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Brief notes on newly discovered teeth of the hybodontiform shark *Strophodus dunaii* (Szabó et Főzy, 2020)

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Abstract – Genus *Strophodus* has been considered as a junior synonym of genus *Asteracanthus* for a long time. The discovery of an articulated skeleton of *Asteracanthus ornatissimus* resurrected the genus *Strophodus*, which is recommended to include all species previously referred to *Asteracanthus*, except for those described by isolated dorsal fin spines. This stands for *Strophodus dunaii* comb. nov. as well, which was established for isolated tooth remains. A new tooth and casts of several previously unknown teeth referable to this species are described here in detail. Notes on future tooth wear pattern analyses in *Strophodus* spp. are also discussed. With 19 figures.

Key words – *Asteracanthus*, Bakonycsernye, Jurassic, *Strophodus*, tooth

INTRODUCTION

The generic name *Asteracanthus* was erected by Agassiz (1837) for enlarged dorsal fin spine remains. The genus *Strophodus* was later created for isolated crushing teeth (Cappetta 2012). Later, when *Asteracanthus* fin spines associated with *Strophodus* teeth were found, *Asteracanthus* was considered as valid and *Strophodus* became a junior synonym (Woodward 1888; Cappetta 2012; Leuzinger *et al.* 2017). For decades, *Asteracanthus* was known only by isolated dorsal fin spines, isolated teeth, and associated or articulated dentitions (Cappetta 2012; Rees & Underwood 2008; Stumpf *et al.* 2021), but skeletons or partial skeletons were not known. Stumpf *et al.* (2021) introduced the first known skeleton of *Asteracanthus* (referred to the species *A. ornatissimus*) from the Upper Jurassic (lower Tithonian) of Solnhofen (Bavaria, Germany). This discovery shed more light on the taxonomic importance of the holotype *Asteracanthus* fin spines, whose morphology gave the generic name of this group. It turned out that the Solnhofen skeleton has high-crowned, multicuspid teeth, markedly different from the low-crowned, mostly oval to bean shaped crushing teeth previously referred to the genus *Asteracanthus*. Therefore, Stumpf *et al.* (2021) resurrected the genus *Strophodus* to include all species previously referred to *Asteracanthus*, except for the species based on isolated fin spines. The validity of species included in genera *Asteracanthus* and *Strophodus* are partly explained and discussed by Sharma & Singh (2021) and Stumpf *et al.* (2021).

The description of the hybodontiform species *Strophodus dunaii* (originally described as *Asteracanthus dunaii*) is based on isolated tooth remains, possibly belonging to the same individual. The remains were found in the Middle Jurassic (Aalenian) Tölgyhát Limestone Formation exposed in the Tűzköves Ravine nearby Bakonycsernye (Hungary). Dentition of this species is characterized by (1) robust teeth with unique occlusal ornamentation that are minutely reticulated towards the crown edges, (2) by the presence of a mesiodistally running, low and wide transversal ridge resulting an asymmetrical, hat-like outline in cross-section view, and (3) by the arched shape of the mesially domed second lateral teeth (Szabó & Főzy 2020). Following the results of Stumpf *et al.* (2021), Sharma & Singh (2021) re-assigned the species as *Strophodus dunaii*, which conclusion is hereby accepted and followed.

As macroscopic fish remains from the Mesozoic of the Carpathian Basin are scarce, all available specimens are of great importance. This especially stands for *S. dunaii*, which was described based on only seven teeth. The present study includes the detailed description of one new original tooth, and casts of three further specimens referable to this hybodontiform shark, together with the taxonomic revision of the species.

MATERIAL AND METHODS

For the geological and locality data of the *S. dunaii* teeth see Szabó & Főzy (2020, p. 297).

Years before the description of the species, an amateur collector, Miklós Hegyi (Csesznek, Hungary) found a tooth at the locality where the type material was unearthed. The originally discovered tooth material of *S. dunaii* included three further, yet undescribed teeth, whose location is currently unknown (Mihály Dunai, pers. comm. 2020). Fortunately, years before the description of *S. dunaii*, Mihály Dunai made casts of these tooth remains, which were donated to the Palaeontological Department of the Eötvös University (ELTE, Budapest).

The fine surface structure of the new tooth and some of the type specimens were investigated with a JSR-IT500 HR scanning electron microscope housed in the Szentágothai Research Centre of the University of Pécs. In his work, Stumpf *et al.* (2021) is followed on the taxonomy and synonymy of *Asteracanthus* and *Strophodus* is accepted for this species.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Order Hybodontiformes Maisey, 1975
Superfamily Hybodontoidea Owen, 1846
Family incertae sedis
Genus *Strophodus* Agassiz, 1838

Strophodus dunaii (Szabó et Főzy, 2020)
(Figs 1–10)

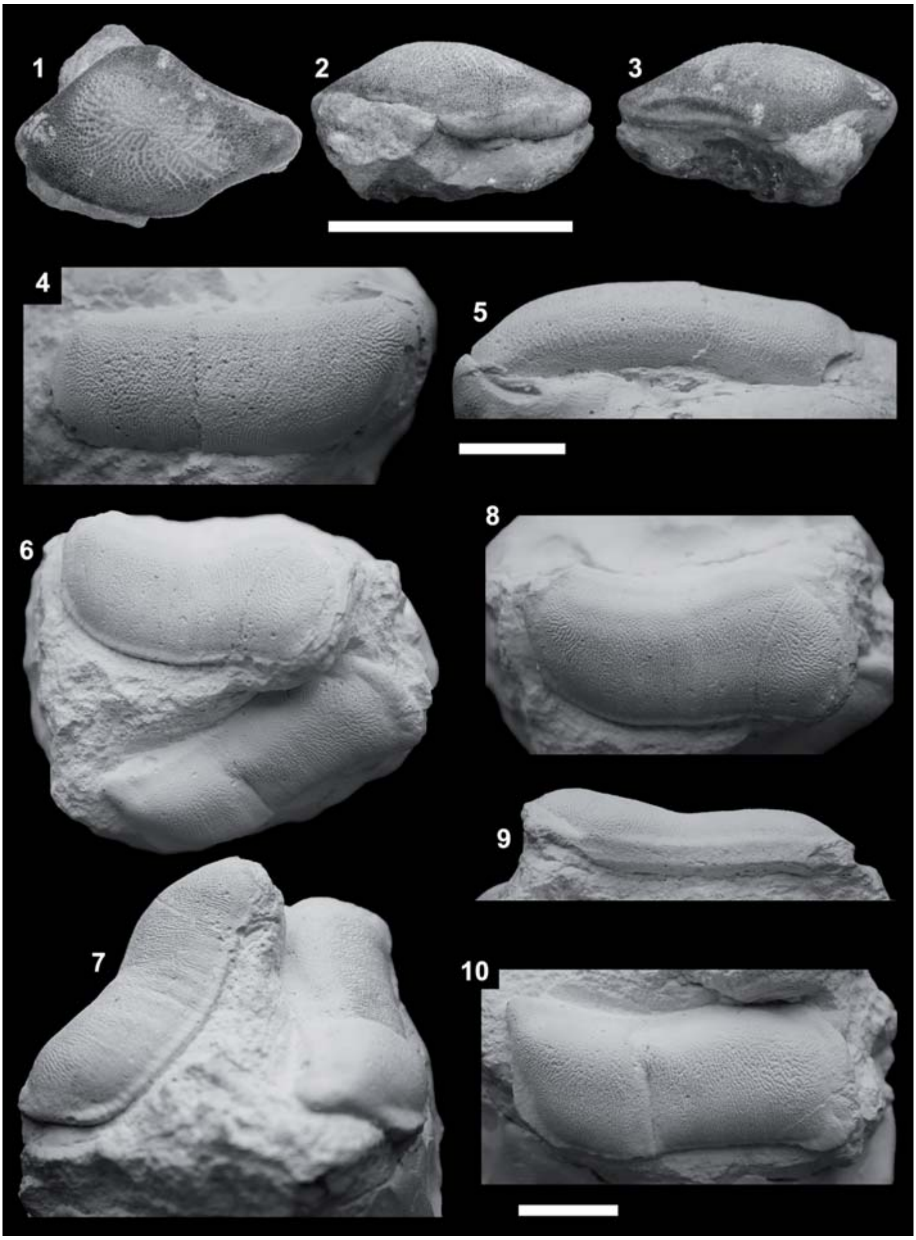
2020 *Asteracanthus dunaii* sp. nov. – Szabó & Főzy, p. 299–303, figs 2, 3.

Referred new material – 1 second anterior tooth (Miklós Hegyi Collection), casts of 1 first lateral tooth and 2 second lateral teeth (ELTE, Palaeontological Collection, ELTE.VER.2021.1–2.).

Description – The private collection specimen (Figs 1–3) represents a second anterior tooth based on the crown's lingually edged, closely triangular outline in occlusal view (see Peyer 1946, pl. 4, figs 1, 2; Rigal & Cuny 2016, fig. 2; Szabó & Főzy 2020, figs 4.18, 4.19). The occlusal ornamentation is composed of frequently branching ridges originating from the higher crown parts and turning into a minute reticulate pattern at the crown edges. No occlusal crest is present. The crown is strongly convex, which makes the low and wide, labially oriented transversal crest barely visible. The specimen lacks the root.

One of the ELTE specimens represents a first lateral tooth (ELTE.VER.2021.1., Figs 4–5) based on its labially projected mesial edge in occlusal view (see Szabó & Főzy 2020, figs 2.3–2.5). The tooth is elongated and exhibits no dome in labial and lingual views. The occlusal surface possesses a low and wide, mesiodistally running transversal ridge near the labial crown edge. An occlusal ornamentation, built up by branching ridges, originates from here. On the lower parts of the crown, this ornamentation turns into a finely reticulate pattern. The vertical crown parts are weakly folded. No remains of the root are visible.

The other cast exposes replicas of two teeth, together with that of the embedding piece of limestone, on which they were originally sitting close to each other (ELTE.VER.2021.2., Figs 6–10). Their position refers them as associable tooth remains, which creates a labiolingual file unit. Both teeth have an almost rectangular, weakly lingually arched outline in occlusal view, referring them as second lateral teeth (see Szabó & Főzy 2020, figs 2.6–2.8). Both extremities of



Figs 1–10. New specimens of *Strophodus dunaii* from the Middle Jurassic of Bakonycsernye (Hungary). – **Figs 1–3.** Second anterior tooth (Miklós Hegyi Collection). – **Figs 4–5.** Cast of a first lateral tooth (ELTE.VER.2021.1.). – **Figs 6–10.** Cast of two second lateral teeth sitting on the same piece of limestone (ELTE.VER.2021.2.). **1, 4, 8, 10** – occlusal view; **2, 5, 9** – labial view; **3** – lingual view; 7 – oblique mesial view. Scale bars: 20 mm

the teeth are angled. The occlusal surface of the teeth is mesially weakly domed, forming the highest part of their crowns. These teeth also show a low and wide, lingually positioned transversal ridge. The surface ornamentation of the crown is built up by branching folds and ridges, which is followed by a folded transition on the vertical part of the crown. This turns into a reticulate ornamentation near to the crown base in all directions. Both teeth lack any remains of the root.

Remarks – Compared to the specimen found by Miklós Hegyi, tooth HNHM PAL.2020.1.1 (second anterior tooth of the type material; see Szabó & Főzy 2020, figs 2.1 and 2.2) has noticeably less convex crown.

One of the casts of the associable second lateral teeth from the Palaeontological Collection of the ELTE possesses a deep mesiodistal fold on the occlusal surface (Figs 6 and 10). This may be regarded as pathology, or may be a link to taphonomy.

SEM OBSERVATIONS

Scanning electron microscope images were taken on the second anterior tooth found by the amateur collector Miklós Hegyi and additionally on a second anterior tooth (HNHM PAL 2020.1.1) and a lateral tooth (HNHM PAL 2020.6.1) from the type material.

The surface of all the three scanned teeth bears a rich ornamentation of diverging folds and ridges on the occlusal surface, turning to a reticulate pattern of pits towards the crown base (Figs 11, 14 and 17). The enamel surface shows no pores or any other features between the ridges and pits (Figs 12–13, 15–16, 18). Unexpectedly, stretchmarks were discovered on the occlusal surface of specimen HNHM PAL 2020.6.1 (Fig. 19). Some of these are more or less parallel to each other; therefore they are tentatively attributed to functional wear as no mechanical preparation was carried out on either of the teeth included in the type material of *S. dunaii* (Mihály Dunai, pers. comm.).

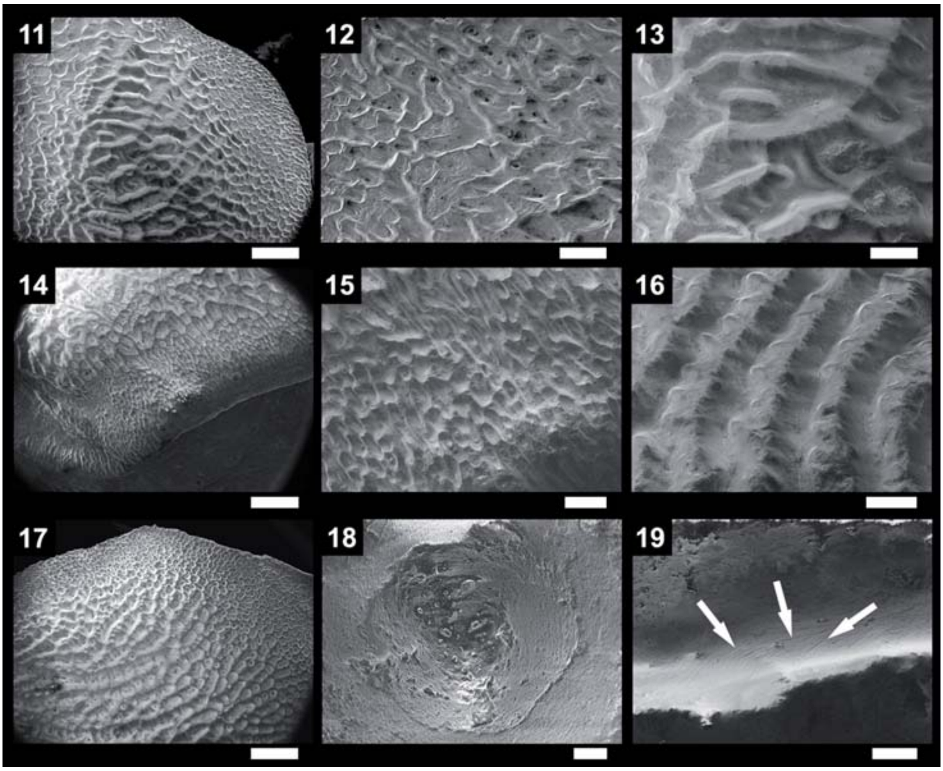
DISCUSSION

The species *Strophodus dunaii* was described based on seven isolated teeth only. Although these teeth provided enough information for the specific description, the number of the remains is still very low. The discovery of new and referable specimens for this taxon, therefore, is of great scientific importance. The genus *Strophodus* itself also includes species which are known only by very low number of specimens (i.e., *S. subreticulatus*, *S. tridentinus*, *S. punctatus*). The scientific evaluation of these species is extremely problematic, mainly due to the poor illustration of the published tooth remains (Agassiz 1838; Pfeil 2011;

Zittel 1870). The above described, additional tooth specimens further support the assignment of *S. dunaii* as a separate species.

The ELTE cast specimen with the two teeth sitting next to each other (ELTE.VER.2021.2.) belongs to a labiolingual unit of a partial second lateral file, and originally were found together with the type material of *S. dunaii*. This supports the theory that the whole type material of *S. dunaii* belongs to the same individual. Future expeditions in the Tűzköves Ravine may reveal further tooth remains.

Nevertheless, the whole material of *S. dunaii* (except for the anterior tooth found by Miklós Hegyi) can be regarded as a disarticulated but associable, partial dentition. Therefore, it is of great importance as the level of heterodonty within *Strophodus* spp. is still poorly known. It may be noted that only *S. magnus*, *S.*



Figs 11–19. Scanning electron microscope images of the occlusal surface of the teeth of *Strophodus dunaii*. – **Figs 11–13.** Second anterior tooth (Miklós Hegyi Collection). – **Figs 14–16.** HNHM PAL.2020.1.1 (second anterior tooth). – **Figs 17–19.** HNHM PAL 2020.6.1 (lateral tooth of undefinable position). White arrows point to some larger stretchmarks. Scale bars: 11, 14, 17: 2 mm; 12, 13, 15, 16: 500 μm; 18: 20 μm; 19: 100 μm

medius, and *S. smithwoodwardi* are known by associated or well-preserved articulated dentitions (Citton *et al.* 2018; Owen 1869; Peyer 1946; Rigal & Cuny 2016). Pfeil (2011) also published an articulated dentition from the Upper Jurassic (Tithonian) of Mühlheim (Germany), referred to as *Asteracanthus* sp. (= *Strophodus* sp.; after Stumpf *et al.* 2021).

Detailed studies on the occlusal wear patterns of the teeth attributed to *Strophodus* spp., combined with other methods could reveal further information on the diet of these durophagous hybodontiforms. The scientific elaboration of the Jurassic fishes of the Carpathian Basin is still low (Dulai *et al.* 1992; Pászti 2004; Szabó 2018, 2019; Szabó & Főzy 2020; Szabó & Pálfy 2019), therefore private collections play an important role as source of information. The present study further emphasizes the importance of private collection specimens in vertebrate palaeontology, since the entire fossil record of *S. dunaii* comes from amateur collections.

Extant Heterodontidae species have a crushing dentition morphologically very similar to that of extinct *Strophodus* spp. (see Cappetta 2012; Hovestadt 2018). The family Heterodontidae includes the genus *Heterodontus* only, which comprises nine nominal species (Ebert *et al.* 2013). These species feed on hard-shelled molluscs, echinoderms, crustaceans, and also small fishes (Froese & Pauly 2021 and references therein). The robust, crushing teeth of *Strophodus* with complex occlusal pattern refer to a diet mainly based on hard-shelled prey (e.g. bivalves and cephalopods) (Szabó & Főzy 2020 and references therein). A large number of the known *Strophodus* tooth materials in museum collections across Europe bear signs of functional wear (pers. obs.). The correlation of dental microwear texture (DMT) and diet in extinct and extant sharks is poorly studied (see in Weber *et al.* 2021; McLennan & Purnell 2021). Weber *et al.* (2021) also highlighted the limits of dental microwear texture analysis (DMTA) in sharks, including the sample sizes and the potentially high number of influencing variables (e.g. post-mortem wear). Yet, with complementing existing technologies (e.g. stable isotope analysis, see Leuzinger *et al.* 2015), DMTA has the potential to be a powerful method for dietary analysis in extinct and living elasmobranchs (McLennan & Purnell 2021), including that of the enigmatic *Strophodus* spp.

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