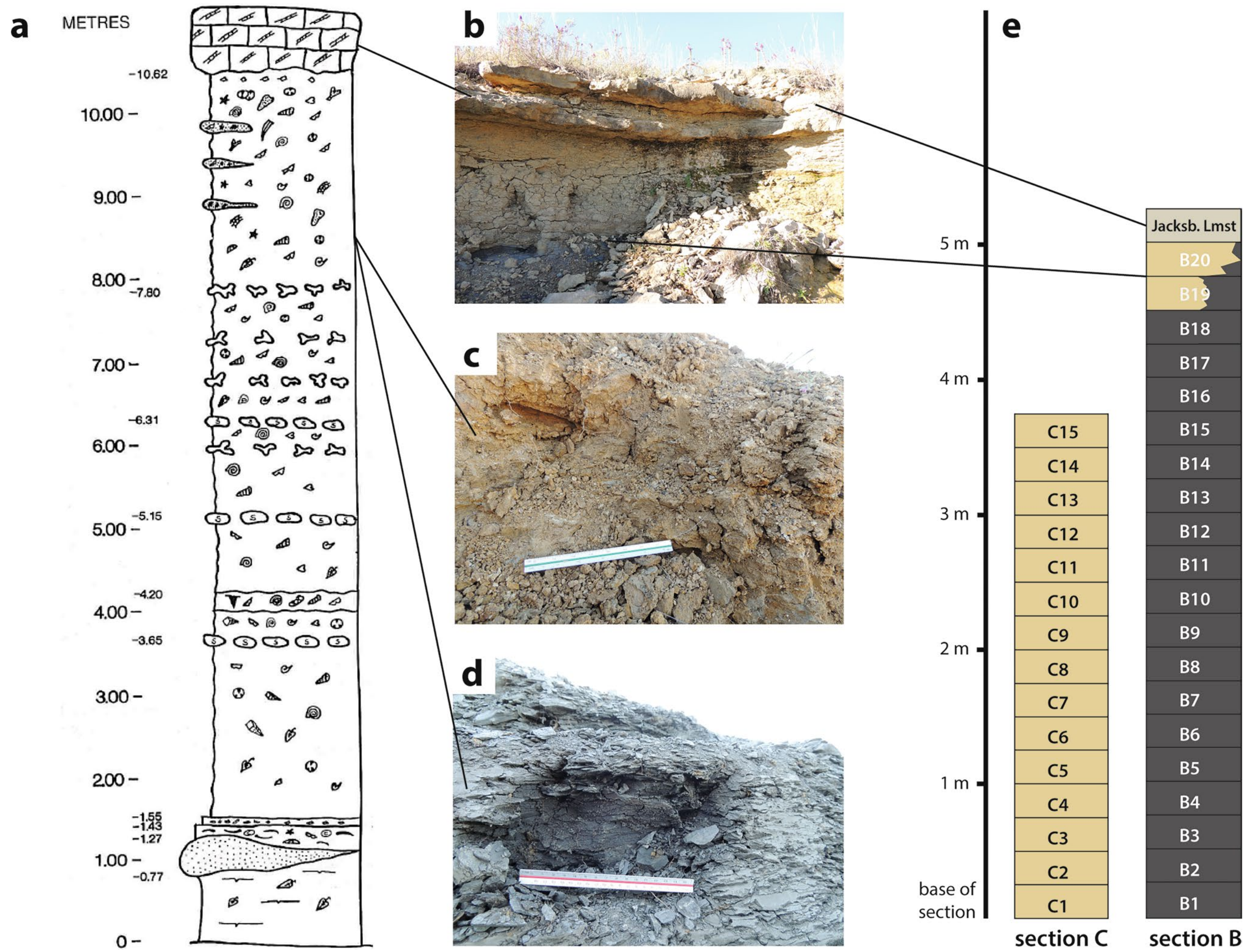

Fig. 2 **a** Profile section by Lobza et al. (1994, Fig. 3). **b** Top of section B with the Jacksboro Limestone covering the Finish Shale which is blending from grey in the lower part of the section into yellowish shale. **c** Yellowish Finis Shale of section C. **d** Greyish Finis Shale of section B. **e** Sections B and C with the samples and their position within the sections indicated

especially fusulinids, are abundant in the lowermost parts of the shale at TXV-200 (e.g. Nestell et al. 2019), but those strata are only recorded subsurface and are not studied here. Overlying deposits comprise a diverse assemblage of fish remains (teeth and bones; Maisey et al. 2017), which are objects of this study. Brachiopods and molluscs are increasingly present throughout the upper parts of the section represented by various cephalopod, gastropod and bivalve species (e.g. Miller and Downs 1950; Boardman et al. 1984; Grossman et al. 1991; Lobza et al. 1994; Forcino et al. 2010; Karapunar et al. 2022; Niko et al. 2022) (Fig. 2a). In addition, echinoderm remains are highly abundant with species ranging from sea urchins, starfish, crinoids, holothurians to brittle stars (personal observation BS; also Boston 1988; Lobza et al. 1994). Plant remains occur occasionally (e.g. Boston 1988; McKinzie and McLeod 2003; personal observation BS).

Geology and geography

The vertebrate remains in the present study were collected from shales at the "Spillway Section" (AMNH locality #5562 = TXV-200) at Lost Creek Lake, Jacksboro (Texas, USA) near its dam. Coordinates of the outcrop are 33° 14′ 12.2″ N / 98° 7′ 12″ W (Figs. 1, 2). Whilst the outcrop was created during the built of the emergency spillway of Lost Creek Lake and previous researchers sampled the lower parts of the shale, we were only able to investigate the upper parts starting at a level covered by remains of conulariids (personal observation BS; Sendino et al. 2023), which we chose as the base of our sampling sections. The entire section of Finis Shale at TXV-200 is approx. 30 m thick (Nestell et al. 2019), but today only 5–6 m of the sequence remains accessible, with a maximum thickness of 10 m above the basal bedding plane. The shales are covered by the Jacksboro Limestone (e.g. Boston 1988; Forcino et al. 2010). Both shale and limestone are part of the Finis transgressive–regressive cycle (Boardman and Heckel 1989; Boardman et al. 1984), which mirrors sea level rise and fall during the Late Paleozoic Ice Age (e.g. Montañez and Poulsen 2013). The Finis Shale and Jacksboro Limestone represent the basal parts of the Graham Formation (Cisco Group; Fig. 2a) (Moore and Plummer 1922; Grossman et al. 1991) of Virgilian (Gzhelian, Upper Pennsylvanian, Carboniferous) age.

The environment is interpreted as non-deltaic based on the amounts of filter-feeders (Boston 1988) and part of the eastern shelf of the western Midland Basin in the North American Midcontinent during an orogenetic event that led to the uplift of the Amarillo and Arbuckle Mountains and the Ouachita Foldbelt to the North and East, respectively (Yang and Kominz 2003).

Material and methods

Fresh stratigraphic sections were studied (Figs. 1c–e, 2b–e) prepared with the help of the Dallas Paleontological Society at the horseshoe-shaped slope (Figs. 1a–e, 2c–e) of TXV-200. The shale was bulk sampled by collecting 2.5 kg of sediment every 25 cm until the top of this stratum was reached and that is covered by the Jacksboro Limestone. The shale itself differs in coloration; whilst lower parts of the sequence often are blackish to deep grey and clayey, weathered shale appears yellowish (Figs. 1d–e, 2c–e).

The collected samples were sent to laboratories at the FAU-GZN Paläoumwelt, Erlangen where they were dried at 35 °C before processing 1.5 kg of each at a time. Since the shale disaggregates easily in tap water, no solvents were required. The samples were then sieved utilising 2 mm, 500 µm, 250 µm and 125 µm mesh sizes. Identifiable fossils were picked from the 2 mm and 500 µm mesh sieves.

The fish microremains were photomicrographed with a scanning electron microscopes (SEM) Tescan VEGA-II XMU, Cambridge CamScan-4 and Hitachi S-3400N. The specimens described herein are housed in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich (BSPG) under collection no. SNSB-BSPG 2020 CXI 129 to SNSB-BSPG 2020 CXI 158.

Results

The fish assemblage from the Finis Shale outcrop includes the microremains of a diverse fauna of chondrichthyans, whilst acanthodians and actinopterygians are rare.

Chondrichthyans

The chondrichthyan microremains contain numerous teeth of a xenacanthimorph, ctenacanthiforms, symmoriiforms, an euselachian, a neoselachian, a petalodontiform and eugeneodontiforms as well as a helodontiform tooth whorl, an euchondrocephalian tooth plate, and rare scales and symmoriiform denticles.

Symmoriiforms

The symmoriiform microremains include faclatid and symmoriid teeth, and denticles. The faclatid teeth belong to *Denaea* sp. and possess a five-cusped cladodont crown with a high central and moderate-sized lateral cusps, and small intermediate cusplets (Fig. 3a, b). The cusps are inclined lingually, recurved and ornamented with straight and delicate cristae. The cusp bases are arranged in a slightly curved line. The tooth base is lingually extended, trapezoidal in shape, with a poorly preserved apical button. The lingual edge of the button is perforated by the foramen of the main vascular canal and forms a narrow median notch.

The teeth of the symmoriid *Stethacanthus* sp. are poorly preserved and have a cladodont crown with very large central cusp and small lateral and intermediate cusps (Fig. 3c). The central cusp is compressed labiolingually. The tooth base is rhomboidal in shape, extended lingually and considerably elongated mesiodistally.

The symmoriiform denticles are represented by two morphotypes. The first morphotype possesses a monocuspid high-conical crown inclined posteriorly and a prominent base (Fig. 5a, b). The crown of some monocuspid denticles is covered by straight cristae (Fig. 5a). This type of denticles was described from the spine-brush complex in some representatives of symmoriiforms (Lund 1974, 1985; Zidek 1993; Coates and Sequeira 2001). The second morphotype is a multicuspid denticle characterised by a crown consisting of elongate cusps consecutively overlapping each other (Fig. 5c). These denticles are buccopharyngeal (Zangerl and Case 1976; Williams 1985; Coates and Sequeira 2001) and were described as the formal taxon “*Stemmatias* (*Stemmatodus*) *simplex*” (St. John and Worthen, 1875).

Ctenacanthiforms

The ctenacanthiform teeth include the teeth of *Heslerodus divergens* (Trautschold 1879) and unidentified ctenacanthiforms. The teeth of *Heslerodus divergens* (Fig. 3e, d) are characterised by a cladodont crown with five to seven cusps including a large central, rather high lateral, moderate-sized inner intermediate and small outer intermediate cusps. The central cusp is slightly larger and higher than the lateral cusps. The cusps are round in cross-section, and covered

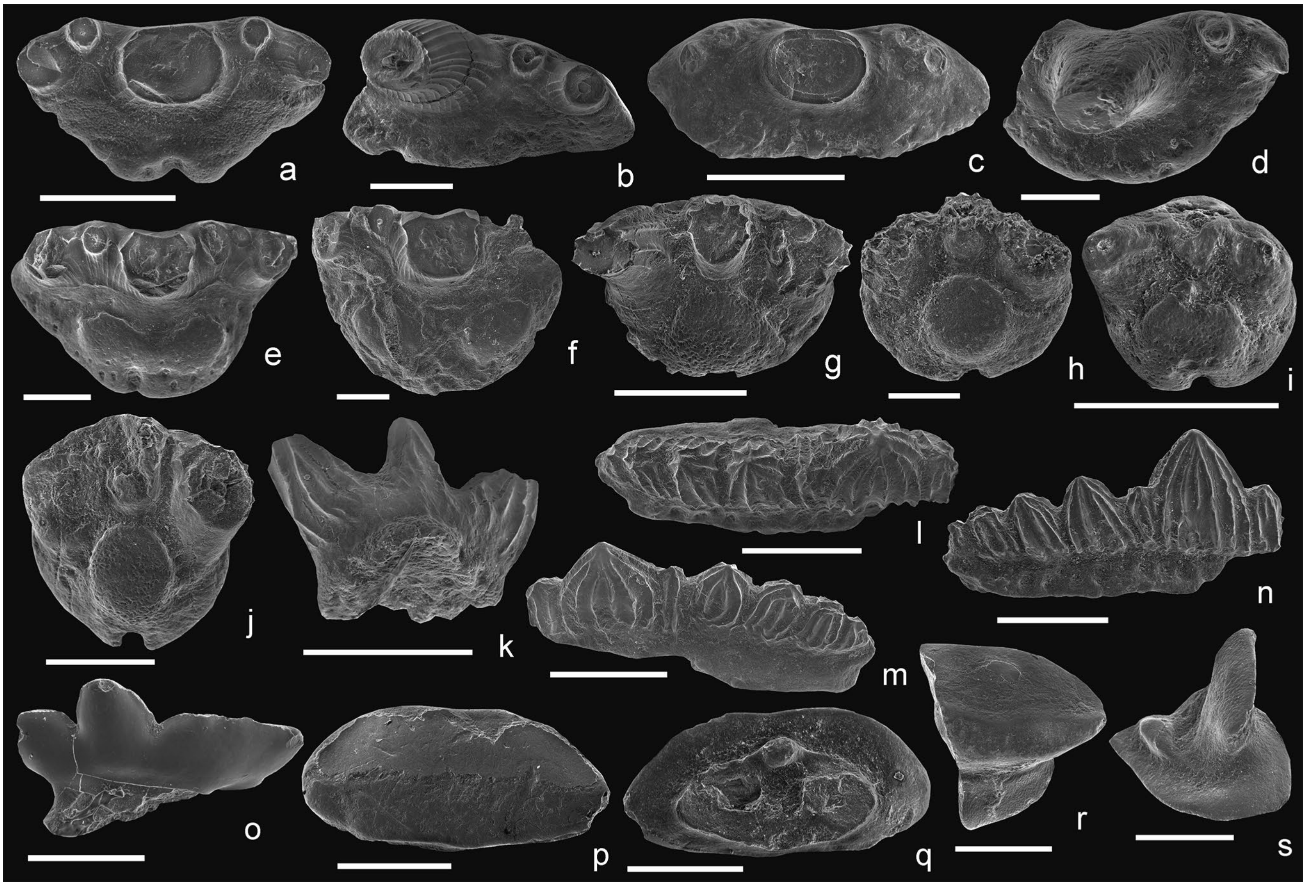

Fig. 3 Elasmobranch teeth. **a, b** *Denaea* sp., occlusal views: **a** SNSB-BSPG 2020 CXI 129, sample B16; **b** SNSB-BSPG 2020 CXI 130, sample C11. **c** *Stethacanthus* sp., occlusal view, SNSB-BSPG 2020 CXI 131, sample B18. **d** Ctenacanthiformes, occlusal view, SNSB-BSPG 2020 CXI 132, sample B20. **e, f** *Heslerodus divergens* (Trautschold 1879), occlusal views:: **e** SNSB-BSPG 2020 CXI 133, sample C14; **f** SNSB-BSPG 2020 CXI 134, sample B6. **g–k** *Bransonella lingulata* Ivanov and Ginter 1996, occlusal (**g–j**) and oblique labial (**k**) views: **g** SNSB-BSPG 2020 CXI 135, sample B19; **h** SNSB-BSPG 2020 CXI 136, sample B14; **i** SNSB-BSPG 2020 CXI 137, sample C12; **j** SNSB-BSPG 2020 CXI 138, sample C11; **k** SNSB-BSPG 2020 CXI 139, sample B19. **l–n** *Sphenacanthus* sp., occlusal (**l**), lingual (**m**) and labial (**n**) views, SNSB-BSPG 2020 CXI 140, sample B15. **o–s** *Cooleyella* cf. *amazonensis* Duffin et al. 1996: **o** lingual view, SNSB-BSPG 2020 CXI 141, sample B5; **p, q** occlusal (**p**) and basal (**q**) views, SNSB-BSPG 2020 CXI 142, sample C11; **r, s** occlusal and oblique lateral views, SNSB-BSPG 2020 CXI 143, sample C11. Scale bars equal 500 µm in **a, b, d–s** and 2 mm in **c**

with coarse cristae on the labial side, and with minute cristae on the lingual side. The tooth base is semicircular in shape, considerably extended lingually, with two oval apical buttons and two oval labio-basal tubercles. The buttons are closely placed (Fig. 3d) or even fused in the middle parts (Fig. 3e). The labial depression is shallow.

Teeth of unidentified ctenacanthiforms are poorly preserved and belong to two types; the first possesses a cladodont crown with a large central and moderate-sized lateral, and small intermediate cusps (Fig. 3d). The central cusp is compressed labiolingually and inclined lingually. The tooth base is semicircular in shape, and slightly extended lingually, with a wide and shallow labial depression. The apical buttons and labio-basal tubercles are not preserved. The second tooth type has a base extending lingually, with a wide and deep labial depression, and two poorly traced round apical buttons. These teeth resemble the teeth of *Glikmanius* sp. (Ginter et al. 2005).

Xenacanthimorphs

The xenacanthimorph remains are represented by numerous teeth of the bransonelliform *Bransonella lingulata* Ivanov and Ginter 1996. *B. lingulata* teeth dominate amongst the microremains of chondrichthyans. These teeth possess a tricuspid, diplodont crown with large lateral and small central cusps (Fig. 3g–k). The lateral cusps are round in cross-section, the central one is compressed mesiodistally. The cusps bear an inverted "V"-nested ornamentation on the labial side reaching the crown/base boundary (Fig. 3k). The lingual side of the cusps is covered with straight cristae. The tooth base is lingually

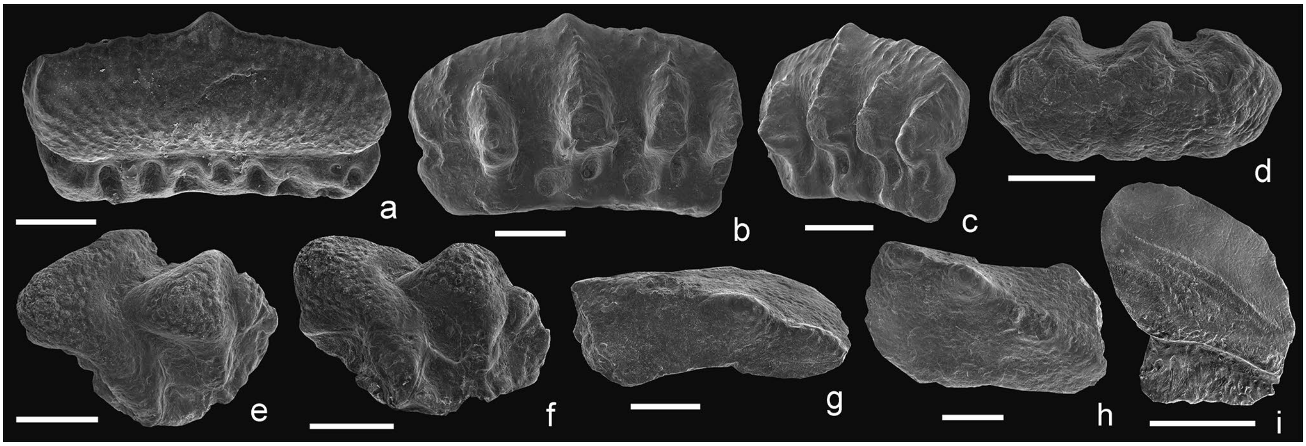

Fig. 4 Euchondrocephalian teeth (**a–d, i**), tooth whorl (**e, f**), and tooth plate (**g, h**). **a–c** *Arpagodus* sp., lingual (**a**), labial (**b**) and oblique lateral (**c**) views, SNSB-BSPG 2020 CXI 144, sample B16. **d** Eugeneodontiformes, occlusal view, SNSB-BSPG 2020 CXI 145, sample B16. **e, f** Helodontiformes, oblique occlusal (**e**) and lateral (**f**) views, SNSB-BSPG 2020 CXI 146, sample B16. **g, h** Euchondrocephali, oblique labial (**g**) and occlusal (**h**) views, SNSB-BSPG 2020 CXI 147, sample C13. **i** *Antliodus* sp., lingual view, SNSB-BSPG 2020 CXI 148, sample B18. Scale bars equal 1 mm in **a–c, e–h;** 500 µm in **d** and 3 mm in **i**

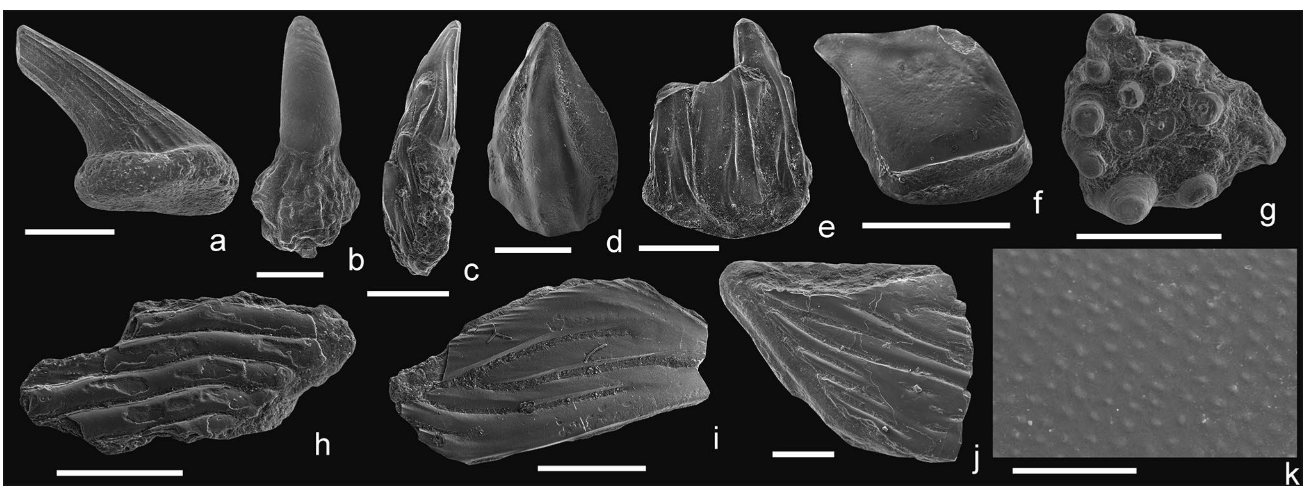

Fig. 5 Fish microremains. **a–c** Symmoriiform denticles: **a, b** brush denticles, lateral (**a**) and anterior (**b**) views; **a** SNSB-BSPG 2020 CXI 149, sample C17; **b** SNSB-BSPG 2020 CXI 150, sample C16; **c** buccopharyngeal denticle, oblique lateral view, SNSB-BSPG 2020 CXI 151, sample B20. **d** Chondrichthyan scale of hybodontid type, crown view, SNSB-BSPG 2020 CXI 152, sample C15. **e** Chondrichthyan scale of ctenacanthid type, crown view, SNSB-BSPG 2020 CXI 153, sample B7. **f** Acanthodiform scale, oblique crown view, SNSB-BSPG 2020 CXI 154, sample B17. **g–k** Actinopterygian remains: **g** tooth plate, crown view, SNSB-BSPG 2020 CXI 155, sample B12; **h–k** scales, crown views, external views: **h** SNSB-BSPG 2020 CXI 156, sample B19; **i** SNSB-BSPG 2020 CXI 157, sample B17; **j, k** SNSB-BSPG 2020 CXI 158, sample C12. Scale bars equal 500 µm in **a–j**, and 50 µm in **k**

extended, from oval to circular in shape. The prominent apical button base occupies almost the entire occlusal surface of the base. The button varies in shape: from round to oval or tear-shaped. The semilunar labio-basal tubercle is located at the labial rim. The foramen of the main vascular canal perforates the lingual rim of the base, frequently forming a distinct notch.

Euselachians

The incomplete tooth of the euselachian *Sphenacanthus* sp. (Fig. 3l–m) possesses a monolithic, pyramidal crown which is elongated mesiodistally. The crown has conical cusps gradually arranged according to their height mesially and distally, the highest at the centre to smallest laterally.

The cusps are rounded in cross-section, fused to each other near the base but separated by narrow triangular depressions. They are ornamented with coarse ridges that diverge from the cusp apex. Two small cusps are closely placed to the central cusp on the mesial and distal sides. The tooth base is slightly extended lingually and perforated by large foramina on the lingual part. These teeth resemble the teeth of *Sphenacanthus delepinei* Fournier and Pruvost 1928.

Neoselachians

The neoselachian microremains are represented by incomplete teeth of the anachronistid *Cooleyella* cf. *amazonensis* Duffin et al. 1996. The crown of these teeth is smooth, with a sloping labial part and a short, inclined lingual part. The labial surface is trapezoidal in shape, with a short and wide labial flange. The tooth base is considerably smaller than the crown, and oval in basal view. The base has an extended, convex lingual and very narrow labial faces. The round small basal tubercle is located beneath the labial flange. The basal tubercle is separated by a narrow transversal groove from the lingual part of the base.

Euchondrocephalians

The euchondrocephalian remains include teeth of eugeneodontiforms and petalodontiform, a helodontiform tooth whorl and an euchondrocephalian tooth plate.

The teeth of the eugeneodontiforms are represented by a single lateral tooth of *Arpagodus* sp. and fragmentary teeth of undetermined taxon. The *Arpagodus* tooth is well preserved, possesses an elongated mesiodistally crown and is strongly compressed labiolingually (Fig. 4a–c). The crown has a crenulated occlusal crest and an acuminated central cusp. The labial face of the crown bears the very prominent, wide buttresses with serrated ridge. The buttresses are separated by deep and wide depressions, and are extended towards the base in the form of narrow ridges. The ridge of the largest, middle buttress originates at the apex of the central cusp. The lingual face of the crown is flat, with numerous tubercles forming vertical rows. The tooth base is extended basally, strongly compressed labiolingually, and perforated with large foramina of vascular canals on both, lingual and labial, sides. The small size of the tooth with large foramina of vascular canals indicates a young tooth. The tooth is similar to the tooth of *Arpagodus rectangulus* Trautschold 1879 (Ginter et al. 2010, Fig. 121C, D) and to some teeth of *Agassizodus variabilis* (Newberry and Worthen 1870) (St. John and Worthen 1875, pl. VIII, Figs. 2, 4, 6), but differs in the tuberculated lingual face missing on the ridges.

The teeth of undetermined eugeneodontiforms are incomplete and poorly preserved, have distinct narrow buttresses on the labial side of the crown and ridges on the lingual side (Fig. 4d). They resemble the teeth of *Agassizodus* and *Eugeneodus* (Ginter et al. 2010).

The tooth of the petalodontiform *Antliodus* sp. possesses the asymmetrical oval crown which is strongly compressed labiolingually and displays several basal ridges (Fig. 4i). These ridges are arranged along a sloping line and occupy approximately half of the lingual face of the crown. The tooth base is considerably smaller than the crown. The tooth is very similar to the *Antliodus* tooth illustrated by Case (1973, Fig. 41).

The helodontiform tooth whorl (or family) includes four teeth with separated crown and fused bases (Fig. 4e, f). Teeth are gradually arranged from smaller to larger ones along a curved line. The crowns are arched, elongated mesiodistally, with a prominent central and sloped mesial and distal parts, and with an extended labial peg and a shallow lingual depression. The occlusal surface of the crown bears large tubule openings. The tooth base of the whorl is extended lingually and arched, with concave basal surfaces.

The euchondrocephalian tooth plate is arched, with sloped lateral surfaces, and wavy occlusal crest (Fig. 4g, h). The tubule openings are traced along the occlusal crest. This tooth plate slightly resembles the tooth plate of *Arcuodus,* but the latter is symmetrical and has an occlusal surface compounded completely of tubular dentine (Itano and Lambert 2018).

Chondrichthyan scales

The chondrichthyan microfossils include scales of ctenacanthid and hybodontid types. The ctenacanthid type (Fig. 5e) possesses a polyodontode crown consisting of long, narrow odontodes. The odontodes are arranged subparallel to each other, and bear the characteristic thin ridges. The scale base is round in outline, with a slightly concave basal side. The scales of hybodontid type (Fig. 5d) have a pyramidal crown covered by robust ridges.

Acanthodians

The acanthodian remains include isolated scales (Fig. 5f). They have a flat, smooth crown almost rhomboid in shape, with acuminated posterior projection, as well as a narrow neck and convex base. The crown is ornamented with tiny microtubercles. These scales belong to the *Acanthodes* type, and are characteristic of representatives of the order Acanthodiformes.

Actinopterygians

Ray-finned fishes are represented by isolated teeth, tooth plates and flank scales. The tooth plate bears conical teeth of various heights and diameters (Fig. 5g). The scales are rhomboidal with elongate ganoine ridges of different width on the free field (Fig. 5h–j). The preserved anterior depressed field is narrow, the upper depressed field has an extended middle part (Fig. 5j). Some ridges give raise to serrated posterior edges (Fig. 5i). The ganoine ridges are covered by rounded microtubercles (Fig. 5k). Some scales are similar to the scales of elonichthyiforms (Lebedev 2001).

Discussion

Distribution and occurrence of fish taxa

The chondrichthyans include widely distributed taxa. The xenacanthimorph *Bransonella lingulata* was recorded in the Carboniferous from the Viséan, Mississippian to the Gzhelian, Pennsylvanian. This species occurs in the Lower Viséan of the Kuznetsk Basin, Russia, the Lower Serpukhovian of the Moscow Region, Russia, the Lower Bashkirian of South Urals, Russia, the Moscovian (Desmoinesian) of Oklahoma, USA, the Lower Kasimovian (Lower Missourian) of New Mexico, USA and possibly in the Upper Bashkirian of Arizona, USA (Hampe and Ivanov 2007; Johnson and Thayer 2009; Ivanov and Hampe 2015; Ivanov et al. 2017; Ivanov and Lucas 2019). This species also was found in the Moscovian of North Greenland and determined as *Bransonella* spp. (Cuny and Stemmerik 2018). The occurrence of *B. lingulata* in the Gzhelian Finis Shales of Texas is the youngest in the world.

The ctenacanthiform *Heslerodus divergens* is known from the Moskovian–Gzhelian, upper Carboniferous of the Moscow Region, Kasimovian–Gzhelian of the Samara Region, and the Carboniferous–Permian boundary beds of the Pechora Sea, Russia (Ivanov 1999, 2005, 2017). It has also been recorded in the Bashkirian (Morrowan) of Wyoming (Ginter 2002), the Moscovian (Desmoinesian) of Indiana, Ohio, Oklahoma, and Pennsylvania (Wiliams 1985; Ginter 2002), the Kasimovian (Missourian) of Missouri (Hoffman et al. 2014), the Gzhelian (Virgilian) of Nebraska and Kansas, USA (Case 1973; Ginter 2002), the Sakmarian (Gearyan), lower Permian of Kansas (Schultze 1985; Ginter 2002) and the Kungurian (Leonardian) of Arizona, USA (Hodnett et al. 2012).

The ctenacanthiform *Glikmanius occidentalis* was reported from the Moscovian, Pennsylvanian, Carboniferous–Kungurian (Leonardian), lower Permian of New Mexico, Arizona, Kansas, Indiana, Illinois, Ohio, Colorado and Texas, USA; occurrences are also present in the Moscovian, Pennsylvanian –Kazanian, middle Permian of the East European Platform and the Urals, Russia and the middle Permian of Japan (Ginter et al. 2005; Johnson 2008; Hodnett et al. 2012).

The anachronistid *Cooleyella amazonensis* occurs in the Moscovian, Pennsylvanian, Carboniferous of Brazil and Oklahoma, USA. It is also recorded from the Kasimovian (Missourian) of New Mexico, USA, the Gzhelian of Kansas, USA, the Artinskian, lower Permian of South Urals, Russia, the Roadian (Kazanian), Guadalupian, middle Permian of Tatarstan, Vladimir and Kirov regions, Russia and the Roadian–Capitanian, middle Permian of Texas, USA (Ivanov et al. 2017, 2021).

Assemblages of the Late Pennsylvanian (Gzhelian) chondrichthyans

Chondrichthyan assemblages from the Mississippian and Early Pennsylvanian (Carboniferous) are abundant and taxonomically diverse in the different regions of the world, and have been quite well studied (e.g. Ginter et al. 2010). The Late Pennsylvanian chondrichthyans are less well known (Ivanov 2022). Besides the reported assemblages from the Finis Shale outcrop rich chondrichthyan assemblages are recorded in the Kasimovian–Gzhelian of the Moscow and Samara regions, Russia, the Gzhelian of the Volgograd Regions, Russia and also from the Missourian of New Mexico and the Virgilian of Nebraska, USA and the Stephanian of Spain, Germany and the Czech Republic.

The fish assemblage of the Finis Shale outcrop, considering the published data but with some new determinations, includes the following taxa: bransonelliform xenacanthimorph *Bransonella lingulata* Ivanov and Ginter 1996; symmoriiforms *Denaea* sp., *Stethacanthus* sp. and undefined taxa; ctenacanthiforms *Heslerodus divergens* (Trautschold 1879), *Glikmanius occidentalis* (Leidy 1859), *Ctenacanthus* sp. and undefined taxa; euselachian *Sphenacanthus* sp.; anachronistid neoselachian *Cooleyella* cf. *amazonensis* Duffin et al. 1996; eugeneodontiforms *Campyloprion* sp., *Arpagodus* sp. and undefined taxa; petalodontiforms *Peripristis semicircularis* Newberry and Worthen 1866, *Petalodus ohioensis* Safford 1853 and *Antliodus* sp.; cochliodontiform *Deltodus* sp.; undefined helodontiform and euchondrocephalian; uncertain chondrichthyan *Physonemus mirabilis* (St. John and Worthen, 1875); undefined acanthodiform and actinopterygians. The bransonelliform species dominates the chondrichthyans in this marine assemblage.

The assemblage from the Onaga Formation, Virgilian of a locality at Peru, Nemaha County, Nebraska contains the bransonelliform *Bransonella nebraskensis*; symmoriiforms *Denaea saltsmani* Ginter and Hansen 2010, *Stethacanthus concavus* Ginter 2018, *Stethacanthus* sp.; ctenacanthiforms *Glikmanius myachkovensis* (Lebedev 2001) and *Heslerodus divergens* (Trautschold 1879); hybodontiforms *Ossianodus nebraskensis* Ginter 2016, "*Polyacrodus" lapalomensis* Johnson 1981, and *"Lissodus"* sp.; euselachians *Sphenacanthus carbonarius* (Giebel 1848), *S. tenuis* Ginter 2016, and Euselachii gen. et sp. indet. eugeneodontiform *Caseodus* sp., petalodontiforms, holocephalans, and iniopterygian (Ginter et al. 2010; Ginter 2016, 2018). The symmoriiforms and hybodontiforms are abundant groups in this marine assemblage.

The chondrichthyans from the Missourian interval of the Horquilla Formation in the Robledo Mountains, New Mexico, USA comprise the remains of the bransonelliforms *Bransonella lingulata* and *Bransonella nebraskensis*; symmoriiforms *Denaea* sp. and *Stethacanthus* sp.; ctenacanthiform *Glikmanius* sp.; jalodontiform *Adamantina foliacea*; euselachians *Protacrodus* sp., Hybodontiformes indet. and Euselachii indet.; neoselachians *Cooleyella amazonensis, Cooleyella* cf. *fordi* (Duffin and Ward 1983) and *C.* sp.; orodontiform *Orodus* sp.; eugeneodontiforms *Agassizodus* sp. and Eugeneodontiformes indet.; helodontiform *Helodus* sp.; petalodontiform and cochliodontiforms (Ivanov and Lucas 2019). The bransonelliforms, jalodontiform and anachronistids dominate amongst other chondrichthyans in this marine assemblage.

The marine chondrichthyans from the Kasimovian–Gzhelian of Moscow and Samara regions, Russia are represented by bransonelliform *Bransonella nebraskensis* (Johnson 1984); symmoriiforms *Denae wangi* Wang, Jin and Wang, 2004), *D.* sp., and *Stethacanthus* sp.; ctenacanthiforms *Heslerodus divergens* (Trautschold 1879), *Heslerodoides triangularis* Ivanov 2022 and *Glikmanius* sp.; jalodontiform *Adamantina foliacea* Ivanov 1999; protacrodontid euselachian *Gzhelodus serratus* Ivanov 2022; neoselachians *Cooleyella amazonensis* Duffin et al. 1996 and *C.* sp.; uncertain elasmobranch *Samarodus flexus* Ivanov 2022; helodontiforms and cochliodontiforms (Ivanov 2017, 2022). The ctenacanthiforms predominate in this fauna.

The chondrichthyan assemblage from the Gzhelian of Volgograd Regions, Russia includes symmoriiforms *Denae wangi, D.* sp. and Symmoriiformes indet.; possible squatinactiform ?*Squatinactis* sp.; euselachians *Gzhelodus serratus,* Lonchidiidae indet. and Sphenacanthidae indet.; neoselachian *Cooleyella amazonensis*; uncertain elasmobranch *Samarodus flexus*; eugeneodontiform *Karpinskiprion ivanovi* (Karpinsky 1924), and Orodontiformes indet. (Lebedev et al. 2023).

The assemblage from the Stephanian C of the Puertollano basin, Spain includes xenacanthiforms *Orthacanthus meridionalis* Soler-Gijón, 1997 and *Triodus* sp.; the euselachian *Sphenacanthus carbonarius* (Giebel 1848), hybodontiforms *"Lissodus" lopezae* Soler-Gijón, 1997, "*Lissodus*" cf. *zideki* (Johnson 1981), and "*L.*" sp. (Soler-Gijón 1997; Schneider et al. 2000; Ginter et al. 2010). The euselachians including sphenacanthid and hybodontiforms are most abundant in this assemblage.

The chondrichthyan assemblage from the Stephanian interval from the Göttelborn—Wahnwegen formation (Kasimovian–Gzhelian) of the Saar-Nahe Basin, Germany contains the xenacanthiforms *Lebachacanthus senckenbergianus* (Fritsch 1889), *Orthacanthus gracilis* (Giebel 1848), *O. kounoviensis* Fritsch 1889, *Xenacanthus meisenheimensis* Hampe 1994, *X. remigiusbergensis* Hampe 1994, *Triodus lauterensis* Hampe 1989; euselachian *Sphenacanthus carbonarius* (Giebel 1848); hybodontiform *"Lissodus" lacustris* Gebhardt 1988, "*Lissodus*" cf. *zideki* (Johnson 1981), and "*L.*" sp. (Schneider et al. 2000; Ginter et al. 2010). The xenacanthiforms strongly predominate in this assemblage.

The chondrichthyan assemblage from the Stephanian B and C of the Kladno-Rakovnfk and Krkonoše Piedmont basins, Bohemia, Czech Republic includes the xenacanthiforms *Orthacanthus kounoviensis* Fritsch 1889, *Xenacanthus parallelus* (Fritsch 1890), *Plicatodus plicatus* (Fritsch 1879), and *Triodus* sp.; ctenacanthiform *Turnovichthys magnus* Štamberg 2001; euselachian *Sphenacanthus carbonarius* (Giebel 1848), hybodontiform *Lissodus lacustris* Gebhardt 1988; *uncertain elasmobranch Platyacanthus ventricosus* (Fritsch 1889) (Zajíc 2000, 2006; Štamberg and Zajíc 2008; Ginter et al. 2010). The xenacanthiforms considerably dominate amongst other chondrichthyans. The fish assemblages from Germany, Bohemia and Spain belong to the lacustrine and palustrine environments in the Late Pennsylvanian but the Puertollano basin demonstrates some marine influences in that time (Schneider et al. 2000).

Conclusion

The Late Pennsylvanian fish assemblage of the Finis Shale outcrop includes the bransonelliform *Bransonella lingulata,* the symmoriiforms *Denaea* sp. and *Stethacanthus* sp., the ctenacanthiforms *Heslerodus divergens*, *Glikmanius occidentalis*, *Ctenacanthus* sp., the euselachian *Sphenacanthus* sp., the anachronistid neoselachian *Cooleyella* cf. *amazonensis,* the eugeneodontiforms *Campyloprion* sp. and *Arpagodus* sp., the petalodontiforms *Peripristis semicircularis*, *Petalodus ohioensis* and *Antliodus* sp., the cochliodontiform *Deltodus* sp. as well as helodontiform and euchondrocephalian remains, *Physonemus mirabilis* and acanthodiform and actinopterygian remains. The bransonelliform species clearly predominate in the assemblage.

Rich assemblages of Late Pennsylvanian chondrichthyans are reported from different regions of the world such as New Mexico and Nebraska of USA, Moscow, Samara and Volgograd regions of Russia, Spain, Germany and Czech Republic. The assemblage from Finis Shale outcrop differs from others by the dominance of bransonelliform remains and the presence of diverse ctenacanthiforms and euchondrocephalians. This locality contains diverse and abundant invertebrates which would have provided a source of food for the fishes. The fishes in the assemblages include representatives with different feeding specialisation: gigantic top predators—ctenacanthiforms, large predators—stethacanthids and heslerodontid ctenacanthiforms, as well as small predators—falcatids and bransonellids, various durophagues such as anachronistid and euchondrocephalians, and probably omnivorous acanthodiforms and actinopterygians.

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Data availability All data are provided in the text and figures.

Declarations

Conflict of interest The authors declare that there are no competing or financial interests in any material discussed in this article.

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