Polyplacophora from the Eocene of Gánt, Hungary

BRUNO DELL'ANGELO, MAURIZIO SOSSO, ANDREAS KROH & ALFRÉD DULAI

The only species of Polyplacophora known from the Eocene of Gánt is *Tonicia pannonica*. Re-examination of the type material of this species indicates that the two syntypes of Szőts belong to two different species. One of those syntypes (the tail valve) is designated as lectotype herein, in order to provide stability to nomenclature by preserving the generic attribution of the species *pannonica* to the genus *Tonicia.* New samples were collected near the type locality, and the nearly 200 valves recovered belong to four species: *Tonicia pannonica*, *Lepidochitona gantensis* sp. nov., *L. szoetsi* sp. nov., and *L. viciani* sp. nov. The paralectotype of *Tonicia pannonica*, an intermediate valve, is here excluded from that species and attributed to *Lepidochitona szoetsi* sp. nov. • Key words: Mollusca, Polyplacophora, systematics, Eocene, Hungary, Gánt.

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Bruno Dell'Angelo, Museo di Zoologia, Via Selmi 3, 40126 Bologna, Italy; bruno.dellangelo@chitons.it • Maurizio Sosso, Via Bengasi 4, 16153 Genova, Italy; sosmauri@gmail.com • Andreas Kroh (corresponding author), Natural History Museum Vienna, Burgring 7, 1010 Wien, Austria; andreas.kroh@nhm-wien.ac.at • Alfréd Dulai, Hungarian Natural History Museum, Department of Palaeontology and Geology, P.O.B. 137, 1431 Budapest, Hungary; dulai@nhmus.hu

In comparison to their Neogene record Palaeogene chitons (Mollusca: Polyplacophora) are poorly known. Only 79 Palaeogene species were reported in a comprehensive review by Dell'Angelo *et al.* (2011). Since then Cabrera & Olivero (2011) and Dell'Angelo *et al.* (2012) each described rare unnamed chiton species from the Eocene of Antarctica and Italy respectively. The large majority of Palaeogene chiton records are from the Eocene of Europe, particularly from Germany, France, the United Kingdom and the Ukraine (reflecting centres of mollusc research rather than chiton palaeobiodiversity hotspots). Oligocene records even are less prevalent, followed by very scare Paleocene examples (Dell'Angelo *et al.* 2011, Appendix 2). Non-European chitons from Palaeogene strata are restricted to few scattered records from the United States, Australia and New Zealand. Moreover, most Palaeogene chiton species are known from single outcrops only, making biogeographic inference impossible. It is clear, however, that this is due to sampling bias rather than to true absence in the fossil record, as exemplified by the study of Dell'Angelo *et al.* (2011) and the present one. Chiton remains are often overlooked by collectors and researchers (Puchalsky *et al.* 2008) due to their resemblance to fragments of other molluscs and, often, small size.

Similarly to the global situation, chitons from the Hungarian Palaeogene Basin are poorly documented, too. The only reports are *Tonicia pannonica* Szőts, 1953 from the Eocene of Gánt and Neszmély (Szőts 1953, Strausz 1974), and *Chiton bernayi* Cossmann, 1888 from the Eocene of Mány (Kecskeméti-Körmendy 1990), which is based on a single head valve that until now could not be located in the collections of the Hungarian Geological and Geophysical Institute (Budapest, Hungary).

The original description of *T. pannonica* is based on two valves, a tail valve and an intermediate valve. Re-examination of the type material (deposited in the Hungarian Geological and Geophysical Institute; inventory number: E.1.) revealed that these two valves are not conspecific, but instead belong to two different species of different generic affinity. Consequently the description and diagnosis of *Tonicia pannonica* needs to be emended. New material collected from the same stratigraphic level near the type locality includes a large number of chiton valves. Based on these new specimens it is possible, for the first time, to characterize the morphology of the head and intermediate valves of this species. In addition, the material revealed the presence of three additional chiton species in Gánt and offers new insights on the chiton fauna from the Eocene of Hungary.

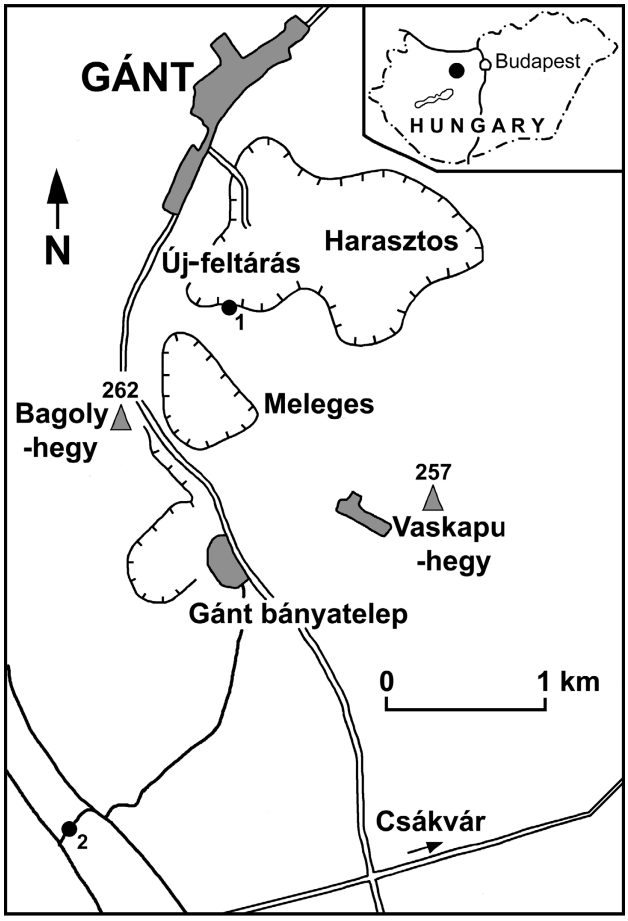

Figure 1. Location map. 1 – Szőts's locality (Új-feltárás = new exposure in Szőts 1953); 2 – Vicián's locality at the vineries around Gánt (2010–2013).

Methods

The present work is based mainly on bulk samples collected by a friend of the authors (Zoltán Vicián, Budapest) between 2010 and 2013. The sediment has been processed by wet-sieving (sieve mesh width 0.5, 1.0, and 2.0 mm). Chiton valves were picked from the 0.5, 1.0 and 2.0 mm fractions using a stereomicroscope. Additional specimens were donated by Helmut Krock (Lüneburg, Germany). SEM-work was carried out at the Natural History Museum Vienna using the JEOL 6400 and 6610LV scanning electron microscopes of the Central Research Laboratories.

Geological setting

The Vértes Hills belong to the NE part of the Transdanubian Range in Hungary. The mass of the Vértes comprises Middle and Upper Triassic dolomite and limestone overlain by Jurassic, Lower Cretaceous, Eocene and Upper Miocene formations with smaller spatial extent and thickness (Budai *et al*. 2008). The SW-NE oriented Gánt Depression is situated inside the Vértes Hills and is part of the Hungarian Palaeogene Basin. The Eocene deposits at Gánt are best exposed in an abandoned open-cast bauxite mine (Fig. 1), where transgressive neritic sediments overly the terrestrial bauxite deposits. The lowermost part of the section is built up of lacustrine and terrestrial deposits overlain by oscillatory succession, which were deposited in a variably restricted brackish-water or marine lagoonal environment (late Lutetian–early Bartonian Forna Formation; Budai *et al*. 2008). The overlying Kincses Formation with very variable lithology accumulated in a shallow-marine lagoon, most probably in the Bartonian. Its lower part contains the so-called "brown molluscan clay", which crops out also at vineries around Gánt (Szőts 1953, Budai *et al*. 2008). These beds are highly fossiliferous and have yielded the rich mollusc fauna monographed by Szőts (1953). Among the other fossil groups the abundant ostracods (Monostori 1977), the charophytes and palynomorphs (Bignot *et al*. 1985), the foraminifers (Halupka 1999) and the fishes (Nolf & Reichenbacher 1999) were studied in detail. The palaeoecological characters of the locality were discussed by Strausz (1962), Mihály (1975) and Mihály & Vincze (1984) (mainly on the basis of the mollusc fauna). Based on the large benthic foraminifers, molluscs, palynomorphs and ostracods this section was attributed to the Middle Eocene. In absence of planktonic fossils, a more precise age is impossible to identify, however, on the basis of lithological analogies with NE Bakony and SW Vértes sections and boreholes, the most probable age of this series is late Lutetian to early Bartonian (Kollányi *et al*. 2003, Budai *et al*. 2008). A detailed description of the Gánt section can be found in Bignot *et al*. (1985, fig. 2). Szőts (1953) outcrop (Loc. 1 in Fig. 1; 47° 22.56´ N, 18° 23.18´ E), is inaccessible today, but new samples could be collected from coeval strata to the south of the bauxite mines (Loc. 2 in Fig. 1; 47° 20.80´ N, 18° 22.60´ E).

Abbreviations. – BD – B. Dell'Angelo Collection, Genova, Italy (will be deposited in MZB); HNHM – Hungarian Natural History Museum, Budapest, Hungary; HGGI – Hungarian Geological and Geophysical Institute, Budapest, Hungary; MNHN – Muséum national d'Histoire naturelle, Paris, France; MZB – Zoological Museum of Bologna University, Bologna, Italy; NHMW – Natural History Museum Wien, Austria; ZISP – Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

Systematic palaeontology

We follow the systematic classification proposed by Sirenko (2006).

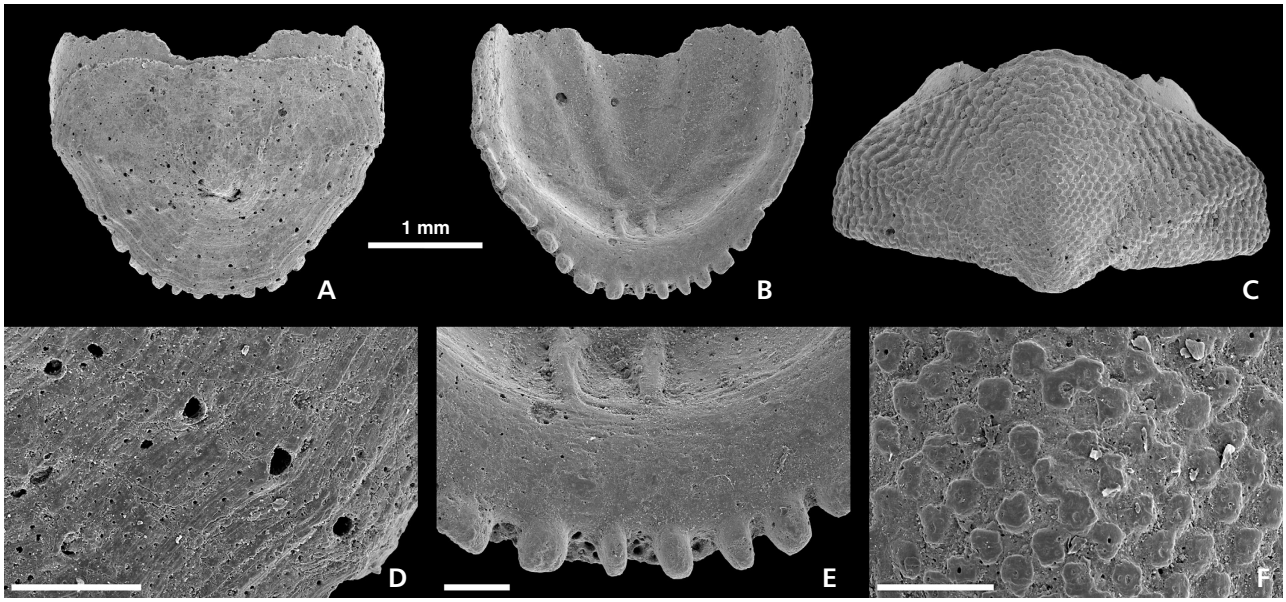

Figure 2. Type material of *Tonicia pannonica* Szőts, 1953 from the Middle Eocene Kincses Formation of Gánt, Hungary. • A, B, D, E – lectotype (tail valve, HGGI E.1a; A – dorsal view, B – ventral view; D – detail of ocelli pores; E – detail of marginal teeth); C, F – paralectotype (intermediate valve, HGGI E.1b; C – dorsal view; F – detail of median area sculpture), here excluded from *T. pannonica* and identified as *Lepidochitona szoetsi* sp. nov. (holotype). Scale bars for D–F equal 200 µm.

Class Polyplacophora Gray, 1821
Subclass Loricata Shumacher, 1817
Order Chitonida Thiele, 1909
Suborder Chitonina Thiele, 1909
Family Chitonidae Rafinesque, 1815
Subfamily Toniciinae Pilsbry, 1893

Genus *Tonicia* Gray, 1847
The genus is known from the Eocene to the Recent.

***Tonicia pannonica* Szőts, 1953**
Figures 2A, B, D, E, 3A–J, 4A–F

p.p. 1953 *Tonicia pannonica* nov. sp.; Szőts, p. 132, pl. 1, figs 3, 4 [not figs 1, 2, = *Lepidochitona szoetsi* sp. nov., see below].
1974 *Tonicia pannonica* Szőts. – Strausz, pp. 9–10, 98, text-fig. 3.
1981 *Tonicia pannonica* Szőts. – Van Belle, p. 55.
2011 *Tonicia pannonica* Szőts. – Dell'Angelo *et al.*, p. 953.

Type. – Lectotype: HGGI, E.1a., a tail valve (Fig. 2A, B, D, E), designated herein. Paralectotype: HGGI, E.1b., an intermediate valve (Fig. 2C, F), excluded from *Tonicia pannonica* and attributed to *Lepidochitona szoetsi* sp. nov. herein.

Type locality. – Gánt, Eocene (Fig. 1). Szőts (1953) indicated the "Új-feltárás = new exposure" as the locality of his two chiton valves (Loc. 1 in Fig. 1; 47° 22.56´ N, 18° 23.18´ E). The new samples collected by Z. Vicián are from the vineries around Gánt (Loc. 2 in Fig. 1; 47° 20.80´ N, 18° 22.60´ E), which were also among Szőts's localities. In both sections the fossils are from the same level (brown molluscan clay).

Type horizon. – Middle Eocene (?late Lutetian to early Bartonian) molluscan clay at the lower part of Kincses Formation.

Additional material examined (from Loc. 2 in Fig. 1). – HNHM: three valves (one head: INV 2013.316; one intermediate: INV 2013.317; one tail: INV 2013.318.) (Fig. 3H–J); NHMW: three valves [one head: NHMW 2014/0203/0001; one intermediate: NHMW 2013/0311/0001 (Fig. 3D–G), and one tail: NHMW 2014/0203/0002]; ZISP 2203: three valves [one head (Fig. 3A–C), one intermediate, and one tail]; BD 101: nine valves (small fragments): two head, two intermediate, and five tail.

Original description. – "Une valve postérieure et une valve médiane appartenant très probablement à la même espèce ont été trouvées à Új-feltárás.

Toute les deux valves, concernant leur ornamentation et les autres caractéristiques morphologiques, sont très voisines de l'espèce *Ch. defrancei* De Rocheb. (Cossm., M.: Cat. Ill. III, p. 15. Pl. I, fig. 9) abondant aux environs de Chaussy; mais elles ne sauraient être identifiées avec celle-cí.

La valve mediane est plus étroite que celle de l'espèce parisienne, son ornamentation est beaucoup plus fine et

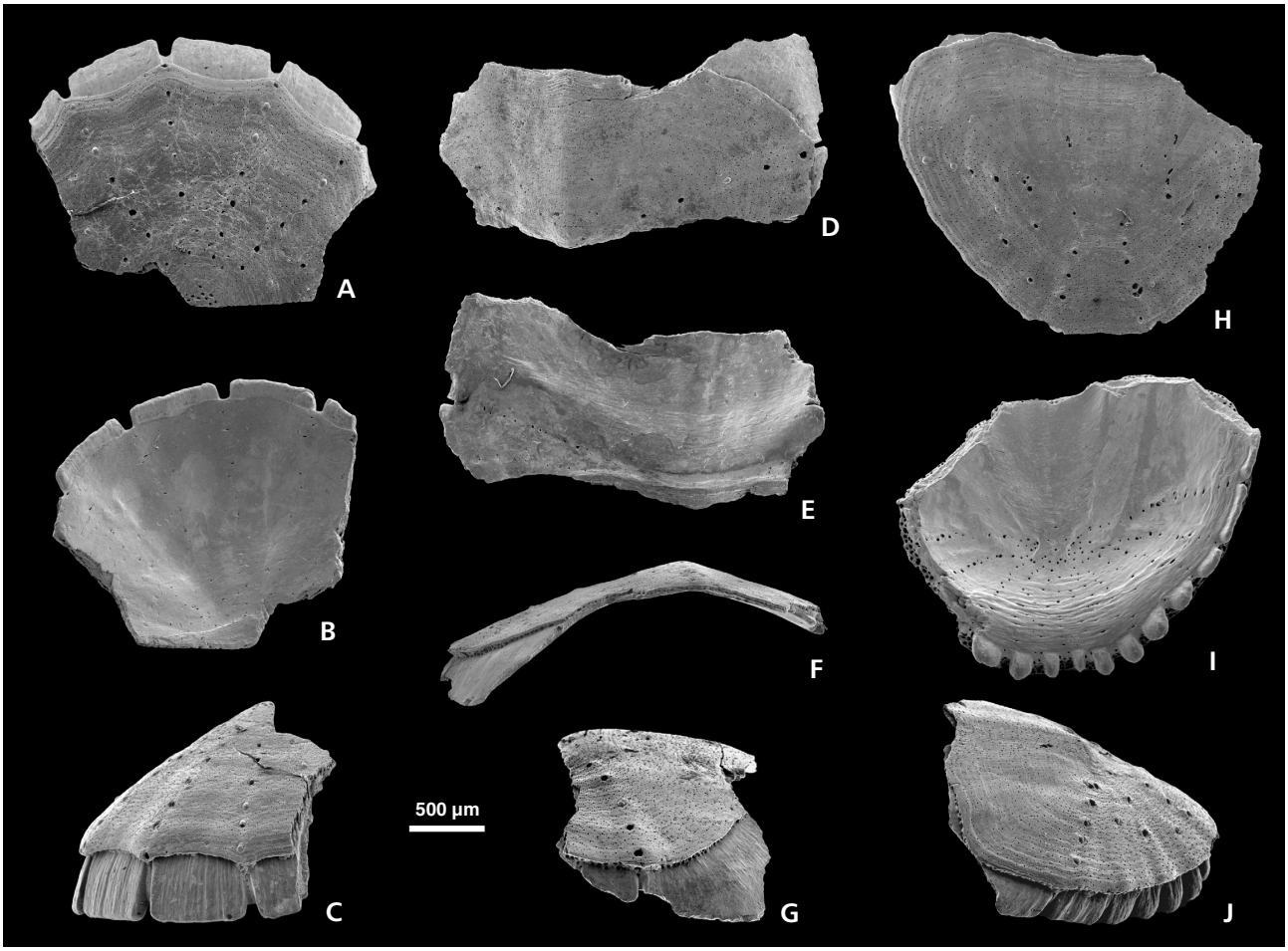

Figure 3. *Tonicia pannonica* Szőts, 1953 from the Middle Eocene Kincses Formation of Gánt, Hungary. • A–C – head valve (ZISP 2203; A – dorsal view, B – ventral view, C – left lateral view); • D–G – intermediate valve (NHMW 2013/0311/0001; D – dorsal view, E – ventral view, F – anterior view, G – right lateral view). • H–J – tail valve (HNHM INV 2013.318; H – dorsal view, I – ventral view, J – right lateral view).

plus serrée. À son aire latérale, on voit aussi quelques carènes obtuses.

La surface de la valve postérieure est, malhereusement, assez roulée. D'après sa taille, il ressemble quand- même à la *Ch. defrancei* De Rocheb.

Aux surfaces intérieures de toutes les deux valves, l'on voit bien les places d'adhésion des muscles et les impressions correspondant aux lames d'insertion.

Dimensions: largeur de la valve postérieure: 2,73 mm, largeur de la valve médiane: 3,64 mm." (Szőts 1953, p. 132)

Emended diagnosis. – Tegmentum smooth; radial ridges of ocelli pores on head valve in the contact between central and lateral areas of intermediate valve, and in postmucronal area of tail valves. Tail valve flattened, mucro subcentral, not prominent, anterior and posterior slopes practically straight. Slit formula 7?/1/13, slits deep, teeth strongly grooved on outside and directed outwards in head and tail valves.

Emended description. – Head valve (Fig. 3A–C) incomplete, semicircular, tegmentum smooth with few radial ridges (7?) bearing regular rows of ocelli on the crest (Fig. 4A). Each row comprising six ocelli of oval shape (Fig. 4B, C), with a maximum diameter *ca* 55 µm. Intermediate valve (Fig. 3D–G) incomplete, rectangular, carinated, posterior margin concave at both sides of the less prominent apex, tegmentum smooth, lateral areas separated from the central area by a slight radial ridge with a row of six ocelli of oval shape (maximum diameter *ca* 52 µm). Tail valve (Fig. 3H–J) elliptical, flattened, front margin straight, mucro subcentral, not prominent, anterior and posterior slopes practically straight, tegmentum smooth, postmucronal area with 13 radial ridges, which bear regular rows of subcircular ocelli (diameter *ca* 54 µm).

Tegmentum smooth, densely covered by irregularly arranged macro- and microaesthetes (Fig. 4D).

Articulamentum with rather wide apophyses; slit formula 7?/1/13; slits deep. The teeth are strongly grooved on

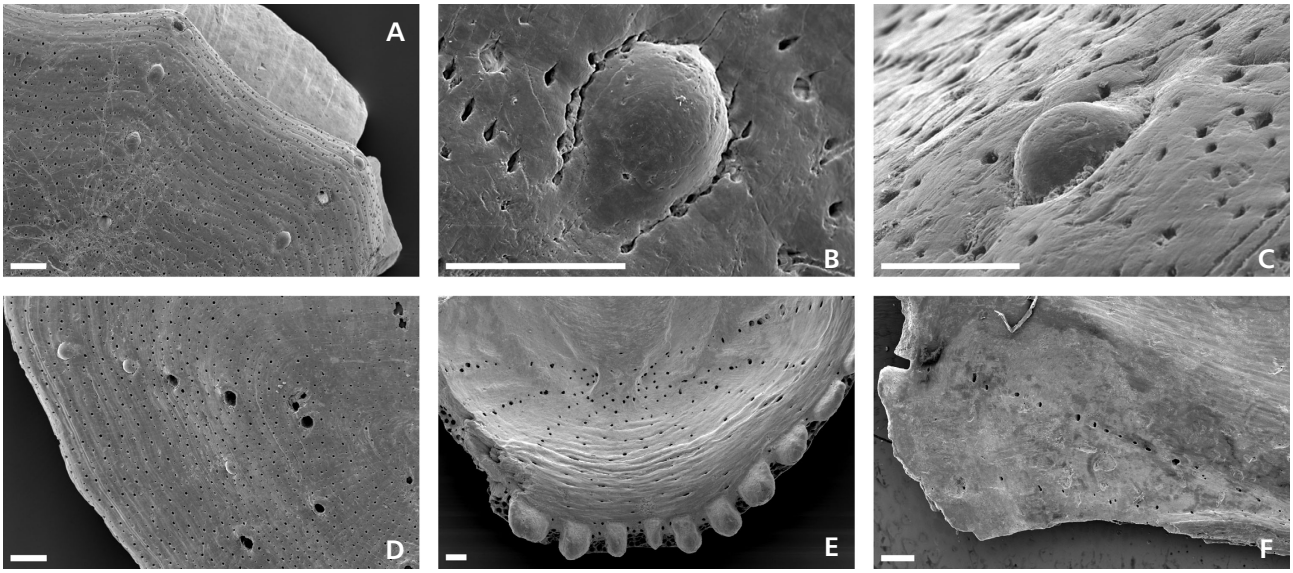

Figure 4. *Tonicia pannonica* Szőts, 1953 from the Middle Eocene Kincses Formation of Gánt, Hungary. • A–C – head valve (ZISP 2203), close-up of surface ornamentation (A) and ocelli in plan (B) and oblique (C) view; • D, E – tail valve (HNHM INV 2013.318), close-up of surface ornamentation (D) and teeth (E); • F – intermediate valve (NHMW 2013/0311/0001), close-up of internal surface. Scale bars for A and D–F equal 100 µm, those in B and C equal 50 µm.

the outside and those of the head and tail valves are directed outwards (Fig. 4E).

Remarks. – Szőts (1953) based his new species *Tonicia pannonica* on two valves (a tail valve and an intermediate valve), which show radically different ornamentation and in the opinion of the present authors belong to two different species. Szőts did not designate a holotype for *T. pannonica*. The tail valve is consistent with the morphology of other *Tonicia* species, characterized by a smooth tegmentum and the presence of ocelli pores (for extra-pigmentary eyes; Kaas *et al*. 2006). The intermediate valve, in contrast, shows characteristics of the genus *Lepidochitona*. The tail valve (Szőts 1953, pl. 1, figs 3, 4), therefore, is designated as lectotype herein, in order to provide stability to nomenclature by preserving the generic attribution of the species *pannonica* to the genus *Tonicia*.

The ornamentation of the head and intermediate valves found in the newly collected samples from Gánt (Figs 3, 4) is identical with that of the lectotype, and are thus considered to be conspecific here.

Szőts (1953) compared the two valves of his new species with *Chiton defrancei* de Rochebrune, 1883, a species from the Eocene of the Paris Basin now attributed to the genus *Lepidochitona*. In that species, the tegmentum is covered by small roundish granules, completely different from the smooth tegmentum of the tail valve designated as lectotype of *T. pannonica*. Szőts's intermediate valve excluded from *T. pannonica* here, in contrast shows similarities to *L. defrancei* (see below under *Lepidochitona szoetsi* sp. nov.).

Some species of chitons known from the Eocene of France (Paris, Cotentin and Loire basins) were attributed to *Tonicia* in the past (Dell'Angelo *et al*. 2011, Appendix 2): *T. brasili* (Cossmann & Pissarro, 1902); *T. edwardsi* de Rochebrune, 1883; *T. lennieri* (Cossmann & Pissarro, 1905); *T. morgani* de Rochebrune, 1883. Unfortunately, the knowledge on the chitons from these basins is poor. Comparison is hampered by the incomplete knowledge on their morphology and lack of SEM documentation. Neither are there any recent revisions of the species reported in the older literature and, the original descriptions are often inadequate. Many of these species thus cannot be attributed with confidence to a specific genus, and are thus considered *gen. inquir.*

New data (Le Renard & Gain 2012, p. 84, fig. 81) show that "*Chiton*" (*Tonicia*) *brasili* Cossmann & Pissarro, 1902 is an elongate chiton, almost vermiform, very different in shape and ornamentation from *T. pannonica.*

Occurrence. – *Tonicia pannonica* is known only from the Middle Eocene of Hungary (Gánt: Szőts 1953 and this paper; Neszmély: Strausz 1974).

Suborder Acanthochitonina Bergenhayn, 1930
Family Tonicellidae Simroth, 1894

Genus *Lepidochitona* Gray, 1821
The genus is known from the Paleocene to the Recent.

***Lepidochitona viciani* sp. nov.**
Figures 5A–L, 6A–F

Type material. – Holotype: NHMW 2013/0311/0006,

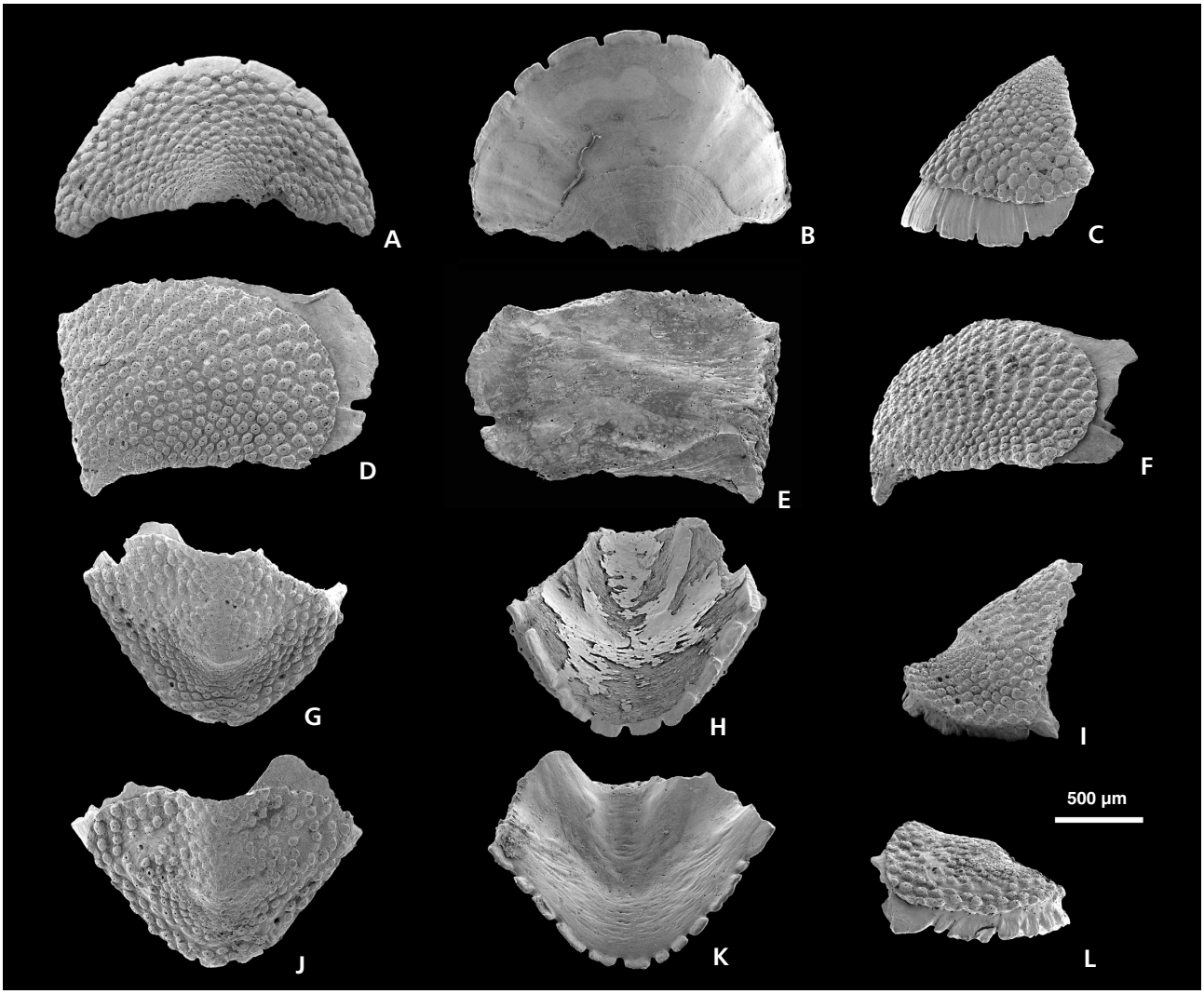

Figure 5. *Lepidochitona viciani* sp. nov. from the Middle Eocene Kincses Formation of Gánt, Hungary. A–C – head valve (paratype NHMW 2013/0311/0002); D–F – partial intermediate valve (paratype NHMW 2013/0311/0003); G–I: tail valve (paratype HNHM PAL 2013.36.1); J–L: tail valve (holotype NHMW 2013/0311/0006); dorsal (left column), ventral (middle column) and lateral views (right column).

an almost complete tail valve (Fig. 5J–L), width 1.6 mm. Paratypes: HNHM: three valves (one head: PAL 2013.34.1, one intermediate: PAL 2013.35.1, and one tail: PAL 2013.36.1) (Fig. 5G–I); NHMW: three valves (one head: NHMW 2013/0311/0002 (Fig. 5A–C); one intermediate: NHMW 2013/0311/0003 (Fig. 5D-F), and one tail: NHMW 2014/0203/0003); ZISP 2204: three valves (one head, one intermediate, and one tail); BD 102: three valves (one head, one intermediate, and one tail).

Other material. – 11 head, 127 intermediate, and 19 tail valves, most of which are fragmentary (BD coll'n; NHMW 2014/0203/0004, 2014/0203/0005, and 2014/0203/0006).

Type locality. – Gánt, road-cut at the vineries (Hungary) (Loc. 2 in Fig. 1).

Type horizon. – Middle Eocene (?late Lutetian to early Bartonian) molluscan clay in the lower part of the Kincses Formation.

Etymology. – The specific name honours our friend Zoltán Vicián (Budapest, Hungary), who collected the sediment samples from Gánt, and has greatly contributed to the knowledge of the Miocene malacofauna of Hungary.

Diagnosis. – Lateral areas of intermediate valves not distinctly separated from central area; tegmentum ornamented by roundish, elevated, well-separated granules, arranged in an irregular quincunx pattern.

Description. – Head valve (Fig. 5A–C, NHMW 2013/0311/0002) almost semicircular, slope slightly con-

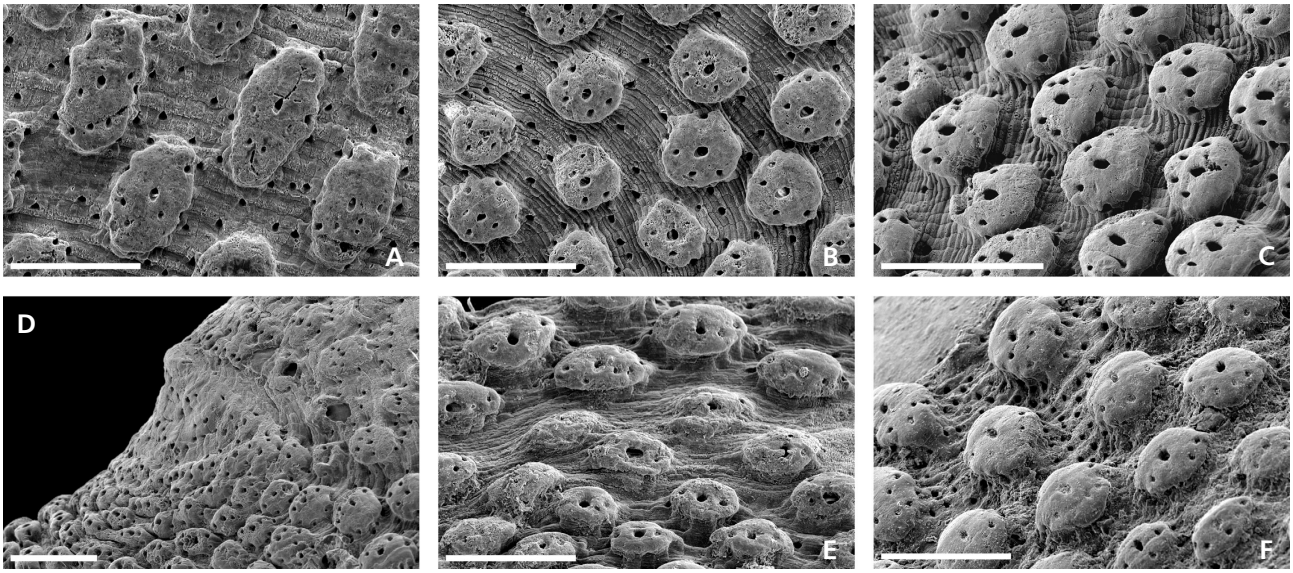

Figure 6. *Lepidochitona viciani* sp. nov. from the Middle Eocene Kincses Formation of Gánt, Hungary. Close-up of surface ornament. • A–C – intermediate valve (paratype NHMW 2013/0311/0003); D – tail valve (paratype HNHM PAL 2013.36.1); E – tail valve (holotype NHMW 2013/0311/0006); F – head valve (paratype NHMW 2013/0311/0002). Scale bars equal 100 µm.

vex. Intermediate valve (Fig. 5D–F) rectangular, subcarinated, lateral margins rounded, hind margin concave at both sides of the prominent apex, beaked, lateral areas not distinctly separated from the central area. Tail valve (Fig. 5J–L, NHMW 2013/0311/0006) subtriangular, wider than long, frontal margin sinuate, concave in the jugal part, mucro subcentral, not prominent, anterior slope almost straight or slightly concave, posterior slope concave just behind the mucro (Fig. 6D).

Tegmentum evenly sculptured all over with roundish (Fig. 6A–F), elevated, well-separated granules, arranged in an irregular quincunx pattern. The granules tending to become more irregularly elongate towards the anterior margin of intermediate (Fig. 6A) and tail valves, but always well separated, not coalescing (except in very few cases, *e.g.* in Fig. 5G, I where two to three coalesced granules can be observed in the antemucronal area of a tail valve). Each granule with a more or less central macroaesthete, and variable number of microaesthetes (three to five, up to seven or eight in more elongate granules) are arranged irregularly along the granule margin. Additional microaesthetes along the bulb of the granule and between granules. Granules roundish, diameter *ca* 60–65 µm in head valves, *ca* 55–65 µm in intermediate valves, *ca* 55–75 µm in tail valves. Elongate granules can reach a maximum length up to *ca* 90–110 µm.

Articulamentum wide, triangular in tail valves, slit formula 8–10/1/8–10, slits deep, teeth strong and very uneven in width, those of the tail valve forwardly directed. Apophyses of intermediate valve not preserved.

Remarks. – This is the most common species found at Gánt, but almost all valves are broken fragments, of 0.5 to 1.5 mm, mostly half valves. This is a common preservation for thin-shelled polyplacophorans (Sigwart *et al.* 2014). Some head and tail valves are almost complete, but the intermediate valves are almost always fragmented, and only two or three are more or less complete.

A few chiton species reported from the European Eocene were attributed to *Lepidochitona* (Dell'Angelo *et al*. 2011, Appendix 2): *L. bernayi* (Cossmann, 1888) from France and U.K., *L. defrancei* (de Rochebrune, 1883) and *L. grinionensis* (Lamarck, 1802) from France. Those three species are characterized by intermediate valves with a diagonal fold between the lateral and central areas. Such a fold is not present in the material studied here (see discussion below).

Lepidochitona vjalovi Makarenko, 1969, and "*Allochiton*" *menneri* (Makarenko, 1969), both from the Paleocene of Ukraine, differ widely from the present specimens, by their tegmentum divided into jugal and pleurolateral areas like species of genus *Acanthochitona*, the very developed and strongly pectinated insertion plates, and are currently being revised and will possibly be attributed to a separate, new genus (Sirenko, pers. com.).

Lepidochitona oligocaena (Rolle, 1862) from the Oligocene of Gaas (France) differs by the shape of the valves, the densely spaced, quadrangular granules, the presence of two slits in intermediate valves (Kroh & Dell'Angelo in prep.).

Lepidochitona corrugis (Boettger, 1869) from the Oligocene of Gienberg, near Waldböckelheim (Germany) differs from our species by the coarser sculpture, the elevated lateral areas of the intermediate valves, which are

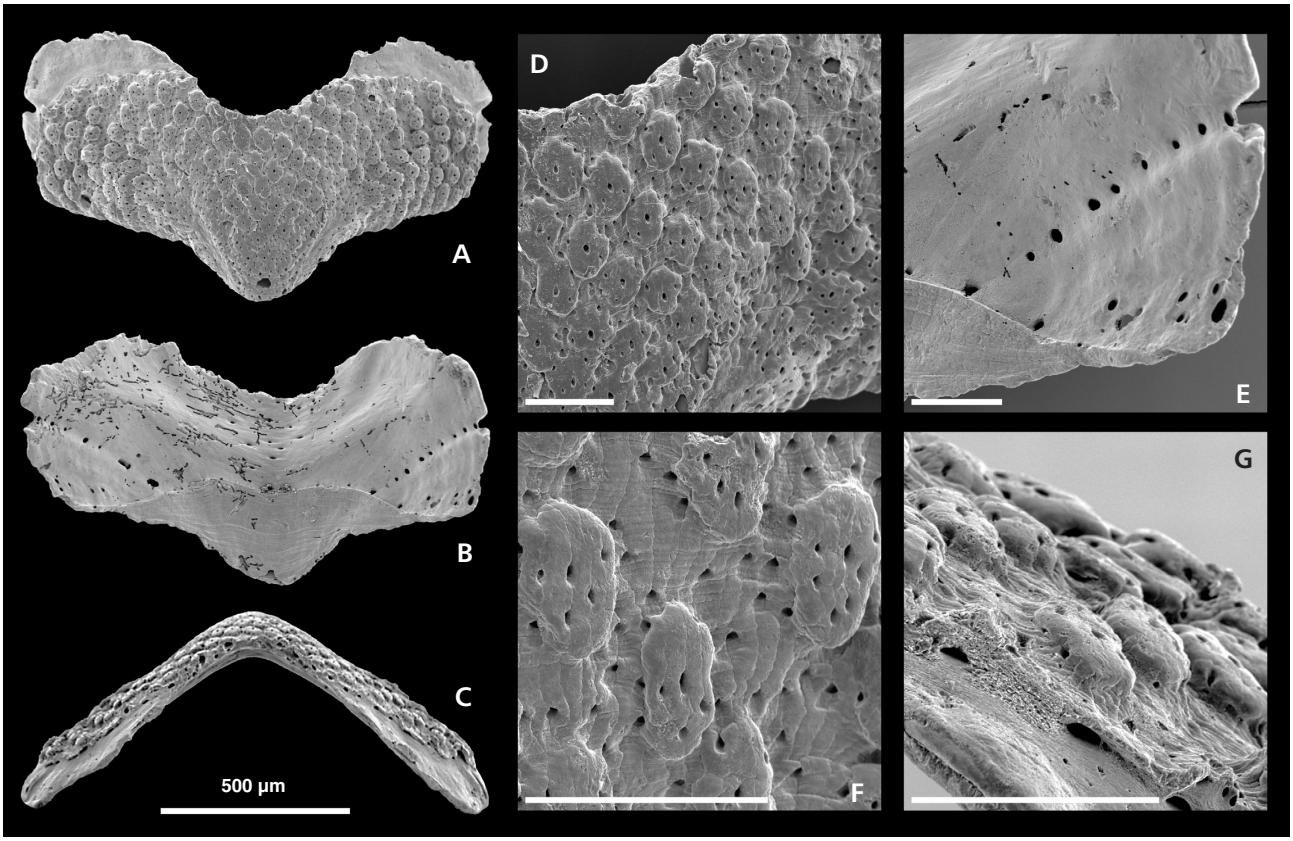

Figure 7. *Lepidochitona gantensis* sp. nov. from the Middle Eocene Kincses Formation of Gánt, Hungary (holotype, NHMW 2014/0448/0001). • A–G – intermediate valve, dorsal (A), ventral (B) and anterior view (C); close-up of surface ornamentation (D), close-up of internal surface (E), granules in dorsal (F) and oblique view (G). Scale bars D–G equal 100 µm.

separated from the central areas by a diagonal fold, and by its granules, which are arranged in rows (Janssen 1978).

Occurrence. – *Lepidochitona viciani* sp. nov. is known only from the Middle Eocene of Gánt (Hungary).

***Lepidochitona gantensis* sp. nov.**
Figure 7A–G

Type material. – Holotype: NHMW: one complete intermediate valve (NHMW 2014/0448/0001, Fig. 7A–C), width 1.2 mm.

Type locality. – Gánt, road-cut at the vineries (Hungary) (Loc. 2 in Fig. 1).

Type horizon. – Middle Eocene (?late Lutetian to early Bartonian) molluscan clay from the lower part of the Kincses Formation.

Etymology. – After the town of Gánt, where the outcrops are situated.

Diagnosis. – Lateral areas of intermediate valves not distinctly separated from central area; tegmentum ornamented by irregular elevated granules arranged in an irregular quincunx pattern; granules well-separated at the valve margin, but coalescing in the jugal area.

Description. — Intermediate valve (Fig. 7A–C) subcarinated, anterior margin with large inward curve in jugal area, lateral margins rounded, hind margin concave at both sides of the prominent and large apex, strongly beaked, lateral areas not distinctly separated from the central area.

Tegmentum evenly sculptured all over with elongate/rectangular (Fig. 7D, F, G), elevated granules, arranged in an irregular quincunx pattern. The granules are not well separated in the jugal area, some of them coalescing, and tending to become more separate towards the lateral margin of the valve. Each granule with a more or less central macroaesthete, and variable number of microaesthetes (three to six) arranged irregularly along the granule margin. Additional microaesthetes along the bulb of the granule and between granules. Granules elongate, length *ca* 60–75 µm.

Articulamentum wide, apophyses not completely preserved, a single deep slit, teeth strong.

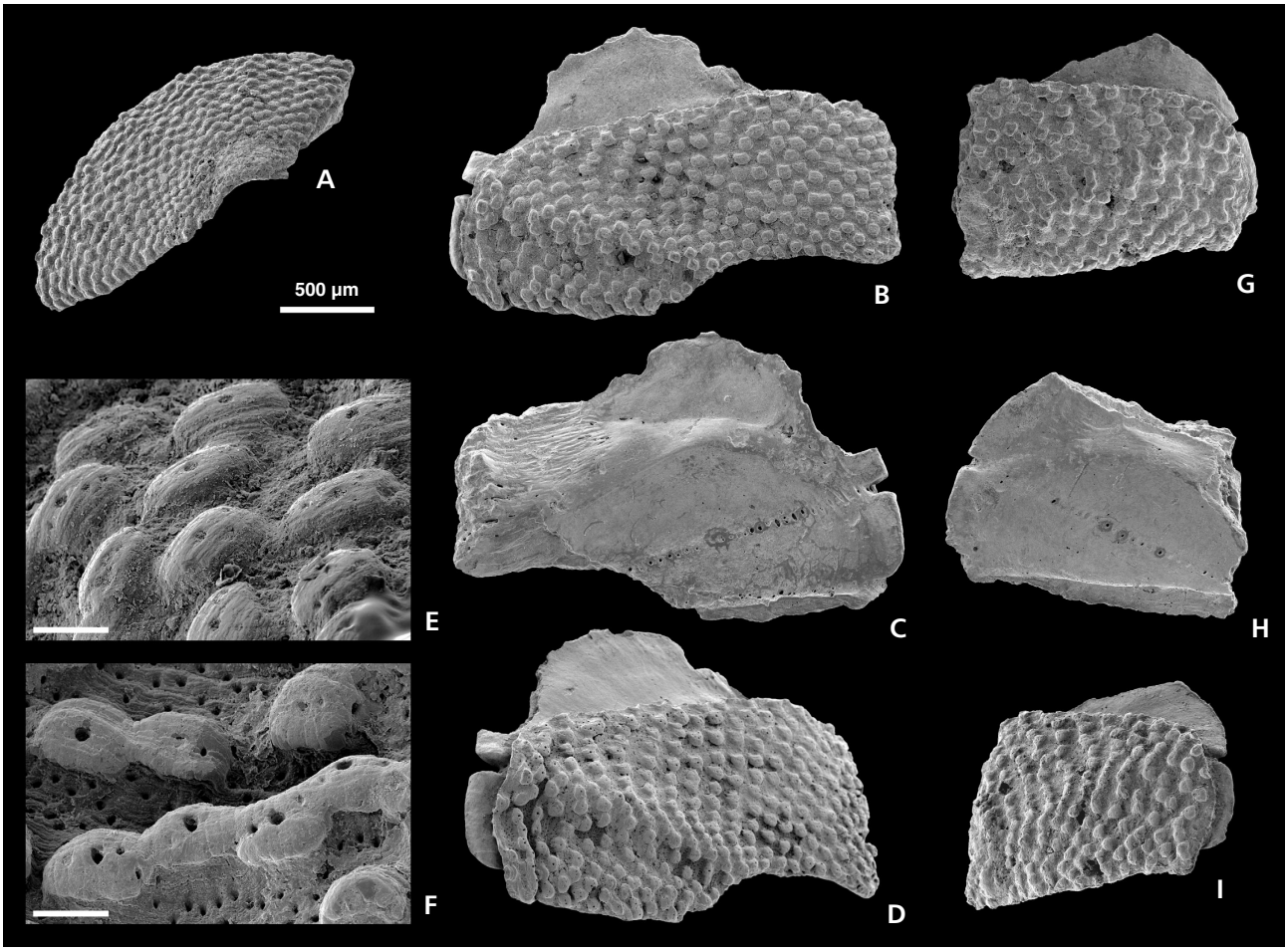

Figure 8. *Lepidochitona szoetsi* sp. nov. from the Middle Eocene Kincses Formation of Gánt, Hungary. • A – head valve; B–F – intermediate valve (paratype, NHMW 2013/0311/0005), dorsal (B), ventral (C) and oblique lateral view (D); close-up of granules on lateral fold (D) and near lateral margin (F); G–I – intermediate valve (paratype, NHMW 2013/0311/0004), dorsal (G), ventral (H) and oblique lateral view (I). Scale bars E, F equal 50 µm.

Remarks. – This single intermediate valve is similar to *Lepidochitona viciani* sp. nov. in having poorly separated lateral areas. It differs from *L. viciani*, however, by its different shape, with a large apex and strongly beaked form, its less roundish and more quadrangular granules (Fig. 7D, F), which are slightly larger (by *ca* 10–15%), more closely spaced and poorly separated. The granules are superficially similar to those of *Lepidochitona szoetsi* sp. nov, but there is no trace of a diagonal fold between the lateral and central areas.

Notwithstanding the scarcity of material, the characters of this species are well defined, and well differentiated from *Lepidochitona viciani* sp. nov. and *L. szoetsi* sp. nov., so we describe *L. gantensis* as a new species here.

Occurrence. – *Lepidochitona gantensis* sp. nov. is known only from the Middle Eocene of Gánt (Hungary).

***Lepidochitona szoetsi* sp. nov.**
Figure 2C, F, 8A–I

1953 *Tonicia pannonica* (non Szőts) – Szőts, p. 132, pl. 1, figs 1, 2.

Type material. – Holotype: HGGI, E.1b.: 1 intermediate valve (figured by Szőts 1953, pl. 1, figs 1, 2) (Fig. 2C, 2F). Paratypes (all from Loc. 2 in Fig. 1): NHMW: 1 right half of intermediate valve (NHMW 2013/0311/0004) (Fig. 8G–I), and 1 left half of intermediate valve (NHMW 2013/0311/0005) (Fig. 8B–F); BD 103: 1 incomplete head valve, width 1.7 mm; BD 104: 1 almost complete intermediate valve, width 3.1 mm.

Additional material examined (all from Loc. 2 in Fig. 1). – 1 head valve (Fig. 8A) (lost during the SEM study); 3 intermediate incomplete valves, maximum width 2 mm (BD coll'n).

Table 1. Main characters of *Lepidochitona* species from the Eocene of Europe.

		L. grinionensis	*L. defrancei*	*L. bernayi*	*L. szoetsi*
head valve	sculpture	small granules	larger granules	larger granules	irregular, elevated granules
	radial ridges	some radial ridges present	absent	9 granulated radial ribs	some radial ridges present
	slits	8	10	9	?
intermediate valves	shape	rectangular, width twice the length	rectangular, narrow	rectangular, narrow	rectangular
	profile	"très arquées"	"très arquées", subcarinated	"peu arquées", rounded	subcarinated
	apex	evident	well evident	less evident	less evident
	sculpture	small granules, also more elongate	larger granules	oblique striae of large granules	irregular, elevated granules, some coalescing
	lateral areas	narrow, and separated from central area by a rib	wide and separated from central area by some ribs	narrow, separated from central area by a large rib	separated from central area by a diagonal fold
	slits				1
tail valve	shape	"scutiforme, autour duquel rayonnent quatre dépressions"	"demi-circulaire, marqué de deux dépressions qui remontent vers le haut"		
	mucro	subcentral, well evident	central, less evident		
	sculpture	small granules	larger granules, more fine in the postmucronal area		
	slits				

Type locality. – Gánt, "new exposure" of Szőts (1953) (Hungary) (Loc. 1 in Fig. 1).

Type horizon. – Middle Eocene (?late Lutetian to early Bartonian) molluscan clay from the lower part of the Kincses Formation.

Etymology. – The specific name honours Endre Szőts, a recognized Hungarian malacologist, who collected the holotype.

Diagnosis. – Head valve with radial ridges; lateral areas of intermediate valves separated from central area by a diagonal fold; tegmentum ornamented by elevated, rectangular granules arranged in a chess-board pattern.

Description. – The head valve bears few radial ridges that correspond to the slits in the insertion lamina. Intermediate valve rectangular, subcarinate, with rounded lateral margins. Hind margin slightly concave at both sides of the apex. Lateral areas distinctly separated from the central area by a diagonal fold.

Tegmentum evenly sculptured all over with irregular polygonal, elevated, poorly separated granules, arranged in an irregular chess-board pattern (Fig. 8E). Those on the head valve are more roundish. Towards the diagonal folds of intermediate valves the granules tend to become coarser, irregularly elongate and coalescing laterally, forming longitudinal rows (Fig. 8F). Each granule bearing a more or less central macroaesthete, and some microaesthetes, which are irregularly arranged along the margin. In addition, microaesthetes are present between granules too. Maximum length of granules: *ca* 45–60 μm in head valve, *ca* 65–80 μm in intermediate valves.

Articulamentum with wide and triangular apophyses in intermediate valves, slit formula ?/1/?, slit deep.

Remarks. – The paralectotype of *Tonicia pannonica* (Szőts, 1953, pl. 1, figs 1, 2) is here excluded from that species and re-assigned to the genus *Lepidochitona*, based on valve shape and ornamentation (Fig. 2C, F). It fits well with the present species and likely represents a second intermediate valve.

In spite of the scarcity of the available material, this species is well characterized by its coarser and dense granules, which tend to coalesce, the presence of radial ridges in the head valve, and a diagonal fold in lateral areas. It differs from the *L. gantensis* sp. nov. by the presence of a distinct fold separating the central and lateral areas. Three other *Lepidochitona* species from the European Eocene show a similar morphology (Dell'Angelo *et al*. 2011, Appendix 2): *L. bernayi* (Cossmann, 1888), *L. defrancei* (de Rochebrune, 1883), and *L. grinionensis* (Lamarck, 1802). The main characters of these species are presented in Table 1, based on the descriptions of Cossmann (1888) for specimens from the Paris Basin.

Material of *Lepidochitona grinionensis* (MNHN J02645, an intermediate valve from Ferme de l'Orme, illustrated in Cossmann & Pissarro 1907) and *L. defrancei* (MNHN J02646, three valves from Chaussy, illustrated in Cossmann & Pissarro 1907) show characters that substantially agree with those deduced from historical descriptions

and reported in Table 1. The intermediate valves of *Lepidochitona szoetsi* sp. nov. are superficially similar to *L. defrancei*. The strong diagonal fold is very similarly developed, as is the ornamentation, but the overall shape of valves of *L. szoetsi* sp. nov. is different, more elongated, and the head valve of *L. defrancei* is also different in shape, with no traces of radial ribs. Unfortunately, we were neither able to trace the types of *L. defrancei*, nor to locate topotypic material (the MNHN specimens come from different localities and it is not clear if they are really conspecific with the type material of de Rochebrune). Notwithstanding the scarcity of the material available, we describe *Lepidochitona szoetsi* sp. nov. as a new species. It must be pointed out, however, that the Paris Basin chitons are poorly known and in need of re-description based on SEM-documentation of the type-material. When more data becomes available, it will be possible to better define the relations between *Lepidochitona szoetsi* sp. nov. and *L. defrancei*.

Occurrence. – *Lepidochitona szoetsi* sp. nov. is known only from the Middle Eocene of Gánt (Hungary).

Discussion

Tonicia pannonica from the Eocene of Gánt was described by Szőts (1953) on the basis of two isolated valves, deposited at the HGGI. New samples were collected near the type locality and were checked specifically for chiton valves. Nearly 200 specimens could be recovered. Although most of them are fragmented, four species could be recognized based on valve shapes and tegmentum ornamentation.

Re-examination of the type material of *Tonicia pannonica* indicates that the two syntypes of Szőts (1953) belong to two different species. One syntype (the tail valve) does indeed belong to the genus *Tonicia* but the other one is a *Lepidochitona*. In agreement with the recommendations of The Code (ICZN 1999, Recommendation 74A), the tail valve is here selected as the lectotype for *Tonicia pannonica*, in order to stabilize nomenclature by preserving the attribution of *pannonica* to *Tonicia*. The paralectotype, an intermediate valve, is excluded from *T. pannonica* here and attributed to *Lepidochitona szoetsi* sp. nov. on base of its ornamentation.

Comparison with other species of *Tonicia* and *Lepidochitona* is generally hampered by the poor or incomplete descriptions for many nominal taxa included in these two genera. Particularly, SEM-documentation of their ornamentation is often lacking and original descriptions are usually presented in general terms. For the Paris Basin chiton fauna no modern revision is available and often repository of the type-material is unknown, making it even more difficult to compare taxa from that region to new finds from elsewhere. As pointed out by Puchalski *et al.* (2008) and exemplified by the present study sampling specifically targeted at the recovery of polyplacophoran valves often results in an increase in local and sometimes global chiton biodiversity since polyplacophoran valves (especially of small species) can easily be overlooked or confused with broken bivalve shells.

Conclusions

Revision of Szőts's (1953) type material of *Tonicia pannonica* from the Eocene of Gánt revealed the presence of a second species among the syntypes and necessitated designation of a lectotype. New material collected near the type locality considerably extended our knowledge of the Hungarian Eocene chiton fauna, as well as the general knowledge of Palaeogene polyplacophorans and resulted in the identification of three *Lepidochitona* taxa in addition to *Tonicia pannonica*: *Lepidochitona gantensis* sp. nov., *L. szoetsi* sp. nov., and *L. viciani* sp. nov.

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