



# Revision of species *Plagiolophus sulcatus* Beurlen, 1939 (Decapoda, Brachyura) from the Oligocene of Hungary and Slovenia

## Revizija vrste *Plagiolophus sulcatus* Beurlen, 1939 (Decapoda, Brachyura) iz oligocena Madžarske in Slovenije

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**Ključne besede:** raki deseteronožci, rakovica, *Glyphtithyreus*, oligocen, rupelij, chattij

### Abstract

The crab species *Plagiolophus sulcatus* Beurlen, 1939 from the Oligocene (Rupelian) Kiscell Clay of Hungary is revised and its holotype is reillustrated for the first time since its original publication. Material from the upper Oligocene (Chattian) of Trbovlje (Slovenia) is here considered conspecific with *P. sulcatus*. Attribution of this species to the genus *Glyphtithyreus*, as proposed by Hiroaki Karasawa and Carrie Schweitzer in 2004, is confirmed. *Glyphtithyreus sulcatus* differs from congeners in possessing protogastric regions that are subtriangular in outline and in having fewer and coarser tubercles on elevated carapace regions.

### Izvleček

Revidirana je vrsta rakovice *Plagiolophus sulcatus* Beurlen, 1939, iz oligocenskih (rupeljskih) kiscellijskih glinenih plasti. Prvič po prvotni objavi je predstavljen holotip in novi primerek iz zgornjega oligocena (chattija) Trbovelj (Slovenija), ki prav tako pripada vrsti *P. sulcatus*. Potrjena je pripadnost te vrste rodu *Glyphtithyreus*, kar sta predlagala Hiroaki Karasawa in Carrie Schweitzer leta 2004. *Glyphtithyreus sulcatus* se od drugih pripadnikov tega rodu razlikuje po tem, da ima trikotno obliko protogastrične regije in manjše število, a izrazitejše oblikovane bradavice na višjih delih oklepa.

### Introduction

Beurlen (1939) described a decapod crustacean faunule from the Oligocene Kiscell Clay of Hungary. The ghost shrimps of this assemblage have since received proper re-evaluation (Hyžný & Dulai, 2014), the three species of brachyuran crabs, including *Plagiolophus sulcatus*, remained unrevised in respect with modern classification until now. This species was tentatively retained in the genus *Plagiolophus* Bell, 1858 (*non* Pomel, 1857) by Karasawa & Schweitzer (2004) in their revision of *Glyphtithyreus* Reuss, 1859. Those authors noted that, “the placement of *G. sulcatus* is somewhat tentative and is based upon our translation of Beurlen’s (1939) original

description in German and the very poorly reproduced illustration in our copy of the work (Karasawa & Schweitzer, 2004, p. 148)”. Thus, since the erection of the species by Beurlen (1939), the type material of *P. sulcatus* has not yet been re-examined.

Bittner (1884) presented an extensive overview of Cenozoic sedimentary rocks and their fossil contents in the vicinity of Sagor (nowadays Zagorje ob Savi) and Trifail (nowadays Trbovlje). Among other faunal elements, Bittner (1884: 29) also mentioned the presence of a crab that was morphologically close to *Plagiolophus*. Several crab specimens from Trbovlje have recently been traced by one of us (MH) during a detailed screen

of the main fossil collections in Austria (Hyžný & Gross, 2016; Hyžný & Zorn, in press). One of these indeed represents *Plagiolophus* (= *Glypithytreus*) and has been considered to be conspecific with *P. sulcatus* by Hyžný & Gross (2016). However, this decision was not based on a first-hand examination of the type material.

The aim of the present note is to provide a revised description of *Glypithytreus sulcatus* on the basis of the type specimen of *Plagiolophus sulcatus* from Hungary and of additional material from Slovenia.

### Geological settings

The material that forms the basis for the present study comes from two localities, as follows:

**Budapest area (Hungary):** the holotype of *Plagiolophus sulcatus* originated from the Kiscell Clay of Óbuda (currently a part of the city of Budapest; Fig. 1). The Kiscell Clay Formation consists of grey, well-bioturbated, calcareous clay and clayey marl (Báldi, 1983), the type area being Óbuda, where brickyards were in operation during the second half of the 19<sup>th</sup> century. The most famous of these was the Újlak brickyard (formerly Holzspach brickyard); this was the type locality of *Plagiolophus sulcatus*.

The calcareous nannoflora of the Kiscell Clay is indicative of the lower part of zone NP 24 (upper Kiscellian) (compare Nagymarosy & Báldi-Beke, 1988). This assemblage probably equates with the topmost part of zone P 20 and the lower part of zone P 21 in the planktonic foraminiferal zonation (Horváth, 1998). In the upper part of the Kiscell Clay, the assemblage also belongs to the upper Kiscellian (NP 24 nannoplankton zone and P 21 planktonic foraminiferal zone) (see Horváth, 1998, 2002). K-Ar dating of glauconite from the Kiscell Clay at Pilisborosjenő, north of Budapest, has yielded a date of 33+/-3 Ma (Báldi et al., 1975). The Kiscellian is a regional stage in the Central Paratethys that is used for part of the Lower Oligocene (Rupelian). It was first proposed by Báldi (1979) and later defined in a type section by Báldi (1986). The Kiscellian is now considered to correspond with the Rupelian (Báldi et al., 1999; Piller et al., 2007).

Generally speaking, the Kiscell Clay is not very rich in macrofossils. Strata assigned to this unit, however, were mined at several brickyards along the margins of the Buda Mountains for nearly a century, which explains why their fauna is relatively well known, including foraminifera (Hantken, 1875; Majzon, 1966; Sztrákos, 1974;

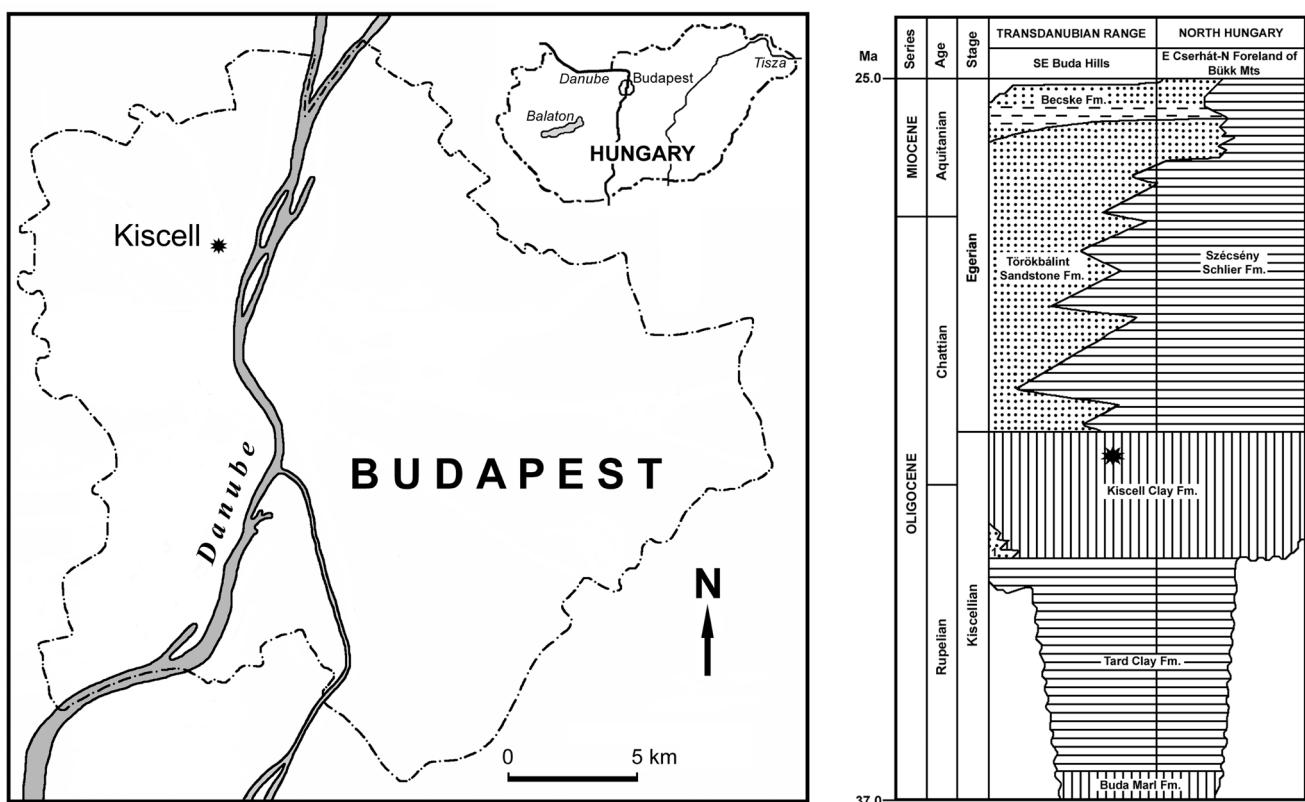


Fig. 1. Left – Simplified map of Hungary and the Budapest area with the position of the former Újlak brickyard (asterisk). Right – Simplified lithostratigraphical scheme of the Hungarian Oligocene at the Buda Hills area (modified after Császár, 1997); the asterisk indicate approximate position of the Kiscell Clay decapod assemblage. 1 = Hárshegy Sandstone Formation

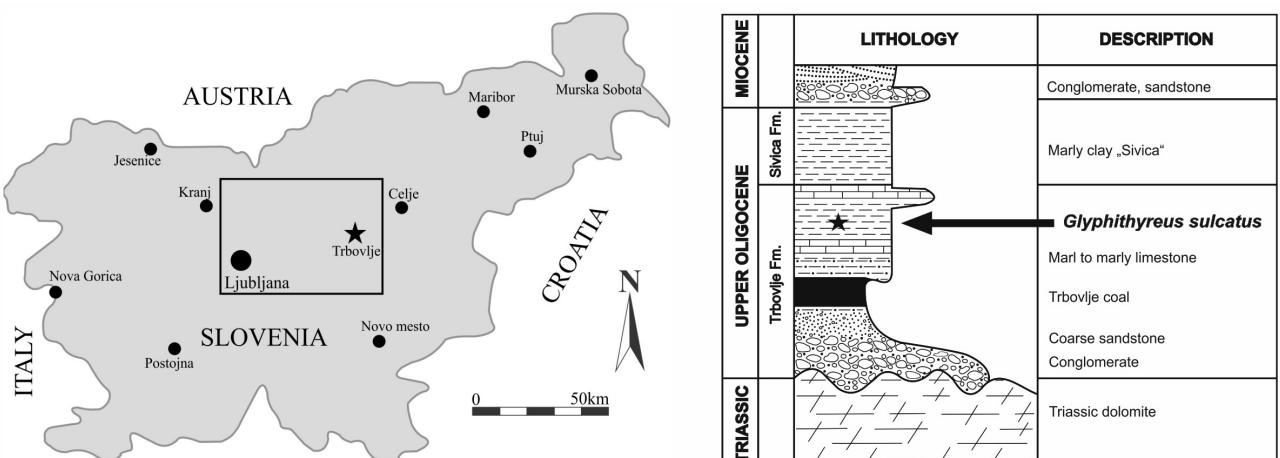


Fig. 2. Left – Simplified map of Slovenia and locality of provenance (star) of specimen of *Glypithyreus sulcatus* (Beurlen, 1939) studied herein. Right – Simplified lithostratigraphical section of the Trbovlje locality (modified after Bechtel et al., 2004); strata that have yielded crab specimens are marked.

Gellai-Nagy, 1988; Horváth, 2002, 2003), gastropods and bivalves (Noszky, 1939, 1940; Báldi, 1986), cephalopods (Szörényi, 1933; Wagner, 1938); brachiopods (Meznerics, 1944), ostracods (Monostori, 1982, 2004), cirripedes (Szörényi, 1934), decapod crustaceans (Beurlen, 1939; Hyžný & Dulai, 2014), and fishes (Weiler, 1933, 1938; Nolf & Brzobohatý, 1994; Szabó & Kocsis, 2016).

**Trbovlje (Slovenia):** The locality of Trbovlje is situated in the Laško Syncline and belongs to geotectonic unit of the Sava folds (Placer, 1999; Jelen & Rifelj, 2002). Oligocene and Miocene sedimentary rocks were laid down disconformably on Triassic and Cretaceous fine-grained, clastic rocks (Hafner, 2000). Successive regressive and transgressive sequences suggest alternating cycles of deepening and shallowing in the depositional environment. The stratigraphical sequence also shows a variably strong influence of marine and terrestrial conditions.

The locality studied is a disused coal pit (GPS co-ordinates: 46°08'56" N, 15°04'03" E), situated some 3 km east of the city of Trbovlje, along the road to Hrastnik (Fig. 2). The area was intensively mined for lignite (brown coal) during the last two centuries. On account of the rich brown coal deposits, the area has been thoroughly studied in the past (Bittner, 1884; Petrascheck, 1952; Kuščer, 1967; Jelen et al., 1992; Placer, 1999; Hafner, 2000).

The Cenozoic sequence here starts with the upper Oligocene Trbovlje Formation, which disconformably overlies Triassic rocks. The coal-bearing Trbovlje Formation is also known as the Socka beds ("Sotzkaschichten") or Pseudo-Socka beds in the older literature (Bechtel et al., 2004). This unit starts with basal conglom-

erates, sandstones layers and greyish coloured marls to marly limestones. The marly beds contained an economically important coal seam. Pollen and coal analysis have demonstrated the taxodiacean–cupressacean origin of the main coal seam (Bruch, 1998; Križnar, 2000) and most likely a transition to a reed marsh in the upper part. The overlying marls and marly limestones are the most fossil-rich beds (Fig. 2), with diverse molluscan and fish assemblages (Križnar, 2015; Buckeridge, in press) and abundant floral remains (Lorencon, 2019). The sequence continues with a horizon of grey marine clay of the Sivica Formation. In the top part of the clay succession occur individual layers and lenses of fine-grained clastic rocks, particularly sandstones and conglomerates. The transition to the clastic beds of the lower Miocene Govce Formation is continuous (Hafner, 2000).

The crab-bearing strata of the Trbovlje Formation are Late Oligocene in age (Odin et al., 1994; Bechtel et al., 2004).

## Material and methods

The crabs studied herein are part of historical collections and have not been prepared further. Specimens were photographed with and without ammonium chloride coating.

## Abbreviations

GBA: Geological Survey of Austria, Vienna (Austria).

HNHM: Department of Palaeontology and Geology, Hungarian Natural History Museum, Budapest (Hungary).

UMJGP: Department for Geology & Palaeontology, Universalmuseum Joanneum, Graz (Austria).

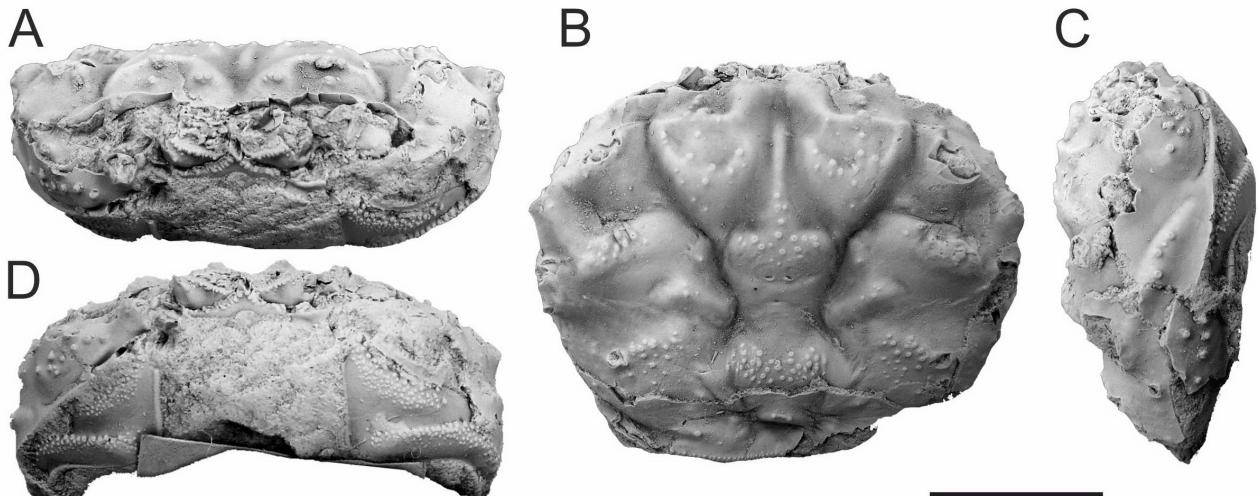


Fig. 3. *Glyphithyreus sulcatus* (Beurlen, 1939), the holotype of *Plagiolophus sulcatus* (HNHM M.59.4692) from the Kiscellian (Rupelian) of the Budapest area, Hungary. A – Frontal view. B – Dorsal view. C – Left lateral view. D – Ventral view. The specimen was coated with ammonium chloride prior to photography. Scale bar equals 10 mm.

Order Decapoda Latreille, 1802  
 Infraorder Brachyura Latreille, 1802  
 Subsection Heterotremata Guinot, 1977  
 Superfamily Xanthoidea MacLeay, 1838  
 Family Panopeidae Ortmann, 1893  
 Subfamily Eucratopsinae Stimpson, 1871  
 Genus *Glyphithyreus* Reuss, 1859  
 (= *Plagiolophus* Bell, 1858, non Pomel, 1857)

**Type species:** *Glyphithyreus formosus* Reuss, 1859, by original designation.

**Diagnosis:** See Karasawa & Schweitzer (2004: 147).

***Glyphithyreus sulcatus*** (Beurlen, 1939) emend.  
 Figures 3–5

\*1939 *Plagiolophus sulcatus* Beurlen, p. 155, pl. 7, fig. 11.  
 2004 *Glyphithyreus sulcatus* (Beurlen) – Karasawa & Schweitzer, p. 148.  
 2010 *Glyphithyreus sulcatus* (Beurlen) – Schweitzer et al., p. 121.  
 2016 *Glyphithyreus sulcatus* (Beurlen) – Hyžný & Gross, p. 110, fig. 15.1.

**Emended diagnosis:** Carapace subhexagonal in outline, widest in anterior one-third of length; fronto-orbital margin about 65 per cent of maximum carapace width; carapace grooves and regions well defined, with granular transverse ridges; regions covered with coarse granules at elevations; protogastric regions subtriangular in outline.

**Material studied:** HNHM M.59.4692, a near-complete carapace, the holotype of *Plagiolophus sulcatus*; Óbuda, Hungary (Fig. 3); UMJGP 56664, a near-complete individual, retaining pereiopods, inclusive of chelipeds, from Trbovlje, Slovenia; GBA 2007/024/0005 (Fig. 4A), counterpart of UMJGP 56664 from Trbovlje, Slovenia (Figs. 4B–C). Interestingly, part and counterpart of the specimen from Trbovlje ultimately landed up in two collections (see also Hyžný & Gross, 2016, fig. 15.1; Hyžný & Zorn, in press, pl. 25, fig. 2).

**Description:** Carapace subhexagonal in outline; L/W (length/width) ratio 0.8, widest in anterior one-third of carapace. Fronto-orbital margin about 65 per cent of maximum carapace width; front broken; orbits poorly preserved. Anterolateral margin strongly convex with four blunt teeth, including outer orbital tooth; posterolateral margin sinuous, converging posteriorly. Carapace grooves and regions well defined; epigastric regions well developed, rectangular in outline; protogastric regions subtriangular in outline, with steep ridges anteriorly; mesogastric region well developed, with elongate, narrow anterior process; metagastric region with granular transverse ridge and two distinct gastric pits posteriorly, separated from smooth urogastric region by narrow groove; cardiac region as wide as metagastric region, with broad, granular transverse ridge; hepatic regions well defined, delimited by deep cervical groove posteriorly; branchial region divided into two portions by distinct branchio-cardiac groove, each bearing granular transverse ridge. Regions covered with coarse granules at elevations, with cardiac region

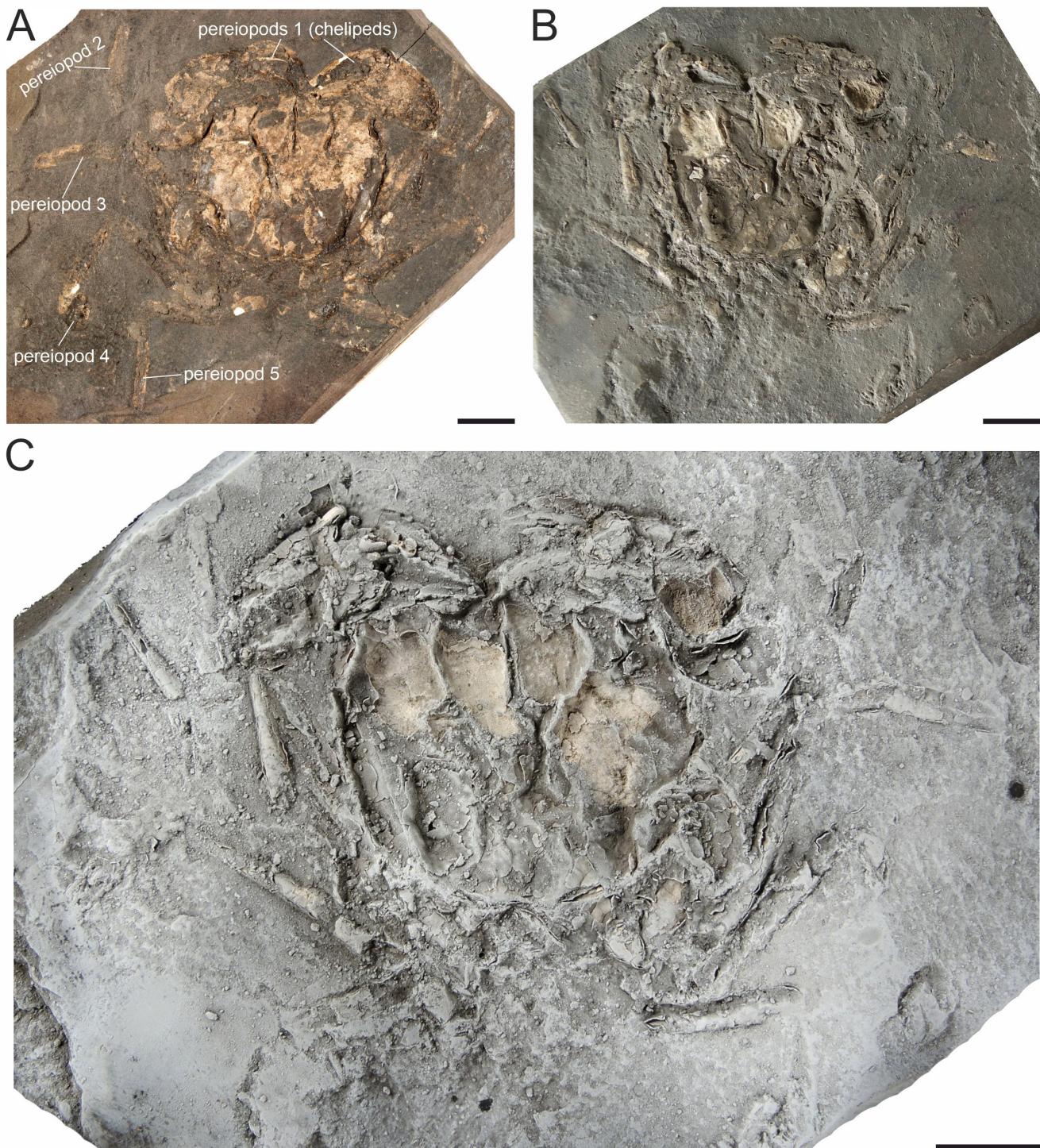


Fig. 4. *Glypithyreus sulcatus* (Beurlen, 1939) from the upper Oligocene (Chattian) of Trbovlje, Slovenia. A – GBA 2007/024/0005 (unwhitened). B – UMJGP 56664 (unwhitened). C – UMJGP 56664 (whitened with ammonium chloride). Scale bars equal 10 mm.

being densely granulated, whereas protogastric, meso- and metagastric and branchial regions having only limited number of relatively large tubercles. Chelipeds (pereiopods 1) with robust chelae, insufficiently preserved; carpus subquadrate in outline; manus approximately two times longer than tall, converging proximally; fingers shorter than manus. Pereiopods 2–5 slender, distal elements not preserved sufficiently.

**Remarks:** Karasawa & Schweitzer (2004, p. 148) noted that, “the description of *G. sulcatus* clearly indicates two transverse ridges on the branchial regions, separated by a very deep cavity, which is certainly characteristic of *Glypithyreus*.” We can confirm this and thus corroborate the transfer of this species to this genus.

As far as carapace outline is concerned, *Glypithyreus sulcatus* appears to be close to *G.*

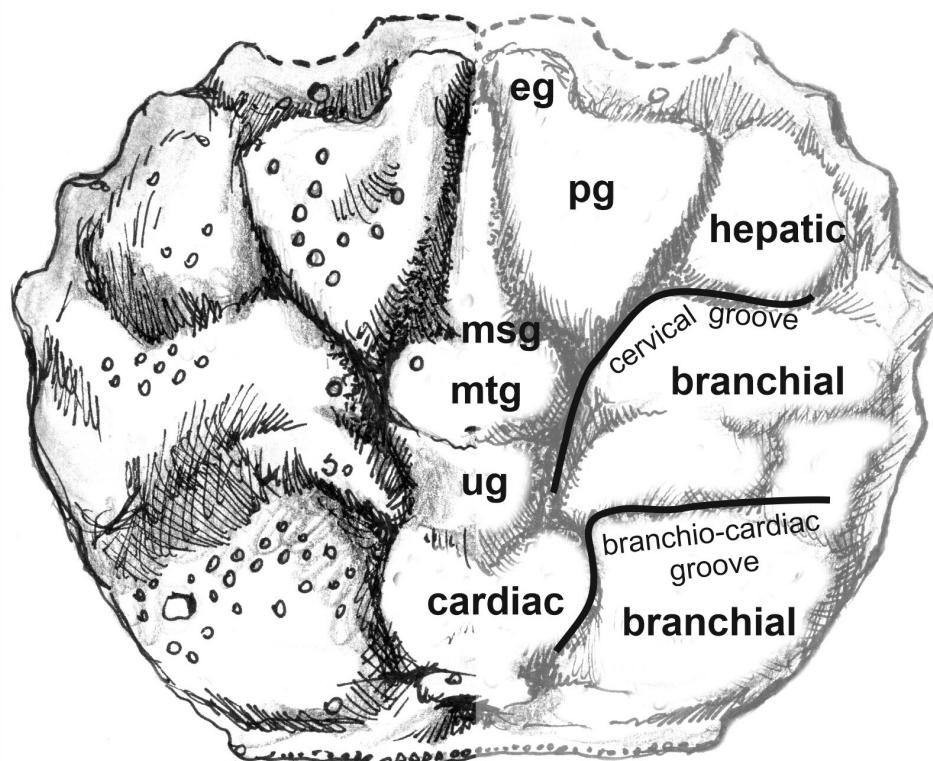


Fig. 5. *Glyphithyreus sulcatus* (Beurlen, 1939), reconstruction scheme of dorsal carapace. Abbreviations: eg = epigastric region, msg = mesogastric regions, mtg = metagastric region, pg = protogastric region, ug = urogastric region.

*ellipticus* Bittner, 1875 from the Eocene of Italy (Bittner, 1875), as far as the published figure allows to judge this. However, the latter differs in having more rounded protogastric regions; these are subtriangular in outline in *G. sulcatus*. Additionally, *G. sulcatus* has fewer granules on the elevated parts of carapace regions (Figs. 3, 5). In this respect, this species differs from all congeners known to date, including *G. formosus* Reuss, 1859 and *G. wetherellii* (Bell, 1858), in which carapace regions have a much finer granulation distributed over a larger area. Moreover, *G. formosus* has a wider fronto-orbital margin (Reuss, 1859, pl. 2, fig. 1) than *G. sulcatus*.

### Conclusions

A revised description of *Plagiolophus sulcatus*, based both on its type specimen from the lower Oligocene (Rupelian) of Hungary and additional material from the upper Oligocene (Chattian) of Trbovlje (Slovenia), is presented. Interestingly, part and counterpart of the specimen from Trbovlje were transferred to the Universal Museum Joanneum at Graz and the Geological Survey at Vienna. The holotype of the species is refigured for the first time here since its original publication. Attribution of *P. sulcatus* to *Glypithyreus*, first suggested by Karasawa & Schweitzer (2004), is confirmed. Comparison with congeners suggests that *G. sulcatus* is differentiated by having subtriangular protogastric regions and fewer and coarser tubercles on elevated carapace regions.

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### References

- Báldi, T. 1979: Changes of Mediterranean (?Indopacific) and Boreal influences in Hungarian marine mollusc faunas since Kiscellian until Eggenburgian times. The stage Kiscellian. Annales Géologiques des Pays Helléniques, VII. Congress CMNS, 1: 19–49.
- Báldi, T. 1983: Magyarországi oligocén és alsó miocén formációk [Oligocene and Lower Miocene formations of Hungary]. Akadémiai Kiadó, Budapest: 293 p. (in Hungarian)
- Báldi, T. 1986: Mid-Tertiary stratigraphy and paleogeographic evolution of Hungary. Akadémiai Kiadó, Budapest: 201 p.
- Báldi, T., Báldi-Beke, M., Horváth, M., Nagymarosi, A., Balogh, K. & Sós, E. 1975: On the radiometric age and the biostratigraphic position of the Kiscell Clay in Hungary. Proceedings of the VIth Congress of RCMNS, Bratislava, Veda: 315–317.

- Báldi, T., Less, G. & Mandic, O. 1999: Some new aspects of the lower boundary of the Egerian stage (Oligocene, chronostratigraphic scale of the Paratethyan area). Abhandlungen der Geologischen Bundesanstalt, 56: 653–668.
- Bechtel, A., Markic, M., Sachsenhofer, R.F., Jelen, B., Gratzer, R., Lücke, A. & Püttmann, W. 2004: Paleoenvironment of the upper Oligocene Trbovlje coal seam (Slovenia). International Journal of Coal Geology, 57/1: 23–48. <https://doi.org/10.1016/j.coal.2003.08.005>
- Bell, T. 1858: A monograph of the fossil malacostracous Crustacea of Great Britain, Part I. Crustacea of the London Clay, 44 p. The Palaeontographical Society, London.
- Beurlen, K. 1939: Neue Dekapoden-Krebse aus dem ungarischen Tertiär. Paläontologische Zeitschrift, 21: 135–161.
- Bittner, A. 1875: Die Brachyuren des vicentini-schen Tertiärgebirges. Denkschriften der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe, 34: 63–106.
- Bittner, A. 1884: Die Tertiär-Ablagerungen von Trifail und Sagor. Jahrbuch der kaiserlich-königlichen Geologischen Reichsanstalt, 34: 236–281.
- Bruch, A. 1998: Palynological Untersuchungen im Oligozän Sloweniens – Paläo-Umwelt und Paläoklima im Ostalpenraum. Tübinger Mikropaläontologische Mitteilungen, 18: 1–193.
- Buckeridge, J.S., Kočí, T., Gašparič, R. & Kočová Veselská, M. in press: *Actinobalanus? sloveniensis* (Thoracica, Balanoidea), a new species of cirripede from the Oligocene and Miocene of Slovenia that grew attached to wood substrates. Neues Jahrbuch für Geologie und Paläontologie – Abhandlungen. Accepted in press March 9th, 2020
- Császár, G. (ed.) 1997: Basic Lithostratigraphic Units of Hungary. Charts and Short Descriptions. Magyar Állami Földtani Intézet, Budapest: 114 p.
- Gellai-Nagy, Á. 1988: Delineation of Hantken's foraminiferal species from the original collection. A Magyar Állami Földtani Intézet Évi Jelentése 1988 évről: 133–173.
- Guinot, D. 1977: Propositions pour une nouvelle classification des Crustacés Décapodes Brachyoures. Comptes rendus hebdomadaires des séances de l'Académie des sciences, D285: 1049–1052.
- Hafner, G. 2000: Sedimentološke značilnosti trboveljskih plasti. Unpublished MSc thesis, University of Ljubljana, Ljubljana: 105 p.
- Hantken, M. 1875: A *Clavulina Szabói* rétegek faunája, I. rész. Foraminiferák (Die Fauna der *Clavulina Szabói* Schichten, I. Teil. Foraminiferen). Jahrbuch der königlichen ungarischen geologischen Anstalt, 4: 1–93.
- Horváth, M. 1998: Paleobathymetrical analysis of Upper Eocene-Lower Miocene Foraminifera of the Hungarian Paleogene Basin. Acta Geologica Hungarica, 41/2: 223–262.
- Horváth, M. 2002: Data to revision and distribution of small foraminifera species described by Hantken (1868, 1875). Part I, Textulariidae and Miliolidae. Fragmenta Palaeontologica Hungarica, 20: 25–42.
- Horváth, M. 2003: Data to revision and distribution of small Foraminifera species described by Hantken (1868, 1875). Part II. Nodosariidae and Vaginulinidae. Fragmenta Palaeontologica Hungarica, 21: 5–32.
- Hyžný, M. & Dulai, A. 2014: Deep-water fossorial shrimps from the Oligocene Kiscell Clay of Hungary: taxonomy and palaeoecology. Acta Palaeontologica Polonica, 59/4: 947–965. <https://doi.org/10.4202/app.2012.0078>
- Hyžný, M. & Gross, M. 2016: From the palaeontological collection of the Universalmuseum Joanneum – The Cenozoic decapod crustaceans (Crustacea: Malacostraca: Decapoda). Joannea, Geologie und Paläontologie, 12: 73–127.
- Hyžný, M. & Zorn, I. in press: A catalogue of the fossil decapod crustaceans in the collections of the Geological Survey of Austria in Vienna. Abhandlungen der Geologische Bundesanstalt.
- Jelen, B. & Rifelj, H. 2002: Stratigraphic structure of the B1 Tertiary tectonostratigraphic unit in eastern Slovenia. Geologija, 45/1: 115–138. <https://doi.org/10.5474/geologija.2002.010>
- Jelen, B., Aničić, B., Brezigar, A., Buser, S., Cimerman, F., Drobne, K., Monostori, M., Kedves, M., Pavšič, J. & Skaberne, D. 1992: Model of positional relationships for Upper Paleogene and Miocene strata in Slovenia. Interdisciplinary Geological Conference on the Miocene Epoch, Abstracts and Field Trips. Ancona, 1–72.
- Karasawa, H. & Schweitzer, C.E. 2004: Revision of the genus *Glypithyreus* Reuss, 1859 (Crustacea, Decapoda, Brachyura, Xanthoidea) and recognition of a new genus. Paleontological Research, 8: 143–154.
- Križnar, M. 2000: Ksilotomske analize rjavih premogov iz Zasavja. Unpublished BSc thesis, University of Ljubljana, Ljubljana: 62 p.

- Križnar, M. 2015: Oligocenska ihtiofavnna (Teleostei) Slovenije - pregled in problematika najdišč. In: Rožič, B. (ed.): Razprave, poročila = Treatises, reports / 22. posvetovanje slovenskih geologov = 22nd Meeting of Slovenian Geologists. Geološki zbornik, 23: 99–104.
- Kuščer, D. 1967: Zagorski terciar (Tertiary formations of Zagorje). Geologija, 10: 5–85.
- Latreille, P.A. 1802: Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres. Vol. 3. F. DuFart, Paris: 467 p.
- Lorencon, R. 2019: Oligocenska flora v okolici Trbovelj. Konkrecija, 8: 12–18.
- MacLeay, W.S. 1838: On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: Smith, A. (ed.) Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835. and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa". Smith, Elder, and Co., London: 53–71.
- Majzon, L. 1966: Foraminifera-vizsgálatok. Akadémiai kiadó, Budapest: 939 p.
- Meznerics, I. 1944: Die Brachiopoden des ungarischen Tertiärs. Annales historico-naturales Musei nationalis hungarici, 36: 10–60.
- Monostori, M. 1982: Oligocene ostracods from the surroundings of Budapest. Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae, Sectio Geologica, 21: 31–102.
- Monostori, M. 2004: Lower Oligocene (Kiscellian) ostracods in Hungary. Annales Universitatis Scientiarum Budapestinensis, Sectio Geologica, 34: 27–141.
- Nagymarosy, A. & Báldi-Beke, M. 1988: The position of the Paleogene formations of Hungary in the standard nannoplankton zonation. Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae, Sectio Geologica, 28: 3–25.
- Nolf, D. & Brzobohatý, R. 1994: Fish otoliths from the Late Oligocene (Eger and Kiscell formations) in the Eger area (northeastern Hungary). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 64: 225–252.
- Noszky, J. 1939: A kiscelli agyag molluszka-faunája. I. rész. Lamellibranchiata (Die Mollusken fauna des Kisceller Tones (Rupelien) aus der Umgebung von Budapest. I. Teil. Lamellibranchiata). Annales historico-naturales Musei nationalis hungarici, 32: 19–146.
- Noszky, J. 1940: A kiscelli agyag molluszka-faunája. II. rész. Loricata, Gastropoda, Scaphopoda. (Die Mollusken fauna des Kisceller Tones (Rupelien) aus der Umgebung von Budapest. II. Teil. Loricata, Gastropoda, Scaphopoda). Annales historico-naturales Musei nationalis hungarici, 33: 1–80.
- Odin, G.S., Jelen, B., Drobne, K., Uhan, J., Skaberne, D., Pavšic, J., Cimerman, F., Cosca, M. & Hunziker, J.C. 1994: Premiers âges géochronologiques de niveaux volcanoclastiques oligocènes de la région de Zasavje, Slovénie. Giornale di Geologia, 56/1: 199–212.
- Ortmann, A.E. 1893: Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. VII. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Thiere, 7/3: 411–495.
- Petrascheck, W. 1952: Der Einfluß der Fazies der Flözablagerung auf die Eigenschaften der Kohle. Zeitschrift der deutschen geologischen Gesellschaft, 104: 1–9.
- Piller, W.E., Harzhauser, M. & Mandic, O. 2007: Miocene Central Paratethys stratigraphy – current status and future directions. Stratigraphy, 4: 71–88.
- Placer, L. 1999: Structural meaning of the Sava folds. Geologija, 41: 191–221. <https://doi.org/10.5474/geologija.1998.012>
- Pomel, A. 1857: Note critique sur les caractères et les limites du genre *Palaeotherium*. Archives des Sciences physiques et naturelles Genève, 5: 200–207.
- Reuss, A.E. 1859: Zur Kenntnis fossiler Krabben. Akademie der Wissenschaften Wien, Denkschrift, 17: 1–90, pls. 1–24.
- Schweitzer, C.E., Feldmann, R.M., Garassino, A., Karasawa, H. & Schweigert, G. 2010: Systematic list of fossil decapod crustacean species. Crustaceana Monographs, 10: 1–222. <https://doi.org/10.1163/ej.9789004178915.i-222>

- Stimpson, W. 1871: Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida by L.F. de Pourtales, Assist. U. S. Coast Survey. Part I. Brachyura. Bulletin of the Museum of Comparative Zoology at Harvard College, 2: 109–160.
- Szabó, M. & Kocsis, L. 2016: A preliminary report on the Early Oligocene (Rupelian, Kiscellian) selachians from the Kiscell formation (Buda Mts, Hungary), with the re-discovery of Wilhelm Weiler's shark teeth. *Fragmenta Palaeontologica Hungarica*, 33: 31–64.
- Szörényi, E. 1933: Adatok a harmadkori *Sepia*-félék ismeretéhez, néhány új magyarországi faj alapján. (Neue tertiäre Sepiinae aus Ungarn nebst Bemerkungen zum zeitlichen Auftreten und zur Entwicklung der Gattung *Sepia*). *Földtani Közlöny*, 63: 1183–1189.
- Szörényi, E. 1934: Oligocén *Scalpellum* maradványok Magyarországról. (*Scalpellum* Reste aus dem ungarischen Oligozän). *Földtani Közlöny*, 64: 272–277.
- Sztrákos, K. 1974: Paleogene planktonic foraminiferal zones in northeastern Hungary. *Fragmenta Mineralogica et Palaeontologica*, 5: 29–81.
- Wagner, J. 1938: A kiscelli közép-oligocén (Rupélien) rétegek kétkopoltyús Cephalopodái és új *Sepia*-félék a magyar eocénből. (Die dibranchiaten Cephalopoden der mitteloligozänen (Rupelien) Tonschichten von Kiscell und eine Sepiinae aus dem ungarischen Eozän). *Annales historico-naturales Musei nationalis hungarici*, 31: 179–199.
- Weiler, W. 1933: Két magyarországi oligocén-korú halfauna. (Zwei oligozäne Fischfaunen aus dem Königreich Ungarn). *Geologica Hungarica, Series Palaeontologica*, 11: 1–54.
- Weiler, W. 1938: Neue Untersuchungen an mitteloligozänen Fischen Ungarns. *Geologica Hungarica, Series Palaeontologica*, 15: 1–31.