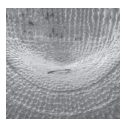


Some Oligocene chitons (Mollusca: Polyplacophora) from Germany and France

BRUNO DELL'ANGELO, MAURIZIO SOSSO & ANDREAS KROH



Four species of chitons (Mollusca: Polyplacophora) described by Sandberger and Rolle from the Oligocene of Germany and France are discussed and illustrated, providing for the first time SEM-images of the type-material and translations of the original descriptions. The material studied includes the holotype of *Chiton modestus* Rolle, 1862 and syntypes of *Lepidopleurus virgifer* Sandberger, 1859, *Chiton oligocaenus* Rolle, 1862, and *Chiton reussi* Rolle, 1862. All these species are considered valid. Redescription of the type material clarifies the identity of the species and enables comparison to related species from coeval deposits. • Key words: Mollusca, Polyplacophora, Cenozoic, Palaeogene, Oligocene, Europe.

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Bruno Dell'Angelo, Via Briscata 16/6, 16154 Genova, Italy; bruno.dellangelo@chitons.it • Maurizio Sosso, Via Bengasi 4, 16153 Genova, Italy • Andreas Kroh, Natural History Museum Vienna, Burgring 7, 1010 Wien, Austria

In comparison with other mollusk classes fossil polyplacophorans did not receive much attention from the academic community. The early authors sometimes mentioned any chiton valves at the end of their monographs on bivalve and gastropod faunas (e.g., Sandberger 1858–1863; Reuss 1860; Cossmann 1888; Boettger 1902, 1906–1907; Cossmann & Peyrot 1909–1935; Zilch 1934). Before the 1950s very few papers focused specifically on fossil polyplacophorans. A notable exception is the work of Šulc (1934), which has remained an indispensable reference for any later study on chitons from the Cenozoic of Europe.

The large majority of European chiton records are from Neogene, while chitons from the Paleogene are poorly known, with greater prevalence of records from Eocene (Cossmann 1888, 1922; Cossmann & Pissarro 1900, 1905; Wrigley 1943; Bielokrys 1999, 2000; Dell'Angelo *et al.* 2011, 2015a; Cherns & Schwabe 2017). Oligocene records even are less prevalent, limited to Germany (Sandberger 1858–1863; Koenen 1892; Janssen 1978; Gürs 1992, 1995; Müller 2011), Belgium (Marquet *et al.* 2008), France (Rolle 1862, Cossmann & Peyrot 1909–1935, Vergneau 1966, Dell'Angelo *et al.* 2018a), Italy (Dell'Angelo & Palazzi 1992, Dell'Angelo *et al.* 2015c). The recent discovery of the type material of four chiton species from the Oligocene of Germany and France preserved in the Natural History Museum Vienna (Šulc collection) is of great importance, and permits a better knowledge of these poorly known species. We provide

for the first time SEM-images of these species, and translations of the original descriptions.

Material & Methods

The material here redescribed comes from two well-known sites, Waldböckelheim (Bad Kreuznach, Germany) and Gaas (Landes, France). Polyplacophoran material originally described and illustrated by Rolle (1862) is preserved in the collection of the Natural History Museum Vienna (Department of Geology and Palaeontology), it derives from the locality Gaas. Additionally, the collection contains polyplacophoran material obtained by exchange from F. Sandberger (in 1862) and as donation from H.C. Weinkauff (in 1863). The Weinkauff collection formed part of the material studied by Sandberger (1858–63) in his monograph “Die Conchylien des Mainzer Tertiärbeckens”, as mentioned in the preface of his work (p. iv). This material is mentioned when Sandberger (1861: p. 184) originally described *Chiton virgifer*: “Von dieser Art sind mehrere Mittel-, Mund- und After-Segmente, theils von Weinkauff, theils von mir selbst [Sandberger] in dem Meeressandes des Gienbergs bei Waldböckelheim gefunden worden. ...”, translating to: “Weinkauff and myself found multiple intermediate, head and tail segments of this species in the marine sand of the Gienberg near Waldböckelheim”. The historical label associated with the specimens, furthermore, proves that Sandberger

studied these very specimens in the year that the original description was published. These facts demonstrate that this material is part of the type-series. The specimens derive from the locality Waldböckelheim.

The site of Waldböckelheim is located 10 kilometers west of Bad Kreuznach (SW Mainz, Germany), a classical locality of the 19th century that has delivered a great number of fossils (predominantly mollusks). The Alzey Formation exposed in the area of Waldböckelheim was deposited during the Oligocene (Rupelian), based on calcareous nannoplankton data (Zones NP23 and lower NP24) (Grimm *et al.* 2000). For additional information, reference is made to Grimm & Grimm (2003) and Bitner & Kroh (2011).

The site of Gaas, referred to the Oligocene (Rupelian) is located 15 kilometers south of Dax (France), in the Chalosse area. The area is well known since the 18th century for its fossiliferous sites. The infra-littoral levels of Gaas consist of mostly clay faluns (*i.e.*, a friable bioclastic marine deposit, sometimes partly consolidated, with a sandy or clayey-sandy matrix) or bioclastic clays. The rich fauna of mollusks was studied by many authors (*e.g.*, Vergneau 1959, 1966; Lozouet & Maestrati 1982; Lozouet 1985, 2011; Cahuzac & Janssen 2010). For additional information, reference is made to Lesport *et al.* (2015) and Dell'Angelo *et al.* (2018a).

Scanning electron microscopy work was carried out at the Natural History Museum Vienna using the JEOL 6400 and 6610LV scanning electron microscopes of the Central Research Laboratories.

Abbreviations. – NHMW – Natural History Museum Wien, Austria; H – height of the valve; L – length of the valve; W – width of the valve.

Systematic palaeontology

The systematic follows Sirenko (2006), except for the genus *Lepidochitona* Gray, 1821, which is attributed to the family Lepidochitonidae Iredale, 1914 according to Kelly & Eernisse (2008) and WoRMS (WoRMS Editorial Board 2018).

Class Polyplacophora Gray, 1821
Subclass Loricata Schumacher, 1817
Order Lepidopleurida Thiele, 1909
Family Leptochitonidae Dall, 1889

Genus *Lepidopleurus* Risso, 1826

Type species. – *Chiton cajetanus* Poli, 1791, by subsequent designation (Herrmannsen 1846). Non *Lepidopleurus* (Carpenter MS) Dall, 1879 (= *Lepidozona* Pilsbry, 1892).

Remarks. – The genus is known from the Eocene to the Recent (Sirenko 2006, Dell'Angelo *et al.* 2018b).

Lepidopleurus virgifer (Sandberger, 1859)

Figures 1, 2A–O

- 1859 *Chiton virgifer*; Sandberger, pl. 14, figs 4, 4a, b.
- 1860 *Chiton virgifer* Sandberger. – Sandberger, pl. 20, figs 15, 15a.
- 1861 *Chiton virgifer* Sandberger. – Sandberger, p. 184.
- non* 1869 *Chiton virgifer?* juv. Boettger (*non* Sandberger, 1859). – Boettger, p. 9, pl. 1, fig. 11a–g [= *Leptochiton maguntiacus* (de Rochebrune, 1882) *partim* and *L. poirieri* (de Rochebrune, 1882) *partim*, *fide* Janssen 1978: pp. 219, 221].
- non* 1870 *Chiton virgifer?* juv. Boettger (*non* Sandberger, 1859). – Boettger, p. 39, pl. 8, fig. 11a–g [= *Leptochiton maguntiacus* (de Rochebrune, 1882) *partim* and *L. poirieri* (de Rochebrune, 1882) *partim*, *fide* Janssen 1978: pp. 219, 221].
- 1882 *Gymnoplax virgifer* (Sandberger). – de Rochebrune, p. 59.
- 1892 *Chiton virgifer* Sandbg. – Koenen, p. 974.
- 1897 *Ch. virgifer* Sandb. – Sacco, p. 90.
- 1912 *Lepidopleurus virgifer* Sandb. – Pompecki, p. 356, fig. 3.
- 1924 *Lepidopleurus virgifer* Sandb. – Zittel, p. 436, fig. 802.
- 1932 *Chiton virgifer* Sandberger. – Wenz, p. 14.
- 1934 *Lepidopleurus virgifer* (Sandb.). – Šulc, p. 3.
- 1957 *Lepidopleurus virgifer* (Sandberger). – Fischer, p. 14.
- 1962 *Lepidopleurus virgifer* (Sandberger). – Malatesta, p. 146.
- 1971 *Lepidopleurus virgifer* (Sandberger). – Sabelli & Spada, p. 6.
- 1977 *Lepidopleurus virgifer* (Sandberger). – Laghi, p. 98.
- 1978 *Lepidopleurus virgifer* (Sandberger). – Janssen, p. 218, pl. 14, figs 3–10.
- 1981 *Lepidopleurus virgifer* (Sandberger). – Van Belle, p. 80.
- non* 1981 *Chiton virgifer?* juv. Boettger (*non* Sandberger, 1859). – Van Belle 1981, p. 80 [= *Leptochiton maguntiacus* (de Rochebrune, 1882) *partim* and *L. poirieri* (de Rochebrune, 1882) *partim*, *fide* Janssen 1978: pp. 219, 221].
- 1983 *Lepidopleurus virgifer* (Sandberger). – Gürs, p. 57.
- 1986 *Lepidopleurus virgifer* (Sandberger). – Hocht, p. 209.
- non* 1989 *Lepidopleurus* (*Lepidopleurus*) *virgifer* (Sandberger). – Dell'Angelo & Palazzi, pl. 3, figs 3, 4; pl. 4, figs 6–9; pl. 22, figs 8, 9 [= *Lepidopleurus benoisti* (de Rochebrune, 1882), *fide* Dell'Angelo *et al.* 2015a: p. 225].
- partim* 1989 *Lepidopleurus* (*Lepidopleurus*) *virgifer* (Sandberger). – Dell'Angelo & Palazzi, p. 50, pl. 3, figs 1, 2, 5; pl. 4, figs 1–5, 10–14.
- 1995 *Lepidopleurus virgifer* (Sandberger). – Gürs, p. 20, pl. 1, figs 8–10.

- 1999 *Lepidopleurus virgifer* (Sandberger). – Dell'Angelo et al., p. 261.
 1999 *Lepidopleurus virgifer* (Sandberger). – Dell'Angelo & Smriglio, pp. 40, 55.
 2010 *Lepidopleurus virgifer* (Sandberger). – Studencka & Dulai, p. 263.
 2011 *Lepidopleurus virgifer* (Sandberger). – Dell'Angelo et al., p. 953.
 2015a *Lepidopleurus virgifer* (Sandberger). – Dell'Angelo et al., p. 225.
 2018a *Lepidopleurus virgifer* (Sandberger). – Dell'Angelo et al., pp. 11, 16.
 2018b *Lepidopleurus virgifer* (Sandberger). – Dell'Angelo et al., pp. 6, 11.

Material. – Syntypes: NHMW 1862/0012/0047 (obtained by the NHMW through exchange with F. Sandberger in 1862): 2 intermediate valves, W 6 and 7.7 mm (Fig. 2E, F); NHMW 1863/0017/0062 (donated to the NHMW by H.C. Weinkauff in 1863; studied by Sandberger on May 4, 1861 as noted on the historical label): 1 intermediate valve, W 7.5 mm, and 2 tail valves, W 5.5 and 5.6 mm (Fig. 2A–D, G–L). Inventory books and historical labels in the NHMW collection were screened for additional specimens that could be associated with Sandberger and/or Weinkauff, but only the two lots listed above can be directly linked to Sandberger.

Additional material: NHMW 1868/0001/0776: 2 tail valves, W 3.8 and 6 mm, from Waldböckelheim; NHMW 1868/0001/0777: 1 tail valve, W 6 mm, from Waldböckelheim (Fig. 2M–O); both lots obtained in 1868 by purchase from Mr. Erber.

Type horizon and locality. – originally referred to as “Meeressand”, today attributed to the Alzey Formation, which is of Oligocene (Rupelian) age (Grimm et al. 2000); Gienberg, near Waldböckelheim, Bad Kreuznach, Germany.

Description. – Original description (translated from Sandberger 1861: pp. 184, 185): “Several intermediate, head, and tail valves of this species were found in the marine sand of the Gienberg near Waldböckelheim, partly by Weinkauff and partly by myself. The intermediate valves are narrow, ribbon-shaped, with almost parallel margins, without projecting tip and short, obtuse angled apophyses. A line running from the center of the anterior margin to the center of the lateral margins separates narrow, acute angled, triangular areas from the main area of the segment. These [lateral] areas are covered with coarse, nodular, often bundle or rod-like dichotomizing, humped folds. The folds project beyond the margin and give it a serrated appearance. They are interrupted by several ledges corresponding to pauses of growth. The

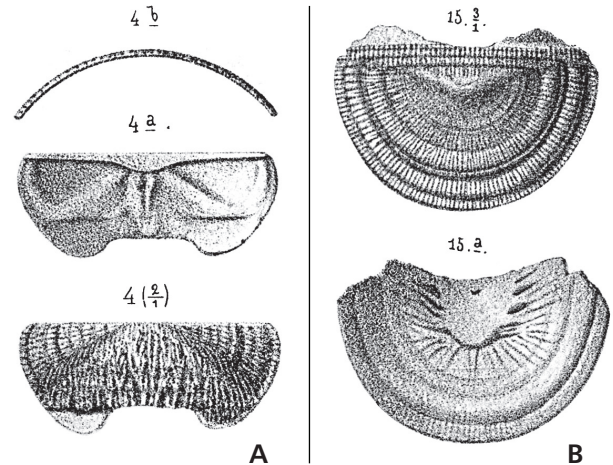


Figure 1. A, B – original figures of *Chiton virgifer* Sandberger, 1859; A – Sandberger (1859: pl. 4, figs 4, 4a–b); B – Sandberger 1860: pl. 20, figs 15, 15a.

main area of the low arched segment is ornamented in a strange way by irregularly nodular longitudinal ridges, which fork repeatedly towards the posterior. The head valve is more strongly curved, almost hemicircular, with eight, roof-like growth ridges projecting above each other, which in turn bear very numerous coarse longitudinal rows projecting beyond the margin of each growth ridge. The tail valve finally, with an almost exactly hemicircular margin, consists of a more narrow anterior area with posteriorly directed, obtuse-triangular hump [mucro] and the same ornamentation which is present on the main area of the intermediate valves. The larger and flatter posterior area, in contrast, is covered by very abundant and delicate beaded ridges which radiate from the hump [mucro].

Based on the peculiarities described here *Chiton virgifer* – as far as the available isolated segments allow a comparison – needs to be compared first with or directly belongs to the subgenus *Tonicia* Gray, which is distributed from the Aleutian Islands, Peru and Chile to the Philippines. But it clearly cannot be accommodated in one of the subgenera occurring in temperate climates.”

Emended description (based on all the material present at NHMW): Intermediate valves wide, broadly rectangular, rounded, moderately elevated, anterior and posterior margins straight, side margins rounded, apex inconspicuous, lateral areas strongly raised. Tail valve semicircular, elevated, width slightly less than twice length ($L/W = 0.53–0.56$), anterior margin from almost straight to slightly convex in jugal area, mucro in anterior position, anterior slope convex, posterior slope concave just behind mucro.

The sculpture of the central area of the intermediate valves is very irregular (Fig. 2A, B, E), agreeing with the Sandberger’s description, while it is generally more regular in the antemucronal area of the tail valve with longitudinal

chains of granules being finer and less subject to split (Fig. 2G, H), tending to be more irregular and rough, shaped by groups of granules branching longitudinally many times (Fig. 2L). The same is true for the coarser sculpture of the lateral areas of the intermediate valves, agreeing well with the Sandberger's description. It is more variable in the postmucronal area of the tail valve, with concentric terraced growth ridges more (Fig. 2L) or less (Fig. 2G, I) evident. Where the sculpture is more regular (Fig. 2H) each granule shows a more or less central macroaesthete, and up to 6 microaesthetes arranged irregularly along the margin.

Articulamentum without insertion laminae, apophyses not well preserved, narrow, triangular in intermediate valves, larger and rounded in tail valves.

Remarks. – The valves present in the NHMW collection as syntypes agree with the original description of Sandberger, and permit to see a certain variability in intermediate and tail valves (head valves are not present).

Sandberger described and figured (1860: pl. 20, fig. 15, also showed in Fig. 1B) a tail valve “with an almost exactly hemicircular margin”, while the syntypes show an anterior margin from almost straight (Fig. 2G) to slightly convex (Fig. 2L, M), and also a more variable position of the mucro, not in such an anterior position as mentioned in the original description (Fig. 2G, L, M). The anterior and posterior slopes of the tail valve (not described and illustrated by Sandberger or Janssen 1978) also show some variability, mainly in the more or less accentuated concavity of the posterior slope (Fig. 2K, O).

The maximum width of the intermediate and tail valves (syntypes) of *Lepidopleurus virgifer* in the NHMW collection is 7.7 and 6 mm, respectively, based on always incomplete intermediate valves. Sandberger (1859) did not give the measurements of his material. The maximum width of the valves figured by Janssen (1978) (based on the scale reported on the figures' caption) is 9.5 (head valve), 13 (intermediate valve), and 8 mm (tail valve), respectively.

The presence of syntypes of *Chiton virgifer* in the NHMW collection is very important, because the type material of Sandberger was not found by Schöndorf (1907), and also the material from the collection of Weinkauff in Munich (Bavarian State Collection of Palaeontology) was destroyed during WW II [*vide* Janssen 1978: p. 218; but note that the part of the collection that Weinkauff had donated to the k. k. Hof-Naturalienkabinet (now the NHMW) in 1863 survived].

Sandberger considered the possibility that *Chiton virgifer* may belong to the subgenus *Tonicia* Gray, 1847, but the lack of insertion plates (Fig. 2F, J) and the similarity with the other known species of *Lepidopleurus* allows attribution of this species to the family Leptochitonidae Dall, 1889. The solid and the coarse sculpture of the valves

are characteristic of the genus *Lepidopleurus* Risso, 1826, and *C. virgifer* was correctly attributed to this genus by all subsequent authors since Šulc (1934).

Šulc (1934) considered large tail valves (width of 18 mm) of *Lepidopleurus decoratus* Reuss, 1860 from the Middle Miocene of Pötzleinsdorf, Austria to be similar to *L. virgifer*. Additionally, these large valves of *L. decoratus* were also interpreted as similar to *L. subcajetanus* (d'Orbigny, 1852) by subsequent authors (*e.g.*, Laghi 1977, Bałuk 1984). Dell'Angelo & Palazzi (1986) considered *L. subcajetanus* a synonym of *Lepidopleurus virgifer*, as already suggested by Sacco (1897). An in-depth study of *L. subcajetanus* and the related species (*Gymnoplax orbigny* de Rochebrune, 1882 and *G. benoisti* de Rochebrune, 1882) has been made by Dell'Angelo *et al.* (2015a), who consider the species previously known as *Chiton subcajetanus* (including the large valves of *L. decoratus* of Šulc) a valid species, the oldest available name of which is *Lepidopleurus benoisti* (de Rochebrune, 1882). This species is surely very similar to *L. virgifer* (see the figures of the syntype of *Middendorffia subcajetana* and of *Gymnoplax benoisti* in Dell'Angelo *et al.* 2015a: pl. 2, figs 1–13, 18–20), but the sculpture is coarser in *L. benoisti*, with more pronounced growth lines, the dimensions are greater (W up to 18 mm in *L. benoisti*, Dell'Angelo *et al.* 2018a), the profile of the tail valve is different, with the postmucronal slope almost straight in *L. benoisti*, vs. concave behind the mucro in *L. virgifer*, and also the geographic and stratigraphic range is different (late Oligocene to middle Miocene of France, North Italy and the Paratethys for *L. benoisti*, vs. Oligocene of Germany for *L. virgifer*).

Another species of *Lepidopleurus* has been recently described from the Miocene (Tortonian) of northwest France, *L. pseudobenoisti* Dell'Angelo, Landau, Van Dingenen & Ceulemans, 2018b, that differs from *L. virgifer* by the strongly pronounced mucro of the tail valve and other characters that are summarized in a table for the three species *L. benoisti*, *L. pseudobenoisti* and *L. virgifer* in Dell'Angelo *et al.* (2018b: tab. 2).

Occurrence. – Lower–upper Oligocene: Germany: Waldböckelheim/Gienberg, Doberg/Böseberg, Weinheim/Zeilstück, Weinheim/Würzmühle (Sandberger 1859, Janssen 1978, this paper).

Order Chitonida Thiele, 1909

Suborder Acanthochitonina Bergenhayn, 1930

Superfamily Mopalioidae Dall, 1889

Family Lepidochitonidae Iredale, 1914

Genus *Lepidochitona* Gray, 1821

Type species. – *Chiton marginatus* Pennant, 1777 (= *Chiton cinereus* Linnaeus, 1767), by monotypy.

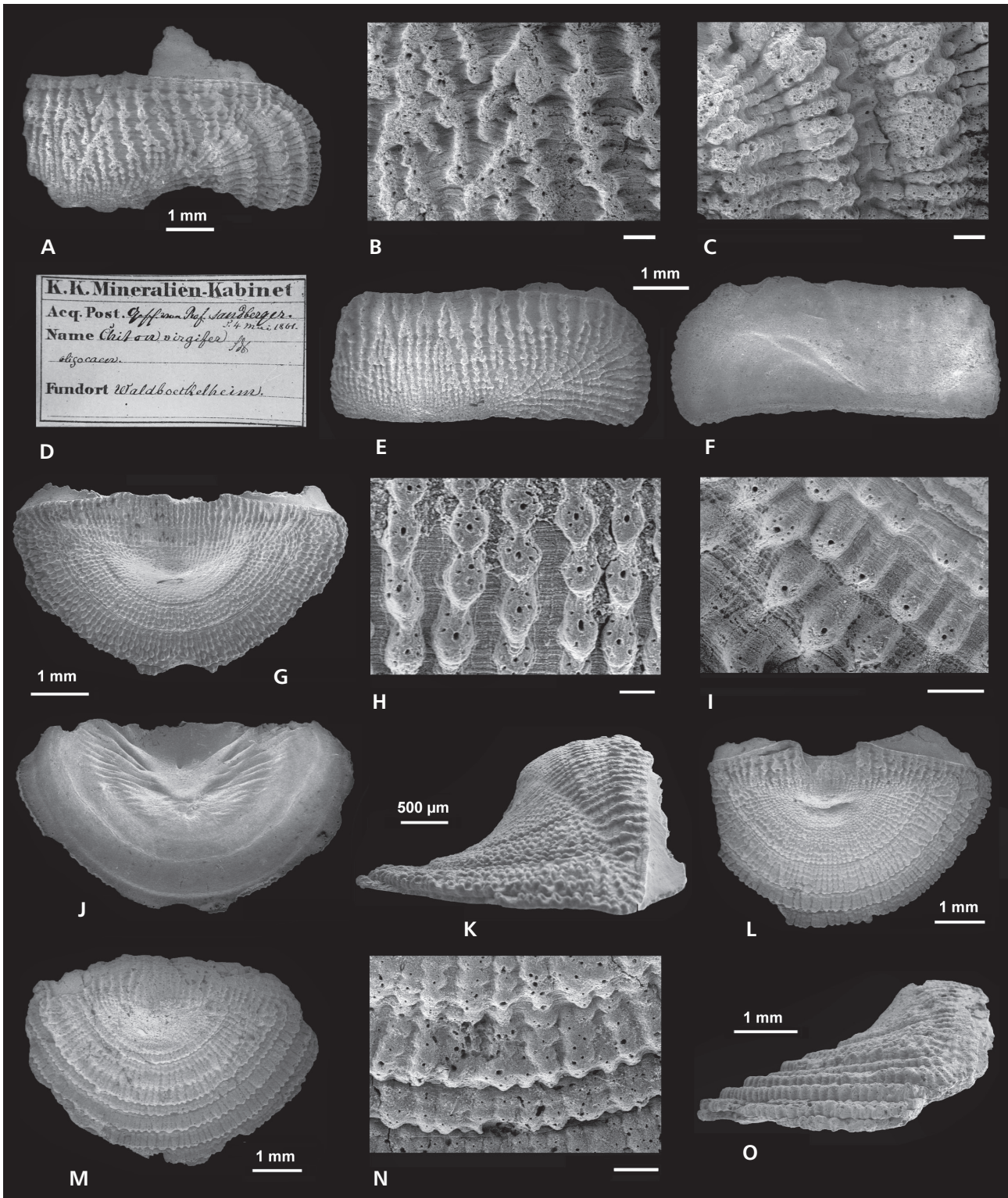


Figure 2. *Lepidopleurus virgifer* (Sandberger, 1859) from Waldböckelheim, Bad Kreuznach, Germany (Oligocene, Rupelian), syntypes (A–L); A–D – NHMW 1863/0017/0062a, intermediate valve, W 7.5 mm, dorsal view (A), close-up of surface ornamentation of central (B) and lateral (C) areas, and historical label (D); E–F – NHMW 1862/0012/0047a, intermediate valve, W 6 mm, dorsal (E) and ventral (F) views; G–K – NHMW 1863/0017/0062b, tail valve, W 5.5 mm, dorsal view (G), close-up of surface ornamentation of antemucronal (H) and postmucronal (I) areas, ventral (J) and lateral (K) views; L – NHMW 1863/0017/0062c, tail valve, W 5.6 mm, dorsal view; M–O – topotypic material, NHMW 1868/0001/0777, tail valve, W 6 mm, dorsal view (M), close-up of surface ornamentation of postmucronal area (N) and lateral view (O). Scale bars = 200 µm (B, C, N); 100 µm (I); 50 µm (H).

Remarks. – The genus is known from the Paleocene to the Recent (Sirenko 2006, Dell’Angelo *et al.* 2015b).

***Lepidochitona oligocaena* (Rolle, 1862)**

Figures 3A, 4A–O

- 1862 *Chiton oligocaenus*; Rolle, p. 213, pl. 1, figs 9–14.
- 1882 *Lepidopleurus oligocaenicus* (Roll.). – de Rochebrune, p. 57.
- 1957 *Ischnochiton oligocaenicus* Rolle. – Fischer, p. 17.
- 1978 „*Chiton*“ *oligocaenus* Rolle. – Janssen, p. 226.
- 1981 *Lepidochitona oligocaena* (Rolle). – Van Belle, p. 54.
- 2011 *Lepidochitona oligocaena* (Rolle). – Dell’Angelo *et al.*, p. 953.
- 2015b *Lepidochitona oligocaena* (Rolle). – Dell’Angelo *et al.*, p. 365.
- 2018a *Chiton oligocaenus* Rolle. – Dell’Angelo *et al.*, p. 11.

Material. – Syntypes NHMW 1858/0018/0255: 9 head (maximum W 2.7 mm), 36 intermediate (maximum W 2.8 mm), and 2 tail (maximum W 2.1 mm) valves (Fig. 4A–L), and NHMW 2011/0009/0006 (ex NHMW 1858/0018/0255): 1 intermediate, W 2.8 mm, and 1 tail valves, W 2.2 mm (Fig. 4M–O). All from a bulk sample of fossiliferous clay from Gaas that was donated to the NHMW in 1858 by Jean-Pierre S. de Grateloup. Bulk sample processed and studied by Friedrich Rolle (Rolle 1862: p. 214), then curator (“Custos-Adjunctus”) at k. k. Hof-Naturalienkabinet (now the NHMW).

Type horizon and locality. – “marnes bleues à *Natica crassatina*”, “stratis tertiariis oligocaenis” (Rolle 1862), Oligocene; now attributed to the Faluns de Gaas of Rupelian age (see *e.g.*, Lozouet 1985); Gaas (Larrat), Dax, Landes, France.

Description. – Original description (translated from Rolle 1862: pp. 213, 214): “Head valve of semi-circular outline, sloping evenly from the apex on all sides. Surface covered densely by warts, sometimes with a few (6–8) slightly raised radial ribs, sometimes without. The inside edge is formed by about 12 unequal teeth, separated by narrow cuts. Intermediate valves 3.8 mm wide, rounded at the apex, but not keeled. Usually they are indistinct divided into five fields, a median one, two paired outer ones and two inner ones; the two outer areas are slightly raised above the surface of the inner ones. They again are subdivided into two smaller fields, of which the outer pair is less elevated. All of these fields, the unpaired and four paired ones converge as against the posterior tip of the segment, like in all other chitons. The tail valve has an elongated, semi-circular outline, raised to an obtuse apex in the center. Above the apex [micro] the curvature [of

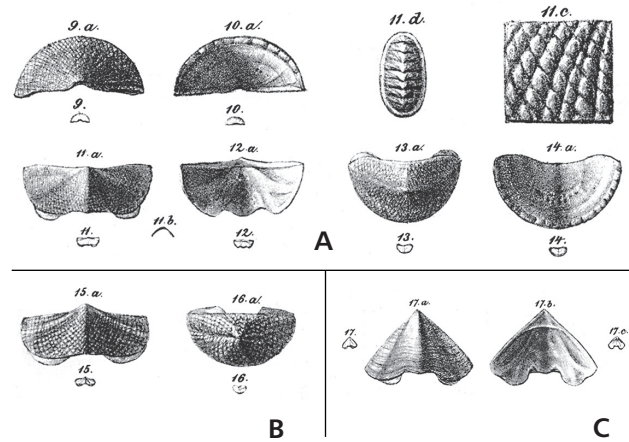


Figure 3. A – original figures of *Chiton oligocaenus* Rolle, 1862 (pl. 1, figs 9–14). • B – *Chiton reussi* Rolle, 1862 (pl. 1, figs 15–16). • C – *Chiton modestus* Rolle, 1862 (pl. 1, fig. 17).

the shell] is greater, below it is distinctly lower. Similar to the head valve, the inside edge is jagged; the number of teeth may well be *ca* 12–14. The surface of the segments is evenly covered with flat grains in a shagreen-like sculpture. Flat, sometimes more rectangular, sometimes more rounded grains or plates are separated by very fine grooves. Under a hundred times magnification, the grains appear flat and not of sharp form, but usually tend to rhombic [pattern] and placed particularly often in quincunx [pattern], so that four or nine [of them], *etc.* form a rhombus. In other places, such as the outer wall of the segments, however, there rather is sometimes an arrangement in rows that run more or less parallel to the margin.

Based on the largest valves, the animal reached about 3.5 mm in maximum width and may therefore have been about 5 millimeters long (= 2.3 Vienna lines.)”

Emended description: Head valve semi-circular, some radial folds (6–8) may be present. Intermediate valve rectangular, L/W = 0.41, rounded in anterior profile (Fig. 4E), highly elevated (H/W = 0.47), anterior margin almost straight or slightly sinuose, just a little concave in the jugum, side margins slightly rounded, posterior margin straight, apex not evident or just highlighted (Fig. 4D, G), lateral areas scarcely differentiated. Tail valve semi-circular, L/W = 0.57, anterior margin slightly sinuose, just a little concave in the jugum, micro subcentral, antimucronal and postmucronal slopes almost straight, just a little concave behind the micro (Fig. 4O).

Tegmentum entirely covered by irregularly arranged granules, very close each other, some coalescing, roundish in the head valves (Fig. 4C), more irregular and tending to rhomboidal in the other valves (Fig. 4H). Each granule with 8–12 aesthetes, of the same dimensions, often one (or more) of them centrally located (Fig. 4C, F, H). Diameter of the roundish granules in head valve *ca* 40–45 μm;

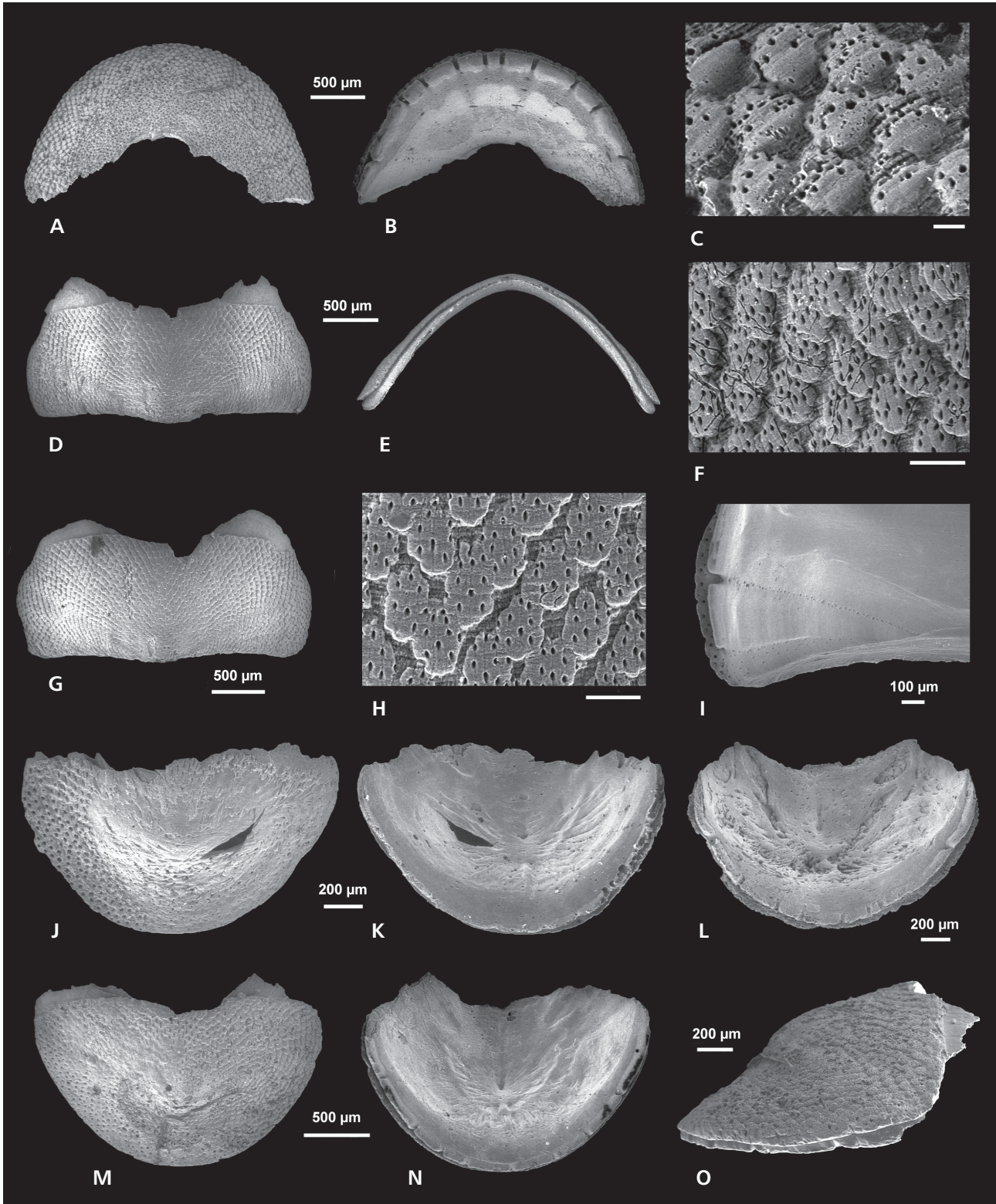


Figure 4. *Lepidochitona oligocaena* (Rolle, 1862) from Gaas, Landes, France (Oligocene, Rupelian); A–L – syntypes, NHMW 1858/0018/0255; A–C – head valve (1858/0018/0255b), W 2.7 mm, dorsal view (A), ventral view (B) and close-up of surface ornamentation (C); D–F – intermediate valve (1858/0018/0255e), W 2.7 mm, dorsal view (D), frontal view (E) and close-up of surface ornamentation (F); G–I – intermediate valve (1858/0018/0255f), W 2.8 mm, dorsal view (G), close-up of surface ornamentation of central area (H) and of internal surface (I); J–K – tail valve (1858/0018/0255d), W 1.6 mm, dorsal (J) and ventral views (K); L – tail valve (1858/0018/0255c), W 2.1 mm, ventral view; M–O – syntypes, NHMW 2011/0009/0006b, tail valve, W 2.2 mm, dorsal (M), ventral (N) and lateral (O) views. Scale bars = 50 µm (F, H); 20 µm (C).

maximum length of the rhomboidal ones in intermediate valves *ca* 50–68 µm.

Articulamentum with rounded apophyses not well preserved, separated by a wide jugal sinus, slit formula: 10–11 / 2 / 9–13, slits inequidistant, slit rays clearly visible in head and intermediate valves (Fig. 4B, I), teeth short.

Remarks. – The original description of Rolle is very detailed and complete, and the attribution of this species to the genus *Lepidochitona* Gray, 1821 by Van Belle (1981) is consistent.

De Rochebrune (1882: p. 57) considered *Chiton reussi* Rolle, 1862 a synonym of the present species: “La similitude parfaite des figures et des descriptions du *C. oligocaenicus* et du *C. Reussi* (Rolle, loc. cit.) nous oblige à les considerer comme étant de la même espèce, et à donner le Reussi en synonymie”, which was followed by Van Belle (1981) and Dell’Angelo *et al.* (2011). The study of the type material of *Chiton reussi* present in the NHMW collection permit us to consider the latter as a valid different species (see below).

The only other chiton species reported from the European Oligocene and attributed to *Lepidochitona* (Janssen 1978, Dell’Angelo *et al.* 2011) is *Lepidochitona corrugis* (Boettger, 1869) from the Oligocene of Waldböckelheim (Germany). This species differs from *L. oligocaena* by the coarser sculpture of granules arranged in rows, the elevated lateral areas of the intermediate valves, which are separated from the central areas by a diagonal fold, the different shape of the more beaked intermediate valves, and the slit formula (8 / 2 / 8 in *L. corrugis* vs. 12 / 2 / 12–14 in *L. oligocaena*).

Rolle also noted the similarity of his species with *Chiton lepidus* Reuss, 1860 from the clay of Rudoltice in Bohemia, but this species, which is present in the NHMW collection and will be discussed in the next part of this work, differs from *L. oligocaena* by several characters *e.g.*, the intermediate valves being semicarinate in anterior profile and with low elevation (not rounded and moderately elevated as in *L. oligocaena*), and the granules structured with a central macroaesthete and numerous microaesthetes (not with aesthetes of the same dimensions, as in *L. oligocaena*).

Also the well-known extant Mediterranean and Atlantic species, *Lepidochitona cinerea* (Linnaeus, 1767), shows some similarity with the present species, mainly in the subquadrangular granules covering the tegmentum (see Dell’Angelo *et al.* 2013: pl. 8, fig. d), but there are a lot of differences that justify the separation of the two species (*e.g.*, the shape of intermediate valves, more elevated, subcarinate in anterior profile, with an evident apex in *L. cinerea* vs. not beaked in *L. oligocaena*, the slit formula, 8–10 / 1 / 8–12 with a single slit in intermediate valves in *L. cinerea* vs. 12 / 2 / 12–14 in *L. oligocaena*).

Occurrence. – Middle Oligocene: northeastern Atlantic (Rupelian); Gaas, France (Rolle 1862, this paper).

***Lepidochitona reussi* (Rolle, 1862)**

Figures 3B, 5A–O

1862 *Chiton reussi*; Rolle, p. 214, pl. 1, figs 15, 16.

1882 *Chiton reussi* Roll. – de Rochebrune, p. 57 [in synonymy of *Lepidopleurus oligocaenicus*].

non 1893 *Chiton reussi* Rzehak (non Rolle, 1862) – Rzehak, p. 171 [an undeterminable species, considered by Rzehak = *Chiton siculus*? Reuss].

non 1900 *Chiton reussi* Procházka (non Rolle, 1862) – Procházka, p. 72, 118, fig. 29 [= *Lepidopleurus cajetanus* (Poli, 1791), *fide* Šulc, 1934, p. 4].

non 1910 *Chiton reussi* (non Rolle, 1862) – Veters, p. 157 [= *Acanthochitona faluniensis* (de Rochebrune, 1882), *fide* Kroh, 2003, p. 134].

1969 *Middendorfia* (sic!) *reussi* Rolle. – Rado, p. 192, pl. 2, fig. 31.

1978 „*Chiton*“ *reussi* Rolle. – Janssen, p. 226.

1981 *Chiton reussi* Rolle. – Van Belle, p. 60 [in synonymy of *Lepidopleurus oligocaenicus*].

2018a *Chiton reussi* Rolle. – Dell’Angelo *et al.*, p. 11.

Material. – Syntypes: NHMW 2011/0009/0002, 1 tail valve, W 1.8 mm; NHMW 2011/0009/0003, 3 intermediate, maximum W 2.3 mm, and 1 tail, W 2 mm (Fig. 5G–O); NHMW 2011/0009/0004, 1 intermediate valve, W 2.4 mm; and NHMW 2011/0009/0008: 5 intermediate valves, maximum W 2.1 mm (Fig. 5A–F). All from a bulk sample of fossiliferous clay from Gaas that was donated to the NHMW in 1858 by Jean-Pierre S. de Grateloup. Bulk sample processed and studied by Friedrich Rolle (Rolle 1862: p. 214), then curator (“Custos-Adjunctus”) at k. k. Hof-Naturalienkabinet (now the NHMW). Originally registered under number NHMW 1858/0018/0255, a lot containing multiple containers (and multiple species); lot split in 2011 in order to be able to refer to the individual sub-lots.

Type horizon and locality. – “marnes bleues à *Natica crassatina*”, “stratis tertiariis oligocaenis” (Rolle 1862), Oligocene; now attributed to the Faluns de Gaas of Rupelian age (see *e.g.*, Lozouet 1985); Gaas, Dax, Landes, France.

Description. – Original description (translated from Rolle 1862: pp. 214, 215): “From this species several intermediate valves and one tail valve were available to me. In shape and sculpture they are very close to those of *Chiton oligocaenus*, only the grains [tubercles/warts] are less common and larger; there are perhaps only half as many as in the previous species. The intermediate

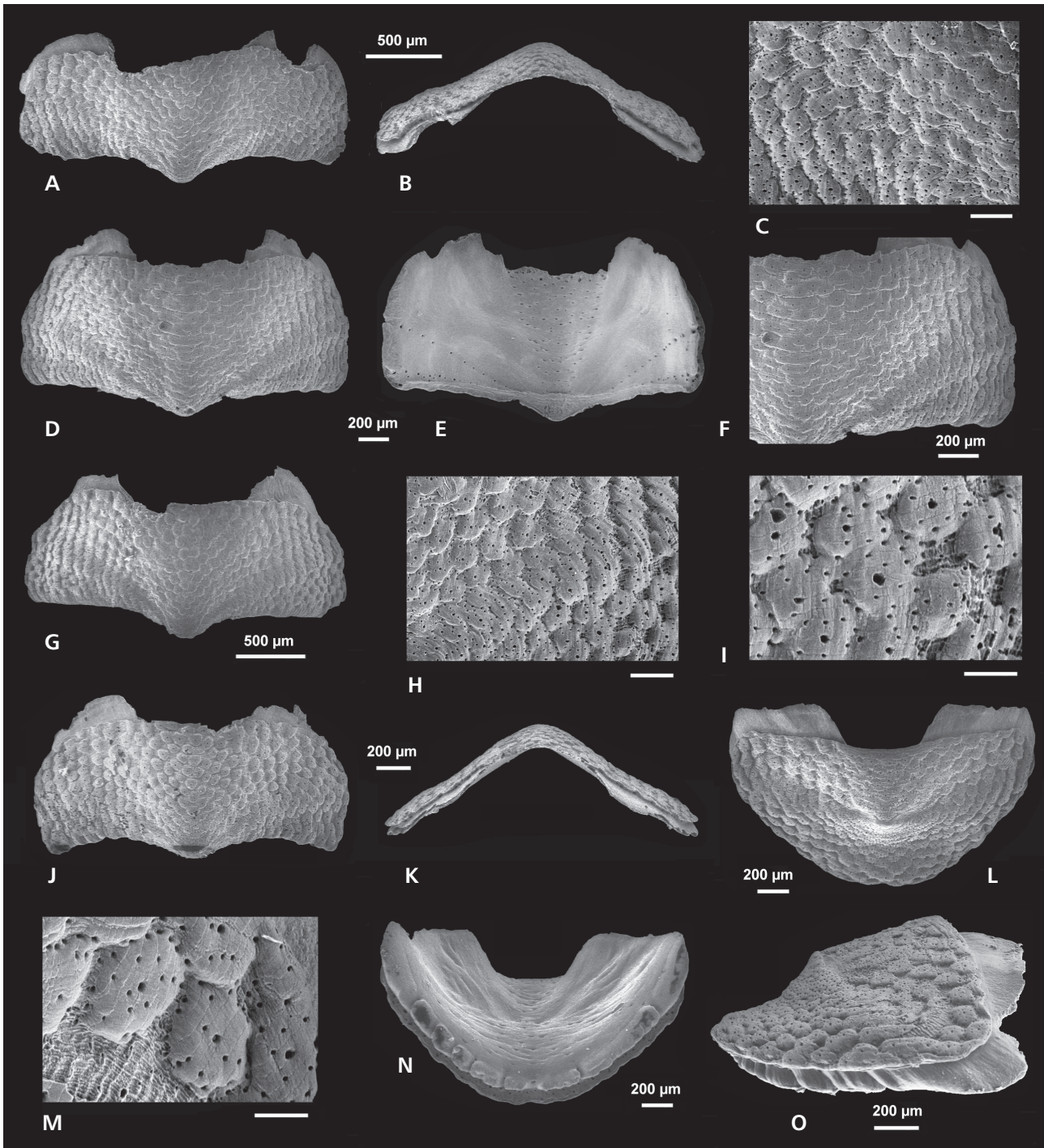


Figure 5. *Lepidochitona reussi* (Rolle, 1862) from Gaas, Landes, France (Oligocene, Rupelian); A–F – syntypes, NHMW 2011/0009/0008; A–C – intermediate valve (2011/0009/0008a), W 2.1 mm, dorsal view (A), frontal view (B) and close-up of surface ornamentation of lateral areas (C); D–F – intermediate valve (2011/0009/0008b), W 2.1 mm, dorsal (D, F) and ventral (E) views; G–O – syntypes, NHMW 2011/0009/0003; G–I – intermediate valve (2011/0009/0003a), W 2.3 mm, dorsal view (G), close-up of surface ornamentation of the diagonal fold separating central and lateral areas (H) and of granules (I); J–K – intermediate valve (2011/0009/0003c), W 1.9 mm, dorsal (J) and frontal (K) views; L–O – tail valve (2011/0009/0003b), W 2 mm, dorsal view (L), close-up of granules (M), ventral (N) and lateral (O) views. Scale bars = 100 µm (C, H); 50 µm (I, M).

valves, 2.8 mm wide, are also keeled in the middle and also divided into five areas, and the outer pair again in two minor areas. Of the areas the inner one is significantly

elevated. The tail valve is similar to that of *Chiton oligocaenus* but wider, the center is inflated to a blunt apex from which a flat fold radiates to each side.”

Emended description: Head unknown. Intermediate valve rectangular (Fig. 5A, D), carinate in anterior profile, moderately elevated ($H/W = 0.28$, Fig. 5B), anterior margin straight or slightly concave, lateral margins rounded, posterior margin slightly concave at both sides of the prominent apex, lateral areas separated from the central areas by a diagonal fold. Tail valve less than semicircular (Fig. 5L), $L/W = 0.45$, anterior margin slightly concave, mucro subcentral, anterior slope straight, posterior slope concave (Fig. 5O).

Tegmentum entirely covered by irregularly arranged and very close to each other roundish granules, not much elevated, some coalescing, diameter up to 83 μm in intermediate valves (Fig. 5C), 96 μm in tail valves (Fig. 5M); each granule bearing a more or less central macroaesthete, and 6–10 microaesthetes arranged irregularly along the margin (Fig. 5I, M), additional microaesthetes are found between the granules.

Articulamentum with apophyses small and triangular in intermediate valves, trapezoidal in tail valve, slit formula $? / 2 / 8-9$, slits deep, teeth strong and very uneven in width, eaves porous.

Remarks. – All intermediate valves and the tail valves of this species present in the NHMW collection have an identical ornamentation (with similar granules and arrangement of aesthetes), and are thus considered to be conspecific here. Like in the previous species, the attribution to the genera *Lepidochitona* Gray, 1821 is consistent for this species.

There is a certain variability in the shape of intermediate valves (the L/W ratio ranges from 0.36 to 0.46, and likewise the carinate anterior profile, with $H/W = 0.28-0.33$).

This species differs from the preceding in several characters: the different shape of the intermediate valves (posterior margin slightly concave at both sides of the prominent apex in *L. reussi*, vs. almost straight without apex in *L. oligocaena*) and tail valves ($L/W = 0.45$ in *L. reussi*, vs. 0.57 in *L. oligocaena*); intermediate valves carinate in anterior profile in *L. reussi*, vs. rounded in *L. oligocaena* ($H/W = 0.28-0.33$, vs. 0.47 in *L. oligocaena*); smaller number of slits of tail valve (8–9, vs. 12–14 in *L. oligocaena*); a different shape and structure of the granules (roundish granules with a central macroaesthete, and 6–10 microaesthetes vs. nearly rhomboidal granules with aesthetes of the same dimension in *L. oligocaena*).

Therefore, we consider *Lepidochitona reussi* (Rolle, 1862) a valid species.

Lepidochitona corrugis (Boettger, 1869) differs from *L. reussi* by the coarser sculpture, the elevated lateral areas of the intermediate valves, the more beaked intermediate valves, and by its granules which are arranged in rows (Janssen 1978).

Lepidochitona lepida (Reuss, 1860) from the clay of Rudoltice in Bohemia is a different species as well, and a few valves not well preserved are deposited at NHMW. Unfortunately, none of the chitons described by Reuss is present at NHMW, which is surprising since much of Reuss' other material is present, particularly foraminifera and ostracods. *Lepidochitona lepida* differs from *L. reussi* by the smaller granules arranged in longitudinal striae in the jugal area, the more evident apex and the different geographic and stratigraphic range, middle Miocene of Paratethys for *L. lepida* vs. Oligocene (Rupelian) of Aquitaine Basin, France for *L. reussi*.

The most similar *Lepidochitona* species is the Mediterranean *L. monterosatoi* Kaas & Van Belle, 1981, regarding the shape of the intermediate valves and tegmental structure. It can be distinguished by, e.g., the arrangement of the granules in curved and diverging longitudinal series on the pleural area of the intermediate valves, the different shape of the tail valve (with the anterior margin being slightly convex, and a different profile), the slit formula ($8 / 1 / 11$ in *L. monterosatoi* vs. $? / 2 / 8-9$ in *L. reussi*).

Occurrence. – Middle Oligocene: northeastern Atlantic (Rupelian); Gaas, France (Rolle 1862, this paper).

Family Tonicellidae Simroth, 1894

Genus *Tonicella* Carpenter, 1873

Type species. – *Chiton marmoreus* Fabricius, 1780, by subsequent designation (Dall 1878).

Remarks. – The genus is known from the Eocene to the Recent (Dell'Angelo *et al.* 2018b).

Tonicella modesta (Rolle, 1862) comb. nov.

Figures 3C, 6A–I

1862 *Chiton modestus*; Rolle, p. 215, pl. 1, fig. 17.

1882 *Tonicia modesta* (Roll.). – de Rochebrune, p. 56.

1981 *Chiton modestus* Rolle. – Van Belle, p. 51 [*gen. inquir.*].

2011 *Chiton modestus* Rolle. – Dell'Angelo *et al.*, p. 953.

2018a *Chiton modestus* Rolle. – Dell'Angelo *et al.*, p. 11.

Material. – Holotype NHMW 2011/0009/0001: 1 intermediate valve (obviously valve II), $W 2.4 \text{ mm}$ (Fig. 6A–E). From a bulk sample of fossiliferous clay from Gaas that was donated to the NHMW in 1858 by Jean-Pierre S. de Grateloup. Bulk sample processed and studied by Friedrich Rolle (Rolle 1862: p. 214), then curator (“Custos-Adjunctus”) at k. k. Hof-Naturalienkabinet (now the NHMW). Originally registered under number NHMW 1858/0018/0255, a lot containing multiple containers (and

multiple species); lot split in 2011 in order to be able to refer to the individual sub-lots.

Additional material: NHMW 2011/0009/0005 (ex NHMW 1858/0018/0255), 1 head valve, W 2.1 mm (Fig. 6F–I). Also from the bulk sample donated by Grateloup, but not originally included in *Chiton modestus* by Rolle (was stored as unidentified “*Chiton*” species), and, therefore, not part of the type series.

Type horizon and locality. – “marnes bleues à *Natica crassatina*”, “stratis tertiariis oligocaenis” (Rolle 1862), Oligocene; now attributed to the Faluns de Gaas of Rupelian age (see e.g., Lozouet 1985); Gaas, Landes, France.

Description. – Original description (translated from Rolle 1862: p. 215): “Only a single segment is available to me, which I think is the second one because of its beak-like, backwards highly elongated shape. The

surface is almost smooth and shows only some weak growth increments parallel to the frontal margin. – The segment is rounded bent in the middle, but not really keeled. Laterally there is a small marginal area on each side. These two are significantly elevated above the rest of the surface and are separated rather sharply. Width 2.8 mm.”

Emended description: Intermediate valve triangular (Fig. 6A), strongly beaked, $L/W = 0.67$, semicarinate in anterior profile (Fig. 6E), highly elevated ($H/W = 0.55$), anterior margin convex, posterior margin almost straight on both sides of the prominent apex, forming an angle of 103° , lateral areas strongly delimited from central area by a diagonal fold.

Tegmentum smooth, displaying very fine microgranulation (Fig. 6C).

Articulamentum with apophyses small and triangular (Fig. 6B), 1 slit for each side (with another just visible close to posterior margin, Fig. 6D), slit rays clearly visible.

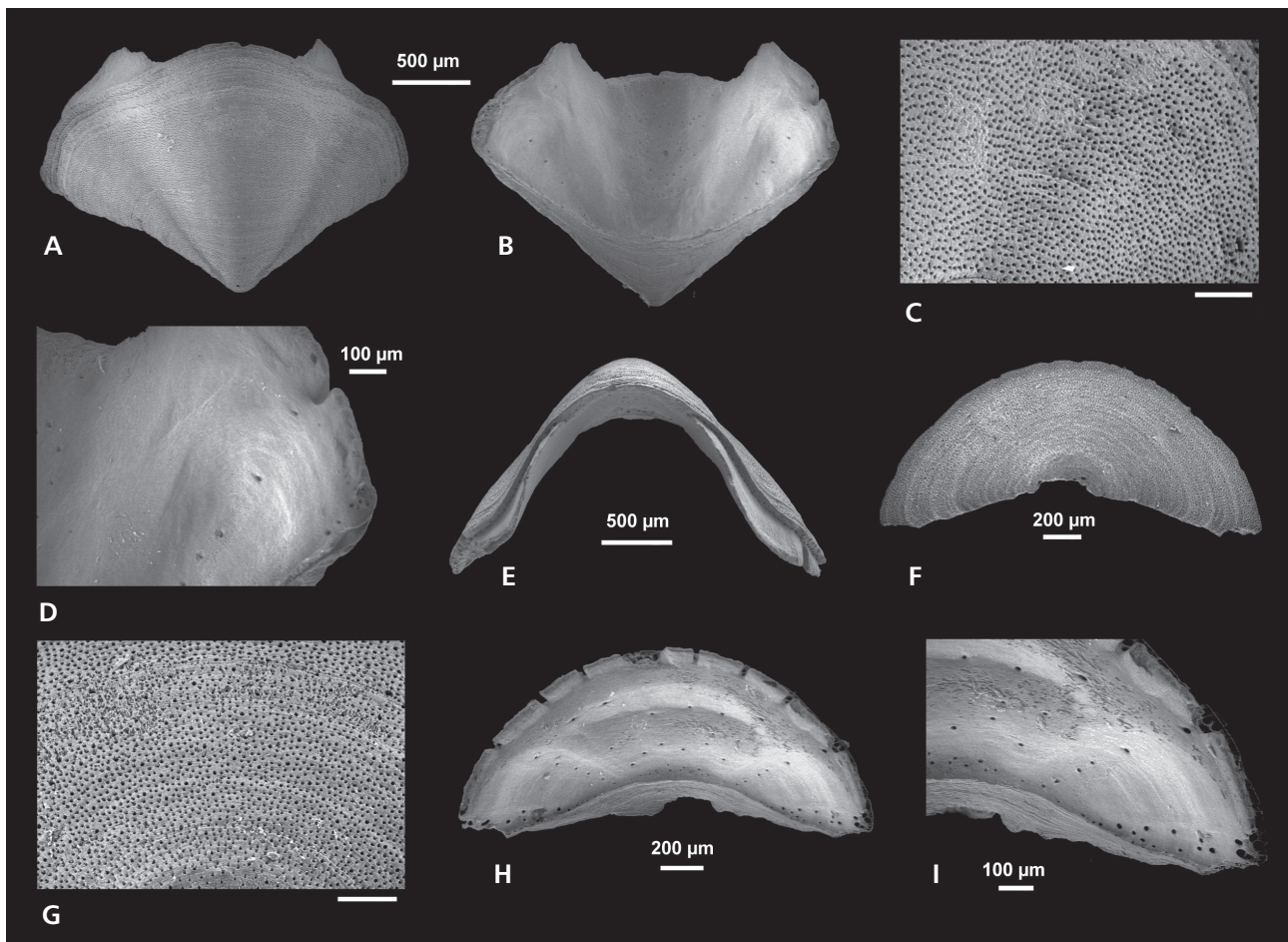


Figure 6. *Tonicella modesta* (Rolle, 1862) from Gaas, Landes, France (Oligocene, Rupelian); A–E – holotype NHMW 2011/0009/0001, intermediate valve, W 2.4 mm, dorsal view (A), ventral view (B, D), close-up of surface ornamentation of lateral area (C) and frontal view (E); F–I – topotypic material, NHMW 2011/0009/0005, head valve, W 2.1 mm, dorsal view (F), close-up of surface ornamentation (G) and ventral view (H, I). Scale bars = 100 µm (C, G).

Remarks. – The original description of Rolle is detailed and complete, and the morphology of the material is consistent with the present attribution to the genus *Tonicella*, characterized by a smooth to microgranulose tegmentum, slit formula: many / 1 / many, eaves generally porous, and lack of extra-pigmentary eyes (Kaas & Van Belle 1985).

In addition to the holotype the NHMW collection contains also a head valve of *Tonicella* (NHMW 2011/0009/0005) from Gaas (Fig. 6F), that we consider conspecific to *T. modesta* due to its tegmental surface. It is smooth and shows arrangement of aesthetes (Fig. 6G) that is similar to that of the holotype. This valve is well preserved and shows 10 slits in the articulamentum (Fig. 6H), the slit rays well visible (Fig. 6I).

Four chiton species attributed to *Tonicella* are reported from the European Palaeogene: *T. tenuissima* (Sandberger, 1859) from the Oligocene (Rupelian) of Waldböckelheim (Germany), *T. implumis* Bielokrysz, 1999 from the upper Eocene beds near Dnepropetrovsk (Ukraine), *T. lira* Cherns & Schwabe, 2017 from the upper Oligocene of France, and *T. redoniensis* Dell’Angelo, Landau, Van Dingenen & Ceulemans, 2018b from the Miocene (Tortonian) of France.

The separation of the *Tonicella* species is not always easy, often the identifying characters are not so clear and overlap in different species, and moreover for some species the head and tail valves are not known. The shape of the intermediate valve (holotype) of *T. modesta* is different from that of the other three species of *Tonicella* reported from the European Palaeogene. Moreover, the number of slits in the head valve differs between *T. tenuissima* (9, according to Janssen 1978) and *T. modesta* (10). *Tonicella implumis* differs from *T. modesta* by the very elongate shape of the intermediate valves (width *ca* three times the length), the central and lateral areas which are not separated, and the head valve with weak radial furrows, and 6–9 slits (*vs.* 10 in *T. modesta*) (Bielokrysz 1999). *Tonicella lira* differs from *T. modesta* by the rugose tegmentum in the lateral areas of the intermediate valves, the fairly straight side margins, and the nearly straight posterior margin with an indistinct apex (Cherns & Schwabe 2017). *Tonicella redoniensis*, differs by the

rectangular shape of the intermediate valves, the almost straight anterior margin, the posterior margin which is almost straight at both sides of the prominent apex (not forming an angle as in *T. modesta*) (Dell’Angelo *et al.* 2018b).

Rolle (1862) compared his new species with *Boreochiton ruber* (Linnaeus, 1767), a living species from the North Atlantic, attributed in the past to the genus *Tonicella*. In *Boreochiton ruber* the shape of intermediate valves is clearly different, more rectangular and elongate, the lateral areas are little or not elevated, poorly defined. The same comparison is also applicable to the other extant *Tonicella* species from North Atlantic, *T. marmorea* (Fabricius, 1780), which features head and intermediate valves that are similar to those of *Boreochiton ruber* (Ferreira 1982, Kaas & Van Belle 1985). Both extant species are scarce in the fossil record, being known only from the Pleistocene of Sweden, Norway, Svalbard (Brogger 1901; Antevs 1917, 1928; Feyling-Hanssen 1955), Alaska (Allison 1973) and Italy (Dell’Angelo & Giusti 1997).

Occurrence. – Middle Oligocene: northeastern Atlantic (Rupelian); Gaas, France (Rolle 1862, this paper).

Conclusions

Four species of chitons from the Oligocene of Germany and France are present in the NHMW collection, including also part of the type material (holotype and syntypes) of each of these species. The status of all the studied species is reported in Tab. 1.

Six species of Polyplacophora have been originally described from the Oligocene of Gaas (France), the three by Rolle (1862) discussed herein (*Lepidochitona oligocaena*, *L. reussi* and *Tonicella modesta*), and three by de Rochebrune (1882), previously reported without descriptions and figures by Benoist (1881): *Tonicia waltebledi*, *Tonicia gaasensis*, and *Lepidopleurus daubrei*. These three last species are poorly known, the original descriptions are inadequate, no modern revision is available, and the generic attribution is considered

Table 1. Emended nomenclature of Oligocene chiton species housed at the NHMW.

Original taxon	Current taxon	Type
<i>Chiton virgifer</i> Sandberger, 1859	<i>Lepidopleurus virgifer</i> (Sandberger, 1859)	Syntypes
<i>Chiton oligocaenus</i> Rolle, 1862	<i>Lepidochitona oligocaena</i> (Rolle, 1862)	Syntypes
<i>Chiton reussi</i> Rolle, 1862	<i>Lepidochitona reussi</i> (Rolle, 1862)	Syntypes
<i>Chiton modestus</i> Rolle, 1862	<i>Tonicella modesta</i> (Rolle, 1862)	Holotype

doubtful (Van Belle 1981), needing further investigation. Further studies are required to define the status of the three species described by de Rochebrune from Gaas, to verify if these are all valid species, or if some of them are referable to the species described by Rolle from the same locality 21 years earlier.

The presence of *Lepidopleurus virgifer* (Sandberger, 1859) from Waldböckelheim (Germany) in the NHMW collection is of great importance because the type material was considered lost previously (*vide* Janssen 1978), and the presence of potential syntypes at NHMW contributes to a better knowledge of this species from the Oligocene of Germany.

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