

## Middle Miocene (Badenian) chitons (Mollusca, Polyplacophora) from the Central Paratethys 1: Várpalota (Bakony Mts, Hungary)

Alfréd DULAI<sup>1</sup> & Lajos KATONA<sup>2</sup>

<sup>1</sup>*Hungarian National Museum Public Collection Centre – Hungarian Natural History Museum, Department of Palaeontology and Geology, H-1083 Budapest, Ludovika tér 2, Hungary.*  
*E-mail: dulai.alfred@nhmus.hu;*

<sup>2</sup>*Hungarian National Museum Public Collection Centre – Bakony Natural History Museum, H-8420, Zirc, Rákóczi tér 1, Hungary. E-mail: katona.lajos@nhmus.hu*

**Abstract** – Várpalota has long been known for its Middle Miocene (mainly mollusc) fossil remains. However, very little information is available on Polyplacophora species. In this paper we discuss the chiton assemblages of two contemporaneous (lower Badenian) sites, the famous Szabó sand pit, and a temporary trench in the Faller Street. The studied material derived from four different collection sources; the Szabó sand pit specimens are from the Hungarian Natural History Museum, Budapest and the Naturalis Biodiversity Center, Leiden, while the Faller Street chitons are from the Bakony Natural History Museum, Zirc and Tibor Berta's private collection in Veszprém. Altogether more than 400 specimens represent mainly eroded fragmentary valves of eight Polyplacophora species. Most of the identified taxa are well known from the Middle Miocene chiton assemblages of the Central Paratethys as well as from the Hungarian localities (*Ischnochiton rissoii* (Payraudeau), *Rhyssoplax corallina* (Risso), *Lepidochitona lepida* (Reuss), *Acanthochitona faluniensis* (Rochebrune), *Cryptoplax weinlandi* Šulc). A further *Acanthochitona* taxon cannot be identified to species level at present due to the scarcity of available material. *Parachiton africanus* (Nierstrasz) was found for the first time from Hungary and *Acanthochitona oblonga* (Leloup) was recorded for the first time not only from Hungary but also from the whole Central Paratethys. With 45 figures.

**Key words** – *Acanthochitona*, *Cryptoplax*, *Ischnochiton*, *Lepidochitona*, lower Badenian, *Parachiton*, polyplacophorans, *Rhyssoplax*

### INTRODUCTION

The Middle Miocene sediments of Hungary, deposited in the former Central Paratethys area are very rich in marine fossils, of which molluscs are particularly common. However, compared to gastropods and bivalves, polyplacophorans are rather rare and, accordingly, little information is available in the literature. CSEP-REGHY-MEZNERICS (1950) described very briefly and without illustration the species *Chiton lepidus* (Reuss) (currently *Lepidochitona lepida*; see SCHWABE 2000) from Hidas in the Mecsek Mts. JAKUBOWSKI & MUSIAŁ (1977) and STUDENCKA &

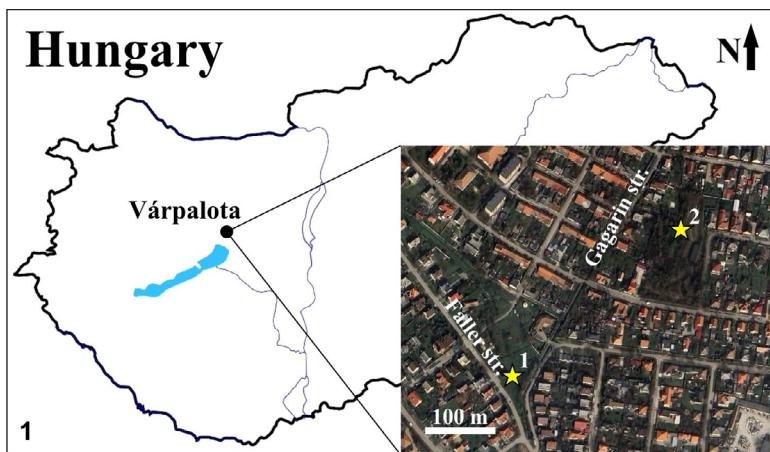
STUDENCKI (1988) mentioned the species *Lepidochitona (Lepidochitona) subgranosa* Bałuk and *Acanthochitona faluniensis* (Rochebrune) from Várpalota in the Bakony Mts, based on material of Muzeum Ziemi in Warsaw, collected by Gwidon Jakubowski. The first publications with detailed descriptions and illustrations appeared in the early 2000s. DULAI (2001) described four species from the Szokolya-2 bore-hole drilled at the eastern edge of the Börzsöny Mts, including *Cryptoplax margitae* Dulai, introduced as a new species. Later, a well-preserved and more diverse assemblage of eight species from two sites in the Bakony Mts (Bánd, Devcser) was described on the basis of materials from private collectors (DULAI 2005).

Since then, smaller or larger Polyplacophora materials have been found from various Middle Miocene (Badenian) localities in Hungary, but these have not been published so far. These new collections are now presented in a series of papers. Smaller, low-diversity assemblage has been found from Borsodbóta in the Bükk Mts (SCHWABE & DULAI 2024). More diverse fauna has been discovered from two sites at Várpalota (this paper), and Devcser (DULAI 2025a) in the Bakony Mts and from Letkés in the Börzsöny Mts (DULAI 2025b). In Mecsekpölöske locality (Mecsek Mts) a relatively diverse and well-preserved chiton assemblage with a high number of specimens will be described by DULAI & SZABÓ (in prep.).

## GEOLOGICAL SETTINGS

The epicontinental sea called Paratethys formed in the Early Oligocene and was intermittently connected to the Mediterranean (RÖGL 1998). The diverse marine fauna (e.g., molluscs, echinoids, corals, decapods, bryozoans, brachiopods, foraminifers, ostracods, fishes) of the Central Paratethys refers to a stable connection with the Mediterranean in the Badenian, most probably in the present-day Slovenia (KÓKAY 1985). The Badenian (16.303 to 12.829 Ma) is a regional stage used in the Central Paratethys for part of the Middle Miocene (Langhian to middle Serravallian) (PAPP *et al.* 1978; HOHENEGGER *et al.* 2014).

Várpalota has long been known in the geological and palaeontological literature for its well-preserved and diverse Mollusca fauna. The protected Szabó sand pit is situated at the SW part of Várpalota, near the Rákóczi residential area (Fig. 1). The section consists of several-metre-thick yellow or grey littoral sand (Puszta-miske Formation, SELMECZI *et al.* 2024; Figs 2–5) full of resedimented mollusc shells (lido facies; KÓKAY 2007). Some of the diverse molluscs are well-preserved, sometimes with original colours, while others are highly eroded. More than 400 Mollusca (Gastropoda and Bivalvia) species were identified in several papers and monographs (e.g. STRAUSZ & SZALAI 1943; STRAUSZ 1954; KECSKEMÉTI-KÖRMENDY 1961, 1962a, b; KÓKAY 1988). GÖRÖG & SOMODY (1988) studied the common and diverse trace fossils on gastropod shells. The lower part of the section



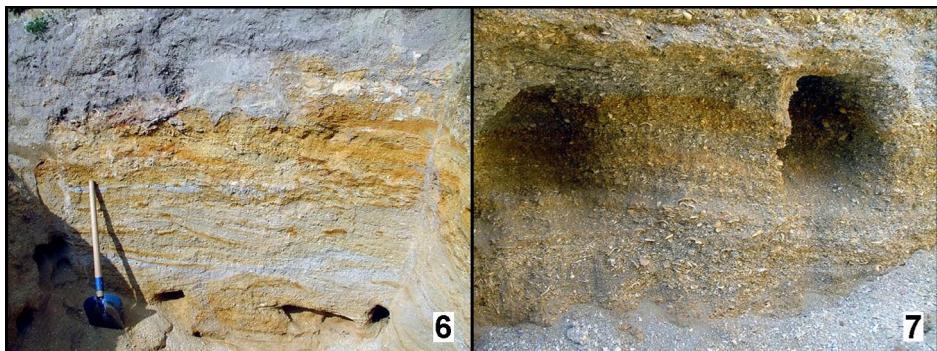
**Fig. 1.** Locality map showing the position of lower Badenian (Middle Miocene) localities in Várpalota. 1 = Faller Street; 2 = Szabó sand pit



**Figs 2–5.** Várpalota, Szabó sand pit locality. – **Fig. 2.** Middle Miocene (lower Badenian) sandy deposits. – **Fig. 3.** Protected section of Pusztamiske Formation (SELMECZI *et al.* 2024). – **Fig. 4.** Cross-bedded sand layers in Szabó sand pit. – **Fig. 5.** Fossil-rich sand layers full of mollusc shells.  
(Photos by Lajos Katona)

contains nearly 100 species of benthic foraminifers and the age of the sand is lower Badenian (upper Lagenidae Zone; KÓKAY 2007). Bryozoa fauna of the sand was investigated by MOISSETTE *et al.* (2006, 2007), and on the basis of 15 identified species they interpreted the locality as shallow-water environment on a terrigenous platform. The sands correspond to a beach environment where skeletal remains from various depth intervals accumulated (MOISSETTE *et al.* 2007). DULAI (2015) mentioned a single brachiopod (*Joania cordata* Rissó) specimen on the basis of a sample in Naturalis Biodiversity Center (Leiden, the Netherlands), collected by Arie W. Janssen in Szabó sand pit in 1979. The same sample contained also some chitons, which are discussed herein. Later fragmentary Discinidae brachiopods were published from the locality by DULAI (2017).

In 2005, a temporary pit was excavated approximately 300 metres southwest of the Szabó sand pit, in Faller Street, where similar fossiliferous sand layers were exposed (Figs 6–7). Three distinct layers could be identified in the section of the pit measuring 4×4 metres and 2.5 metres deep. The bottom layer consisted of 0.5



Figs 6–7. Várpalota, Faller Street locality. – Fig. 6. View of the section in the temporary pit. – Fig. 7. Closer view of lower Badenian sediments containing several mollusc shells. (Photos by Lajos Katona)

metre flat-lying coarse-grained grey sand, which contained almost no mollusc shells. Above this was a 1.5-metre-thick cross-bedded coarse sand layer that contained a significant amount of mollusc shell fragments. This stratigraphic sequence was capped by approximately half a metre of redeposited sediment. From the thin stratigraphic sequence, it was determined that a high-energy environment was overlain by lower-energy cross-bedded sand. Based on the size and orientation of the channels, the transport direction was likely North-Northeast, and the layers may have been deposited in several metres of water depth. We also found bioturbation traces in the cross-bedded sand, indicating that the intensive sedimentation was periodically interrupted by calmer periods. From the medium-grained

cross-bedded sand, 250 species of molluscs were identified, and in addition, a significant amount of vertebrate remains were found, including shark, ray, and other fish teeth, otoliths, and rhinoceros tooth fragments, as well as Polyplacophora skeletal elements (KATONA *et al.* 2011).

The sedimentological and faunal data suggest a sublittoral beach facies. The minimal presence of freshwater and terrestrial species indicates that smaller streams may have flowed into the sea, potentially washing in the specimens. The age of the fauna is late early Badenian (M4b) (KATONA *et al.* 2011).

## MATERIAL AND METHODS

The Polyplacophora material of the Szabó sand pit comes from two museum collections. Generally, poorly-preserved, mostly fragmentary chiton valves were found in the collection of the Department of Palaeontology and Geology of the Hungarian National Museum Collection Centre – Hungarian Natural History Museum, Budapest, where part of the screen-washed residues collected by Anna Kecskeméti-Körmendy in the 1960s are kept. She carried out stratigraphic studies on the basis of the material collected bed-by-bed in the Szabó sand pit (KECSKEMÉTI-KÖRMENDY 1961), and then described the Gastropoda and Bivalvia fauna of the section (KECSKEMÉTI-KÖRMENDY 1962a, b). The following Polyplacophora assemblage was found in a subset of her samples.

Abbreviations used in the text: H = head valve; I = intermediate valve; T = tail valve; fr = fragments; HNHM = Hungarian National Museum Public Collection Centre – Hungarian Natural History Museum, Budapest; NBC = Naturalis Biodiversity Center, Leiden, the Netherlands; BNHM = Hungarian National Museum Public Collection Centre – Bakony Natural History Museum, Zirc.

230–240 cm:

*Ischnochiton rissoi* (Payraudeau, 1826), 1 I (HNHM INV 2024.561);

300–310 cm:

*Ischnochiton rissoi* (Payraudeau, 1826), 1 H (HNHM INV 2024.562; Fig. 11);  
2 I (HNHM INV 2024.563);

*Lepidochiton lepida* (Reuss, 1860), 2 H (HNHM INV 2024.564–565; Fig. 22), 47  
I (HNHM INV 2024.566–570; Fig. 23), 2 T (HNHM INV 2024.571–572; Fig. 24);

*Rhyssoplax corallina* (Risso, 1826), 13 I (HNHM INV 2024.573–575; Figs  
28–29), 1 T (HNHM INV 2024.576);

*Acanthochiton faluniensis* (Rochebrune, 1883), 29 I (HNHM INV 2024.577);

*Acanthochiton oblonga* (Leloup, 1981), 1 H (HNHM INV 2024.578), 5 I  
(HNHM INV 2024.579–582; Figs 39–42);

Polyplacophora indet., 1 H, 36 I, 1 T (HNHM INV 2024.583);

330–340 cm:

- Ischnochiton rissoi* (Payraudeau, 1826), 1 T (HNHM INV 2024.584);  
*Lepidochitona lepida* (Reuss, 1860), 3 I (HNHM INV 2024.585);  
*Acanthochitona faluniensis* (Rochebrune, 1883), 3 I (HNHM INV 2024.586);  
*Acanthochitona oblonga* (Leloup, 1981), 1 I (HNHM INV 2024.587);

430–440 cm:

- Lepidochitona lepida* (Reuss, 1860), 5 I fr. (HNHM INV 2024.588);  
*Rhyssoplax corallina* (Risso, 1826), 1 I (HNHM INV 2024.589);  
*Acanthochitona faluniensis* (Rochebrune, 1883), 1 I (HNHM INV 2024.590);  
*Acanthochitona* sp., 1 I (HNHM INV 2024.591);

670–680 cm:

- Lepidochitona lepida* (Reuss, 1860), 1 I (HNHM INV 2024.592).

Some chiton valves were also found in the Várpalota 1 and 3 samples collected for bryozoan studies by DULAI *et al.* (2010) and stored in HNHM:

- Rhyssoplax corallina* (Risso, 1826), 1 I (HNHM INV 2024.593);  
*Acanthochitona faluniensis* (Rochebrune, 1883), 2 H (HNHM INV 2024.594), 2 I (HNHM INV 2024.595);  
*Acanthochitona oblonga* (Leloup, 1981), 1 H (HNHM INV 2024.596).

Limited chiton material from the Szabó sand pit was found in the collection of the Naturalis Biodiversity Centre in Leiden (the Netherlands). Here, on the basis of a collection by Arie W. Janssen (15 October 1979), some Polyplacophora valves from this locality were found, in addition to the very rare Brachiopoda remains (DULAI 2015).

- Lepidochitona lepida* (Reuss, 1860), 9 I (NBC RGM.793895);  
*Lepidochitona lepida* (Reuss, 1860), 2 I (NBC RGM.793893; Figs 25–26);  
*Ischnochiton rissoi* (Payraudeau, 1826), 1 H (Fig. 10), 3 I (Fig. 12) (NBC RGM.793900–793902);  
*Rhyssoplax corallina* (Risso, 1826), 2 I (NBC RGM.793894);  
*Acanthochitona faluniensis* (Rochebrune, 1883), 4 H, 36 I, 2 T (NBC RGM.793896–793899).

The majority of the Polyplacophora material from the Várpalota, Faller Street site is in the Bakony Natural History Museum, Zirc, while a smaller part is in the private collection of Tibor Berta (Veszprém). Two specimens repre-

senting rare species from this locality are deposited in the collection of the Hungarian National Museum Collection Centre – Hungarian Natural History Museum, Budapest.

Bakony Natural History Museum, Zirc:

*Ischnochiton rissoi* (Payraudeau, 1826), 4 I, 5 T (Figs 13–18), (BNHM 2025.2.1);

*Lepidochitona lepida* (Reuss, 1860), 3 H (Figs 19–21), 16 I (BNHM 2025.2.2);

*Rhyssoplax corallina* (Risso, 1826), 1 H, 4 I (BNHM 2025.2.3);

*Acanthochitona faluniensis* (Rochebrune, 1883), 7 H (Fig. 30), 102 I (Figs 32–33), 9 T (Figs 36–38) (BNHM 2025.2.4);

*Acanthochitona oblonga* (Leloup, 1981), 4 I (BNHM 2025.2.5);

Polyplacophora indet., 1 H, 12 I, 2 T (BNHM 2025.2.6).

Tibor Berta private collection:

*Lepidochitona lepida* (Reuss, 1860), 1 I;

*Rhyssoplax corallina* (Risso, 1826), 1 I (Fig. 27);

*Acanthochitona faluniensis* (Rochebrune, 1883), 1 H (Fig. 31); 16 I (Figs 34–35);

*Acanthochitona oblonga* (Leloup, 1981), 1 I;

Polyplacophora indet., 7 I, 1 T.

Hungarian National Museum Public Collection Centre – Hungarian Natural History Museum, Budapest:

*Parachiton africanus* (Nierstrasz, 1906), 1 T (HNHM INV 2024.597; Figs 8–9);

*Cryptoplax weinlandi* Šulc, 1934, 1 T (HNHM INV 2024.598; Figs 43–45).

## SYSTEMATIC PALAEONTOLOGY

Class Polyplacophora Gray, 1821

Subclass Neoloricata Bergenhayn, 1955

Order Lepidopleurida Thiele, 1909

Family Leptochitonidae Dall, 1889

Genus *Parachiton* Thiele, 1909

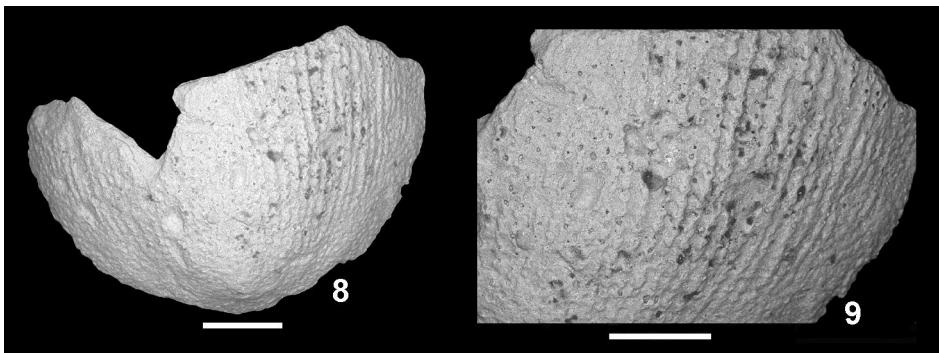
*Parachiton africanus* (Nierstrasz, 1906)  
(Figs 8–9)

1999 *Lepidopleurus (Parachiton) africanus* Nierstrasz, 1906 – DELL’ANGELO & SMRIGLIO, pp. 80–84, pl. 23–24, figs 30–33. (cum syn.)

2015 *Parachiton africanus* (Nierstrasz, 1906) – RUMAN & HUDÁČKOVÁ, p. 158, fig. 2.1. (cum syn.)

**Material – Faller Street (HNHM, 1 T).**

**Remarks** – The only available fragmentary tail valve is semi-oval in outline, but the anterior end is missing (Fig. 8); if reconstructed the potential original length of the valve, the length of the valve can reach or even exceed the width. The lateral area is slightly prominent, with some short concentric growth lines. Rounded mucro strongly shifted almost to the posterior margin. The surface of the antemucronal area is ornamented with longitudinally arranged rows of granules; the granules fuse in the longitudinal direction and thus form a continuous rib-like ornamentation, while laterally the knots are separated from each other (Fig. 9).



Figs 8–9. *Parachiton africanus* (Nierstrasz, 1906). Fragmentary tail valve, Faller Street, HNHM INV 2024.597. – Fig. 8. Dorsal view. – Fig. 9. Enlarged part of the shell ornamentation. Scale bars: 8: 0.5 mm; 9: 0.4 mm

This form was previously identified as *Lepidopleurus thielei* Šulc in the Central Paratethys (ŠULC 1934; BAŁUK 1971). *Lepidopleurus africanus* Nierstrasz was rediscovered by KAAS (1977) and later LAGHI *et al.* (1980) confirmed the presence of this species in the present-day Mediterranean and considered the Paratethyan Miocene species, *thielei* to be conspecific with the recent taxon. This synonymy was later also accepted by researchers of the Central Paratethyan chitons (BAŁUK 1984; RUMAN & HUDÁČKOVÁ 2015).

The species *africanus* was initially assigned to the genus *Lepidopleurus* and later to the genus *Leptochiton*, often using the subgenus *Parachiton* Thiele within both genera. IREDALE (1914) raised the subgenus *Parachiton* to generic rank, but this was followed mainly by New Zealand and Australian workers only. Our current genus conception is based on SAITO (1996). *Parachiton* can be distinguished from *Lepidopleurus* on the basis of the large tail valve and the posteriorly displaced mucro besides morphological differences of the radulae. Currently, 22 recent *Parachiton* species are distinguished, of which *P. africanus* is the only species from the

Mediterranean, all others are known from the Indo-Pacific region (DELL'ANGELO *et al.* 2015).

*Habitat* – This species is considered to be a typical member of the bicoenoses of coastal detritus and marl (25–150 m, high organogenic content, strong bottom currents) (DELL'ANGELO & SMRIGLIO 1999).

*Distribution within the Central Paratethys* – This species is one of the rarer polyplacophorans of the Central Paratethys (Austria: ŠULC 1934; Poland: BAŁUK 1971; Slovakia: RUMAN & HUDÁČKOVÁ 2015). The tail valve from Várpalota is the first record of *P. africanus* from the Hungarian Miocene. In addition to the Central Paratethys, fossil representatives of the species have been found in the Plio-Pleistocene sediments of Italy (LAGHI *et al.* 1980; DELL'ANGELO & SMRIGLIO 1999).

Order Chitonida Thiele, 1909  
Suborder Chitonina Thiele, 1909  
Superfamily Chitonoidea Rafinesque, 1815  
Family Ischnochitonidae Dall, 1889  
Subfamily Ischnochitoninae Dall, 1889  
Genus *Ischnochiton* Gray, 1847

*Ischnochiton rissoi* (Payraudeau, 1826)  
(Figs 10–18)

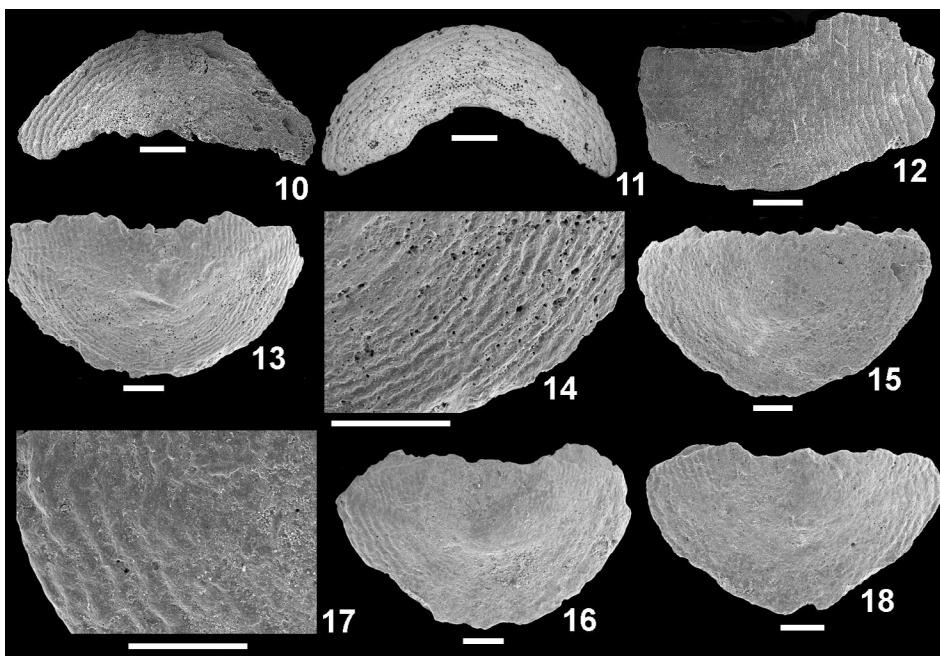
1999 *Ischnochiton (Ischnochiton) rissoi* (Payraudeau, 1826) – DELL'ANGELO & SMRIGLIO, pp. 100–105, pl. 29–31, figs 40–48. (cum syn.)

2005 *Ischnochiton rissoi* (Payraudeau, 1826) – DULAI, pp. 33–36, pl. 3, figs 1–5. (cum syn.)

*Material* – Szabó sand pit: HNHM: 300–310 cm (1 H, 2 I); 330–340 cm (1 T); NBC (1 H, 3 I); Faller Street: BNHM (4 I, 5 T).

*Remarks* – A Polyplacophora species occurring in both Várpalota localities. Head (Figs 10–11), intermediate (Fig. 12) and tail valves (Figs 13–18) are equally known. Although most of the valves are fragmentary, they are consistent with the illustrations in the literature. Fossils of the genus *Ischnochiton* Gray are common in the Badenian Polyplacophora assemblages of the Central Paratethys and mostly representatives of the species *I. rissoi* were found. ŠULC (1934) described the species *I. rudolticensis* from the Vienna Basin, and BAŁUK (1971) considered it to be an ancestral form of *I. rissoi*. However, it was later identified by LAGHI (1977) as a junior synonym of the species *rissoi*, which was accepted by subsequent authors.

The other *Ischnochiton* species of the Central Paratethys is *I. korytnicensis* Bałuk, described from the Miocene of Poland, which differs in its surface orna-



Figs 10–18. *Ischnochiton rissoei* (Payraudeau, 1826). – Fig. 10. Head valve, Szabó sand pit, NBC RGM.793900. – Fig. 11. Head valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.562. – Fig. 12. Fragmentary intermediate valve, Szabó sand pit, NBC RGM.793901. – Figs 13–14. Tail valve, Faller Street, BNHM. – Fig. 13. Dorsal view. – Fig. 14. Enlarged part of the shell surface to show details of the ornamentation. – Fig. 15. Tail valve, Faller Street, BNHM. – Figs 16–17. Tail valve, Faller Street, BNHM. – Fig. 16. Dorsal view. – Fig. 17. Enlarged part of the shell ornamentation. – Fig. 18. Tail valve, Faller Street, BNHM. Scale bars: 0.5 mm

mentation (radial ribs instead of concentric wrinkles; see e.g. in DELL'ANGELO *et al.* 1999). The material of *I. rudolticensis* described by BAŁUK (1965) from Niskowa, was assigned to *I. rissoei* by DULAI (2005) with a question mark, but those specimens most probably belong to *I. korytnicensis*.

*Habitat* – *I. rissoei* adheres to stones and dead shells in very shallow water (1–5 m; rarely down to 100 m) (DELL'ANGELO & SMRIGLIO 1999). Locally it can be very common under stones on clean sandy bottoms (POPPE & GOTO 1991).

*Distribution within the Central Paratethys* – Widespread in the Badenian sediments of the Central Paratethys: Austria (KROH 2002, 2003); Czech Republic (ŠULC 1934); Hungary (DULAI 2005, 2025a, b; this paper); Poland (BAŁUK 1971, 1984); Romania (DELL'ANGELO *et al.* 2007); Ukraine (STUDENCKA & DULAI 2010). It is also well-known from the Mediterranean (Miocene, Pliocene, Pleistocene, Recent; see e.g. DELL'ANGELO *et al.* 2021).

## Subfamily Lepidochitoninae Iredale, 1914

Genus *Lepidochitona* Gray, 1821*Lepidochitona lepida* (Reuss, 1860)

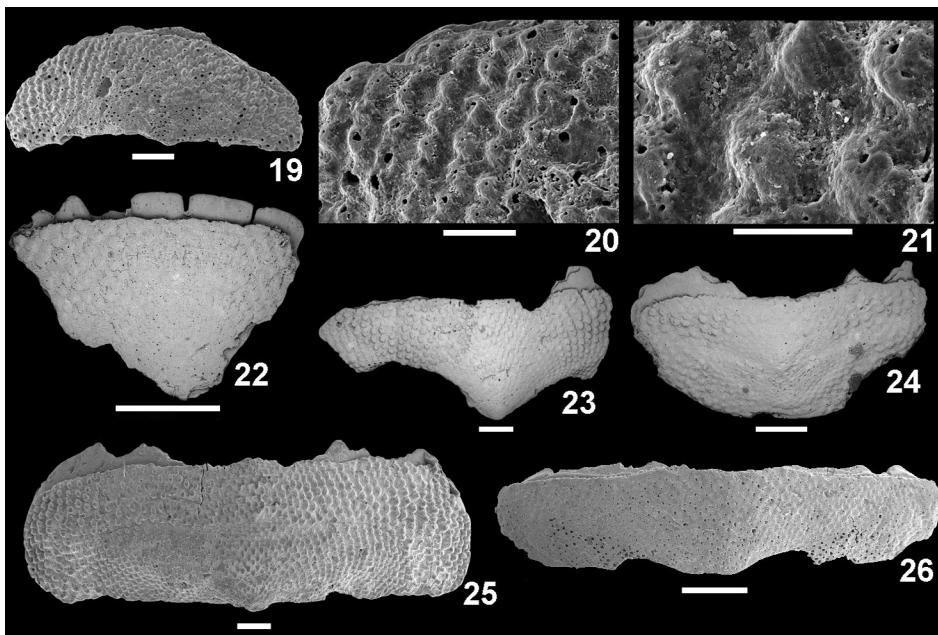
(Figs 19–26)

2010 *Lepidochitona lepida* (Reuss, 1860) – STUDENCKA & DULAI, pp. 267–268, text-fig. 6A–B. (cum syn.)2015 *Lepidochitona lepida* (Reuss, 1860) – RUMAN & HUDÁČKOVÁ, p. 164, fig. 5.6. (cum syn.)

**Material – Szabó sand pit:** HNHM: 300–310 cm (1 H, 46 I, 2 T), 330–340 cm (3 I), 430–440 cm (5 I), 670–680 cm (1 I); NBC (11 I); **Faller Street:** BNHM (3 H, 16 I), Berta Collection (1 I).

**Remarks –** *Lepidochitona* Gray valves are the second most common Polyplacophora remains from the Várpalota sites. They are represented mainly by intermediate valves, but some head and tail valves also occur. The entire surface of the tegmentum is ornamented with fine rounded granules, the central and lateral areas are not separated. The posterior margin of the head valve is almost straight (Fig. 19) and the granules are arranged in obliquely running rows (Figs 19–20). The radial ridges mentioned by BAŁUK (1971, pl. 4, fig. 6) are not observed on the head valves of Várpalota. Some of the intermediate valves have a broad, angular outline, with rounded lateral margins and not very prominent apexes (Figs 25–26). These are similar to the Ukrainian material of STUDENCKA & DULAI (2010, text-fig. 6A) (but the shells from Várpalota are broader), or to the Korytnica specimens of BAŁUK (1971, pl. 4, fig. 10 and 1984, pl. 7, fig. 2). The fragmentary apophysis of the specimen shown in Fig. 25 is also very similar to the asymmetrically subtriangular shape of the Ukrainian valve. However, less broad intermediate valves with a prominent large apex (Fig. 23) also occur at Várpalota, which resemble the Vienna Basin material presented by ŠULC (1934, fig. 14). The tail valves of Várpalota (Fig. 24) also show a good correspondence with ŠULC (1934, fig. 15)'s material. Due to the highly eroded surface of the specimens, only the larger macroaesthetes are usually visible on the granules, the number and arrangement of the smaller microaesthetes being not visible (Fig. 21), which does not facilitate a clear species classification of these specimens.

The Polish authors (JAKUBOWSKI & MUSIAŁ 1977; STUDENCKA & STUDENCKI 1988) mentioned the species *L. subgranosa* without illustration from the Szabó sand pit. The species *subgranosa* was described from Korytnica by BAŁUK (1971), and was also mentioned later by Polish authors (BAŁUK 1984; STUDENCKA & STUDENCKI 1988). According to KAAS (1977), the species *subgranosa* is conspecific with *L. cinerea*, but according to BAŁUK (1984), the species described by him is more similar to *L. canariensis* (Thiele) among the recent forms. DELL'ANGELO *et*



Figs 19–26. *Lepidochitona lepida* (Reuss, 1860). – Figs 19–21. Head valve, Faller Street, BNHM. – Fig. 19. Dorsal view. – Fig. 20. Enlarged part of the surface ornamentation. – Fig. 21. Enlarged part of the surface ornamentation. – Fig. 22. Head valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.564. – Fig. 23. Intermediate valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.566. – Fig. 24. Tail valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.571. – Fig. 25. Intermediate valve, Szabó sand pit, NBC RGM.793893. – Fig. 26. Intermediate valve, Szabó sand pit, NBC RGM.793893. Scale bars: 19, 22–26: 0.5 mm; 20: 0.2 mm; 21: 0.1 mm

al. (2004) also suggest a probable identity to the species *canariensis*. The numerous *Lepidochitona* species described from the Central Paratethys would require a more thorough revision, but unfortunately the poorly preserved, highly eroded material from the Várpalota sites is not suitable for this. For this reason, the specimens found here are for the time being assigned to the most widespread and commonly used *Lepidochitona* species of the Central Paratethys.

**Habitat** – *L. lepida* is an extinct, mainly Central Paratethyan species. Among the closely related recent species, *L. cinerea* prefers areas free of currents up to 10 m depth in the lower mesolittoral and infralittoral zone (DELL'ANGELO & SMRIGLIO 1999). *L. canariensis* is typical of the intertidal zone (DELL'ANGELO & SMRIGLIO 1999).

**Distribution within the Central Paratethys** – This species is known mainly from the Middle Miocene of the Central Paratethys: Czech Republic (REUSS 1860; ŠULC 1934); Hungary (CSEPREGHY-MEZNERICS 1950; DULAI 2001, 2025a; this

paper); Poland (BAŁUK 1965, 1971, 1984; MACIOSZCZYK 1988; STUDENCKA & STUDENCKI 1988); Romania (ŠULC 1934); Slovakia (RUMAN & HUDÁČKOVÁ 2015); Ukraine (STUDENCKA & DULAI 2010). It was also recorded in the Mediterranean, from Northern Italy (SACCO 1897, as *Lepidopleurus* cf. *marginatus* Pennant).

Family Chitonidae Rafinesque, 1815  
Subfamily Chitoninae Rafinesque, 1815  
Genus *Rhyssoplax* Thiele, 1893

*Rhyssoplax corallina* (Risso, 1826)  
(Figs 27–29)

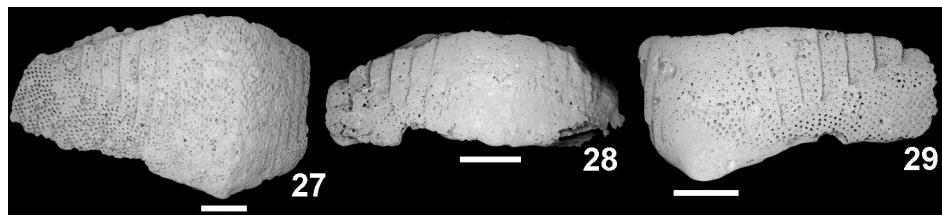
1999 *Chiton (Rhyssoplax) corallinus* (Risso, 1826) – DELL’ANGELO & SMRIGLIO, pp. 174–178, pls 58–59, figs 97–107. (cum syn.)

2015 *Chiton corallinus* (Risso, 1826) – RUMAN & HUDÁČKOVÁ, pp. 160–162, figs 3.7, 4.1. (cum syn.)

**Material – Szabó sand pit:** HNHM: 300–310 cm (12 I, 1 T), 430–440 cm (1 I), NBC (2 I); **Faller Street:** BNHM (1 H, 4 I), Berta Collection (1 I).

**Remarks** – From both localities at Várpalota, *Rhyssoplax* Thiele is known mainly for intermediate valves (Figs 27–29), with head and tail valves being rare. The lateral areas of the intermediate valve are clearly visible with a smooth surface, making them distinguishable from the species *R. olivacea* (Spengler). On average, 7 grooves are observed in the pleural area of the intermediate valve, all of which run to the anterior border, which distinguishes it from the species *phaseolinus*, which is also about half the size of *corallina* (DELL’ANGELO & SMRIGLIO 1999). In some earlier literature, this species was described from the Central Paratethys as *C. denudatus* Reuss (REUSS 1860; ROCHEBRUNE 1883; PROCHÁZKA 1895; BAŁUK 1971).

**Habitat** – Recent *R. corallina* is considered an eurybathial species between 0 and over 100 metres depth and often recorded from coralligenous bottoms (DELL’ANGELO & SMRIGLIO 1999).



**Figs 27–29.** *Rhyssoplax corallina* (Risso, 1826). – Fig. 27. Intermediate valve, Faller Street, Berta Collection. – Fig. 28. Intermediate valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.573. – Fig. 29.

Intermediate valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.574. Scale bars: 0.5 mm

*Distribution within the Central Paratethys* – One of the most common chiton species in the Middle Miocene of the Central Paratethys (several records from Austria, Czech Republic, Hungary, Poland, Romania, Slovakia, Ukraine; see details in DELL'ANGELO *et al.* 2007; RUMAN & HUDÁČKOVÁ 2015; and SCHWABE & DULAI 2024).

Suborder Acanthochitonina Bergenhayn, 1930

Family Acanthochitonidae Pilsbry, 1893

Subfamily Acanthochitoninae Pilsbry, 1893

Genus *Acanthochitona* Gray, 1821

*Acanthochitona faluniensis* (Rochebrune, 1883)

(Figs 30–38)

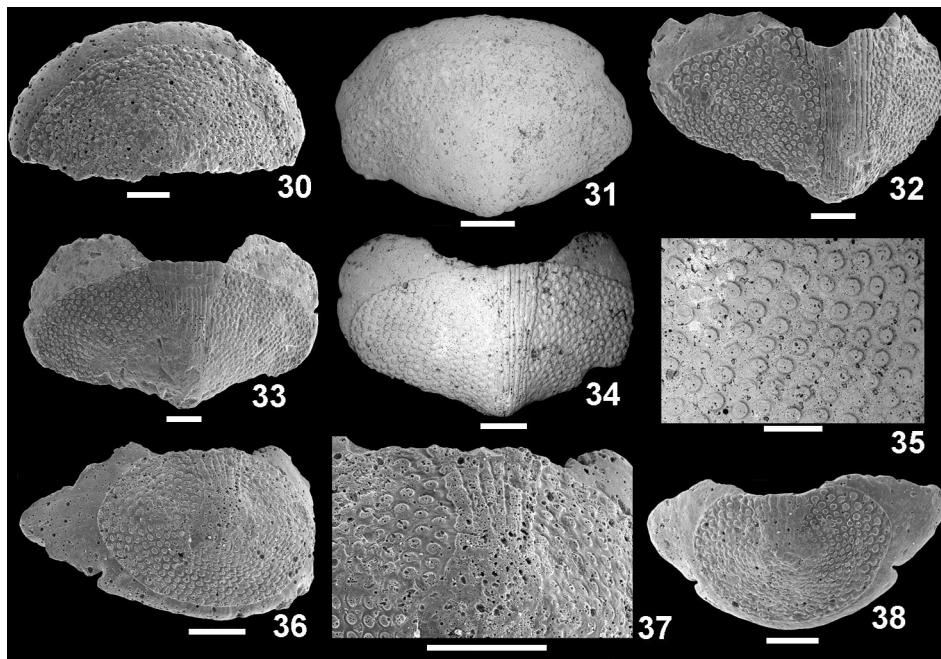
2005 *Acanthochitona faluniensis* (Rochebrune, 1883) – DULAI, pp. 39–40, pl. IV, figs 5–10, pl. V, figs 1–4. (cum syn.)

2015 *Acanthochitona faluniensis* (Rochebrune, 1883) – RUMAN & HUDÁČKOVÁ, pp. 164–165, figs 4.5.–4.10. (cum syn.)

*Material* – Szabó sand pit: HNHM: 300–310 cm (22 I), 330–340 cm (3 I), 430–440 cm (1 I), NBC (4 H, 36 I, 9 T); Faller Street: BNHM (7 H, 102 I, 9 T), Berta Collection (1 H, 16 I).

*Remarks* – It is unambiguously the most common Polyplacophora species of the Middle Miocene sites of Várpalota, half of the valves found belong to this species. In the earlier literature, two Polish papers (JAKUBOWSKI & MUSIAŁ 1977; STUDENCKA & STUDENCKI 1988) also mentioned this species in the material collected by Gwidon Jakubowski. *A. faluniensis* is among the dominant faunal elements not only in the Várpalota sites, but also in the Middle Miocene chiton assemblages of the Central Paratethys in general. Accordingly, descriptions and illustrations are abundant in the literature.

The species is controversial, as some authors consider the species *faluniensis* to be synonymous with the recent *A. communis* Risso or the conspecific *A. fascicularis* Linnaeus (e.g. LAGHI 1977; DELL'ANGELO & SMRIGLIO 1999; DELL'ANGELO *et al.* 2007), while researchers working in the Central Paratethyan area have so far uniformly made a stand for the validity of the species *faluniensis*. Comparisons of the mentioned two species have been discussed in detail by BAŁUK (1984), DULAI (2005), and STUDENCKA & DULAI (2010), among others. An additional distinguishing character is mentioned by SCHMIDT-PETERSEN *et al.* (2015), who diagnosed that the granules of *fascicularis* are small, rounded in outline, densely packed, and have an incision on their sides (l.c. fig. 6). In reviewing both the



Figs 30–38. *Acanthochitona faluniensis* (Rochebrune, 1883). – Fig. 30. Head valve, Faller Street, BNHM. – Fig. 31. Strongly eroded head valve, Faller Street, Berta Collection. – Fig. 32. Intermediate valve, Faller Street, BNHM. – Fig. 33. Intermediate valve, Faller Street, BNHM. – Figs 34–35. Intermediate valve, Faller Street, Berta Collection. – Fig. 34. Dorsal view. – Fig. 35. Enlarged detail of surface ornamentation. – Figs 36–37. Tail valve, Faller Street, BNHM. – Fig. 36. Dorsal view. – Fig. 37. Enlarged detail of surface ornamentation around the mucro. – Fig. 38. Tail valve, Faller Street, BNHM. Scale bars: 30–34, 36–38: 0.5 mm, 35: 0.2 mm

studied specimens from Várpalota and the *faluniensis* illustrations in the literature (e.g. BAŁUK 1984: pl. 8, figs 1b, 5; DULAI 2001: pl. II, figs 2–3; KROH 2003: fig. 7; DULAI 2005: pl. 4, figs 6, 9; STUDENCKA & DULAI 2010: text-fig. 7B, D; RUMAN & HUDÁČKOVÁ 2015: figs 4.10a, b) we found no evidence of such incisions on the sides of the granules. This confirms that the Central Paratethyan *A. faluniensis* species is not conspecific with the Mediterranean *A. fascicularis*.

*Habitat* – *A. faluniensis* is an extinct species, while the closely related *A. fascicularis* occurs in shallow-water environments, often on the lower surface of algae-covered rocks. DELL'ANGELO & SMRIGLIO (1999) mentioned depths down to 73 m.

*Distribution within the Central Paratethys* – One of the most common Polyplacophora species in the Middle Miocene sediments of the Central Paratethys (for more details on the localities see RUMAN & HUDÁČKOVÁ 2015): Austria (ŠULC

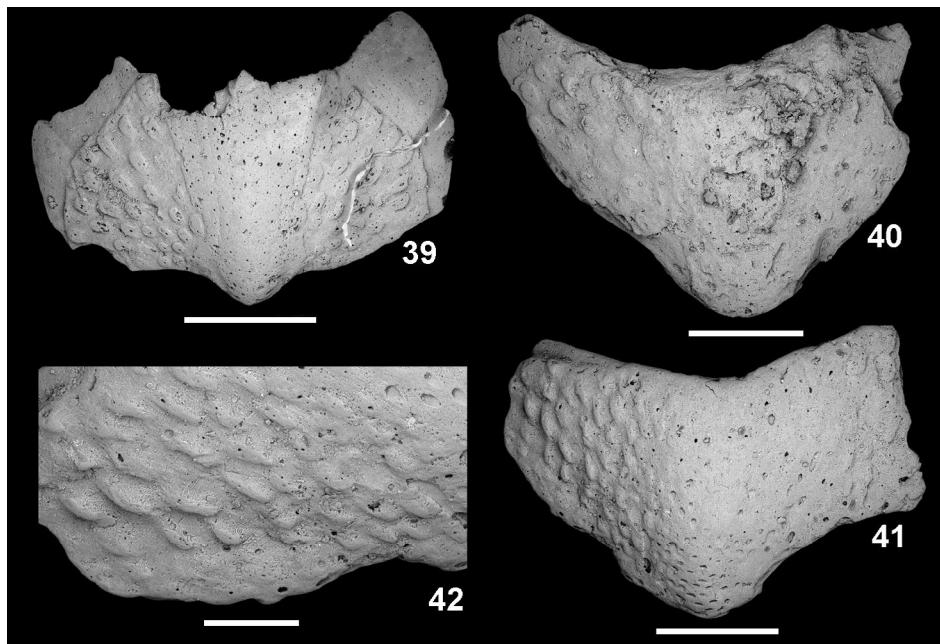
1934; KROH 2003); Czech Republic (ŠULC 1934; KROH 2002, 2003; ZÁGORŠEK 2006); Hungary (JAKUBOWSKI & MUSIAŁ 1977; STUDENCKA & STUDENCKI 1988; DULAI 2001, 2005, 2025a, b; this paper; DULAI & SZABÓ in prep.); Poland (BAŁUK 1971, 1984; JAKUBOWSKI & MUSIAŁ 1977, 1979; MACIOSZCZYK 1988; STUDENCKA & STUDENCKI 1988); Romania (ZILCH 1934; STANCU & ANDREESCU 1968; RADO 1969, 1971; RADO & MUȚIU 1970; DELL'ANGELO *et al.* 2007); Slovakia (TOMAŠOVÝCH 1998; RUMAN & HUDÁČKOVÁ 2015); Ukraine (STUDENCKA & DULAI 2010).

*Acanthochitona oblonga* (Leloup, 1981)  
(Figs 39–42)

- 1981 *Acanthochiton oblongus* sp. nov. – LELOUP, p. 1, figs 1a–d, pl. 1.  
1983 *Acanthochitona oblonga* Leloup, 1981 – DELL'ANGELO & CUPPINI, pp. 77–78, textfig. (without number).  
1985 *Acanthochitona crinita* (Pennant) – KAAS, p. 596, figs 39–43.  
1992 *Acanthochitona crinita* f. *oblonga* Leloup – BASCHIERI *et al.*, p. 68, fig. 4.  
1994 *Acanthochitona crinita* f. *oblonga* Leloup – BASCHIERI, p. 40, fig. 2.  
1995 *Acanthochitona crinita* f. *oblonga* Leloup – DELL'ANGELO & FORLI, p. 237, fig. 6.  
2011 *Acanthochitona oblonga* (Leloup, 1981) – BONFITTO *et al.*, p. 174, text-figs 3, 4C, 6C.  
2013 *Acanthochitona oblonga* (Leloup) – DELL'ANGELO *et al.*, p. 97, pl. 10, figs N–Q. (cum syn.)  
2016 *Acanthochitona oblonga* (Leloup, 1981) – DELL'ANGELO *et al.*, p. 89, pl. 6, figs. 3–4.  
2019 *Acanthochitona oblonga* Leloup, 1981 – AMATI & OLIVERIO, pp. 142–143, figs 2B, 3.

**Material – Szabó sand pit:** HNHM: 300–310 cm (5 I), 330–340 cm (1 I);  
**Faller Street:** BNHM (4 I), Berta Collection (1 I).

**Remarks** – The species *Acanthochiton oblongus* was described by LELOUP (1981) from the Gulf of Salina, Malta, on the basis of the very highly elongated and sharp-edged granules ornamenting the tegmentum. It was later recovered from some other sites in the Mediterranean, but because of the transitional characters of the ornamentation, it was considered by several authors as a subspecies of *crinita* (Pennant) (BASCHIERI 1994; DELL'ANGELO & FORLI 1995) or as a junior synonym of *crinita* (KAAS 1985; DELL'ANGELO & SMRIGLIO 1999; DELL'ANGELO & ZAVODNIK 2004). According to KAAS (1985), it is only a local form of *crinita*, characterized by highly elongated granules. Later, however, it was found in many other parts of the Mediterranean outside Malta, so it was by no means a local form. BONFITTO *et al.* (2011) confirmed the validity of the species *oblonga* based on morphological and molecular studies. Subsequently, several recent occurrences were published, mainly from waters around Italy (see e.g. AMATI & OLIVERIO 2019, fig. 3). SCHMIDT-PETERSEN *et al.* (2015) described a new species of *Acanthochitona* (*A. pilosa*) from the Mediterranean Sea, and provided useful descriptions and illustrations for the separation of *A. oblonga*. According to their identification key, the granules in *A. fascicularis* are small, densely spaced and round in outline with a



Figs 39–42. *Acanthochitona oblonga* (Leloup, 1981). – Fig. 39. Intermediate valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.579. – Fig. 40. Intermediate valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.580. – Figs 41–42. Intermediate valve, Szabó sand pit, 300–310 cm, HNHM INV 2024.581. – Fig. 41. Dorsal view. – Fig. 42. Enlarged detail of surface ornamentation. Scale bars: 39–41: 0.5 mm, 42: 0.2 mm

lateral incision, whereas in the other three species (*oblonga*, *pilosa*, *crinita*) they are oval or drop-shaped. In the latter three species, *A. oblonga* can be clearly distinguished by the length of the granules being 3–5 times their width, whereas in the other two species the difference is only 1–2 times. On the basis of this definition, the studied specimens from Várpalota, despite their highly eroded surface, can be well classified as *A. oblonga* (Figs 39–42).

In addition to the increasing number of recent Mediterranean occurrences, some fossil *A. oblonga* records have also been described in Italy: from Late Miocene Tortonian strata (DELL'ANGELO *et al.* 2016), from the Ligurian Pliocene (DELL'ANGELO *et al.* 2013) and from the Pleistocene of Riparbella (DELL'ANGELO & FORLI 1995). The Várpalota occurrence is the first fossil record outside the Mediterranean. For this reason, unlike the other species described in this paper, a detailed synonymy list is given here.

The closely related species, *A. crinita* (under this name) has not yet been mentioned from the Central Paratethys area, but similar forms have been represented under various names. BAŁUK (1971) described the species *A. lacrimulifera* from

Korytnica, which is characterized by an elongated, raindrop-like ornamentation. This was later considered by LAGHI (1977) to be conspecific with the recent species *A. fascicularis*. Laghi's statement was accepted by BAŁUK (1984), who described the newly found specimens from Korytnica as *A. fascicularis*. The same species name was applied by STUDENCKA & STUDENCKI (1988), referring to the work of BAŁUK (1984). Later, however, Dell'Angelo considered the fossil occurrences in Poland as representatives of *crinita* (e.g. DELL'ANGELO *et al.* 2004). The interpretation of *A. lacrimulifera* will be discussed in the following parts of this article series on the basis of the new materials from the Devecser (DULAI 2025a), Letkés (DULAI 2025b), and Mecsekpölöske (DULAI & SZABÓ in prep.) sites.

*Habitat* – Low-oxygen microhabitats under stones or in clefts with a larger depth range (SCHMIDT-PETERSEN *et al.* 2015).

*Distribution within the Central Paratethys* – It is the first record of this species from the Central Paratethys. It is currently found in the Mediterranean Sea (Malta, Italy), and its fossil records are also known from Italy (Late Miocene – Pleistocene; DELL'ANGELO & FORLI 1995; DELL'ANGELO *et al.* 2013, 2016).

#### *Acanthochitona* sp.

*Material – Szabó sand pit:* HNHM: 430–440 cm (1 I).

*Remarks* – The ornamentation of an *Acanthochitona* intermediate valve differs from both species described from Várpalota above, as the granules are not elongated as in *oblonga* and are less sparsely spaced and larger than in *faluniensis*. The single poorly preserved specimen does not allow a more precise identification, but a similar form also occurs in the recently collected Badenian material from Mecsekpölöske, which will be discussed later (DULAI & SZABÓ in prep.).

Family Cryptoplacidae H. et A. Adams, 1858

Genus *Cryptoplax* De Blainville, 1818

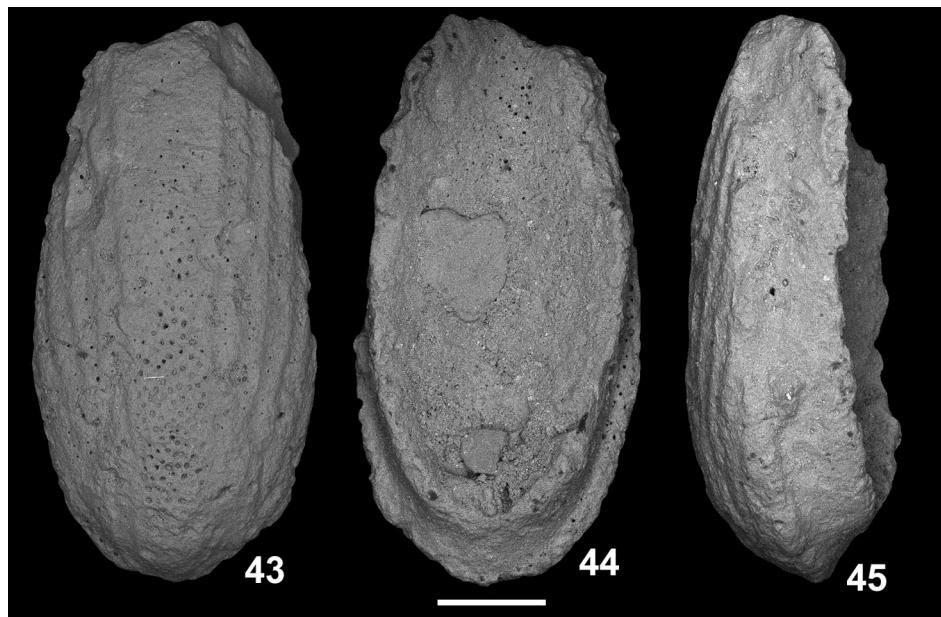
#### *Cryptoplax weinlandi* Šulc, 1934 (Figs 43–45)

2007 *Cryptoplax weinlandi* Šulc, 1934 – DELL'ANGELO *et al.*, pp. 45–47, figs 2, 3, 5. (cum syn.)

2015 *Cryptoplax weinlandi* Šulc, 1934 – RUMAN & HUDÁČKOVÁ, pp. 165–166, Fig. 5.5. (cum syn.)

*Material – Faller Street:* HNHM (1T).

*Remarks* – Although *C. weinlandi* Šulc is a common chiton species in many sites of the Central Paratethys and Hungary, until now only one tail valve has been found at Várpalota in the temporary excavation of Faller Street. It is likely



Figs 43–45. *Cryptoplax weinlandi* Šulc, 1934. Fragmentary tail valve, Faller Street, HNMH INV 2024.598. – Fig. 43. Dorsal view. – Fig. 44. Ventral view. – Fig. 45. Lateral view. Scale bar: 0.5 mm

that the highly mobile sandy beach environment was not very favourable for *Cryptoplax*. This species is described and analysed in detail in DULAI (2005) and DELL'ANGELO *et al.* (2007). The only other *Cryptoplax* species of the Central Paratethys, *C. margitae* Dulai, can be distinguished by its granular ridges. It is less common than *C. weinlandi*, but occurs in some Hungarian sites (Szokolya, Bánd, Mecsekpolöske).

*Habitat* – *C. weinlandi* Šulc is an extinct species, the living representatives of the genus occur in temperate and tropical areas of the Indo-Pacific and the Red Sea (GOWLETT-HOLMES 1998). The southern Australian *C. striata* Lamarck is an opportunistic grazing omnivore (KANGAS & SHEPHERD 1984).

*Distribution within the Central Paratethys* – The extinct *C. weinlandi* Šulc was one of the most common Middle Miocene Polyplacophora species in the Central Paratethys: Austria (KARRER 1877; ŠULC 1934; ZILCH 1934; SIEBER 1956; KROH 2002, 2003); Czech Republic (ŠULC 1934; ZILCH 1934; ZÁGORŠEK 2006); Hungary (DULAI 2001, 2005, 2025a, b; this paper; DULAI & SZABÓ in prep.); Poland (BAŁUK 1971, 1984); Romania (ŠULC 1934; ZILCH 1934; MARINESCU *et al.* 1962; MARINESCU 1964; RADO 1969, 1971; RADO & MUȚIU 1970; FLOREI 1978 (as *C. teinlandi*); STUDENCKA & STUDENCKI 1988; DELL'ANGELO *et al.* 2007); Slovakia (HYŽNÝ *et al.* 2012; RUMAN & HUDÁČKOVÁ 2015).

## CONCLUSIONS

So far, very little information is available on the Middle Miocene Polyplacophora fauna of Várpalota, but two species have been mentioned by Polish authors (JAKUBOWSKI & MUSIAŁ 1977 and STUDENCKA & STUDENCKI 1988) based on material from an occasional collection. In this paper, we describe the chiton fauna of two lower Badenian sites (the famous Szabó sand pit and a temporary trench at Faller Street) in Várpalota, based on material from four different sources (three museum collections and one private collection). A total of 221 (HNHM: 162, NBC: 59) Polyplacophora valves from the Szabó sand pit and 200 (BNHM: 170, Berta Collection: 28, HNHM: 2) from Faller Street were identified.

Based on more than 400 valves available, we were able to separate eight Polyplacophora species. More than half (50.8%) of the valves belonged to the species *Acanthochitona faluniensis*, while the second most common group included the remains of *Lepidochitona* (21.5%). (It is no coincidence that these two taxa were mentioned by Polish researchers in the collection of the Muzeum Ziemi in Warsaw). Among the less common and actually surprising species, *Acanthochitona oblonga* is the only one with a marked occurrence (2.6%). Three taxa (*Parachiton africanus*, *Acanthochitona* sp., and *Cryptoplax weinlandi*) were found in only 1–1 specimen (0.2–0.2%), which motivates the authors to further investigations. It is worth highlighting that the number of indeterminable Polyplacophora specimens (14.7%) is extremely high due to the highly eroded and poorly preserved valves.

More than half of the identified species are well known from other Middle Miocene sites of the Central Paratethys, and are common species elsewhere (*A. faluniensis*, *L. lepida*, *R. corallina*, *I. rissoii*, *C. weinlandi*). However, the surprisingly high proportion of species found for the first time (three of the eight taxa identified) represents a new element for the Hungarian Miocene fauna, or even for the entire Central Paratethys. *Acanthochitona oblonga* had been for a long time of uncertain status in the Recent Mediterranean fauna, but its presence has now become certain. Until now, it was known in the fossil record only from the Mediterranean region of Italy, making the occurrence in Várpalota the first Central Paratethyan and the first record from outside the Mediterranean. *Parachiton africanus* is a rare chiton species in the Central Paratethys, and this is its first known record from Hungary. The undetermined *Acanthochitona* valve differs from both identified species, but the single eroded valve did not allow a more precise identification. It may be a step forward that valves of similar appearance also occur in the material from Mecsekpölöske, which will be processed later (DULAI & SZABÓ in prep.).

The ecological requirements of the species found are very varied, with shallow sea-dwelling forms (*rissoii*, *faluniensis*) and eurybath forms (*corallina*), as well

as forms living on coastal detritus, coralligenous substrate or possibly algae-covered rocks. This confirms the reconstructions of the palaeoenvironment established for the Várpalota site on the basis of other groups of fossil remains (e.g. Mollusca, Bryozoa): near-shore, shallow-water sandy beach faunas, where remains of specimens originally living at different depths were accumulated by strong water movement (KÓKAY 2007; MOISSETTE *et al.* 2007).

Although we have significantly increased our knowledge of the Middle Miocene Polyplacophora fauna of Várpalota compared to previous data, we do not consider the work on this topic to be complete. Only a small part of the Kecske-méti-Körmenty screen-washed samples in the HNHM collection have been checked for chiton valves. On the other hand, although only a temporary trench was excavated in Faller Street in 2005, the limited quantity of screen-washed samples examined from there also yielded one-one valve each of two species not previously known from Hungary. For this reason, we plan to collect further samples in Faller Street in the future, if possible.

\*

*Acknowledgements* – The scanning electron microscope photos were taken partly at the Hungarian Natural History Museum, Budapest, partly at the Department of Materials Engineering at the University of Pannonia, Veszprém, and partly at the Plant Protection Institute of the HUN-REN Centre for Agricultural Research; Martonvásár. We thank Adrienn Fitos-Boros, Márton Szabó and Barna Pál-Gergely for their contribution to the preparation of the SEM photos. Constructive review by Enrico Schwabe (Munich) helped to improve the manuscript. The authors are grateful to Tibor Berta for offering his chiton material to study and publish.

## REFERENCES

- AMATI B. & OLIVERIO M. 2019: First record of *Acanthochitona pilosa* Schmidt-Petersen, Schwabe & Haszprunar, 2015 (Mollusca, Polyplacophora) in Spain and Algeria. – *Bollettino Malacologico* **55**: 140–144.
- BAŁUK W. 1965: Chiton z piasków tortonskich kotliny Sadeckiej. (Chitons from the Tortonian of the Nowy Sącz Depression, Poland.) – *Acta Palaeontologica Polonica* **10**(3): 365–378.
- BAŁUK W. 1971: Lower Tortonian chitons from the Korytnica clays, southern slopes of the Holy Cross Mts. – *Acta Geologica Polonica* **21**(3): 449–472.
- BAŁUK W. 1984: Additional data on chitons and cuttlefish from the Korytnica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). – *Acta Geologica Polonica* **34**(3–4): 281–297.
- BASCHIERI L. 1994: Un’insolita concentrazione di due specie di Poliplacofori. – *La Conchiglia* **26**(270): 40–42.
- BASCHIERI L., DELL’ANGELO B. & PALAZZI S. 1992: Recenti ritrovamenti di Polyplacophora anomali nel Mediterraneo. – *Bollettino Malacologico* **28**(1–4): 65–68.
- BONFITTO A., DELL’ANGELO B., EVANGELISTI F. & SABELLI B. 2011: The genus *Acanthochitona* (Mollusca: Polyplacophora) in the Mediterranean Sea: morphological and molecular data. – *Scientia Marina* **75**(1): 171–180. <https://doi.org/10.3989/scimar.2011.75n1171>

- CSEPREGHY-MEZNERICS I. 1950: A Hidas (Baranya M.) tortonai fauna. (Die tortonische Fauna von Hidas, Kom. Baranya, Ungarn). – *Annales Instituti Geologici Publici Hungarici* **39**(2): 1–106.
- DELL'ANGELO B. & CUPPINI S. 1983: Prima segnalazione di *Acanthochitona oblonga* Leloup, 1981 lungo le coste Italiane. – *Bollettino Malacologico* **19**(1–4): 77–78.
- DELL'ANGELO B. & FORLI M. 1995: I Polyplacophora del Pleistocene inferiore di Riparbella (Pisa), con elenco dei molluschi rinvenuti. – *Bollettino Malacologico* **30**(1994): 221–252.
- DELL'ANGELO B., GIUNTELLI P., SOSSO M. & ZUNINO M. 2015: Polyplacophora from the Miocene of North Italy. Part 1: Leptochitonidae, Hanleyidae, Ischnochitonidae and Callistoplacidae. – *Rivista Italiana di Paleontologia e Stratigrafia* **121**(2): 217–242. <https://doi.org/10.13130/2039-4942/6514>
- DELL'ANGELO B., GIUNTELLI P., SOSSO M. & ZUNINO M. 2016: Polyplacophora from the Miocene of North Italy. Part 2: Callochitonidae, Chitonidae, Lepidochitonidae, Acanthochitonidae and Cryptoplacidae. – *Rivista Italiana di Paleontologia e Stratigrafia* **122**(3): 71–102. <https://doi.org/10.13130/2039-4942/7699>
- DELL'ANGELO B., GRIGIS M. & BONFITTO A. 2007: Notes on fossil chitons. 2. Polyplacophora from the Middle Miocene of Lăpușiu (Romania). – *Bollettino Malacologico* **43**: 39–50.
- DELL'ANGELO B., LANDAU B. & MARQUET R. 2004: Polyplacophora from the Early Pliocene of Estepona (Málaga, southwest Spain). – *Bollettino Malacologico Supplemento* **5**: 25–44.
- DELL'ANGELO B., PALAZZI S. & PAVIA G. 1999: I Molluschi del Messiniano Inferiore di Borelli (Torino). 4. Polyplacophora. – *Bollettino del Museo Regionale di Scienze Naturali - Torino* **16**(1–2): 257–302.
- DELL'ANGELO B. & SMRIGLIO C. 1999: *Chitoni viventi del Mediterraneo*. – Edizioni Evolver, Roma, 256 pp.
- DELL'ANGELO B., SOSSO M., PRUDENZA M. & BONFITTO A. 2013: Notes on Fossil Chitons. 5. Polyplacophora from the Pliocene of Western Liguria, Northwest Italy. – *Rivista Italiana di Paleontologia e Stratigrafia* **119**: 65–107. <https://doi.org/10.13130/2039-4942/6025>
- DELL'ANGELO B., SOSSO M. & TAVANO M.L. 2021: Chitons (Mollusca, Polyplacophora) from the Lower Pliocene of Borzoli (Genova). – *Annali del Museo Civico di Storia Naturale „G. Doria”* **114**: 403–449.
- DELL'ANGELO B. & ZAVODNIK D. 2004: Marine fauna of the Mljet National Park (Adriatic Sea, Croatia). 4. Mollusca: Polyplacophora. – *Natura Croatica* **13**(4): 319–341.
- DULAI A. 2001: Middle Miocene (Badenian) Polyplacophora (Mollusca) remains from borehole Szokolya-2 (Börzsöny Mts, Hungary, Central Paratethys). – *Fragmента Palaeontologica Hungarica* **19**: 39–49.
- DULAI A. 2005: Badenian (Middle Miocene) Polyplacophora from the Central Paratethys (Bárd and Devecser, Bakony Mountains, Hungary). – *Fragm. Palaeontologica Hungarica* **23**: 29–50.
- DULAI A. 2015: Central Paratethyan Middle Miocene brachiopods from Poland, Hungary and Romania in the Naturalis Biodiversity Center (Leiden, the Netherlands). – *Scripta Geologica* **149**: 185–211.
- DULAI A. 2017: First record of Discinidae brachiopods from the Miocene of Hungary. – *Fragm. Palaeontologica Hungarica* **34**: 63–74. <https://doi.org/10.17111/FragmPalHung.2017.34.63>
- DULAI A. 2025a: Middle Miocene (Badenian) chitons (Mollusca, Polyplacophora) from the Central Paratethys 3: additional data from Devecser (Bakony Mts, Hungary). – *Fragm. Palaeontologica Hungarica* **40**: in press.
- DULAI A. 2025b: Middle Miocene (Badenian) chitons (Mollusca, Polyplacophora) from the Central Paratethys 4: Letkés (Börzsöny Mts, Hungary). – *Fragm. Palaeontologica Hungarica* **40**: in press.
- DULAI A., MOISSETTE P. & MÜLLER P.M. 2010: Badenian (Middle Miocene) bryozoan fauna of Hungary: basic data of localities and samples. – *Fragm. Palaeontologica Hungarica* **28**: 33–69.

- DULAI A. & SZABÓ M. in prep.: Middle Miocene (Badenian) chitons (Mollusca, Polyplacophora) from the Central Paratethys 5: Mecsek-pölöske (Mecsek Mts, Hungary).
- FLOREI N. 1978: Asupra minutinelor badeniene de la Delineşti (Banat). – *Studia Universitatis Babeş-Bolyai, Seria Geologia* 23(1): 21–23.
- GOWLETT-HOLMES K.L. 1998: Family Cryptoplacidae. – In: BEESLEY P.L., ROSS G.J.B. & WELLS A. (eds): *Mollusca – The Southern Synthesys*. Part A, Fauna of Australia Volume 5: 189. – CISRO, Melbourne.
- GÖRÖG Á. & SOMODY Á. 1988: Trace fossils on Badenian (Miocene) gastropods from Várpalota, Hungary. – *Annales Universitatis Scientiarum Budapestinensis de Rolando Eötvös Nominatae, Sectio Geologica* 28: 121–160.
- HOHNEGGER J., ČORIĆ S. & WAGREICH M. 2014: Timing of the Middle Miocene Badenian Stage of the Central Paratethys. – *Geologica Carpathica* 65(1): 55–66. <https://doi.org/10.2478/geoca-2014-0004>
- HYŽNÝ M., HUDÁČKOVÁ N., BISKUPIČ R., RYBÁR S., FUJKI T., HALÁSOVÁ E., ZÁGORŠEK K., JAMRICH M. & LEDVÁK P. 2012: Devínska Kobyla – a window into the Middle Miocene shallow-water marine environments of the Central Paratethys (Vienna Basin, Slovakia). – *Acta Geologica Slovaca* 4(2): 95–111.
- IREDALE T. 1914: The chiton fauna of the Kermadec Islands. – *Proceedings of the Malacological Society of London* 11(1): 25–51. <https://doi.org/10.1093/oxfordjournals.mollus.a063530>
- JAKUBOWSKI G. & MUSIAŁ T. 1977: Lithology and fauna from the Upper Tortonian sands of Monastyrz and Długi Goraj (Southern Roztocze, Poland). – *Prace Muzeum Ziemi* 26: 63–126.
- JAKUBOWSKI G. & MUSIAŁ T. 1979: Lithology and fauna of the Middle Miocene deposits of Trzęsiny (Roztocze Tomaszowskie Region, South-eastern Poland). – *Prace Muzeum Ziemi* 32: 37–70.
- KAAS P. 1977: Notes on Loricata, 9. On the rediscovery of *Lepidopleurus africanus* Nierstrasz, 1906 and the systematic position of the taxon *Parachiton* Thiele, 1909. – *Basteria* 41: 81–86.
- KAAS P. 1985: The genus *Acanthochitona* Gray, 1821 (Mollusca, Polyplacophora) in the north-eastern Atlantic Ocean and in the Mediterranean Sea, with designation of neotypes of *A. fascicularis* (L., 1767) and of *A. crinita* (Pennant, 1777). – *Bulletin du Museum National d'Histoire Naturelle* (4)7(A3): 579–609. <https://doi.org/10.5962/p.285863>
- KANGAS M. & SHEPHERD S.A. 1984: Distribution and feeding of chitons in a boulder habitat at West Island, South Australia. – *Journal of the Malacological Society of Australia* 6: 101–111. <https://doi.org/10.1080/00852988.1984.10673963>
- KARRER F. 1877: Geologie der Kaiser Franz Josefs Hochquellen-Wasserleitung. Eine Studie in den Tertiär-Bildungen am Westrande des Alpinen Theiles der Niederung von Wien. – *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 9: xiii, 420 pp.
- KATONA L.T., KÓKAY J. & BERTA T. 2011: A várpalotai Faller utcai badeni korú üledék molluszka faunája. (Badenian mollusc fauna from Várpalota (Faller Street)). – *Földtani Közlöny* 141(1): 3–22.
- KECSKEMÉTI-KÖRMENDY A. 1961: A várpalotai természetvédelmi terület homokréteg-összletének finomrétegtani vizsgálta. (Feinstratigraphische Untersuchungen im Naturschutz-Gebiet von Várpalota.) – *Földtani Közlöny* 91(4): 426–431. (in Hungarian with German abstract)
- KECSKEMÉTI-KÖRMENDY A. 1962a: Új Molluszka-fajok a várpalotai középsőmiocénből I. Gastropoda. (Neue Molluskenarten aus dem Mittelmiozän von Várpalota. I. Gastropoden.) – *Földtani Közlöny* 92(1): 81–99. (in Hungarian with German abstract)
- KECSKEMÉTI-KÖRMENDY A. 1962b: Új Molluszka fajok a várpalotai középsőmiocénből II. Lamelli-branchiata. (Neue Molluskenarten aus dem Mittelmiozän von Várpalota. II. Lamellibranchiata.) – *Földtani Közlöny* 92(2): 217–229. (in Hungarian with German abstract)
- KÓKAY J. 1985: Central and Eastern Paratethyan interrelations in the light of Late Badenian salinity conditions. – *Geologica Hungarica, Series Palaeontologica* 48: 9–95.

- KÓKAY J. 1988: *Várpalota, Szabó-féle homokbánya*. [Várpalota, Szabó sandpit.] – Magyarország geológiai alapszelvényei, Magyar Állami Földtani Intézet, Budapest, 6 pp.
- KÓKAY J. 2007: Várpalota, Szabó-féle homokbánya. Miocén (badeni), Pusztamiske Formáció. [Várpalota, Szabó sand pit. Miocene (Badenian), Pusztamiske Formation.] – In: PÁLFY J. & PAZONYI P. (eds): *Őslénytani kirándulások Magyarországon és Erdélyben*. Hantken Kiadó, Budapest, pp. 81–82. (in Hungarian)
- KROH A. 2002: Die Polyplacophoren des Badenium (Mittel-Miozän) von Gainfarn, Niederösterreich. – *Berichte des Institutes für Geologie und Paläontologie der Karl-Franzens-Universität Graz* 5: 10–11.
- KROH A. 2003: The Polyplacophora (Mollusca) of the Langhian (Lower Badenian) of the Molasse Zone and the Northern Vienna Basin (Austria). – *Annalen des Naturhistorischen Museums in Wien* 104A: 129–143.
- LAGHI G.F. 1977: Polyplacophora (Mollusca) neogenici dell’Appennino settentrionale. – *Bollettino della Società Paleontologica Italiana* 16(1): 87–115, pls 1–4.
- LAGHI G.F., RUSSO F. & DELL’ANGELO B. 1980: Recenti ritrovamenti di *Lepidopleurus (Parachiton) africanus* Nierstrasz, 1906 (Polyplacophora, Mollusca). – *Atti della Società dei Naturalisti e matematici di Modena* 111: 1–7.
- LELOUP E. 1981: *Acanthochiton oblongus* sp. nov. – *Bulletin Institut Royale des sciences Naturelles de Belgique* 53(5): 1–3.
- MACIOSZCZYK W. 1988: Polyplacophora from the Badenian deposits of Węglinek, Węglin and Łychów (Western Rostocze – Poland). – *Prace Muzeum Ziemi* 40: 47–58.
- MARINESCU J. 1964: Reprezentati ai clasei Amphineura in Miocenul din Oltenia. – *Dări de Seamă ale Ședințelor* 50(1): 179–185.
- MARINESCU J., HÎNCULOV L. & TURCULEȚ L. 1962: Contribuționi la studiul faunei tortoniene din vestul Olteniei. – *Dări de Seamă ale Ședințelor* 47(1): 73–85.
- MOISSETTE P., DULAI A., ESCARGUEL G., KÁZMÉR M., MÜLLER P. & SAINT MARTIN J.-P. 2007: Mosaic of environments recorded by bryozoan faunas from the Middle Miocene of Hungary. – *Palaeogeography, Palaeoclimatology, Palaeoecology* 252(3–4): 530–556. <https://doi.org/10.1016/j.palaeo.2007.05.010>
- MOISSETTE P., DULAI A. & MÜLLER P. 2006: Bryozoan faunas in the Middle Miocene of Hungary: biodiversity and biogeography. – *Palaeogeography, Palaeoclimatology, Palaeoecology* 233: 300–314. <https://doi.org/10.1016/j.palaeo.2005.10.001>
- PAPP A., CICHA I., SENEŠ J. & STEININGER F.F. (eds) 1978: *M4 Badenien (Moravien, Wielicien, Kosovien). Chronostratigraphie und Neostratotypen, Miozän der Zentralen Paratethys*. – Verlag der Slowakischen Akademie der Wissenschaft, Bratislava, 594 pp.
- POPPE G.T. & GOTO Y. 1991: *European Seashells. Volume 1 (Polyplacophora, Caudofoveata, Solenogastra, Gastropoda)*. – Wiesbaden, Christa Hemmen Verlag, 340 pp.
- PROCHÁZKA V.J. 1895: Miocean východočeský. – *Archiv pro přírodověcké prozkoumání Čech* 10(2): 1–149.
- RADO G. 1969: Grupe noi de organisme în fauna Tortoniană de la Buituri (Amfineure și Pești). – *Studii și cercetări de geologie, geofizică, geografie, Seria geologie* 14(1): 189–204.
- RADO G. 1971: Asupra faunei miocene din bazinul Beiuș (Badenian). – *Analele Universității București, Geologie* 20: 171–184, pls 1–5.
- RADO G. & MUȚIU R. 1970: Studiul faunei Tortoniene din Forajele de la Islaz. – *Analele Universității București, Geologie* 19: 141–171.
- REUSS A.E. 1860: Die marinen Tertiärschichten Böhmens und ihre Versteinerungen. – *Sitzungsberichte der Mathematischen-Naturwissenschaften Classe der Kaiserlichen Akademie der Wissenschaften* 34: 207–285.

- ROCHEBRUNE A.T. 1883: Monographie des espèces fossiles appartenant à la classe des Polyplaxiphores. – *Annales des Sciences Géologiques* **14**(1): 1–74, pls 1–3.
- RÖGL F. 1998: Palaeogeographic considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). – *Annalen des Naturhistorischen Museums in Wien* **99**: 279–310.
- RUMAN A. & HUDÁČKOVÁ N.H. 2015: Middle Miocene chitons (Polyplacophora) from the Slovak part of the Vienna Basin and the Danube Basin (Central Paratethys). – *Acta Geologica Slovaca* **7**(2): 155–173.
- SACCO F. 1897: *I Molluschi dei terreni terziarii del Piemonte e della Liguria* **22**: 1–130. <https://doi.org/10.5962/bhl.title.12269>
- SAITO H. 1996: Seven new species of the genus *Parachiton* (Polyplacophora: Leptochitonidae) from the northwest Pacific. – *Venus* **55**(3): 161–187. [https://doi.org/10.18941/venusjjm.55.3\\_161](https://doi.org/10.18941/venusjjm.55.3_161)
- SCHMIDT-PETERSEN J., SCHWABE E. & HASZPRUNAR G. 2015: *Acanthochitona pilosa* spec. nov., a new species of *Acanthochitona* Gray, 1821 from the Mediterranean (Mollusca, Polyplacophora). – *Spixiana* **38**(1): 11–20.
- SCHWABE E. 2000: *Chiton lepidus* Reuss, 1860 (currently *Lepidochitona lepida*; Mollusca, Polyplacophora): proposed conservation of the specific name. – *Bulletin of Zoological Nomenclature* **57**: 204–209. <https://doi.org/10.5962/bhl.part.20726>
- SCHWABE E. & DULAI A. 2024: Middle Miocene (Badenian) chitons (Mollusca, Polyplacophora) from the Central Paratethys 2: Borsodbóta (Bükk Mts, Hungary). – *Fragmata Palaeontologica Hungarica* **39**: 55–68. <https://doi.org/10.17111/FragmPalHung.2024.39.55>
- SELMECZI I., FODOR L., LUKÁCS R., SZEPESI J., SÉBE K., PRAKFALVI P. & SZTANÓ O. 2024: Lower and Middle Miocene. – In: BABINSZKI E., PIROS O., CSILLAG G., FODOR L., GYALOG L., KERCSMÁR Zs., LESS Gy., LUKÁCS R., SÉBE K., SELMECZI I., SZEPESI J. & SZTANÓ O. (eds): *Lithostratigraphic units of Hungary II. Cenozoic formations*, SARA Budapest, pp. 52–115.
- SIEBER R. 1956: Die Tortonfauna von Mattersburg und Forchtenau (Burgenland). – *Verhandlungen der Geologischen Bundesanstalt* **1956**(3): 236–249.
- STANCU I. & ANDREESCU E. 1968: Fauna Tortoniană din regiunea Rugi-Delinești (Bazinul Caransebeșului). – *Studii și cercetări de geologie, geofizică, geografie, Seria geologie* **13**(2): 455–471.
- STRAUSZ L. 1954: Várpalotai felső-mediterrán csigák. (Les Gastropodes du Méditerranéen supérieur (tortonien) de Várpalota.) – *Geologica Hungarica, Series Palaeontologica* **25**: 1–150.
- STRAUSZ L. & SZALAI T. 1943: Várpalotai felső-mediterrán kagylók. [Upper Mediterranean bivalves of Várpalota.] – *A Magyar Királyi Földtani Intézet Évi Jelentése függelékei, Beszámoló a Magyar Királyi Földtani Intézet Vitaüléseinek munkálatairól*, **5**(3): 112–153. (in Hungarian)
- STUDENCKA B. & DULAI A. 2010: Chitons (Mollusca: Polyplacophora) from the Middle Miocene sandy facies of Ukraine, Central Paratethys. – *Acta Geologica Polonica* **60**: 257–274.
- STUDENCKA B. & STUDENCKI W. 1988: Polyplacophora from the Badenian (Middle Miocene) marine sandy facies of the Holy Cross Mts (Central Poland). – *Prace Muzeum Ziemi* **40**: 37–46.
- ŠULC J. 1934: Studie über die fossilen Chitonen – I. Die fossilen Chitonen im Neogen des Wiener Beckens und der angrenzenden Gebiete. – *Annalen des Naturhistorischen Museums in Wien* **47**: 1–31.
- TOMAŠOVÝCH A. 1998: Bádenské mäkkýse z tehelne Devinská Nová Ves (Bratislava, Slovensko). – *Mineralia Slovaca* **30**: 357–386.
- ZÁGORŠEK K. 2006: The Polyplacophora (Mollusca) of the Badenian from the Moravian part of the Carpathian Foredeep (Czech Republic). – *Scripta Journal of the Faculty of Science, Masaryk University, Brno, Geology* **33–34**: 96–98.
- ZILCH A. 1934: Zur Fauna des Mittel-Miozäns von Kostej (Banat). – Typus-Bestimmung und Tafeln zu O. Boettger's Bearbeitungen. – *Senckenbergiana* **16**: 193–302.



*Eocene wildlife of the Carpathian Basin*  
edited by Alfréd Dulai

Available in our webshop:

<https://commerce.nhmus.hu/productdisplay/eocén-élővilág-kárpát-medencében>