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ISOLATED FISH SCALES (TELEOSTEI) FROM THE PALEOGENE AND NEOGENE SEDIMENTS OF THE CENTRAL PARATETHYS (CZECH REPUBLIC, SLOVAK REPUBLIC)

IZOLOVANÉ RYBÍ ŠUPINY (TELEOSTEI) Z PALEOGENNÍCH A NEOGENNICH SEDIMENTŮ CENTRÁLNÍ PARATETHYS (ČESKÁ REPUBLIKA, SLOVENSKÁ REPUBLIKA)

RŮŽENA GREGOROVÁ

Abstract

Gregorová, R., 2023: Isolated fish scales (Teleostei) from the Paleogene and Neogene sediments of the Central Paratethys (Czech Republic, Slovak Republic). – Acta Musei Moraviae, Scientiae geologicae, 108, 2, 283–308 (with Czech summary).

Isolated fish scales (Teleostei) from the Paleogene and Neogene sediments of the Central Paratethys (Czech Republic, Slovak Republic)

Isolated scales and parts of the squamation were analyzed from the Paleogene and Neogene sediments of the Central Paratethys (Oligocene to Miocene, Czech Republic, Slovak Republic). The structure and morphology of the scales could be studied in detail due to their excellent preservation. This paper presents the fish scales from the families Clupeidae, Sternoptychidae, Myctophidae, Zeidae, Gadiformes fam. indet, Gadidae, Merluciidae, Macrouridae, Trachichthyidae, Holocentridae, Gobiidae, Echeneidae, Sphyraenidae, Palaeorhynchidae, Scopthalmidae, Syngnathidae, Scombridae, Euzaphlegidae, Leiognathidae, Percoidei fam. indet., Triglidae, Moronidae, Sparidae, Caproidae, Ostraciidae and Teleostei gen. indet. 1, 2, 3. This comparative analysis shows that isolated remnants have important taxonomic value and helps in the identification of incomplete fish skeletons. Four principal scale type are described in the paper: true cycloid: *Oligophus moravicus*, Gadiformes fam. indet., *Paleogadus* sp. 1, 2, ? *Paleomolva* sp., *Palimphyes* sp., *Leiognathoides* sp., *Sphyraena* sp., *Palaeorhynchus* sp., Echeneidae gen. indet.; cycloid crenate: *Maicopiella longimana, Alosa* sp., cycloid spinoid: *Coelorinchus* sp., *Gephyroberyx* cf. *darwinii*, Holocentridae gen. indet., Scopthalmidae gen. indet., Triglidae gen. indet., *Capros* sp.; ctenoid: *Diplodus* sp., *Gobius jarosi*, Moronidae gen. indet., Percoidei gen indet.; specialised scales: *Argyropelecus priscus, Syngnathus* sp., *Gephyroberyx* cf. *darwinii, Zenopsis clarus, Oligolactoria bubiki.*

Key words: squamation, Teleostei scales, cycloid, spinoid, ctenoid, Paratethys, Paleogene, Neogene.

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INTRODUCTION

Paleogene and Neogene sediments (Menilitic Formation, Hustopeče Marlstone) of the Westem Carpathian Flysh zone and Miocene sediments of the Vienna basin are famous for their rich fossil fish remnants. Both whole skeletons and their isolated parts including scales are found. The very good preservation of fossil scales is due to their structure. Fish scales from modern teleost fish are high-performance materials made of cross-plies of collagen fibers (elasmodine) reinforced with hydroxyapatite (Khayer Dastjerdi and Barthelat

2014). Based on comparative analysis, these isolated remnants have similar taxonomic value as complete skeletons. Scales are often mentioned only as part of the description of the entire skeletons of fossil fish and have not been given a special attention. However, fossil scales can play an important role as otoliths in sediments where entire skeletons are missing or for instance in drill cores. HECKEL (1850) and RZEHAK (1880) were probably the first to use scale morphology in the taxonomy of clupeids. However, all taxa are considered as nomen dubium (e. g. KOVALCHUK *et al.* 2020). Until now, no publication has dealt with fossil fish scales in detail from the Oligocene and Miocene and this paper fills a gap in the field of paleoichthyological study in the Central Paratethys region. The basic morphological features of each scale are given in the paper. This study can thus expand the number of taxa and complete our knowledge of the fossil assemblages. Due to the fragmentary nature of the fossil material it was not possible in most cases to study scale shape variation over the body.

MATERIAL AND METHODS

The majority of the studied material comes from the collections of the Department of Geology and Paleontology of the Moravian Museum in Brno (MM). Museum numbers are given for individual taxa in the systematic part and description. The material was studied under an Olympus SZX10 microscope and photographed by author with a Canon EOS1100D and Nikon D90 digital cameras.

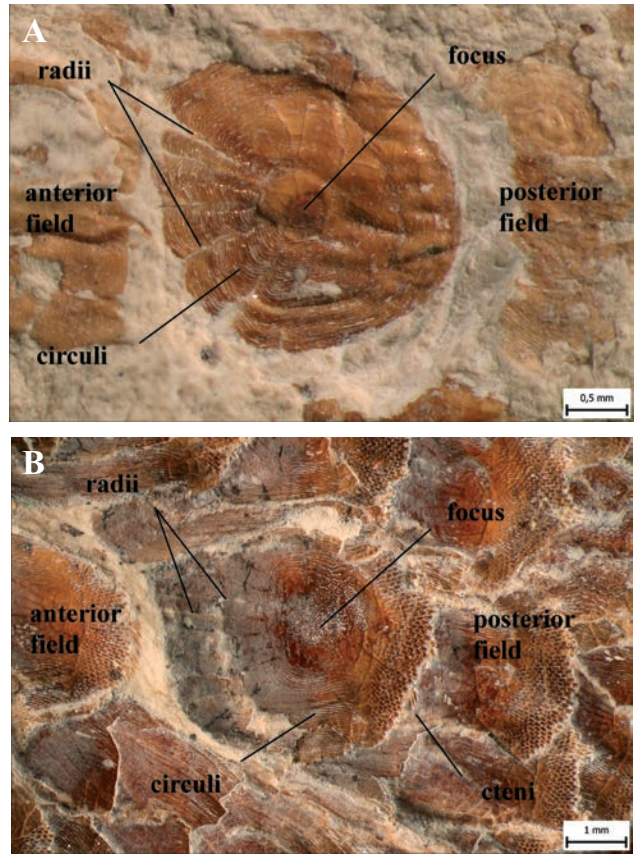


Fig. 1. Scale characteristics shown for a cycloid scale – *Oligophus moravicus* (PAUCA), (A) and a ctenoid (regenerated) scale – Moronidae gen. indet (B).

Obr. 1. Morfologie cykloidní šupiny – *Oligophus moravicus* (PAUCA), (A), ktenoidní (regenerované) šupiny – Moronidae gen. indet (B).

Order and family classifications in the systematic part follow those of NELSON *et al.* (2016). Methodology of scale analysis of extant species, terminology of scale types, scale shapes follow BRÄGER and MORITZ (2016, figs. 2–4), ROBERTS (1993) and PATTERSON *et al.* (2002). Basic scale characteristics are shown on the own fossil material (fig. 1 A, B). Description of the scale in the systematic part follow BRÄGER and MORITZ (2016). The arrow in the pictures points to the head (anterior field of the scale).

Skeletal remnants are mostly found as two halves of the slate and often only the inner side of the squamation is exposed for observation. So we can see the anterior edge of the scales (head direction), which is not normally visible from the external part because it is nested under the skin and covered by the previous row (fig. 2 A). The artificial resin transfer method (ARTM) has been used in some cases (e.g. BORNHARDT 1975, MICKLICH, DROBEK 2007)). This made, it possible to study the scales from the outside (surface of the body), (fig. 2 B). In most cases, the identification of scales is supported by the analysis of the entire skeleton or isolated bones or otoliths. Otherwise it is stated – there are no skeletal remains. Paleoecology of most taxa see (GREGOROVÁ 2013).

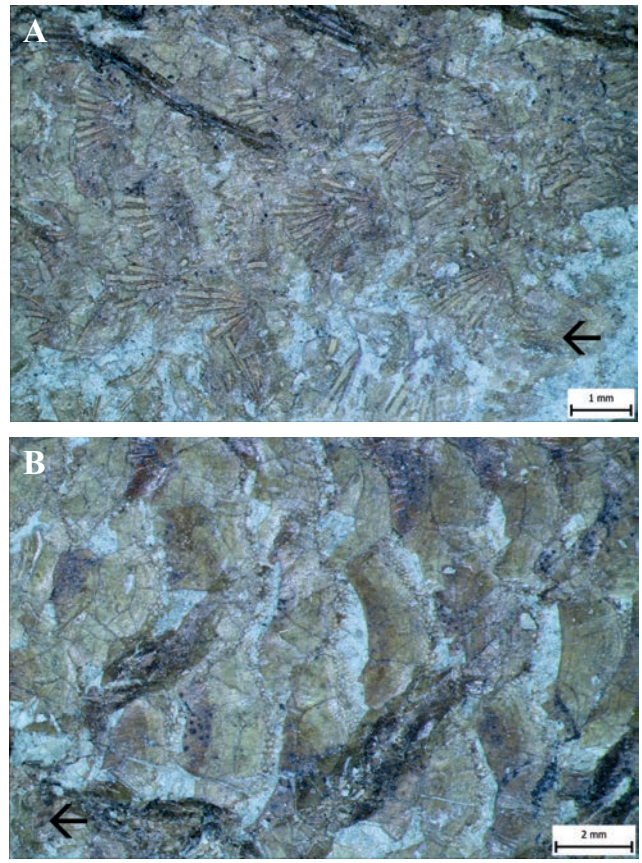


Fig. 2. Serranidae gen. indet. Děvínská Nová Ves, Vienna basin, Badenian, A – Scale squamationn from the inner side of the body, where the anterior part with radii is preserved. B – Scale squamation from the outer side of the body, where the posterior part with ctenii is preserved, specimen prepared by ARTM, Ge 28 472.

Obr. 2. Serranidae gen. indet. Děvínská Nová Ves, vídeňská pánev, baden, A – šupinový pokryv z vnitřní strany těla, kde je zachována přední strana šupin s radiálními rýhami (radii), B – šupinový pokryv z vnější strany těla, kde je zachována zadní strana šupin s ostny (cteni), exemplář je preparován medotou ARTM, Ge 28 472.

TYPES OF THE SCALES (according Bräger and Moritz (2016)

Cycloid scales. Scales without additional separate ossifications. Marginal indentations or spine-like projections might occur. Cycloid scale subtypes are:
True cycloid. Cycloid scale without any spine projections or marginal increments.
Crenate. Cycloid scale with marginal increments termed here as crenate.
Spinoid. Cycloid scale with spines that is continuous with the main body of the scale. Spines can be restricted to the posterior margin or scattered over the posterior field.
Ctenoid scales. Scales with additional separate ossifications, that form discrete spines called cteni. Ctenoid scales can occur with three types of cteni:
Peripheral cteni. Ctenoid scale with separate ossifications that occur as whole spines in one row at the posterior margin.
Transforming cteni. Ctenoid scale with separate ossifications that arise as whole spines in two or more alternating rows marginally and transform into truncated spines sub-marginally.
Whole cteni. Ctenoid scale with separate ossifications that occur as whole spines marginally and sub-marginally.

SYSTEMATIC PART

Order Clupeiformes

Family Clupeidae

Scales of clupeids are distinguishable from other fish species, by having distinctive grooves (radii) arranged in transverse, longitudinal or irregular orientation. They are the most numerous scales that we find in the Menilitic Formation.

Szymczyk (1978) studied in detail the variability of clupeid scales of the species *Clupea sardinites* (Heckel) an older synonym of *Maicopiella longimana* (Heckel) and *Alosa* cf. *sagorensis* Steindachner from the Menilite beds of the Polish flysh Carpathians. However, the material studied in this article does not allow us to use the results of the above-mentioned article due to its fragmentary nature.

Maicopiella longimana (Heckel)
Fig. 3 A, B

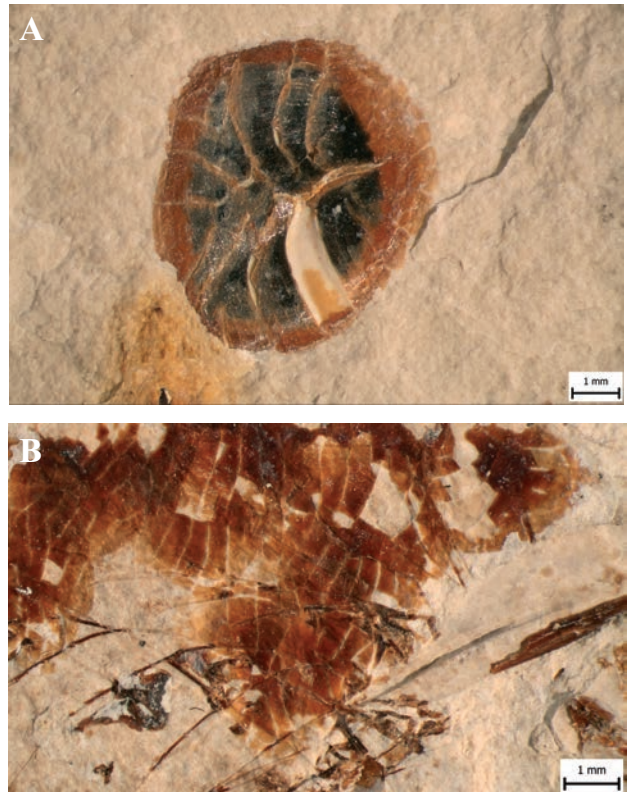
Type: cycloid: crenate. *Shape:* circular to oval or slightly quadrilateral: generally cordate to discoidal. *Shape variability:* moderate. *Anterior field:* flattened to convex with smooth margin.

Lateral fields: flattened to convex and extended in dorso-ventral axis. *Posterior field:* rounded to tapered end with slightly crenulated margin. *Circuli:* distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. *Radii:* transverse grooves are present.

Comment: Clupeid scales, unlike whole skeletons, are very abundant in the Menilitic formation. Kovalchuk *et al.* (2020) consider *Maicopiella longimana* (Heckel) to be the only species in the Oligocene of the Carpathians. Due to the large shape variability of the clupeid scales, it is currently not possible to determine them at the level of species or genera.

Fig. 3. *Maicopiella longimana*, Litenčice, Dynów Marlstone, Oligocene, A – isolated scale, Ge 29604, B – part of the squamation, Ge 33434.

Obr. 3. *Maicopiella longimana*, Litenčice, dynowské slínovce, oligocén, A – izolovaná šupina, Ge 29604, B – část šupinového pokryv, Ge 33434.



Alosa sp.

Fig. 4

Type: cycloid: *Shape:* circular to oval or slightly quadrilateral: generally cordate to discoidal. *Anterior field:* flattened with low conical apex and smooth margin.

Lateral fields: flattened to convex and extended in dorso-ventral axis.

Posterior field: rounded.

Circuli: distinct and discontinuous in the anterior and lateral fields, indistinct in the posterior field. *Radii:* Subhorizontal grooves are present in the posterior field. In the central field there are a number of nodules forming a network-like structure.

Fig. 4. *Alosa sp.*, isolated scale, Bystřice/Olší, Šitbořice beds, Oligocene, Ge 26862.

Obr. 4. *Alosa sp.*, izolovaná šupina, Bystřice/Olší, šitbořické vrstvy, oligocén, Ge 26862.

Order Stomiiformes

Family Sternoptychidae
Argyropelecus priscus (PAUCA)
Fig. 5

Type: specialised. *Shape:* rectangular. Ventral angular keel scales extend in living species below the abdominal photophores; the scales do not overlap each other. GREGOROVÁ (1993, 2013) described complete skeleton material from the Šitbořice Beds of the Menilitic Formation from Moravian localities.

Fig. 5. *Argyropelecus priscus*, specialised rectangular scales in the ventral keel of the body, Bystřice/Olší, Šitbořice Beds, Oligocene, Ge 26929.

Obr. 5. *Argyropelecus priscus*, specializované hranaté šupiny na břišní straně těla, Bystřice/Olší, šitbořické vrstvy, oligocén, Ge 26929.

Order Myctophiformes

Family Myctophidae
Oligophus moravicus (PAUCA)
Fig. 6 A, B, C

Type: cycloid: true cycloid. *Shape:* circular to shell-shaped. *Shape variability:* low. *Anterior field:* ronded. The margin of this field is deeply scalloped. *Lateral fields:* ronded or flatened and slightly extended in dorso-ventral axis. *Posterior field:* rounded with smooth margin. *Focus:* central. *Circuli:* distinct and discontinuous in the anterior field, distinct and continuous in the lateral fields and in the posterior field. *Radii:* radii are present in the anterior field in radial orientation. There are three radii on the scales above lateral line (fig. 6A), four to six radii in the ventral part, above photophores bearing scales. In myctophids, modified lenticular scales are developed on the ventral side of the body (for detail see GREGOROVÁ (2004)), which are very well preserved on the fossil material from the Dynow Marlstone of the Menilitic formation (Litenčice locality).

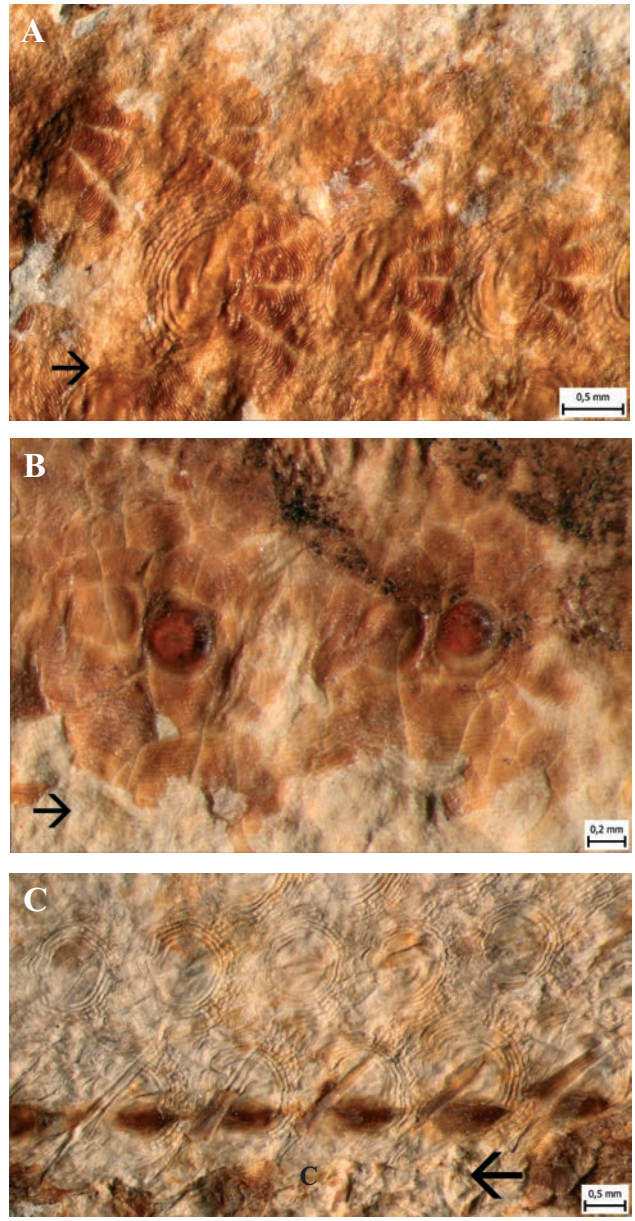


Fig. 6. *Oligophus moravicus*, Litenčice, Dynów Marlstone, Oligocene, A – scales from the dorsal part of the body, Ge 33435, B – scales with the ventral photophores (VO), Ge 23980, C – imprints of the scales rows and specialized scales of lateral line, Ge 33436.

Obr. 6. *Oligophus moravicus*, Litenčice, dynowské slínovce, oligocén, A – šupiny z hřbetní části těla, Ge 33435, B – šupiny s břišními fotofory (VO), Ge 23980, C – otisky šupinových řad a specializované šupiny laterální linie, Ge 33436.

Order Zeiformes

Family Zeidae
Zenopsis clarus (Daniltshenko)
Fig. 7

Type: specialised,Ge 29970.

Large buckler plates ventrally from pelvic fin to anal fin. Spine buclers lining the ventral and dorsal contours of the body.

Whole skeletons were analysed by Gregorová (2011)

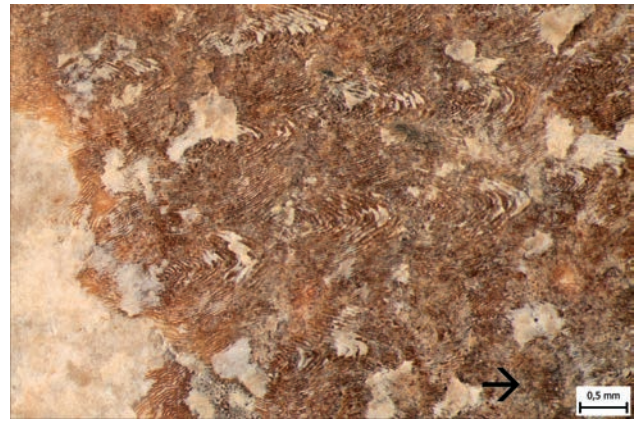
Fig. 7. *Zenopsis clarus*, buckler plates, Litenčice, Dynow Marlstone, Oligocene, Ge 29970.
Obr. 7. *Zenopsis clarus*, kýlovité šupiny, Litenčice, dynowské slínovce, oligocén, Ge 29970.

Order Gadiformes

Gadiformes gen. indet.
Fig. 8

Type: cycloid: true cycloid. *Shape:* diamond-shaped. *Shape variability:* low. *Anterior field* and *posterior field*: strongly convex with pointed apex and smooth margin. *Lateral fields:* flattened to convex and elongated in antero-posterior axis. *Focus:* central. *Circuli:* distinct and continuous, densely arranged. Radii: absent. The structure of gadiform caudal fin supports the systematic identification of the scales.
Family Merlucciidae

Fig. 8. Gadiformes gen. indet. incomplete specimen with the squamation, Litenčice, Dynów Marlstone, Oligocene, Ge 33440.
Obr. 8. Gadiformes gen. indet., nekompletní exemplář s šupinami, Litenčice, dynowské slínovce, oligocén, Ge 33440.



Palaeogadus sp. 1
Fig. 9

Type: cycloid: true cycloid. *Shape:* oval: ovoid to oblong. *Shape variability:* low. *Anterior field:* strongly convex with rounded apex and smooth margin. *Lateral fields:* flattened to convex and elongated in antero-posterior axis. *Posterior field:* convex or rounded with smooth margin. *Focus:* central. *Circuli:* distinct and continuous, densely arranged. Radii: absent.

Fig. 9. *Paleogadus* sp. 1, isolated scales, Mouchnice, Dynów Marlstone, Oligocene, Ge 33441.

Obr. 9. *Paleogadus* sp. 1, izolované šupiny, Mouchnice, dynowské slínovce, oligocén, Ge 33441.

Paleogadus sp. 2
Fig. 10

Type: cycloid: true cycloid. *Shape:* oval: ovoid. *Shape variability:* low. *Anterior field:* strongly convex with rounded apex and smooth margin. *Lateral fields:* flattened to convex and elongated in antero-posterior axis. *Posterior field:* rounded end with smooth margin. *Focus:* central. *Circuli:* distinct and continuous. *Radii:* absent.

Skeletal remains were analysed by Gregorová (2013).

Comment. *Paleogadus* sp. 2 differs from *Paleogadus* sp. 1 in its less elongated shape of the scales.

Fig. 10. *Paleogadus* sp. 2, detail of the squamation of complete specimen, Bystřice/Olší, Šitbořice beds, Oligocene, Ge 26858.

Obr. 10. *Paleogadus* sp. 2, detail šupin šupin kompletního jedince, Bystřice/Olší, šitbořické vrstvy, oligocén, Ge 26858.

Family Gadidae
? Paleomolva sp.
Fig. 11

Type: cycloid: true cycloid. *Shape:* oval: ovoid to oblong.

Shape variability: low. *Anterior field:* strongly convex with rounded apex and smooth margin.

Lateral fields: flattened to convex and elongated in antero-posterior axis. *Posterior field:* rounded end with smooth margin. *Focus:* central. *Circuli:* distinct and continuous, low number of circuli in comparison with previous specimen *Paleogadus* sp. *Radii*: absent.

Comment: there are no skeletal remains.

Fig. 11. ? *Paleomolva* sp., cycloid scales, Mouchnice Dynów Marlstone, Oligocene, MM, collection Rzehak, Ge 33442.

Obr. 11. ? *Paleomolva* sp., cyklodní šupiny, Mouchnice dynowské slínovce, oligocén, kolekce Rzehak, Ge 33442.

Family Macrouridae

Coelorinchus sp.

Fig. 12 A, B

Type: cycloid: spinoid. Shape: circular to polygonal.

Shape variability: unknown. *Anterior field:* convex with pointed apex and smooth margin. The antero-lateral corners are extended and pointed. *Lateral fields:* convex and extended in dorso-ventral axis. *Posterior field:* rounded to tapered end with spinous posterior field. *Focus:* antero-central. *Circuli:* distinct and continuous in the anterior and lateral

Fig. 12. *Coelorinchus* sp., A – spinoid scales from the inner side, B – detail of the spines developed on the posterir field (outer side), Cerová-Lieskové, Karpatian (Late Burdigalian) „schlier“ facies, collection of comenius University Bratislava, unnumbered.

Obr. 12. *Coelorinchus* sp., A – spinoidní šupiny z vnitřní strany, B – detail ostnů na zadním okraji šupiny (vnější strana), Cerová-Lieskové, karpat (Burdigalian) šlírová facie, sbírka Univerzity Comenského v Bratislavě, neočíslované.

fields, distinct and discontinuous in the posterior field. Radii: absent. *Spines:* 5–8 thorn-shaped spines rows are arranged in entire posterior field.

A preserved otolith and other osteological features support the identification (GREGOROVÁ in preparation).

Order Holocentriformes

Family Trachichthyidae
Gephyroberyx cf. *darwinii* (JOHNSON)
Fig. 13 A, B, C.

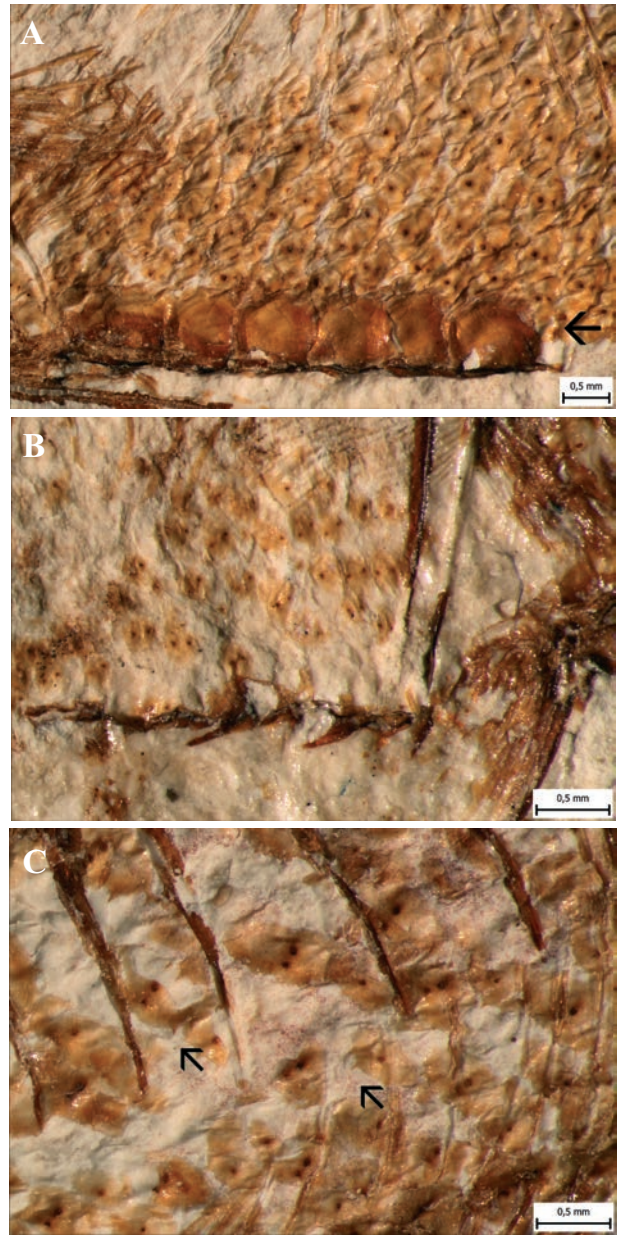


Fig. 13. *Gephyroberyx* cf. *darwinii*, large keeled scales between pelvic and anal fins, A – keeled and body scales, Ge 29 968, B – spines of the keeled scales, Ge 29 969, C – detail of the spinoid scales with the posteriorly oriented spine – arrow, Ge 29968, Litenčice, Dynów Marlstone, Oligocene.

Obr. 13. *Gephyroberyx* cf. *darwinii*, specializované šupiny mezi břišní a anální ploutví, A – kýlovité šupiny, Ge 29968, B – ostny kýlovitých šupin, 29969, C – detail spinoidních šupin s dozadu orientovaným ostnem – šipka, Ge 29968, Litenčice, dynowské slínovce, oligocén.

Two types of the scales are developed: cycloid – spinoid and large scutes on the ventral part of the body.

Type: cycloid: spinoid. The body scales small, thin, irregularly arranged. *Shape:* semicircular. *Anterior field:* convex. *Lateral fields:* flattened to convex and extended in dorso-ventral axis. *Posterior field:* slightly rounded, flatened, irregular with a spine projecting posteriorly (fig. 8 B, C). One or two dark spots indicate spines in the central part of the scales. *Focus:* not observable. *Circuli:* not observable.

Type: specialised large keeled scales between pelvic and anal fins (fig. 8 A, B).

Skeletal remains were analysed by GREGOROVÁ (2011).

Family Holocentridae
Holocentridae gen. indet.,
Fig. 14

Type: cycloid: spinoid. *Shape:* polygonal: pentagonal to hexagonal. *Shape variability:* high.

Anterior field: flattened to slightly ronded with smooth margin. *Lateral fields:* flattened to convex and elongated in dorso-ventral axis. *Posterior field:* rather flattened with spinous margin. *Focus:* central. *Circuli:* distinct and continuous in the anterior and lateral fields, indistinct in the posterior field. *Radii:* absent. *Spines:* about 10 teeth-like spines emerge from the posterior margin. The scales are robust and thick.

Osteological characters support the identification (GREGOROVÁ in preparation).

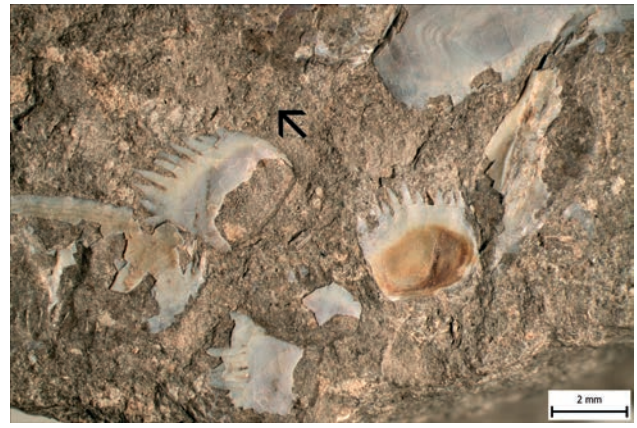


Fig. 14. Holocentridae gen. indet., isolated spinoid scales, Bystřice/Olší, Šitbořice Beds, Oligocene, akc. 2/90.

Obr. 14. Holocentridae gen. indet., izolované spinoidní šupiny, Bystřice/Olší, šitbořické vrstvy, oligocén, akc. 2/90.

Order Gobiiformes

Familly Gobiidae
Gobius jarosi (PŘIKRYL et REICHENBACHER)
Fig. 15

Type: ctenoid: peripheral cteni. *Shape:* circular: true circular or discoidal. *Shape variability:* low. *Anterior field:* no observable. *Lateral fields:* no observable. *Posterior field:* rounded end with ctenous margin. *Focus:* posterior.

Circuli: distinct and discontinuous; continuous only in the postero-lateral section.

Radii: primary, secondary and tertiary radii are present in the anterior and lateral fields in parallel to radial orientation. Radii often extend to the posterior field.

Cteni: peripheral cteni.

The scales are relatively large and are arranged in about five – six rows. Each row appears to contain slightly more than 30 scales (Reichenbacher *et al.* 2017).

Fig. 15. *Gobius jarosi*, squamation with ctenoid scales with typical peripheral ctenii, Vážany/Litavou, Hustopeče Marl, early Miocene, Ge 25032.

Obr. 15. *Gobius jarosi*, ktenoidní šupiny s typickými periferními ostny, Vážany/Litavou, hustopečské slíny, spodní miocén, Ge 25032.

Order Carangiformes

Family Echeneidae

Echeneidae gen. indet.

Fig. 16

Type: Cycloid. *Shape:* diamond. Anterior field and posterior field: symmetrical shape with sharp edge. Lateral fields: slightly convex elongated in the antero-posterior axis *Focus:* central. *Circuli:* distinct and continuous. *Radii:* absent.

Skeletal remains were analysed by Gregorová (2013). Micklich *at al.* (2016) described detail of squamation of *Oligoremora rhenana* n. g. n. sp. that are very similar to the scales of the representative presented here.

Fig. 16. Echeneidae gen. indet., cycloid diamond shaped scales, Litenčice, Šitbořice Beds, Oligocene, Ge 32996.

Obr. 16. Echeneidae gen. indet., cykloidní kosočtverečné šupiny, Litenčice, šitbořické vrstvy, oligocén, Ge 32996.

Order Istiophoriformes

Family Sphyraenidae
Sphyraena sp.
Fig. 17

Type: cycloid. *Shape:* circular: true circular to discoidal. *Shape variability:* low. *Anterior field:* no observable. *Lateral fields:* convex. *Posterior field*: rounded, smooth ?. *Focus:* central. *Circuli:* distinct.

Comment: Detail of the squamation (fig. 25) is taken from partially preserved skeleton. Osteological characters and an otolith support the determination of the genus (Gregorová in preparation).

Fig. 17. *Sphyraena* sp., squamation with circular scales, Děvínska Nová Ves, Vienna basin, Badenian, private collection.
Obr. 17. *Sphyraena* sp., cyklodní kulaté šupiny, Děvínska Nová Ves, vídeňská pánev, baden, soukromá sbírka.

Family Palaeorhynchidae
Palaeorhynchus sp.
Fig. 18

Type: cycloid: true cycloid. *Shape:* circular to oval: true circular to ovoid.

Size variability: hight. Anterior field: convex with smooth margin. Lateral fields: convex. Posterior field: rounded end with smooth margin. Focus: central. Circuli: dense, distinct and continuous. Radii: absent.

Skeletal remains were analysed by Gregorová (2013).

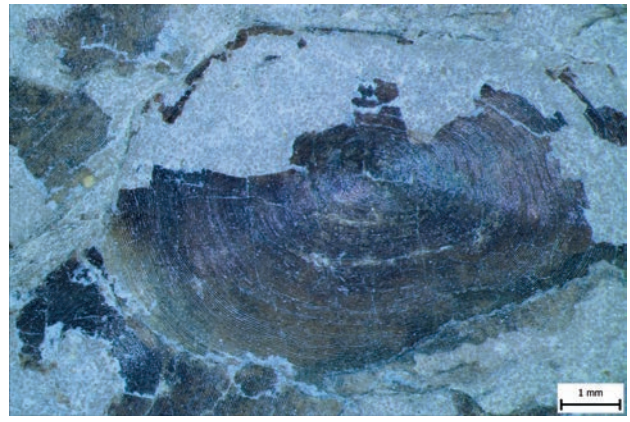


Fig. 18. *Palaeorhynchus* sp., cycloid scale, Litenčice, Šitbořice Beds, Oligocene, Ge 33062.
Obr. 18. *Palaeorhynchus* sp., cyklodní šupina, Litenčice, šitbořické vrstvy, oligocén, Ge 33062.

Order Pleuronectiformes

Familly Scopthalmidae gen. indet.
Fig. 19

Type: ctenoid. *Shape:* rounded. *Shape variability:* low. *Anterior field:* ronded *Lateral fields:* convex. *Posterior field:* slightly tapered end with ctenous margin. *Focus:* postero-central. *Circuli:* distinct continuous in the anterior field and lateral fields. *Radii:* primary occur in the anterior field in radial orientation. *Cteni:* transforming cteni.

Comment: this specimen was assigned to the genus of *Scopthalmus* by Gregorová (2011), but its recent representatives have cycloid scales, so the question of the systematic classification of the fossil representative remains open.

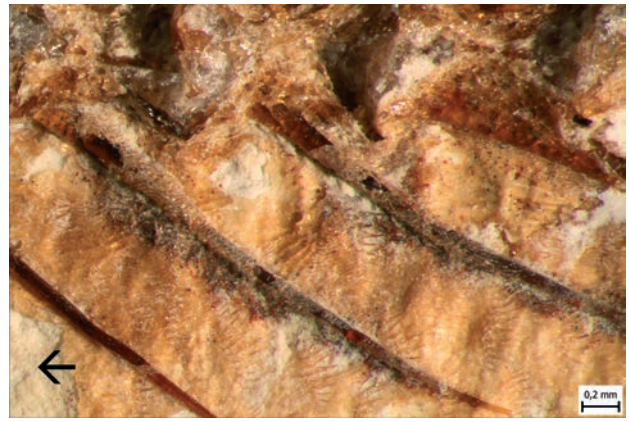


Fig. 19. Scopthalmidae gen. indet., detail of the spinoid scales from the caudal region, Litenčice, Dynow Marlstone, Oligocene, Ge 29977.

Obr. 19. Scopthalmidae gen. indet., detail spinoidních šupin z kaudální oblasti, Litenčice, dynowské slínovce, oligocén, Ge 29977.

Order Syngnathiformes

Family Syngnathidae
Syngnathus sp.
Fig. 20 A, B

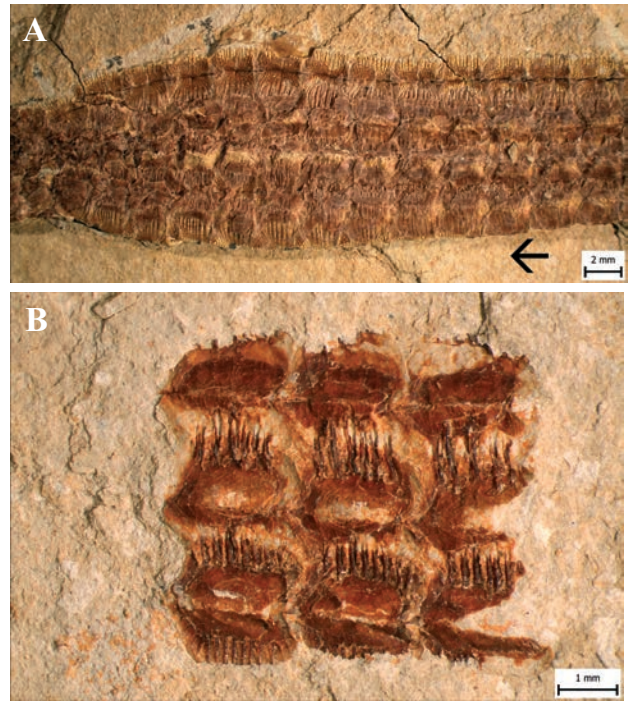


Fig. 20. *Syngnathus* sp., specialised scales of carapace, Krumvíř, Hustopeče Marl, Egerian, A – Ge 33437, B – Ge 33438.

Obr. 20. *Syngnathus* sp., specializované šupiny karapaxu, Krumvíř, hustopečské slíny, eger, A – Ge 33437, B – Ge 33438.

Type: specialized. *Shape:* Quadrilateral to rectangular. *Shape variability:* low. The scales possess in the middle a ridge from which parallel grooves extend vertically. They are connected finger-like with the grooves of the adjacent scales forming a solid carapace.

Skeletal remains were analysed by GREGOROVÁ (2013).

Order Scombriformes

Family Scombridae
Scomber sp.
Fig. 21 A, B

Type: cycloid. *Shape:* oval, irregular rectangular or rhomboidal. *Shape variability:* high. *Anterior field:* flattened with smooth margin. *Lateral fields:* flattened or sligtly ronded extended in dorso-ventral axis. *Posterior field:* rounded. *Focus:* central. *Circuli:* distinct and continuous. *Radii:* absent.

Whole skeleton was described by GREGOROVÁ (2013).

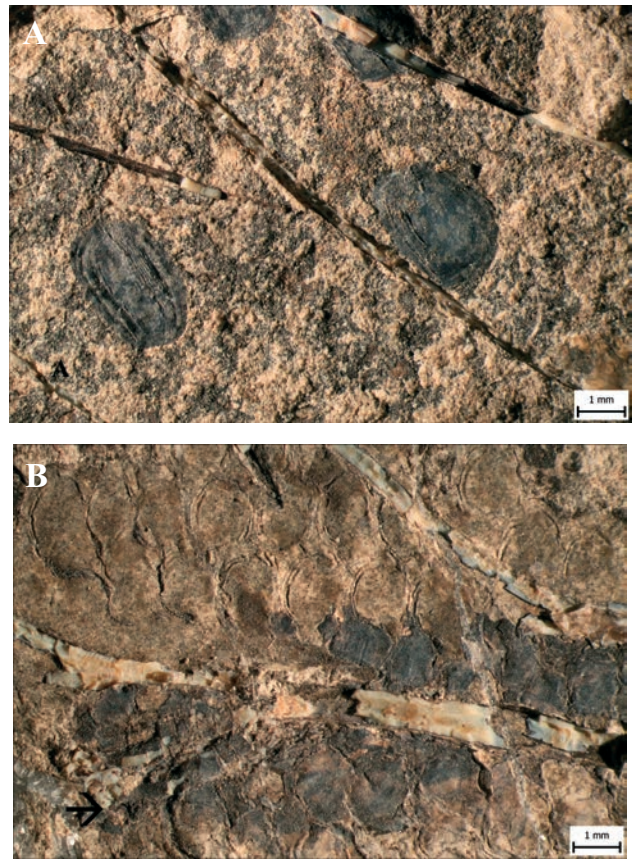


Fig. 21. *Scomber* sp., A – isolated cycloid scales, B – squamation from the dorsal part of the body, Bystřice/Olší, Šitbořice beds, Oligocene, Ge 27064.

Obr. 21. *Scomber* sp., A – izolované cykloidní šupiny, B – šupinový pokryv z dorzální části těla, Bystřice/Olší, šitbořické vrstvy, oligocén, Ge 27064.

Family Euzaphlegidae
Palimphyes sp.
Fig. 22 A, B

Type: cycloid: true cycloid. *Shape:* quadrilateral: square. *Anterior field:* flattened with a striate margin. *Lateral fields:* flattened to convex *Posterior field:* slightly ronded with smooth margin. *Focus:* antero – central. *Circuli:* distinct and continuous in the anterior and the lateral fields, wrap around the focus and run semiparallel to the posterior field. *Radii:* about 22 radii present in the anterior field in radial orientation.

Skeletal remains were analysed by Gregorová (2011).

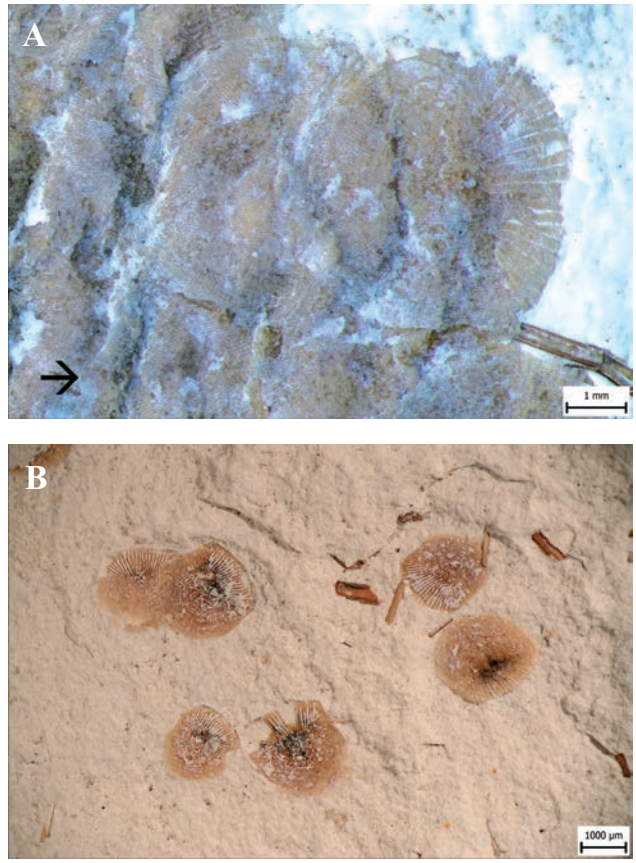


Fig. 22. *Palimphyes* sp. A – detail of the squamation, Ge 30206, B – isolated scales, Ge 33439 (Fig. B), Litenčice, Dynow Marlstone, Oligocene.

Obr. 22. *Palimphyes* sp. A – detail šupinového pokryvu, Ge 30206, B – izolované šupiny, Ge 33439 (obr. B), Litenčice, dynowské slínovce, oligocén.

Order Perciformes

Family Leiognathidae
Leiognathoides minutus (Daniltshenko)
Fig. 23

Type: cycloid: true cycloid. *Shape:* circular. *Shape variability:* low. *Anterior field:* strongly convex with rounded apex and smooth margin. *Lateral fields:* flattened to convex and elongated in antero-posterior axis. *Posterior field:* rounded end with smooth margin. The scales are small, there are 3–4 rows between hemal spines. *Focus:* central. *Circuli:* distinct and continuous. *Radii:* absent.

Whole skeletons were analysed by Gregorová (2013). Micklich *et al.* (2017) describe skeletons and scales of *Leiognathoides* cf. *altapinna*, from the Oligocene of the Grube Unterfeld ("Frauenweiler") clay pit. These authors describe radii on scales in the caudal part of the body. This character is not observable on our material.

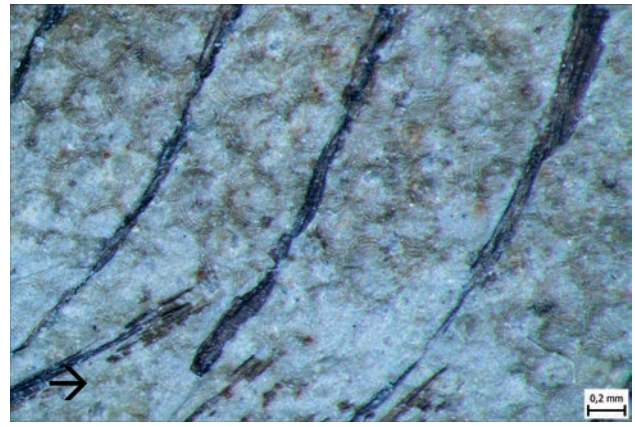


Fig. 23. *Leiognathoides* sp. cycloid scales, Hustopeče marl, Vážany nad Litavou, Early Miocene, Ge 25026.
Obr. 23. *Leiognathoides* sp., cykloidní šupiny, hustopečské slíny, Vážany nad Litavou, spodní miocén, Ge 25026.

Family insertae sedis
? *Oligoserranoides* sp.
Fig. 24

Type: ctenoid: transforming cteni. *Shape:* quadrilateral: square or rectangular. *Shape variability:* unknown. *Anterior field:* flattened with striate to slightly scalloped margin. The antero-lateral corners are at right angle. *Lateral fields:* flattened and elongated in antero-posterior axis. *Posterior field:* rounded to tapered end with ctenous margin. *Focus:* postero-central. *Circuli:* distinct; discontinuous in the anterior field, continuous in the lateral fields, discontinuous in the posterior field. *Radii:* at least 13 radii are present in the anterior field in radial orientation. *Cteni:* transforming.

These scales belong probably to the most common percoid genus *Oligoserranoides* that has been revised by Bienkowska-Wasiluk and Paldyna (2018).

Fig. 24. *Oligoserranoides* ? sp., ctenoid scales, Litenčice, Šitbořice beds, Oligocene, Ge 33055.
Obr. 24. *Oligoserranoides* ? sp., ktenoidní šupiny, Litenčice, šitbořické vrstvy, oligocén, Ge 33055.

Order Scorpaeniformes

Family Triglidae gen. indet.
Fig. 25

Type: spinoid. Due to the small size of the specimen, only spines are observable on the specimen and no other morphological characters.

Whole skeletons were analysed by Gregorová (2013).

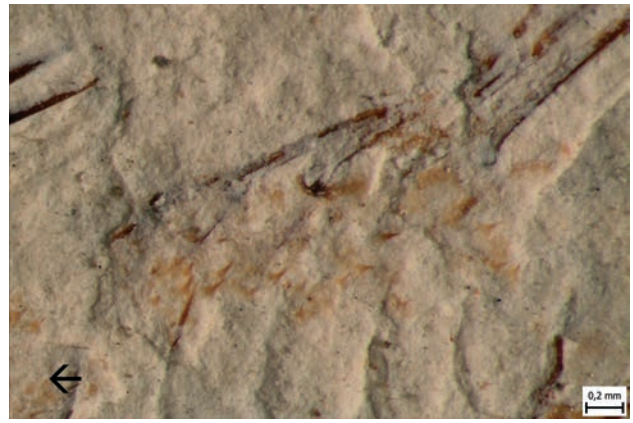


Fig. 25. Triglidae gen. indet., detail of the preserved scale spines, Litenčice, Dynow Marlstone, Oligocene, Ge 29972.
Obr. 25. Triglidae gen. indet., detail šupinových ostnů, Litenčice, dynowské slínovce, oligocén, Ge 29972.

Order Moroniformes

Moronidae gen. indet.
Fig. 26 A, B

Type: ctenoid: transforming cteni.

Shape: quadrilateral to polygonal: square or rectangular to pentagonal. *Shape variability:* moderate. *Anterior field:* flattened with striate to slightly scalloped margin. The antero-lateral corners are slightly pointed. *Lateral fields:* flattened and elongated in antero-posterior axis.

Posterior field: rounded to tapered end with ctenous margin. *Focus:* postero-central.

Circuli: distinct; discontinuous in the anterior field, continuous in the lateral fields, discontinuous in the posterior field. *Radii:* primary and secondary radii are present inthe anterior field in radial orientation. *Cteni:* transforming.

Identification of the skeletal remains and scales were anlysed by Gregorová *et al.* (2016).

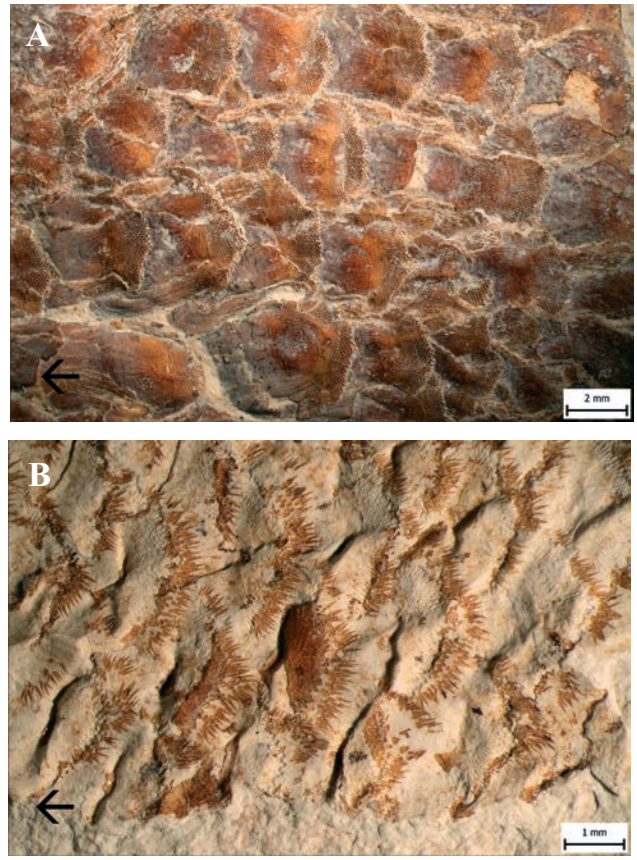


Fig. 26. Moronidae gen. indet., A – slightly disarticulated squamation of ctenoid scales – both the front and back of the scale are visible, Ge 31065, B – outer side squamation with the posteriot ctenous field of the scales, Ge 33443, Litenčice, Dynow Marlstone, Oligocene.

Obr. 26. Moronidae gen. indet., A – část mírně disartikulovaného pokryvu ktenoidních šupin – je viditelná přední i zadní část šupiny, Ge 31065, B – vnější šupinový pokryv se zadní stranou ktenoidního okraje šupin, Ge 33443, Litenčice, dynowské slínovce, oligocén.

Order Spariformes

Family Sparidae
Diplodus sp.
Fig. 27 A, B

Type: ctenoid: transforming cteni. *Shape:* circular. *Shape variability:* moderate. *Anterior field:* rounded with waved margin. *Lateral fields:* ronded. *Posterior field:* rounded with ctenous margin.

Focus: central. *Circuli:* distinct and continuous in the anterior and lateral fields, indistinct in posterior field. Four distinct circuli around focus. *Radii:* radii are present in the anterior field in radial orientation. Eight radii were counted on the scales of the ventral part of the body.

Analysis of skeletal remains (Gregorová 2009) supports taxonomic affinity of scales.

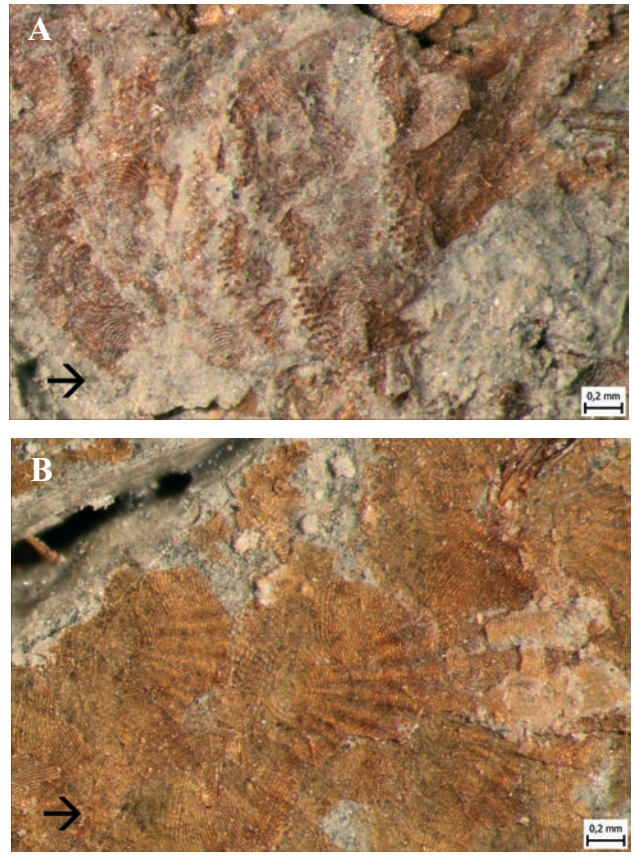


Fig. 27. *Diplodus* sp., A – partial squamation with posterior exposed part, B – anterior part with radii, Devinska Nová Ves, Badenian, Vienna Basin, Ge 29816.

Obr. 27. *Diplodus* sp., A – šupinový pokryv se zadní viditelnou částí. B – přední část s radii (zakrytá část), Děvínská Nová Ves, Baden, vídeňská pánev, Ge 29816.

Order Caproiformes

Family Caproidae
Capros sp.
Fig. 28

Type: cycloid: spinoid. *Shape:* not observable. *Shape variability:* not observable. *Anterior field:* are not observable. *Lateral fields:* are not observable. *Posterior field:* rounded end with smooth margin but spinous posterior field. Spines: numerous, long and thin spines are scattered within the entire posterior field; they overreach the posterior margin. *Focus:* postero-central. *Circuli:* distinct and continuous in the anterior and lateral fields, discontinuous to indistinct in the posterior field. *Radii:* absent.

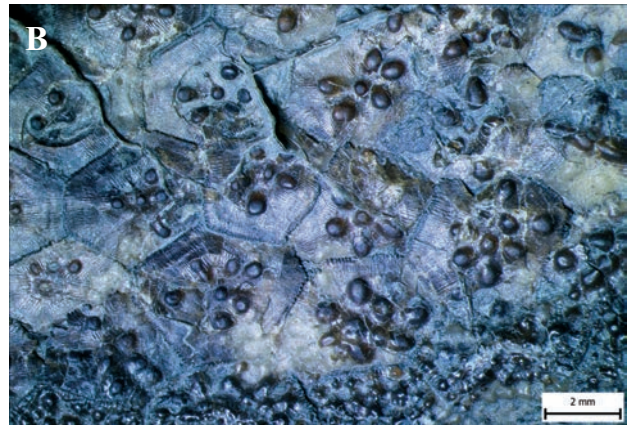
Osteological analysis supports the systematic identification of the scales (Gregorová in preparation).

Fig. 28. *Capros* sp., numerous semiparalel scales spines, Bystřice/Olší, Šitbořice beds, Oligocene, Ge 26933.
Obr. 28. *Capros* sp., četné semiparalení šupinové ostny, Bystřice/Olší, šitbořické vrstvy, oligocén, Ge 26933.

Order Tetraodontiformes

Family Ostraciidae
Oligolactoria bubiki (Tyler et Gregorová)
Fig. 29 A, B

Fig. 29. *Oligolactoria bubiki*, A – group of scales in almost articulated position, Bystřice/Olší, Šitbořice beds, Oligocene, Ge 26830, B – ventral carapace of the body, Litenčice, Šitbořice beds, Oligocene, Ge 32990.
Obr. 29. *Oligolactoria bubiki*, A – skupina šupin v téměř artikulované pozici, Bystřice/Olší, šitbořické vrstvy, oligocén, Ge 26830, B – ventrální karapax, Litenčice, Ge 32990, šitbořické vrstvy, oligocén.



Type: specialised scales. *Shape:* robust hexagonal scales are finely denticulate for interdigitation with opposing plates to form a solid carapace of the body. They are tuberculate on the outer surface, with the central tubercle tending to be larger and more elevated than the others.

Whole skeletons were described by TYLER and GREGOROVÁ (1990).

Teleostei gen.indet. 1

Fig. 30 A, B

Type: cycloid crenate. *Shape:* quadrilateral: square or rectangular. *Shape variability:* unknown. *Anterior field:* flattened with smooth margin. *Lateral fields:* flattened and elongated in dorso-ventral axis. *Posterior field:* flattened to rounded end with marginal increments termed as crenae. *Focus:* postero-central.

Circuli: distinct; discontinuous in the anterior field, continuous in the lateral fields, discontinuous in the posterior field. *Radii:* no radii.

No whole skeletons.

Fig. 30. Teleostei gen. indet 1, cycloid crenate scales, Křepice, Dynow Marlstone, Oligocene, Ge 3356.

Obr. 30. Teleostei gen. indet 1, cyklodní „crenate“ šupiny, Křepice, dynowské slínovce, oligocén, Ge 3356.

Teleostei gen. indet. 2

Fig. 31

Type: cycloid. *Shape:* quadrilateral: semirectangular. *Shape variability:* unknown. *Anterior field:* flattened with deeply scalloped margin creating two lobes. *Lateral fields:* flattened and elongated in dorso-ventral axis. *Posterior field:* flattened to slightly rounded. Ronded and pointed protuberance cover posterior field below focus. Larger protuberance are irregulary developed along two deep lobes. *Focus:* posterior field. *Circuli:* distinct; continuous in the anterior and lateral field. *Radii:* one radius.

Comment: this taxon is know only by the scales. Considering the size of the scale, it was a very large individual. There are no whole skeletons.

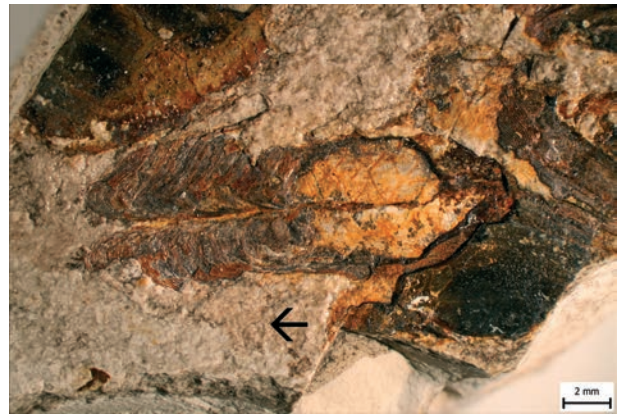
Fig. 31. Teleostei gen indet. 2, cycloid scale, Bystré, Oligocene, Slovak Republic, Ge 33444.
Obr. 31. Teleostei gen indet. 2, cykloidní šupina, Bystré, oligocén, Slovensko, Ge 33444.

Teleostei gen. indet. 3
Fig. 32

Type: cycloid: *Shape:* oval. *Anterior field:* two tapered lobes. *Lateral fields:* flattened and elongated in antero-posterior axis. *Posterior field:* rounded. *Focus:* posterior field. *Circuli:* distinct; continuous in the anterior and lateral field.

Comment: this species is know only by scales. Considering the size of the scale, it was a very large individual as the previous fish.

Fig. 32. Teleostei gen. indet. 3 cycloid scale, Mouchnice, Dynow Marlstone, Oligocene, Ge 33445.
Obr. 32. Teleostei gen. indet. 3, cykloidní šupina, Mouchnice, dynowské slínovce, oligocén, Ge 33445.



CONCLUSION

Scales of thirty taxa of Teleostei from the Paleogene and Neogene sediments of the Central Paratethys are presented and figured in this paper. Most of the material came from the Menilitic Formation and from the Ždánice-Hustopeče Formation of the Moravian part of the Carpathian flysh zone, some examples come from the Central Carpathian Paleogene and the Miocene of the Vienna Basin (Slovak Republic). Four principal scale type are described: true cycloid: *Oligophus moravicus*, Gadiformes fam. indet., Paleogadus sp.1, 2, ? *Paleomolva* sp., *Palimphyes* sp., *Leiognathoides* sp., *Sphyraena* sp., *Palaeorhynchus* sp., Echeneidae gen. indet.; cycloid crenate: *Maicopiella longimana*, *Alosa* sp., cycloid spinoid: *Coe-*

lorinchus sp. (first record of skeletal remains), *Gephyroberyx* cf. *darwinii*, Holocentridae gen. indet., Scopthalmidae gen. indet., Triglidae gen. indet., *Capros* sp.; ctenoid: *Diplodus* sp., *Gobius jarosi*, Moronidae gen. indet., Percoidei gen indet.; specialised scales: *Argyropelecus priscus, Syngnathus* sp., *Gephyroberyx* cf. *darwinii, Zenopsis clarus, Oligolactoria bubiki.*

Analysis of isolated scales or partial squamation indicated that the fish fauna assembalge was more diversified than the study of entire and partial skeletons has shown. Identification of scales in terms of their taxonomic affiliation is an important tool for paleontological evaluation of fossil remains where the entire skeletons are unknown. The size of some of the scales (*Palaeorhynchus* sp. Teleostei gen. indet. 2 and 3) indicates that much larger fish lived in the assemblage than we would expect based on the skeletons.

SOUHRN

Článek presentuje šupiny třiceti taxonů ryb (Teleostei) z paleogenních a neogenních sedimentů centrální oblasti Paratethys. Většina materiálu byla studována z menilitového souvrství a ždánicko-hustopečkého souvrství moravské části flyšové zóny Karpat; některé příklady pochází ze vnitrokarpatského paleogénu a z miocénu vídeňské pánve (Slovensko). Jsou zde popsány čtyři hlavní typy šupin: pravé cykloidní: *Oligophus moravicus*, Gadiformes fam. indet., *Paleogadus* sp.1, 2, ? *Paleomolva* sp., *Palimphyes* sp., *Leiognathoides* sp., *Sphyraena* sp., *Palaeorhynchus* sp., Echeneidae gen. indet.; „crenate“ cykloidní: *Maicopiella longimana*, *Alosa* sp., cycloidní spinoidní: *Coelorinchus* sp., *Gephyroberyx* cf. *darwinii*, Holocentridae gen. indet., Scopthalmidae gen. indet., Triglidae gen. indet., *Capros* sp.; ktenoidní: *Diplodus* sp., *Gobius jaroši*, Moronidae gen. indet., Percoidei gen indet.; specializované šupiny: *Argyropelecus priscus, Syngnathus* sp., *Gephyroberyx* cf. *darwinii, Zenopsis clarus, Oligolactoria bubiki.*

Studium šupin je významným nástrojem při indentifikaci rybích zbytků a dokládá, že rybí společenstvo bylo diverzifikovanější, než ukazuje analýza pouze celých skeletů. Identifikace šupin z hlediska jejich taxonomické příslušnosti je důležitým nástrojem pro paleontologické a paleoekologické hodnocení fosilních pozůstatků, kde celé kostry chybí. Velikost některých šupin naznačuje, že ve společenstvech žily mnohem větší ryby, než bychom na základě koster očekávali.

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