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# A new family of giant Jurassic–Cretaceous littorinoid gastropods from the northern Tethys shelf

MATHIAS HARZHAUSER and SIMON SCHNEIDER



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The giant, up to 40 cm high littorinoid gastropods from the Middle Tithonian to Berriasian carbonates of the Alpine-Carpathian northern Tethys margin are assigned to the genus *Leviathania*. The genus is distributed from Spain to the Caucasus. Some species formed dense populations in the wide-spread, highly productive lagoonal environments situated on the carbonate platforms of Ernstbrunn (Austria), Mikulov, Štramberk (both Czech Republic), and Nyzhniv (Ukraine). The conspicuous morphology, comprising very large shells with strongly angulated whorls and especially the phaneromphalous umbilicus exclude the traditional attributions of this genus to the families Purpurinidae and Purpuroideidae. Therefore, we establish the new family Leviathaniidae for the type genus *Leviathania*. The family comprises the largest pre-Cenozoic gastropods, represented by a yet unnamed gigantic *Leviathania* species from the latest Tithonian or early Berriasian of Ukraine. The gastropods are tentatively assumed to have fed omnivorous, i.e., on a mixed detrital-algal diet, based on comparable population densities as the large modern queen conch *Lobatus gigas* from the Caribbean Sea.

Key words: Mollusca, Gastropoda, *Leviathania*, carbonate platform, body size, Jurassic–Cretaceous, Tethys, Tithonian, Ernstbrunn Limestone, Austria.

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## Introduction

Approximately 50 km to the north of Vienna a chain of salient hills arises, which extends in north-eastern direction, crosses the Austrian-Czech Republic border, and finally reaches the river Thaya (Fig. 1). Several of these hills are formed by massive, light-coloured, fossiliferous carbonate rocks, known as the Ernstbrunn Limestone since the publication of Boué (1830), and dated as Middle to Late Tithonian based on ammonite biostratigraphy (Zeiss and Hofmann 2001; Fig. 2). For more than 200 years, people have been collecting fossils from this limestone in the surroundings of Ernstbrunn (Haidinger 1782), and the gastropods discussed herein may have been among the first species that struck their eyes, simply because of their impressive size of up to 30 cm. The species was named *Pterocera gigantea* and first described from the Ernstbrunn Limestone by Makowsky (1874) based on a single internal mould from Bergen (now Perná) north of Nikolsburg (now Mikulov; southern Moravia, Czech Republic). Few years later, comparable fossils were also recorded from the Tithonian to Berriasian rocks of the Nyzhniv (formerly Niżniów) Formation of southern Ukraine (Fig. 1) and thoroughly described by Alth (1881, 1882). However, he and later authors attributed their finds to a different, stratigraphically much older species of *Purpuroidea* Lycett, 1848. Herein, we provide an update of the taxonomy and comprehensive re-description of the species from the Ernstbrunn Limestone, including hitherto unknown characters of the external shell surface and the umbilicus. For the first time, the palaeoecology of these gastropods is evaluated in context of their environment and compared to the life habits of modern taxa of similar size.

*Institutional abbreviations*.—NHMW, Natural History Museum Vienna, Austria; MHNG, Muséum d'histoire naturelle et Musée d'histoire des sciences de la Ville de Genève, Switzerland.

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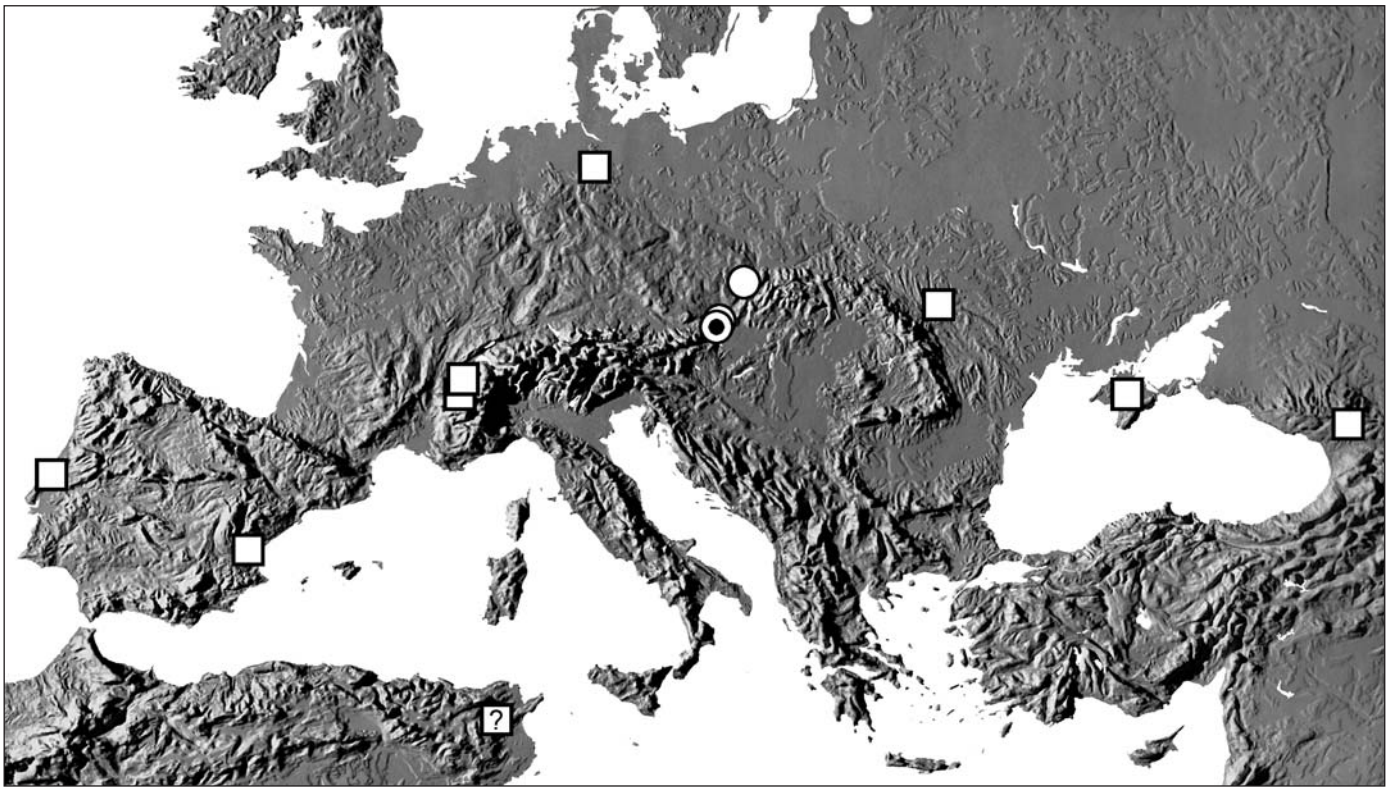



Fig. 1. Geographical overview of Europe. The type locality (circle with black dot) and occurrences (circles) of *Leviathania gigantea* (Makowsky, 1874) and the occurrences of *Leviathania* spp. (squares) are indicated. African occurrences need verification (?).

# Geological setting

**Ernstbrunn Limestone.**—The Ernstbrunn Limestone forms several isolated blocks within the Waschberg-Ždánice Unit, which is a SW-NE trending, tectonically delimited area representing the most distal Alpine-Carpathian Nappe (Fig. 1), and is regarded as the sole structural element that directly connects the Alps and Carpathians at surface. During the late Alpine orogeny, the rocks of the Waschberg-Ždánice Unit were pushed northward onto the sediments of the North Alpine and Carpathian foreland basins; they were in turn overthrust by the Rhenodanubian Flysch from the south (Wessely 2006). As a result of these movements, large blocks of Upper Jurassic to Palaeogene rocks were scoured off the autochthonous strata below the thrusted nappes, dragged to surface, and are now preserved as tectonic klippen, surrounded by fine-grained siliciclastics of Neogene age.

The oldest of the klippen are formed by two closely related, highly fossiliferous lithostratigraphic units. The Kimmeridgian to Upper Tithonian Klentnice Beds consist of a variety of mixed siliciclastic-carbonate shallow water facies. From the Middle Tithonian onwards, they are locally replaced by or intercalate with the pure carbonates of the Ernstbrunn Limestone, but still persist as a lateral equivalent of the newly developed carbonate platform until the end of the Tithonian (Fig. 2). At top, both strata are capped by erosion.

Major portions of the Ernstbrunn Limestone preserve carbonate skeletons but fossils can usually not be mechanically separated from the matrix. Rarely, shells have been exposed by natural weathering in karst fissures. However, the quarries of Dörfles have become famous for their abundant, large-sized internal moulds of epidiceratids, cardioids, and gastropods, including the giant *Leviathania* described herein. Besides Dörfles, these huge gastropods are known from the Ernstbrunn Limestone from the historical Marienmühle Quarry at Mikulov (Nikolsburg) and from Perná (Bergen) north of Mikulov.

**Štramberk Limestone**.—Widely equivalent un-rooted carbonate rocks of Late Tithonian to Berriasian age are found in and around the well-known Štramberk quarry in northern Moravia (Czech Republic), being part of the Silesian Nappe of the Outer Carpathians, a flysch nappe consisting mainly of Cretaceous sediments. At the type locality, the Štramberk Limestone is severely faulted and locally mingled with different strata of Cretaceous age. Two contrasting hypotheses exist, which try to explain the formation of these rocks and their relation to the Cretaceous sediments and the surrounding flysch deposits. The first theory, mainly established by Eliaš (1970, 1979), considers all Jurassic rocks, including the kilometre-sized one of Štramberk, as olistolithes that were deposited as over-sized components of the Chlebovice Conglomerate, which is a local member of the Těšin-Hradiště Formation. The second scenario, supported by Houša (1975, 1989), regards the Jurassic rocks as true tectonic klippen, and the Štramberk Limestone as well as the various Cretaceous

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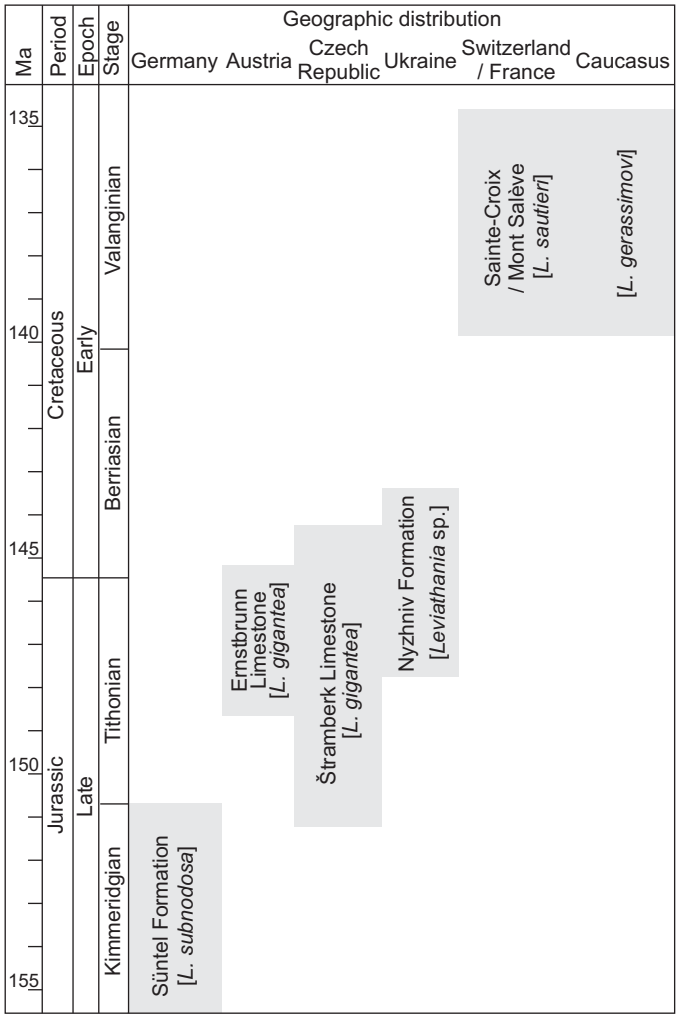



Fig. 2. Schematic stratigraphic positions of the strata yielding species of *Leviathania* discussed in the text. Please note that lower and upper limits of most of these strata are tentative.

rock types are considered separate lithostratigraphic units (Vašíček and Skupien 2004).

Although both Štramberk and Ernstbrunn limestone preserve more or less the same flora and fauna, the relative abundance of taxa differs strongly between these two occurrences, since most of the fossils are found in different areas of the respective carbonate platforms. While major portions of the Ernstbrunn Limestone consist of variable lagoonal facies, the Štramberk Limestone is mainly composed of reef and fore reef facies. Lagoonal carbonates, and consequently also the giant gastropods, are relatively scarce at Štramberk.

**Nyzhniv (Niżniów) Formation**.—In contrast to all other similar strata of the circum-Carpathian region at surface the Upper Tithonian to Lower Berriasian limestone beds of the Nyzhniv Formation in southern Ukraine are preserved in the form of autochthonous, extra-Carpathian deposits that onlap the southern margin of the Eurasian continent (Gutowski et al. 2005). The succession of the Nyzhniv Formation starts with a conglomerate, exemplifying the transgression of the Late Tithonian Tethys Sea onto a relief of Palaeozoic rocks. Gradually, the siliciclastic sediments pass into a marginal carbonate ramp (Gutowski et al. 2005). Only the most proximal parts of the formation have been preserved at outcrop, hardly exceeding 20 m in thickness. The carbonates are capped by erosion and overlain by Upper Cretaceous strata. Similar to the Ernstbrunn Limestone, the Nyzhniv Formation is composed of different lagoonal facies, and thus also yields a similar fauna including giant *Leviathania* gastropods (Alth 1881, 1882). Based on microfauna, the formation has been dated as uppermost Jurassic to earliest Cretaceous (Gutowski et al. 2005), and is thus at least in part slightly younger than the Ernstbrunn Limestone (Fig. 2).

# Material and methods

More than 90 specimens of *Leviathania* from the Ernstbrunn Limestone are stored in NHMW. All specimens are preserved as casts or moulds. The original cavities of the shells are perfectly filled by sediment whereas the original shell wall is usually completely dissolved without having been replaced by sediment or pseudomorphotic calcite. Therefore, it is possible to produce silicone moulds, representing the former shell, allowing insights in the internal architecture of the gastropod shell. Specimens labelled as *Natica* (?) *subnodosa* Roemer, 1836 from its type area in northern Germany, and several other species, traditionally placed in the Purpurinidae Zittel, 1895 or Purpuroideidae Guzhov, 2004, are present in the collections of the NHMW and have been studied for comparison.

# Systematic palaeontology

## Class Gastropoda Cuvier, 1795

## Subclass Caenogastropoda Cox, 1960

## Order Littorinimorpha Golikov and Starobogatov, 1975

## Superfamily Littorinoidea Children, 1834

## Family Leviathaniidae nov.

*Type genus*: *Leviathania* Pčelincev, 1927.

*Diagnosis*.—Large sized shells with gradate spire and globular last whorl with wide sutural ramp. Sculpture consisting of nodes, which are confined to the shoulder. In many species, the nodes are only present on the spire whorls, if developed at all, whilst a bulge-like keel appears on the last whorl. Sculpture may also be completely reduced to a keel-like shoulder. No axial sculpture known so far. Umbilicus phaneromphalous. The inner wall of the umbilicus has a strong concavity reflecting a central swelling of the inner lip; a weak anterior canal is present. Protoconch unknown.

*Remarks*.—The species attributed to *Leviathania* and its monogeneric family have usually been classified within the Purpurinidae Zittel, 1895 (e.g., Wenz 1939) or Purpuroidei-

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dae Guzhov, 2004. The main argument for this assignment seems to have been the large last whorl and the angulated whorls. Kaim (2004) provided a revised diagnosis of the type genus of the Purpurinidae, which characterises members of this family as moderately sized with prominent axial and spiral sculpture. The umbilicus is reduced to a chink, which is covered by a thin inner lip. Numerous nominal species of *Purpurina* d'Orbigny, 1850 have been described by Eichwald (1868), Hudleston (1888), Brösamlen (1909), and Kaim (2004). The morphology of these taxa matches the diagnosis of *Purpurina* by Kaim (2004) and clearly excludes a close relation with the Leviathaniidae fam. nov. A revision of the family Purpurinidae Zittel, 1895 was presented by Guzhov (2004) who includes the genera *Angularia* Koken, 1892*, Eucycloidea* Hudleston, 1888, *Moerckeia* Böhm, 1895, *Pseudoscalites* Kittl, 1894, *Purpurina* d'Orbigny, 1850, *Tretospira* Koken, 1892, and *Ptychostoma* Laube, 1868. Following earlier suggestions by Golovinova and Korotkov (1986), Guzhov (2004) doubted that *Purpuroidea* Lycett, 1848 and *Leviathania* Pčelintzev, 1927 can be maintained within that family and consequently introduced the new family Purpuroideidae for these genera. He based this family on "large or extremely large multispiral shells that lack an umbilicus and possess a siphonostomatous aperture bearing a short half-closed siphonal canal." This diagnosis fits well to the numerous representatives of *Purpuroidea* Lycett, 1848, as listed by Guzhov (2004), but obviously excludes *Leviathania*, which possesses a very distinct and deep umbilicus. Already Guzhov (2004) discussed the possibility that *Leviathania* should be removed from the Purpuroideidae but refrained from doing so due to the inadequate material known to him.

In the original description, Pčelincev (1927) considered this genus to be anomphalous. This misinterpretation might be explained by the fact that the gastropods are represented only by internal moulds consisting of the identical sediment as the umbilical filling. Therefore, the umbilical area differs hardly from the rest of the gastropod and appears to be closed at first sight. The character of the umbilicus is usually revealed only if cross sections are studied, allowing to trace the otherwise enigmatic shell outline.

## Genus *Leviathania* Pčelincev, 1927

?= *Tuberleviathania* Golovinova and Korotkov, 1986

(= *Turboleviathania* Guzhov, 2004, lapsus calami pro *Tuberleviathania*)

*Type species*: *Natica leviathan* Pictet and Campiche, 1863 (the junior synonym of *Strombus sautieri* Coquand, 1856). Sainte-Croix (Kanton Waadt, Switzerland), "calcaire roux dans les marnes à bryozoaires" (Pictet and Campiche 1863), Valanginian.

*Species included*: *Leviathania gigantea* (Makowsky, 1874), Tithonian, Czech Republic and Austria; *Leviathania* sp., Tithonian or Berriasian, Ukraine; *Leviathania sautieri* (Coquand, 1856), Valanginian, Switzerland, France; *Leviathania gerassimovi* Pčelincev, 1927, Valanginian, Caucasus; *Leviathania subnodosa* (Roemer, 1836), Kimmeridgian, Northern Germany (Fig. 2). Doubtful species which probably belong to *Leviathania*, but are based on poorly preserved specimens: *Leviathania sulcata* Pčelincev, 1963, Cretaceous, Crimea; *L.* sp., Tithonian, Crimea (Korotkov 1989); *L. beschterikensis* Golovinova, 1982, Cretaceous, Crimea; *L. gabonensis* (Meunier, 1887), Albian?, Gabon.

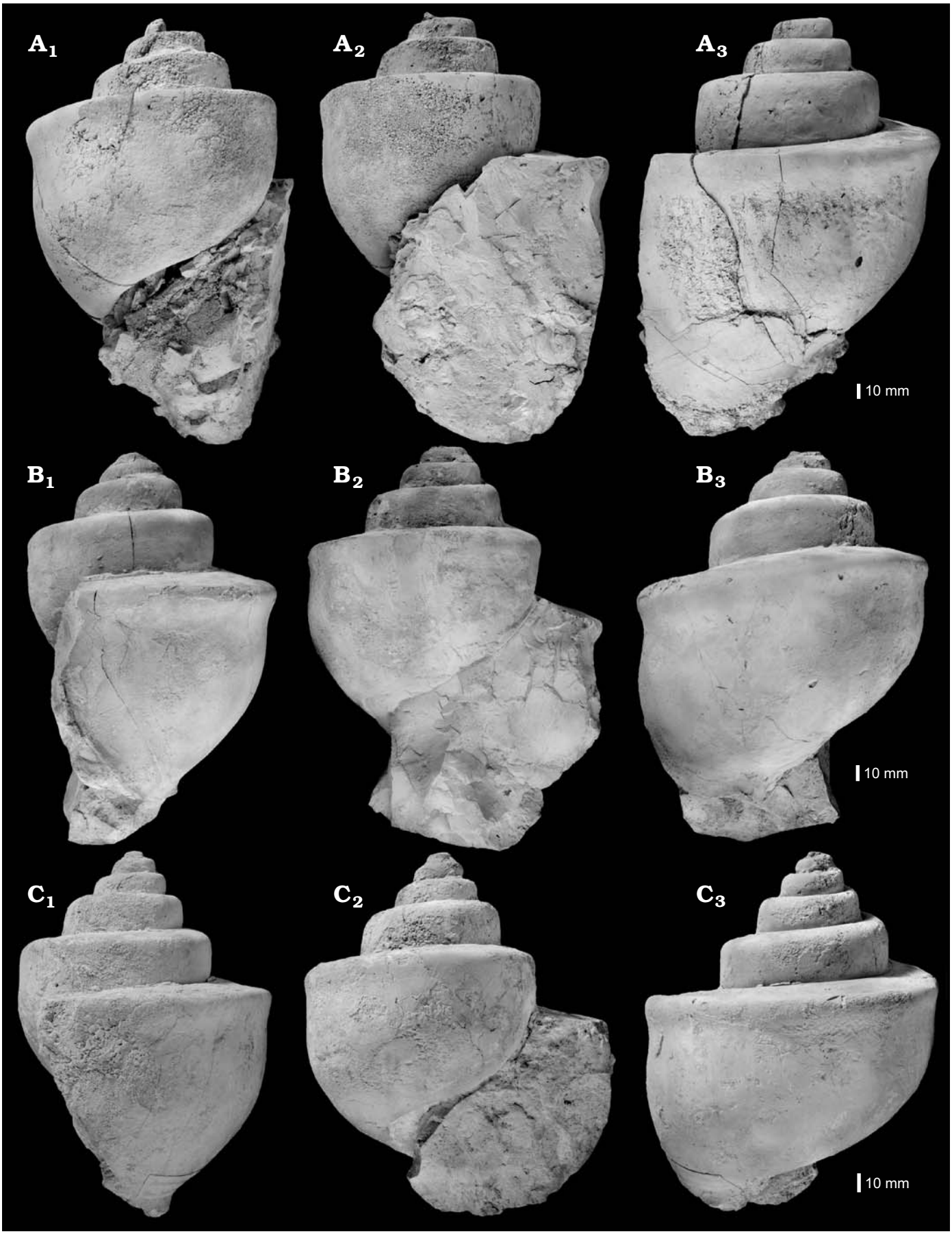
*Diagnosis*.—As given for family Leviathaniidae. If *Tuberleviathania* Golovinova and Korotkov, 1986 might be accepted as valid genus, the definition of *Leviathania* could be reduced to species with weak to obsolete nodes on the last whorls.

*Discussion*.—The species detailed below was usually placed in the genus *Purpuroidea* Lycett, 1848. *Purpuroidea* is still used in a much too broad sense and needs revision as done by Kollmann (1984) for alleged Late Cretaceous representatives of that genus. In fact, this genus is based on the type species *Murex*? *nodulatus* Young and Bird, 1828 from the Bathonian of England (note that Wenz [1939] erroneously mentioned *Purpuroidea maureausea* [Buvignier, 1852] as type species). This species has a steep sutural ramp, blunt nodes and a rugose axial sculpture on the last whorl and develops a basal spiral cord. Its spire is high and coalescing. Other representatives of *Purpuroidea*, as described by Buvignier (1852) and Hudleston (1880), are also characterised by a moderately high spire and strong sculpture of the last whorl, which is bulbous naticoid. These morphologies have little in common with the huge shells from the Tithonian of Austria and the related specimens from Ukraine. In contrast, *Leviathania* Pčelincev, 1927 comprises large species with a gradate spire, smooth shell and anteriorly strongly expanding aperture. The sculpture is restricted to nodes or a keel along the shoulder. Its Valanginian type species is *Natica leviathan* Pictet and Campiche, 1863, which is a junior synonym of *Strombus sautieri* Coquand, 1856. Thus, it has to be referred to as *Leviathania sautieri* (Coquand, 1856).

Several species which have been assigned to *Leviathania* by Pčelincev (1927) and Golovinova (1982) from the Cretaceous of Russia have been transferred to *Tuberleviathania* Golovinova and Korotkov, 1986, with the type species *Leviathania gerassimovi* Pčelincev, 1927. Golovinova and Korotkov (1986) separated this genus from *Leviathania* based on the presence of nodes on the shoulder, the large size and the broad last whorl. The size and the width of the last whorl, however, are no distinguishing features. The size is even topped by some *Leviathania* species, as discussed below, and the broad last whorl is also developed in the type species of *Leviathania*, *L. sautieri*. Only the prominent nodes would be of interest, but there are also *Tuberleviathania* species with weakly developed nodes (Guzhov 2004). Moreover, all taxa which have been assigned to *Tuberleviathania* in the literature are based on poorly preserved internal moulds and are rather dubious. Therefore, we follow Guzhov (2004) and treat *Tuberleviathania* Golovinova and Korotkov, 1986 tentatively as synonym of *Leviathania*.

Fig. 3. Littorinoid gastropod *Leviathania gigantea* (Makowsky, 1874) → from the Tithonian of Dörfles, Lower Austria; in lateral ($A_1$–$C_1$), ventral ($A_2$–$C_2$), and dorsal ($A_3$–$C_3$) views. **A**. Neotype NHMW2011/0347/0001. **B**. Reference specimen NHMW2011/0264/0001. **C**. Reference specimen NHMW2011/0347/0002.

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*Stratigraphic and geographic range*.—Kimmeridgian to Valanginian: Portugal, Spain, France, Switzerland, Austria, Czech Republic, Germany, Ukraine, Crimea, Caucasus, Gabon (Green 1934; Foucault 1971; Bosca 1922; Pictet and Campiche 1863; Makowsky 1874; Alth 1881, 1882; Pčelincev 1963, Golovinova 1982; Golovinova and Korotkov 1986; Meunier 1887).

## *Leviathania gigantea* (Makowsky, 1874)

Figs. 3A–C, 4A–C, 5B, 6.

1874 *Pterocera gigantea* nova species; Makowsky 1874: 123, pl. 2 [non *Rostellaria gigantea* Geinitz, 1842].
1910 *Purpuroidea subnodosa*; Abel 1910: 9.
1940 *Purpuroidea subnodosa* Roemer; Bachmayer 1940: 14.
1954 *Purpuroidea subnodosa* Roemer; Bachmayer 1954: 462, 463, fig. 20.
1964 *Purpuroidea subnodosa* (Roemer); Bachmayer 1964: 104; fig. 124.
1969 *Purpuroidea subnodosa* (Roemer); Bachmayer 1969: 116; fig. 141.
1974 *Purpuroidea subnodosa* Roemer; Thenius 1974: 58, fig. 112/20.
2002 *Purpuroidea subnodosa*; Plöchinger and Karanitsch 2002: 42, 198, figs. 33, 431.
2006 *Purpuroidea*; Wessely 2006: 74, fig. 148.

*Type material*: Neotype: specimen NHMW2011/0347/0001, height: 268 mm, width: 225 mm (Figs. 3A, 4B).

*Type locality*: Dörfles "Quarry 5" sensu Bachmayer (1940), GPS WGS 84: N48°32'37.28", E16°20'58.12", north of Ernstbrunn, ca. 50 km north of Vienna; Lower Austria.

*Type horizon*: Ernstbrunn Limestone (Ernstbrunn formation); Middle to Late Tithonian (Zeiss and Hofmann 2001).

*Material*.—Reference specimen 1: NHM 2011/0264/0001: height: 255 mm, width: 195 mm (Fig. 3B). Reference specimen 2: NHMW2011/0347/0002, height: 182 mm, width: 158 mm (Fig. 3C).

*Diagnosis*.—An extraordinary large species, attaining 300 mm in height, with gradate spire and nearly flat sutural ramp. Early whorls bear indistinct shoulder nodes, which are replaced by a bulgy keel on later whorls. The bulbous last whorl is very large, rapidly expanding in diameter compared to spire, with a distinct concavity below the keel. A narrow "columellar" fold occurs close to the suture on the columellar wall, which develops a very prominent central swelling. Aperture anteriorly widening; phaneromphalous umbilicus deep and wide with dense sculpture of scaly growth increments.

*Description*.—Very large gastropods, which have attained up to 30 cm in height. The protoconch and the earliest teleoconch are unknown. Teleoconch consisting of at least 7–8 whorls. The earliest preserved whorls are moderately convex with a faint median angulation; no sculpture is detectable on the available material at that stage of growth. The angulation shifts quickly into the upper portion of the following whorl and grades into a very prominent shoulder. This angulation separates a feebly concave sutural ramp from the nearly straight sided to slightly convex outer face which is subparallel to the spire axis. The suture is thread-like without incision and adjoined by a delicate, thin sutural collar. The slight concavity of the ramp is caused by the indistinct, wide spaced knobby swellings at the angulation, which are directed in adapical direction but do not protrude abaxially over the periphery. These swellings become blunt nodes on the subsequent spire whorl. Although the exact number cannot be counted, they may have ranged around 15 on the penultimate spire whorl. There, the nodes become spirally elongate, low and poorly defined, but still with adapical orientation. On the last spire whorl and the body whorl, the nodes disappear completely and are replaced by a prominent bulgy keel. This structure pretends a somewhat allometric growth with quickly broadening sutural ramp. The ramp is divided into a weakly convex adsutural part and a shallow concavity close to the bulge. Similarly, the outer face develops a considerable concavity below the bulge, which is a very characteristic feature of this species. On the last whorl, this concavity passes into the strongly convex but rapidly contracting base. The peristome is lost in all specimens, but the preserved terminal parts of the last whorl show that the aperture widens significantly anteriorly. Consequently, the base forms a marked neck. The entire shell is smooth except for faint growth lines. On spire whorls, these comprise a strongly prosocline part along the outer face which passes via a shallow sulcus into an opisthocline adsutural part on the ramp. On the broad sutural ramp of the last spire whorl, the growth lines are sigmoidal with a shorter prosocyrt part close to the bulge and a wider, deeper opisthocyrt adsutural part.

The columella is divided into a deeply concave anterior part which passes into a prominent convex central swelling, followed by a slightly narrower posterior concavity. The surface is smooth except for a narrow but strongly raised fold situated a few millimetres below the suture. Due to the central swelling, the inner lip is strongly curved, robust and becomes adapically thinner, forming a thin columellar plate at the base. Anteriorly, it thickens considerably and passes into a broad and blunt fasciole. This structure borders a phaneromphalous, perspectivic umbilicus which reaches up to the earliest spire whorls. A strong concavity in the umbilicus causes the prominent central swelling in the columellar wall (Fig. $4A_2$, $A_3$, B). The most characteristic feature of the umbilical surface is a dense succession of growth increments, which cause a rough and scaly sculpture (Figs. $4A_1$, $A_2$, 6). A weak anterior canal is developed. Its exact morphology and transition into the outer lip is unknown. The prosocline growth lines of the outer face seem to define also the margin of the outer lip (Fig. $3B_1$).

*Remarks*.—Makowsky (1874) correctly recognized that this huge species is still undescribed and proposed *Pterocera gigantea* as new name. He was not aware that this name was preoccupied by the Cretaceous *Rostellaria gigantea* Geinitz, 1842, which has been placed into *Pterocera* by Reuss (1846), and thus created a junior secondary homonym. However, since *Pterocera gigantea* Makowsky, 1874 is now referred to *Leviathania*, the junior secondary homonym becomes avail-

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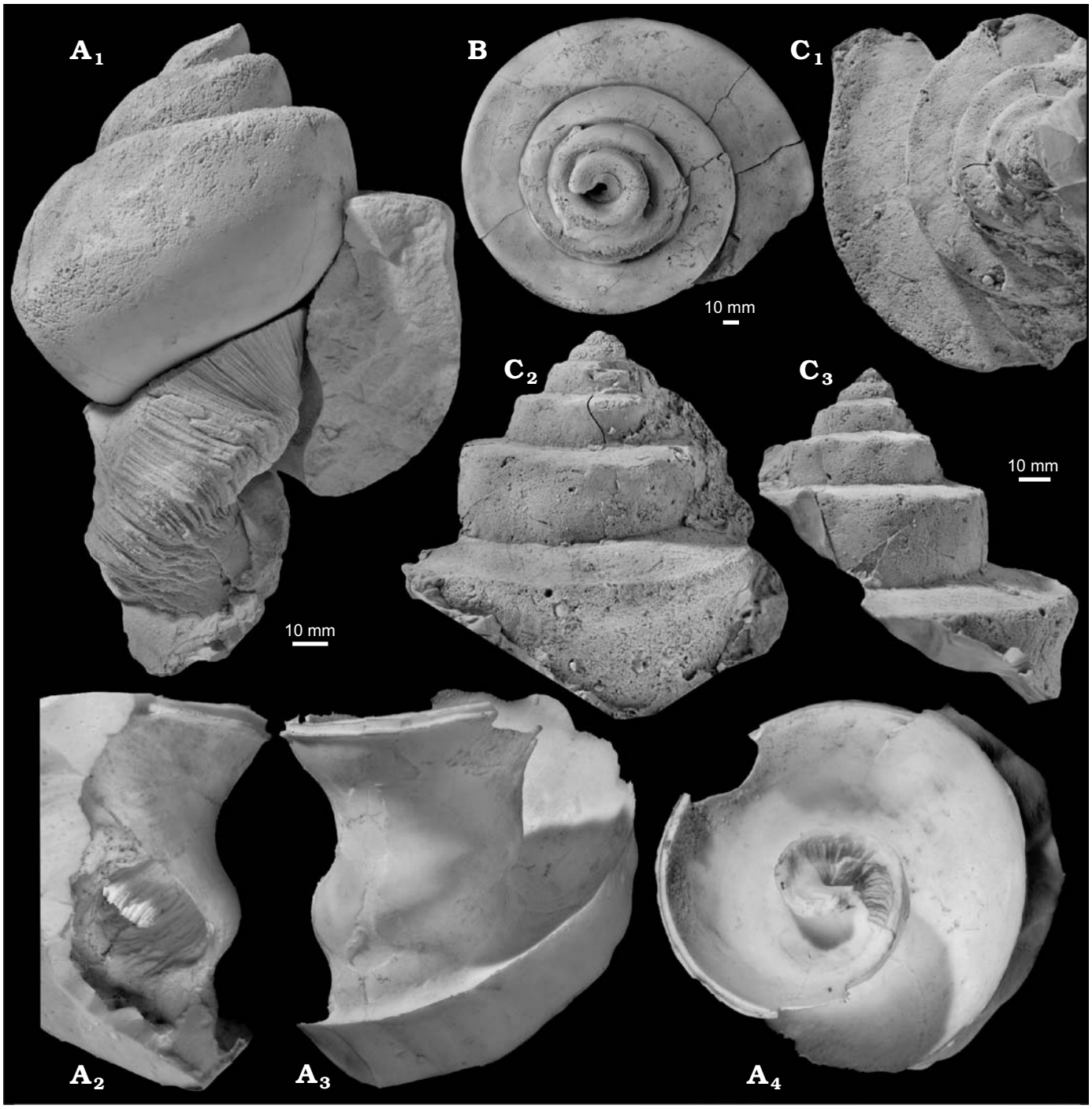



Fig. 4. Littorinoid gastropod *Leviathania gigantea* (Makowsky, 1874) from the Tithonian of Dörfles in Lower Austria. **A**. Specimen NHMW2011/0347/0003, showing the natural cast of the umbilical cavity with the scaly surface of the growth increments ($A_1$). Silicone casts of the cavities, which remained from dissolution of the original shell in different views ($A_2$–$A_4$). View into the original umbilical cavity ($A_2$), note the prominent swelling on the columellar wall which corresponds to the umbilical concavity. Lateral view on the columella with central swelling and narrow fold directly below the upper suture ($A_3$). Apical view showing the umbilical cavity ($A_4$). **B**. Specimen NHMW2011/0347/0001, apical view of the neotype. **C**. Specimen NHMW2011/0347/0004, silicone cast of the surface of the spire in apical ($C_1$) and lateral ($C_2$, $C_3$) views; the growth line is indicated by a black line in $C_2$.

able (ICZN 1999: Article 59.2), and the valid species name is *Leviathania gigantea* (Makowsky, 1874).

The holotype of *Pterocera gigantea* Makowsky, 1874, originally part of the collections of the Naturforschender Verein Brünn, has been lost (personal communication Růžena Gregorová, Moravian Museum, Brno). Makowsky (1874) stated that his specimen had been collected from a quarry near Bergen (nowadays Perná) north of Mikulov. Since no outcrops of Ernstbrunn Limestone exist in the surroundings of Perná, the fossil gastropod was presumably derived from the southern part of the Děvin hill. As already stated by Makowsky (1874), no additional fossils have been reported from

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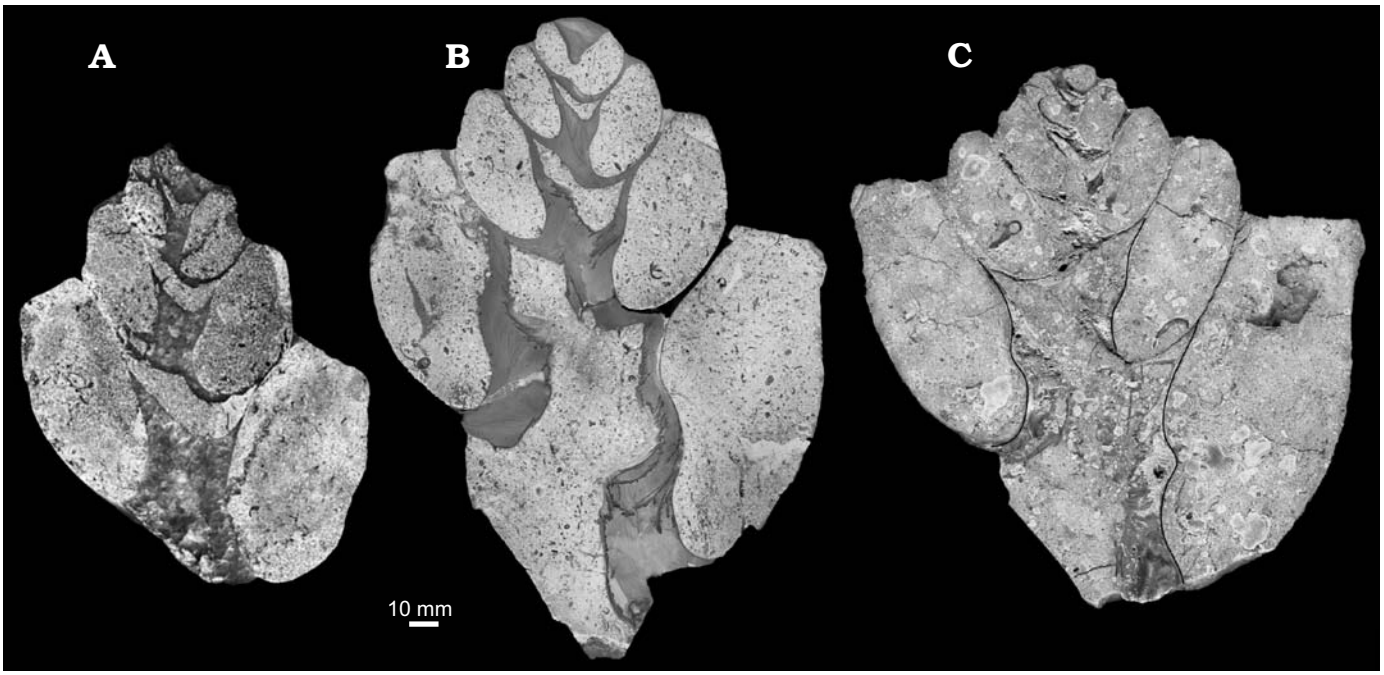



Fig. 5. Cross-sections of three species of Leviathaniidae. **A**. *Leviathania subnodosa* (Roemer, 1836) from the Kimmeridgian of Tönjesberg at Hannover in Germany, NHMW1861/0036/0107. **B**. *Leviathania gigantea* (Makowsky, 1874) from the Tithonian of Dörfles in Lower Austria, NHMW2011/0347/0005. **C**. *Leviathania sautieri* (Coquand, 1856) from the Valanginian of Mont Salève, Haute-Savoie, France, MHNG GEPI 78423; note that the shell borders are highlighted by line drawings.

this outcrop. In order to clarify the taxonomic status of the species, we herein select a fully grown, well-preserved specimen of *Leviathania gigantea* from the Ernstbrunn Limestone of Dörfles near Ernstbrunn (Lower Austria) as a neotype.

Most authors, aside from Makowsky (1874), have identified the specimens as *Purpuroidea subnodosa* (Roemer, 1836). This species derives from the Kimmeridgian Süntel Formation of Northern Germany (Fig. 5A; Menning and Hendrich 2002) and is thus distinctly older than the Tithonian *Leviathania gigantea*. Aside from the stratigraphic gap, it differs considerably from *L. gigantea* in its smaller size, the steeper sutural ramp and the absence of a marked shoulder-bulge. It develops also a concavity on the inner wall of the umbilicus, but this is weaker compared to *L. gigantea*. The type of this species is lost, but material from the Roemer collection in the Roemer- und Pelizaeus-Museum Hildesheim and specimens from the NHMW suggest that *L. subnodosa* developed prominent and large nodes even on the last whorl. The general shape and the deep and wide umbilicus place this taxon clearly within the newly established family Leviathaniidae.

*Leviathania sautieri* (Coquand, 1856) (= *L. leviathan* [Pictet and Campiche, 1863]), from the Valanginian of France and Switzerland, represents a closely related species (Fig. 5C). It agrees largely in outline with the characteristic gradate spire and broad sutural ramp on the last whorl. The spire, however, is much lower and the sutural shelf of the last whorl is wider. It develops a keel, which is slightly less bulgy but lacks any nodes on the spire whorls. It is only slightly smaller and seems to lack the anterior widening of the aperture (cf. Pictet and Campiche 1863: 562, pl. 89: 1, 2). The concavity on the inner wall of the umbilicus of *Leviathania sautieri* is distinct (Fig. 5C) but less prominent.

Alth (1881: 29, pl. 2: 1; 1882: 207, pl. 19: 1) described a specimen from the Ukrainian Nyzhniv Formation as *Purpurina subnodosa*, which is clearly related with *Leviathania gigantea*. This gigantic specimen attained nearly 40 cm in height. It differs from *L. gigantea* in the absence of the characteristic concavity below the shoulder and lacks a distinct bulge. Further, it lacks nodes on early spire whorls and the nearly straight outer face of the spire whorls is slightly scalate. Finally, its spire is higher. These differences suggest that the Ukrainian shell is not conspecific with *Leviathania gigantea*, which displays a quite constant morphology. Except for the outstanding size, the Ukrainian species is intermediate between the Tithonian *L. gigantea* and the Valanginian *L. sautieri* (Coquand, 1856). We consider it to represent a distinct, yet unnamed, species, which already heralds the typical Cretaceous morphology. Therefore, we did not include this reference in the chresonymy of *Leviathania gigantea.* Since we have not studied any specimens from Nyzhniv, we refrain from assigning a new name.

*Leviathania sulcata* Pčelincev, 1963, from the Cretaceous of Crimea, is stout and has a convex shoulder without nodes or a bulge but is reminiscent of our species concerning the widening of the aperture (cf. Pčelincev 1963: 49, pl. 15: 1). *Leviathania beschterikensis* Golovinova, 1982 differs from *Leviathania gigantea* in its strong nodes on the shoulder and the more regular growth, resulting in a comparatively slender shell. *Leviathania gerassimovi* Pčelincev, 1927 from the Valanginian of the Caucasus differs in its convex whorls

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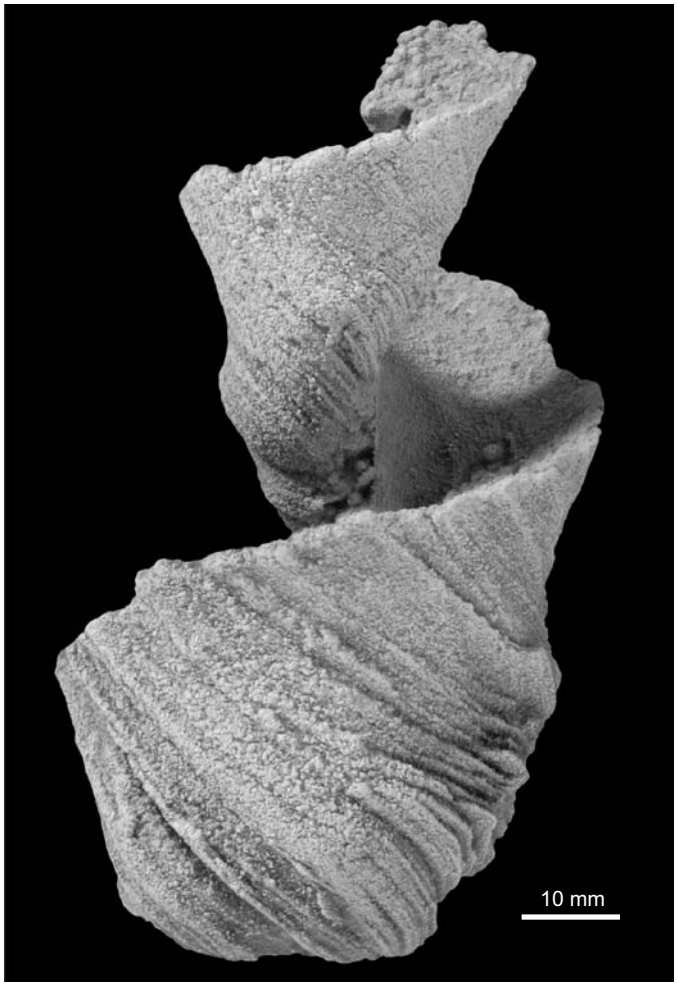



Fig 6. Natural internal cast of the umbilical cavity of *Leviathania gigantea* (Makowsky, 1874) from Ernstbrunn (Austria); NHMW2012/0121/0001.

and the rapidly increasing diameter of the whorls; it lacks a sutural ramp.

The stratigraphically closest species with similar morphology is *Purpuroidea carpathica* Zittel, 1873 (Zittel 1873: 316, pl. 343: 3, 4) from the Tithonian of Štramberk. This species differs from the new species in its distinctly smaller size of less than 15 cm height, the prominent nodes and the higher spire. The growth lines are steeply prosocline on the sutural ramp, thus differing strongly from *L. gigantea*.

*Distribution.*—*Leviathania gigantea* is frequently found in the Tithonian Ernstbrunn Limestone in the quarries at Dörfles and Ernstbrunn in Lower Austria and Mikulov in southern Moravia (Czech Republic). Additional Tithonian material was found at Štramberk in Czech Republic (private collection of Lubomir Martinásek, Kopřivnice, Czech Republic).

*Discussion.*—The whitish to light-grey Ernstbrunn Limestone typically consists of almost 100% of calcium carbonate (Moshammer and Lobitzer 1997). At Dörfles Quarry 5 (denomination sensu Bachmayer 1940), which has yielded most of the discussed gastropods, the rocks comprise a patchwork of slightly variant, highly fossiliferous facies, dominated by bio-pelmicrites (wacke- and packstones), bio-pelsparites, algal bindstones and oncoid pack- and grainstones. Characteristic facies fossils include dasycladalean, codiacean, and solenoporacean algae, foraminifers, nerineid gastropods, and epidiceratid, lucinid and cardioid bivalves. Small scleractinian and coralline sponge patch reefs occur locally (Hofmann 1990).

Bachmayer (1957) proposed a diversity of more than 500 fossil species for the Ernstbrunn Limestone, which evidently was no overestimate. With regard to species numbers, the assemblage is macroscopically dominated by gastropods, bivalves, and crustaceans. Still relatively diverse are ammonites, scleractinian corals, echinoderms, and brachiopods. Among these groups, the bivalves presumably accounted for the major portion of biomass, since they were represented by numerous extraordinarily large species of, e.g., *Epidiceras*, *Pachyrismella*, and *Pterocardia*, and abundant Astartidae and Lucinidae. Gastropods also comprise several large taxa, mainly within the Pleurotomariidae, Aporrhaidae, and Nerineidae. The latter occur in large quantities, and represent one of two major components of the epidiceratid-nerineid biofacies distinguished by Hofmann (1990). In this respect, dasycladalean algae also have to be considered, as they dominate the assemblage at places, and surely played an effective role in the production of biomass. The largest fossils of the Ernstbrunn Limestone community, however, are the giant *Leviathania* gastropods.

A similar assemblage is documented from the Nyzhniv Formation in Ukraine by Alth (1881, 1882). He described a total of 180 species, 93 of them gastropods, and 57 bivalves. In contrast to Ernstbrunn-Dörfles, epidiceratids are only represented by a few extremely small specimens, and thus not important for biofacies. Crustaceans are represented only as indeterminable fragments. Interestingly, four species of Dasycladales are also present.

Although a palaeoecological evaluation of the respective assemblages is lacking, a comparable environment can be inferred for *Leviathania sautieri*. On one hand, the gastropod mould from Mont Salève is composed of bio-pelmicrite with small oncoids (Fig. 5C); on the other hand, the fauna from Sainte-Croix comprises many taxa typical of lagoonal settings (e.g., nerineids; Pictet and Campiche 1861–1864).

Hence, tropical lagoonal environments of the northern coasts of the Tethys Ocean seem to have been the preferred habitat of the Leviathaniidae. This is also supported by the comparatively scarce occurrences in the reef and fore reef settings represented by the coeval Štramberk Limestone.

The Leviathaniidae have no living relatives and the interpretation of their palaeoecology remains speculative. The large number of specimens in the collection of the NHMW is not a sampling bias due to the attractive size of these fossils, but indeed reflects the high abundance of the gastropods in the field, which can still be observed in the quarries around Ernstbrunn. Obviously, this species lived in huge populations. The shells are rarely associated with scleractinian and

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coralline sponge patch reefs but are typically filled with bio-pelmicrites, bio-pelsparites, and oncoid pack- and grainstones (Fig. 5). Hence, the animals seem to have preferred the rather mobile bioclastic sediment which provided a sandy substratum. In modern marine faunas, only herbivore strombids are found in comparable size and population densities in shallow marine, lagoonal settings. The huge *Lobatus gigas* (Linnaeus, 1758) occurs in densities of 70–80 specimens/ha in the Bahamas and the Dominican Republic (Stoner and Ray 1996; Posada et al. 1999). A direct comparison of the ecology of both taxa, however, is hampered by the fact that the extant strombid is largely bound to seagrass meadows, which have not been in existence in Jurassic times (Eva 1980; Hemminga and Duarte 2000). Another huge strombid, which forms considerable populations is *Lambis truncata* ([Lightfoot], 1786), which was counted to occur in densities of 1.3 specimens/ha in protected lagoons in Kenia (McClanahan 1989). Other extant gastropod species of comparable size are the carnivores *Cassis cornuta* (Linnaeus, 1758) and *Charonia tritonis* (Linnaeus, 1758), which occur in distinctly lower densities even in areas which have not been exposed to fishery (McClanahan 1989). Therefore, we suggest that the abundance of the large-sized *Leviathania* might rather correspond to a herbivorous/omnivorous life style comparable to the extant strombids.

# Conclusions

Despite the eye-catching size and morphology of the various species belonging to the newly defined family Leviathaniidae, these taxa have been treated as Purpurinidae Zittel, 1895 or Purpuroideidae Guzhov, 2004. A separation from these families is based on the phaneromphalous umbilicus of the Leviathaniidae, their weak sculpture and large size. Herein, we consider the family as part of the order Littorinimorpha Golikov and Starobogatov, 1975 but leave the question of its phylogenetic relations open due to a lack of adequate data.

The family comprises currently only one well defined genus and several species, which suggest an origin of the group during the Kimmeridgian, when it is known from northern Germany. During the latest Jurassic the family was represented along the northern Tethys shelf, from Austria in the west to the Ukraine in the east. During the Early Cretaceous, the family spread from Spain and France via Switzerland as far east as the Caucasus. Occurrences from southern areas, such as those in Arabia (Banner and Wood 1964) or from the Cretaceous of the early Atlantic Ocean (Meunier 1887; Green 1934) are based on poor illustrations or geological reports and will need detailed confirmation. Similarly, records from the Aptian of Tunisia (Heldt et al. 2009) have to be treated with caution.

The species currently assigned to the family Leviathaniidae seem to have been characteristic members of the benthic assemblages of the tropical lagoons of the northern Tethys shelf. They were less frequent in reefal settings but rather preferred mobile bioclastic sediment. The population densities and the shell-size-class are comparable in modern faunas only with those of the stromboidean gastropods. Therefore, we tentatively suggest a comparable herbivorous/omnivorous life style.

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