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STEM CYPRAEID GASTROPODS – A REVISION OF THE GENUS *ZITTELIA* GEMMELLARO, 1869

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Abstract: *Zittelia* is an extinct genus of the family Colombellinidae, which originally was described from the Upper Jurassic–?Lower Cretaceous (Tithonian–?Valanginian) of Sicily, Italy, and subsequently reported from several localities across Europe. Its shell is oval, with a thickened, siphonostomatous peristome, a narrow, slit-like aperture displaying distinct abapical sinuosity, and a denticulate outer lip that is bent outward. In contrast to members of the Cypraeidae, the shells of which are convolute, the spire of *Zittelia* remains elevated. A thorough examination of the type material has enabled a comprehensive revision of the taxonomic composition of the genus and clarification of its diagnostic characteristics. Species of *Zittelia* share morphological affinities with *Colombellina*, the type genus of the Colombellinidae, and are closely related to early representatives of the cypraeids. This is reflected in changes in the shell morphology of *Zittelia* during the Late Jurassic, including a progressive enlargement of the last whorl, elongation of the aperture, and a substantial expansion of the columellar lip. The species most closely resembling early cypraeids is the type species, *Zittelia cipraeaeformis* Gemmellaro, 1869, which possesses a broadly expanded columellar lip and a low spire. The occurrence of *Zittelia* is restricted to peri-Tethyan carbonate facies. Its co-occurrence with the earliest cypraeids in the uppermost Jurassic of Sicily indicates that the Late Jurassic reefs and associated lagoons of the Tethys may have served as centres of diversification for the Colombellinidae and as potential areas of emergence for the Cypraeoidea.

Key words: Gastropoda, Colombellinidae, cowries, taxonomy, systematics, evolutionary relationships, diversification.

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INTRODUCTION

The Late Jurassic and Early Cretaceous were crucial periods in the evolution of "higher" caenogastropods (Neomesogastropoda sensu Bandel, 1991 and Latrogastropoda sensu Riedel, 2000), when the stem groups gave rise to the crown groups, including Neogastropoda Wenz, 1938, Tonnoidea Suter, 1913 and Cypraeoidea Rafinesque, 1815 (e.g., Bakayeva *et al.*, 2024; Nützel *et al.*, 2025). One such stem group is the extinct family Colombellinidae Fischer, 1884, which is currently classified among taxa of uncertain position within Latrogastropoda

Riedel, 2000 in Bouchet *et al.* (2017) and considered to be the ancestral group of the Cypraeoidea (Nützel *et al.*, 2025). Ponder and Lindberg (2020, p. 680) noted that Colombellinidae is unplaced but formerly included in the Stromboidea Rafinesque, 1815. The family comprises two genera: *Zittelia* Gemmellaro, 1869 and *Colombellina* d'Orbigny, 1842. Colombellinids differ from other Mesozoic gastropods in their thick oval shells with coarse nodular ornamentation and a narrow aperture, which terminates with both an anterior and a posterior canal. Despite their thick shells, which facilitated good preservation, colombellinid occurrences are scarce and geographically restricted. So far, species of *Zittelia* have been recorded exclusively in the Upper Jurassic (upper Oxfordian–Tithonian; Fig. 1) and possibly lowermost Cretaceous (Berriasian–Valanginian) carbonate sediments from several localities within Europe (Fig. 2; Tab. 1; Étallon, 1859; Guirand and Ogérien, 1865; Gemmellaro, 1869; Zittel, 1873; Futterer, 1892; Brösamlen, 1909; Joukowsky and Favre, 1913; Gründel *et al.*, 2019, 2022).

This study presents a comprehensive revision of the genus *Zittelia*, based on the 19th-century collections described by Guirand and Ogérien (1865), Gemmellaro (1869), and Zittel (1873) as well as a re-assessment of the type material of the corresponding species. It is worth noting that the type material from the Upper Jurassic–lowermost Cretaceous (Tithonian–Valanginian) of Sicily, Italy, on which the genus was based, has not been systematically examined since its original description by Gemmellaro (1869). This paucity of thorough studies has led to a misleading and limited understanding of the diagnostic features of the type species, casting doubt on the validity of the genus itself (Gründel *et al.*, 2019). The revision also is prompted by the relationship of *Zittelia* with the family Cypraeidae Rafinesque, 1815 – a group of predatory crown latrogastropods, which are currently distributed predominantly in tropical and pantropical seas, with their greatest diversity in the Indo-Pacific region, and are commonly known as cowries. The initial discussion of this relationship was undertaken by Sayn (1932), and subsequently, the family Colombellinidae was designated as a probable stem group of the Cypraeoidea and the Tonnoidea by Taylor and Morris (1988), as they possess some cowry and cymatiid-like species, a hypothesis that has never been critically assessed.

A detailed study of the earliest representatives of Cypraeidae (Nützel *et al.*, 2025), complemented by the revision of the family Colombellinidae, argues that *Zittelia* resembles *Cypraea*. The purpose of this paper is to compare *Zittelia* to other early latrogastropods, in particular to other colombellinids and cypraeids, and to discuss their phylogenetic importance for crown latrogastropods.

Abbreviations: MDC – Museum of Confluences in Lyon, France; MGUP – Geological Museum of Palermo University, Italy; SMNS – Staatliches Museum für Naturkunde in Stuttgart, Germany; SNSB-BSPG – Bavarian State Collection for Palaeontology and Geology in Munich, Germany.

HISTORICAL BACKGROUND

The genus *Zittelia* was originally described by Gemmellaro (1869) from the Upper Jurassic–Lower Cretaceous of Sicily, Italy. Because *Zittelia* was very similar to *Colombellina* d'Orbigny, 1842, Gemmellaro (1869) placed it in Buccinidae Rafinesque, 1815, where *Colombellina* was originally classified by d'Orbigny (1842). Gemmellaro (1869) described two new species, *Zittelia cipraeaeformis* Gemmellaro, 1869 and *Z. picteti* Gemmellaro, 1869, and suggested that *Colombellina sofia* Guirand and Ogérien, 1865, from the Kimmeridgian of France (Guirand and Ogérien 1865; Ogérien, 1867), should also be included in *Zittelia*. Later, *Z. sofia* was synonymized with *Z. oppeli* (Étallon, 1859) by Zittel (1873), who also described four new species of *Zittelia* – *Z. crassissima* Zittel, 1873, *Z. globulosa* Zittel, 1873, *Z. laeviuscula* Zittel, 1873, and *Z. gemmellaroi* Zittel, 1873, from the Tithonian–?Berriasian of Czechia. Subsequently, Futterer (1892) described *Z. striata* Futterer, 1892, from the re-deposited Tithonian limestone of Polcenigo, in northern Italy.

De Loriol (1886–1888) redescribed two species, assigned to the genus from the Kimmeridgian of France. These included *Z. oppeli* (Étallon, 1859), originally described by Étallon (1859) without providing any illustrations, and *Z. victoria* (Guirand and Ogérien, 1865). His study was based on the collections of M. A. Étallon (Étallon, 1859) and E. Guirand (Guirand and Ogérien, 1865), which he examined at the Museums of Dijon and Lyon, respectively.

Another new species of *Zittelia* – *Z. globosa* Brösamlen, 1909 – from the Upper Jurassic of Nattheim, Germany, was described by Brösamlen (1909). Later, this species was synonymised by Joukowsky and Favre (1913) with *Z. picteti*.

Two species of *Zittelia*, *Z. picteti* and *Zittelia* sp. were recorded from the Upper Jurassic (Tithonian) of southern France by Tsan-hsun (1931). However, the validity of these identifications remains questionable, due to the absence of illustrations or descriptions of the aperture.

Sayn (1932, p. 32, text-fig. 10, pl. 3, figs 8, 9) described the species *Zittelia drumensis* Sayn, 1932 from the Barremian–Aptian (Lower Cretaceous) near Barcelonne (France), which therefore was considered to be the latest representative of this genus. Sayn (1932) did not indicate the exact number of specimens that he had examined, noting only that the species is rare. Sayn (1932) also noted that *Z. drumensis* exhibits the typical sinuosity characteristic of *Zittelia* and possesses about twenty thin columellar teeth – a feature absent in other species of the genus. He further suggested a similarity to some species of *Palaeocypraea* Schilder, 1928, from the Danian, Paleocene. However, the shell outline and aperture morphology of this species more closely resembles the recently described genus *Coffeacypraea* Nützel & Schneider, 2025 (in Nützel *et al.*, 2025).

Cossmann (1916) described *Z. gymna* Cossmann, 1916 from the Barremian of Orgon (France), a species that has been reclassified with some doubt into the genus *Liocarenus* Harris and Burrows, 1891, in the family Acteonidae d'Orbigny, 1842 (Gründel and Kollmann, 2013).

Finally, Gründel *et al.* (2019, p. 133) considered *Zittelia* a synonym of *Columbellaria* Rolle, 1861, noting that upon comparing the type species of both genera, the authors

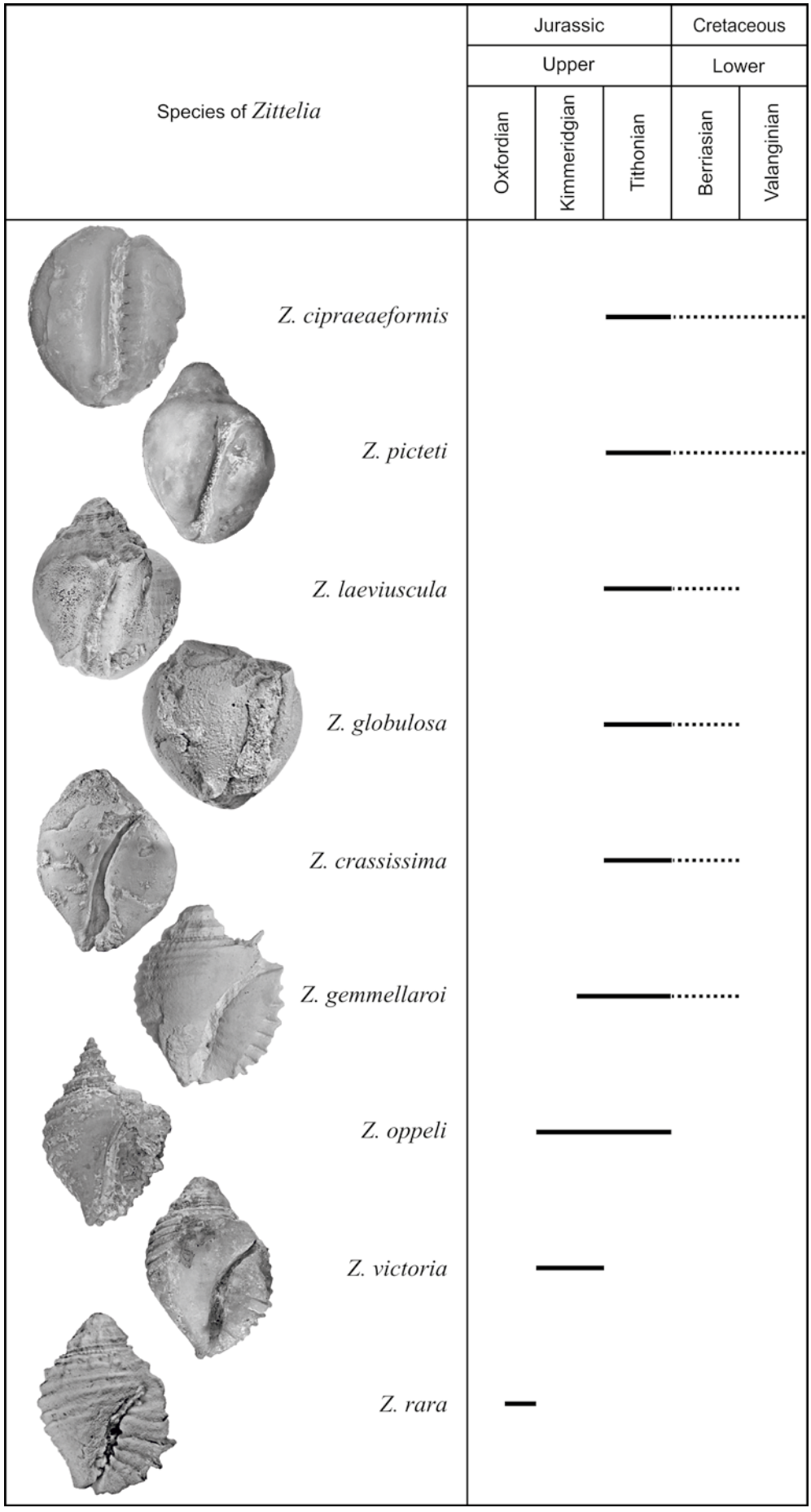

Fig. 1. Stratigraphic distribution of *Zittelia* in the Upper Jurassic and Lower Cretaceous. Dotted lines indicate uncertain ranges.

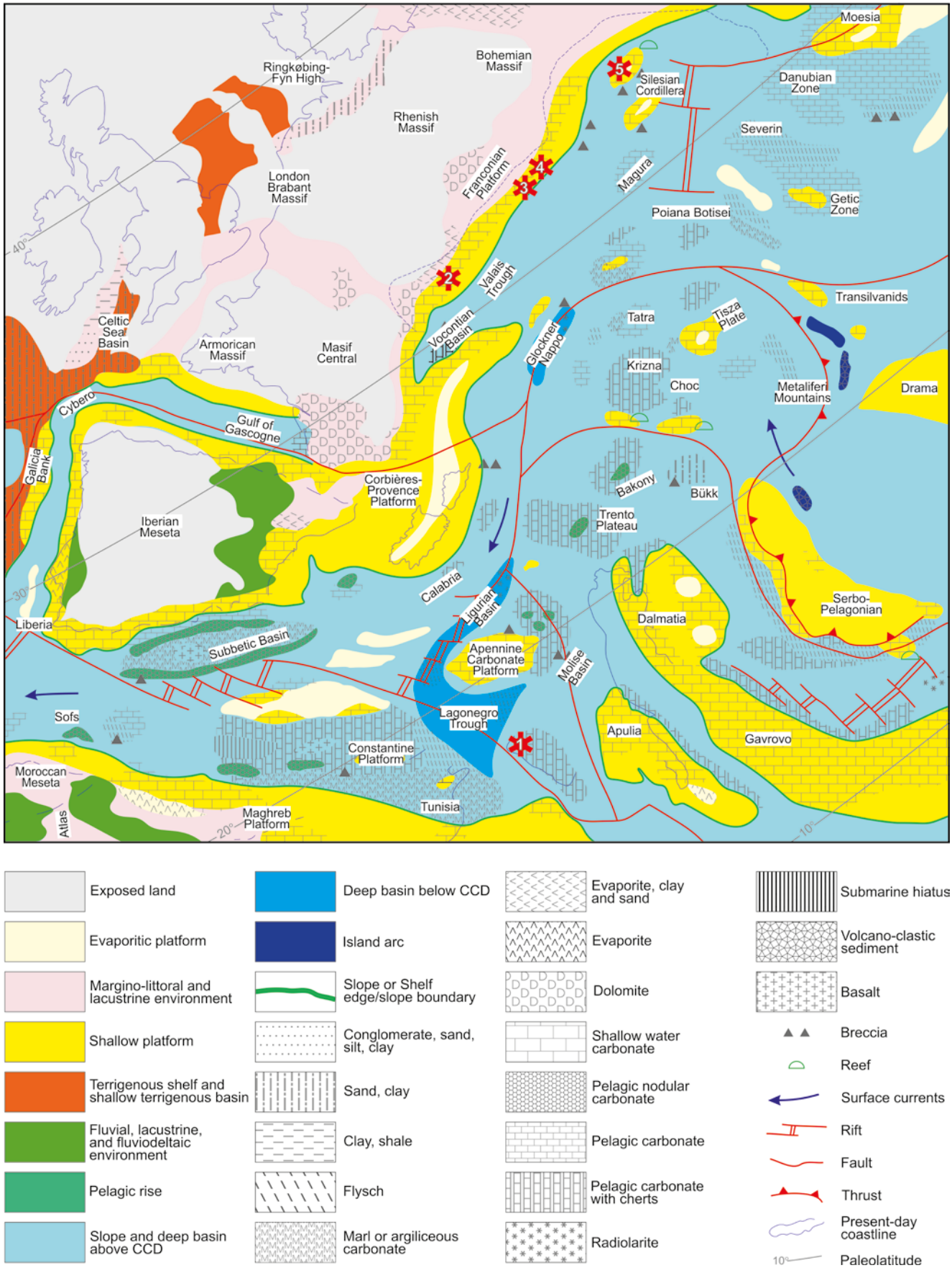

Fig. 2. Late Tithonian palaeoenvironments (redrawn and simplified from Fourcade *et al.*, 1993) with records of *Zittelia*: 1 – Sicily, Italy, 2 – Rhône-Alpes, France, 3 – St-Ursanne, Switzerland, 4 – Swabia, Germany, 5 – Moravian-Silesian region, Czechia and Poland.

Table 1

List of species included in *Zittelia*. Taxa, for which the type material has been revised, are marked with an asterisk.

Age	Location	Revised taxonomic name	Taxon name, according to original description	Reference
Middle Oxfordian	Switzerland	*Zittelia rara* (Gründel, Hostettler & Menkveld-Gfeller, 2022)	*Columbellaria rara* Gründel, Hostettler & Menkveld-Gfeller, 2022	Gründel *et al*., 2022
Kimmeridgian	France	*Zittelia oppeli* (Etallon, 1859)	*Columbellina Oppeli* Et.	Étallon, 1859
			Columbellina Sofia (Guirand et Ogérien)*	Guirand and Ogérien, 1865; Ogérien, 1867
			Zittelia Oppeli (Etallon)	de Loriol, 1886–1888
			Columbellina (Zittelia) Oppeli (Etallon)	Cossmann, 1904, 1913
		Zittelia victoria (Guirand & Ogérien, 1865)	*Columbellina Victoria* (Guirand et Ogérien)*	Guirand and Ogérien, 1865, Ogérien,, 1867
			Zittelia Victoria Guirand et Ogérien	de Loriol, 1886–1888
			Columbellina (Zittelia) Victoria (Guir. et Ogér.)	Cossmann, 1904, 1913
Late Jurassic–?Early Cretaceous (Tithonian–?Valanginian)	Sicily, Italy	*Zittelia picteti* Gemmellaro, 1869	*Zittelia Picteti* Gemm.*	Gemmellaro, 1869
		Zittelia cipraeaeformis Gemmellaro, 1869	*Zittelia cipraeaeformis* Gemm.*	Gemmellaro, 1869
Tithonian	Germany	*Zittelia gemmellaroi* Zittel, 1873	*Zittelia globosa* Brösamlen	Brösamlen, 1909
Tithonian–?Berriasian	Czechia	*Zittelia crassissima* Zittel, 1873	*Zittelia crassissima* Zitt.*	Zittel, 1873
		Zittelia globulosa Zittel, 1873	*Zittelia globulosa* Zitt.*	Zittel, 1873
		Zittelia laeviuscula Zittel, 1873	*Zittelia laeviuscula* Zitt.*	Zittel, 1873
		Zittelia gemmellaroi Zittel, 1873	*Zittelia Gemmellaroi* Zitt.	Zittel, 1873
Tithonian	France	*Zittelia picteti* Gemmellaro, 1869	*Zittelia Picteti* Gemmellaro	Roman, 1897
		Zittelia picteti Gemmellaro, 1869	*Zittelia picteti* G. Gemm.	Joukowsky and Favre, 1913
		Zittelia? *picteti* Gemmellaro, 1869	*Zittelia picteti* Gemmellaro	Tsan-hsun, 1931
		Zittelia oppeli (Etallon, 1859)	*Zittelia oppeli* (Et.)	Joukowsky and Favre, 1913
Tithonian?	Northern Italy	Cypraeoidea	*Zittelia striata* n. sp.	Futterer, 1892
Barremian–Aptian	France	*Coffeacypraea*? *drumensis* (Sayn, 1932)	*Zittelia drumensis* (nov. sp.)	Sayn, 1932

could not identify any differences that would justify their separation at the generic level.

Thanks to the efforts of the staff at the G. G. Gemmellaro Geological Museum of the University of Palermo, the Museum of Confluences in Lyon, and the Bavarian State Collection for Palaeontology and Geology in Munich, the type materials of most of the species of *Zittelia* (except for *Z. gemmellaroi*) have been rediscovered and made available for study. This allows a better understanding of the diagnostic characteristics of genus *Zittelia* and its species diversity.

MATERIAL AND METHODS

This study is based on the materials from 19th-century collections, stored at the Museum of Geology G. G. Gemmellaro in Palermo, Sicily, Italy (11 specimens), the Museum of Confluences in Lyon, France (16 specimens) and the Bavarian State Collection for Palaeontology and Geology in Munich, Germany (14 specimens; see Tab. 2 for the list of localities). The MGUP specimens were photographed by CDA, and the MDC specimens were photographed by DB.

Table 2

List of examined material.

Species	Stratigraphy	Locality	Number of specimens	Accession number and specimen status
Zittelia cipraeaeformis Gemmellaro, 1869	Tithonian–?Valanginian	Carini near Palermo, Sicily, Italy	3	MGUP-20-361A.1, 361A.2, 361A.3 (lectotype)
		Santa Maria di Gesù in Palermo, Sicily, Italy	3	MGUP-20-361B.1, 361B.2, 361B.3
		Rotoli in Palermo, Sicily, Italy	3	MGUP-20-361C.1, 361C.2, 361C.3
Zittelia crassissima Zittel, 1873	Tithonian–?Berriasian	Koňákov (Koniakau), Czechia	2	SNSB-BSPG AS III 896, 899
		Štramberk, Czechia	4	PG AS III 897, 898 (lectotype), 909, 910
Zittelia gemmellaroi Zittel, 1873	Upper Kimmeridgian	Saal, Germany	1	SNSB-BSPG 2016 XXI 1
Zittelia globulosa Zittel, 1873	Tithonian–?Berriasian	Štramberk, Czechia	2	SNSB-BSPG AS III 900, 901
Zittelia laeviuscula Zittel, 1873	Tithonian–?Berriasian	Štramberk, Czechia	5	SNSB-BSPG AS III 902 (lectotype), 904, 905, 906, 907
		Wilamowice (Willamowitz), Poland	1	SNSB-BSPG AS III 903
Zittelia oppeli (Étallon, 1859)	Kimmeridgian	Valfin, France	13	MDC 20014062
Zittelia picteti Gemmellaro, 1869	Tithonian–?Valanginian	Carini near Palermo Sicily, Italy	2	MGUP-20-362.1 (lectotype), 362.2
Zittelia victoria (Guirand & Ogérien, 1865)	Kimmeridgian	Valfin, France	3	MDC 20014042.1 (lectotype), 20014042.2, 20014042.3

The SNSB-BSPG specimens were coated with ammonium chloride and photographed by Katharina Peter (Bremen) during the course of an internship at SNSB-BSPG.

The material housed in Palermo apparently has remained untouched since the time of its study by Gemmellaro (1869), until the present studies (Nützel *et al.*, 2025 and herein). We could not trace any publications containing a redescription or new illustrations of this collection. The shells were collected by G. G. Gemmellaro in the surroundings of Palermo during field research carried out for the compilation of the geological map of Sicily. All Tithonian fossils collected were grouped in the collection entitled "La fauna dei calcari a Terebratula Janitor" (Catalogue Number MGUP 020). Subsequently, Gemmellaro (1869) provided detailed descriptions of all the recognized species in the corresponding publication, enriching it with splendid illustrations. The specimens are stored in glass vials, sealed with cotton plugs and cork stoppers (Fig. 3), accompanied by labels indicating their localities and adhered images that were published by Gemmellaro (1869). The shells are well preserved, with one specimen even exhibiting the colour pattern (Fig. 4J).

The Bavarian State Collection for Palaeontology and Geology in Munich houses a part of Ludwig Hohenegger's collection from the Moravian-Silesian region (now in Czechia and Poland), which was studied by Zittel (1873). The repository for the remaining portion has not yet been determined and it is possible that these specimens are lost. The preservation of the shells of colombellinids varies; often apertures, including the outer lip and other morphological elements, are damaged, or the original aragonite has been replaced by calcite during diagenesis; some specimens are internal moulds. Evidently, they were extracted from much harder rocks, compared to the Sicilian material.

Fig. 3. *Zittelia* type material with drawings from original description by Gemmellaro (1869). **A**. Box MGUP-20-361 with nine specimens of *Zittelia cipraeaeformis* Gemmellaro, 1869 from three localities: Carini near Palermo, Santa Maria di Gesù and Rotoli in Palermo, Sicily, Italy; Tithonian–?Valanginian. **B**. Box MGUP-20-362 with two specimens of *Zittelia picteti* Gemmellaro, 1869 from Carini near Palermo, Sicily, Italy; Tithonian–?Valanginian. Scale bars represent 10 mm.

The specimens housed at the Museum of Confluences in Lyon, France (Fig. 5) were originally described by Guirand and Ogérien (1865) and subsequently investigated again by de Loriol (1886–1888). The material originates from the Edmond Guirand collection, which was acquired by the Lyon Natural History Museum on March 28, 1873. On the basis of the detailed description of the exposed deposits in Valfin, France, provided by Guirand and Ogérien (1865), it is highly probable that the specimens were collected by Guirand. The shells are well preserved, and the numbers on them allow for an easy correlation with the illustrations by de Loriol (1886–1888). Unfortunately, we could not relate the specimens to the illustrations in Guirand and Ogérien (1865), and assume that their figures are composites of several specimens.

The carbonate deposits from around Palermo range continuously from the upper Tithonian (Upper Jurassic) through Berriasian to Valanginian (Lower Cretaceous; Basilone and Sulli, 2016 and references therein), therefore we consider this long stratigraphic interval as the possible range of the studied Sicilian specimens. Likewise, until new materials with precise stratigraphic information from the Štramberk area localities (as in Vaňková *et al.*, 2019) are collected, we have to assume a Tithonian–?Berriasian age for specimens from the Moravian-Silesian region (i.e., Štramberk, Koňákov, and Wilamowice), deposited in old collections.

We adopted the higher-level taxonomy scheme of Bouchet *et al.* (2017). The conchological terminology in the descriptions is based on the glossaries of Cox (1960) and Arnold (1965).

SYSTEMATIC PALAEONTOLOGY

Superorder LATROGASTROPODA F. Riedel, 2000
Family COLOMBELLINIDAE Fischer, 1884
(= COLUMBELLARIIDAE Zittel, 1895;
= ZITTELIIDAE Schilder, 1936)

Genus *Zittelia* Gemmellaro, 1869

Type species: *Zittelia cipraeaeformis* Gemmellaro, 1869; subsequent designation by Cossmann (1901, p. 230); Upper Jurassic–?Lower Cretaceous, Sicily, Italy.
Emended diagnosis: Thick oval shell with low spire, ornamented with tuberculated spiral cords and axial ribs; last whorl large and inflated with tuberculated spirals; peristome siphonostomatous, thickened; aperture narrow, slit-like, and slightly curved with a distinct sinuosity in the abapical part; columellar lip widely expanded; outer lip denticulate, thickened, and bent outward.
Species included: Nine species are considered valid herein: *Zittelia cipraeaeformis* Gemmellaro, 1869, *Z. crassissima* Zittel, 1873, *Z. gemmellaroi* Zittel, 1873, *Z. globulosa* Zittel, 1873, *Z. laeviuscula* Zittel, 1873, *Z. oppeli* (Étallon, 1859), *Z. picteti* Gemmellaro, 1869, *Z. rara* (Gründel, Hostettler & Menkveld-Gfeller, 2022), and *Z. victoria* (Guirand & Ogérien, 1865).
Remarks: *Zittelia* differs from *Colombellina* in having a more globose shell outline with a lower spire, a narrower aperture, and a wider expansion of the columellar lip, which tightly adheres to the last whorl, forming a callus. The columellar lip of *Zittelia* is smooth instead of denticulate, as in *Colombellina*. However, the main difference is the presence of a sinuosity in the abapical part of the aperture, which Gemmellaro (1869) considered a diagnostic character for establishing his new genus. This sinuosity occurs in each

Fig. 4. Type series of *Zittelia cipraeaeformis* Gemmellaro, 1869, Tithonian–?Valanginian, province of Palermo, Sicily, Italy. **A–B**. Lectotype MGUP-20-361A.3 (designated herein); A – apertural view, arrow indicates sinuosity; B – abapertural view, arrows indicate margin of the inner lip. **C –** MGUP-20-361A.1, abapertural view. **D–E.** MGUP-20-361A.2; D – apertural view; E – abapertural view. **F**. MGUP-20-361B.1, abapertural view. **G –** MGUP-20-361B.2, apertural view. **H–I**. MGUP-20-361B.3; H – apertural view; I – abapertural view. **J**. MGUP-20-361C.1, abapertural view with the colour pattern preserved. **K–L**. MGUP-20-361C.2; K – apertural view; L – abapertural view. **M–N.** MGUP-20-361C.3; M – apertural view; N – abapertural view. Scale bars represent 5 mm.

Fig. 5. Collection of Guirand and Ogérien (1865). **A**. Box MDC 20014042 with type material of *Zittelia victoria* (Guirand & Ogérien, 1865), **B**. Box MDC 20014062 with 13 specimens of *Zittelia oppeli* (Étallon, 1859). All specimens were collected from the Kimmeridgian of Valfin, France. Scale bars represent 10 mm.

species of *Zittelia* in approximately the same location and may vary slightly in size – smaller in the early forms from the middle Oxfordian and Kimmeridgian, and larger in the species from the Tithonian–?Valanginian.

Futterer (1892, p. 117, pl. 10, fig. 16) described a single specimen as *Zittelia striata* from the rudist facies of Calloniche, Northern Italy, and considered it to have been redeposited from the Tithonian carbonate platform of Polcenigo. Futterer (1892) noted the good preservation of the shell and highlighted the presence of denticles on the columellar lip, which are absent in other species of *Zittelia*. Another specimen, identified as *Z. striata*, from the upper Albian of Tannenboden, Chiemgau, Germany, is housed at SNSB-BSPG (SNSB-BSPG 1970 VI 88; unpublished material). It is poorly preserved and cannot be identified with confidence. On the basis of the original description, shell outline and presence of denticles on the columellar lip, this species appears to more closely resemble an early cypraeid than any colombellinid and is pending revision of the original material.

Stratigraphic and geographic occurrence: Upper Jurassic (middle Oxfordian–Tithonian) to ?lowermost Cretaceous (Valanginian); Rhône-Alpes (France), St-Ursanne (Switzerland), Swabia (Germany), and Moravian-Silesian region (Czechia and Poland).

Zittelia cipraeaeformis Gemmellaro, 1869
Figs 3A, 4

*1869 *Zittelia cipraeaeformis* sp. nov. – Gemmellaro, p. 88, pl. 15, figs 7–12.

1940 *Zittelia cipraeaeformis* Gemmellaro – Wenz, p. 927, fig. 2713.

1994 *Zittelia cipraeaformis* Gemmellaro – Groves, p. 27 [refigured from Wenz, 1940].

Material: 9 specimens from Sicily, Italy: 3 from Carini near Palermo (MGUP-20-361A.1, MGUP-20-361A.2, lectotype MGUP-20-361A.3 (designated herein)), 3 from Santa Maria di Gesù in Palermo (MGUP-20-361B.1, 361B.2, 361B.3), and 3 from Rotoli in Palermo (MGUP-20-361C.1, 361C.2, 361C.3).

Description: Shell thick, globular; apex blunt, elevated; teleoconch consists of 4 convex whorls, which increase rapidly in size, separated by moderately incised suture; last whorl large, its height being about three-quarters of the entire shell height; last whorl ornamented with 7–9 strong nodular spiral cords, with four stronger cords in the middle part and one weaker subsutural nodular cord; peristome siphonostomatous, thickened; aperture narrow, slit-like, straight in the central part and slightly curved in the abapical and parietal parts; columellar lip widely expanded, callous, smooth with a distinct sinuosity in the abapical part; outer lip denticulate, thickened, and bent outward.

Remarks: The coarse ornamentation of the last whorl is similar to that of *Z. oppeli*; however, the shell outline differs significantly. This species is distinguished from others by its globular shell (Tab. 3) with a low spire, which is almost not visible from the ventral side, and a widely expanded, callous columellar lip extending onto the dorsal side.

Table 3

Measurements (mm) of *Zittelia cipraeaeformis* Gemmellaro, 1869.
Abbreviations: H – shell height, W – shell width, PA – pleural angle.

Specimen number	H	W	PA
MGUP-20-361A.1	12.70	10.57	97°
MGUP-20-361A.2	15.76	14.25	90°
Lectotype MGUP-20-361A.3	13.20	11.35	90°
MGUP-20-361B.1	17.22	14.39	–
MGUP-20-361B.2	16.92	15.66	–
MGUP-20-361B.3	13.27	11.87	94°
MGUP-20-361C.1	9.34	6.85	–
MGUP-20-361C.2	10.75	9.22	94°
MGUP-20-361C.3	11.13	8.81	92°

Gemmellaro (1869) noted that this species is not related to any contemporaneous species. He did not indicate the number of studied specimens but mentioned that many specimens of this species are present in the Museum of Geology and Mineralogy of the University of Palermo (Gemmellaro, 1869, p. 88).

Stratigraphic and geographic occurrence: Tithonian–?Valanginian of Palermo and surroundings, Sicily (Italy).

Zittelia crassissima Zittel, 1873
Figs 6, 7

*1873 *Zittelia crassissima* sp. nov. – Zittel, p. 206, pl. 40, figs 11–13.

1903 *Zittelia crassissima* Zittel – Zittel, p. 374, fig. 915.

? 1919 *Zittelia crassissima* Zittel – Faure-Marguerit, p. 70.

Material: 6 specimens from Czechia: 2 from Koňákov (SNSB-BSPG AS III 896, 899), and 4 from Štramberk (lectotype SNSB-BSPG AS III 898 (designated herein), SNSB-BSPG AS III 897, 909, 910).

Description: Shell thick, oval, with low spire; apex not preserved; teleoconch consists of 4 preserved convex whorls, separated by moderately incised suture; spire whorls ornamented with widely spaced wide axial ribs and 3–4 thin spiral cords; last whorl large, its height being approximately four-fifths of the entire shell height; last whorl ornamented with 15–16 strong spiral cords including with two subsutural nodular cords; cords narrower than interspaces; peristome siphonostomatous, thickened; aperture narrow, slit-like, and s-shaped; it terminates with a short anterior canal and a relatively long inclined posterior canal, expanded at the end; columellar lip widely expanded, callous, smooth with sinuosity in the abapical part; outer lip denticulate, thickened, and bent outward.

Remarks: It is probable that the preservation of the studied specimens is the reason for the weak expression of the denticles on the inner part of the outer lip, which are only observable on one specimen (Fig. 6A) and were described by Zittel (1873) on the basis of the moulds. Zittel (1873) also noted that *Z. crassissima* possesses the thickest shell among all *Zittelia* species. It is worth noting that this species is the largest among the representatives of the genus (Tab. 4; Fig. 8).

Zittel (1873) described this species on the basis of the study of 10 specimens from the collection of Hohenegger. Of those, six specimens are currently present at SNSB-BSPG. Faure-Marguerit (1919) identified a single specimen as *Z. crassissima* from the Upper Jurassic of Echaillon, France.

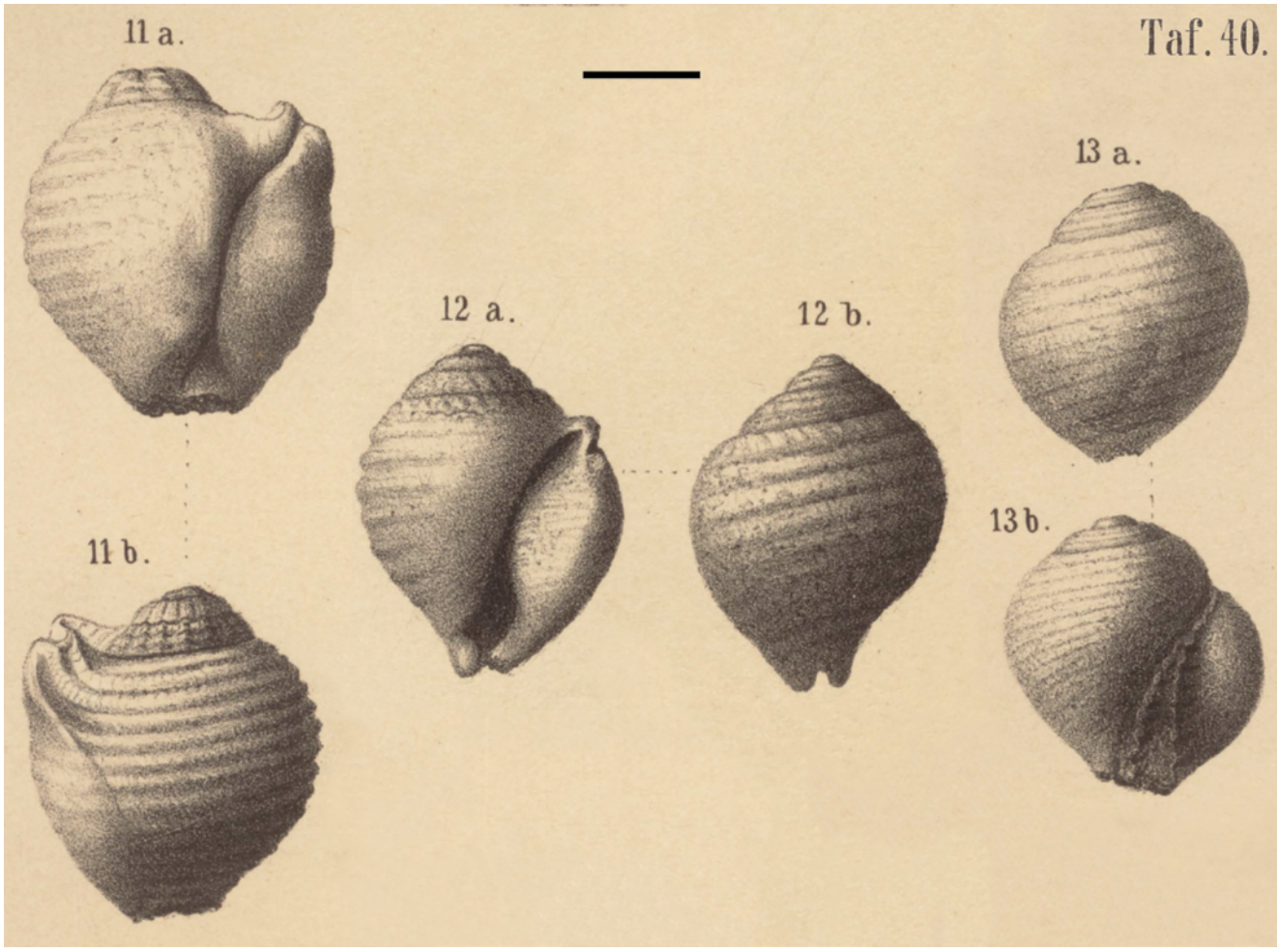

Fig. 6. Reproduction of Zittel's (1873, pl. 40, figs 11–13) drawings of three specimens of *Zittelia crassissima* Zittel, 1873, from Štramberk (11, 12) and Koňákov (13), Czechia, illustrating differences in sizes and in shell shape: more elongated (12a, b) and almost globose (13a, b). An approximate scale bar represents 5 mm.

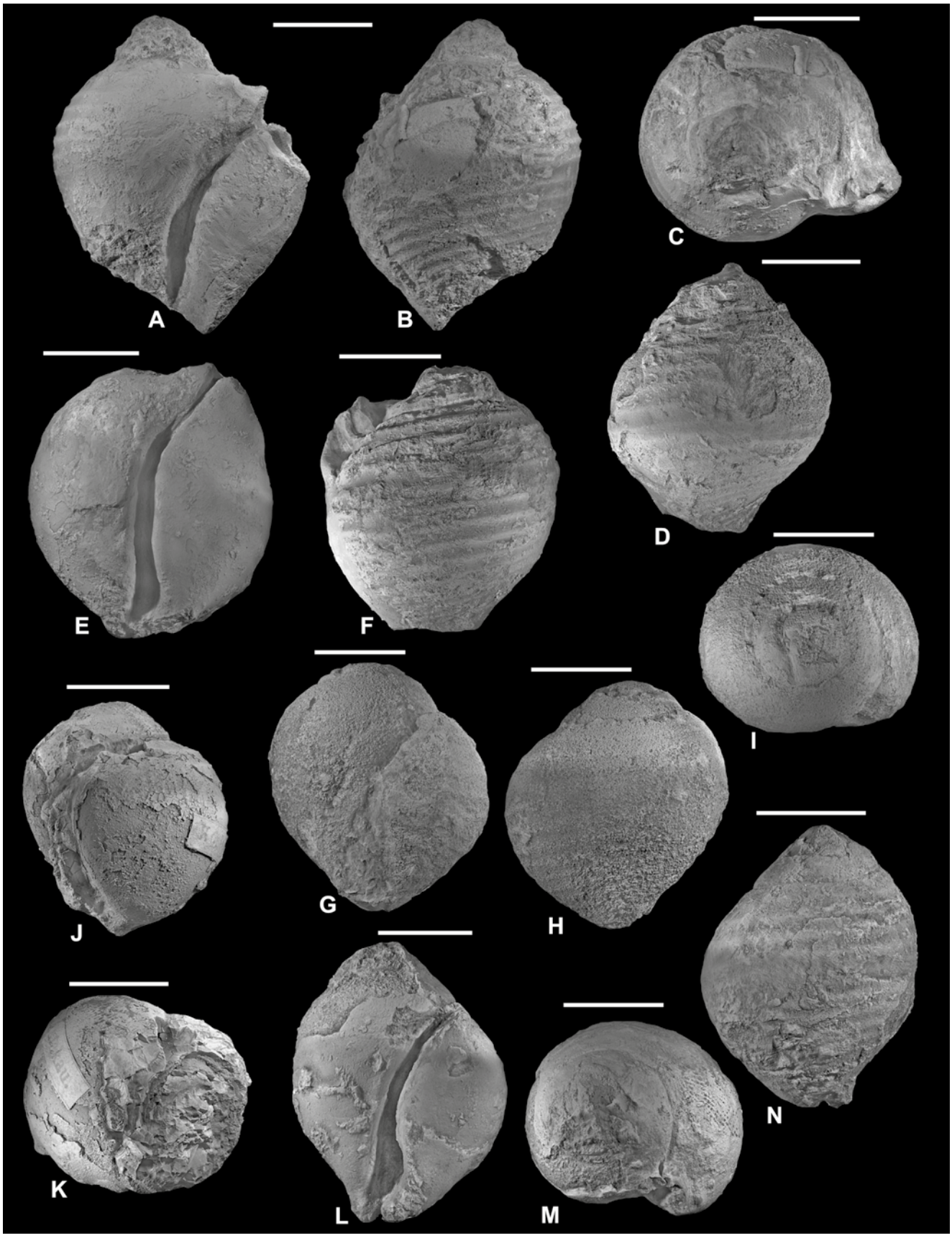

Fig. 7. *Zittelia crassissima* Zittel, 1873, from the Tithonian–?Berriasian of Czechia. **A–C**. SNSB-BSPG AS III 909, Štramberk; A – apertural view; B – abapertural view; C – apical view. **D**. SNSB-BSPG AS III 910, Štramberk, abapertural view. **E–F**. SNSB-BSPG AS III 897, Štramberk; E – apertural view; F – abapertural view. **G–I**. SNSB-BSPG AS III 896, Koňákov; G – apertural view; H – abapertural view, I– apical view. **J–K**. SNSB-BSPG AS III 899, Koňákov; J – abapertural view; K – basal view. **L–N**. Lectotype SNSB-BSPG AS III 898 (designated herein), Štramberk; L – apertural view; M – apical view; N – abapertural view. Scale bars represent 10 mm.

Table 4

Measurements (mm) of *Zittelia crassissima* Zittel, 1873.

Specimen number	H	W	PA
SNSB-BSPG AS III 896	27.49	24.44	94°
SNSB-BSPG AS III 897	28.86	25.67	90°
Lectotype SNSB-BSPG AS III 898	29.95	22.95	84°
SNSB-BSPG AS III 899	22.96	21.10	–
SNSB-BSPG AS III 909	32.25	26.08	85°
SNSB-BSPG AS III 910	27.48	22.86	83°

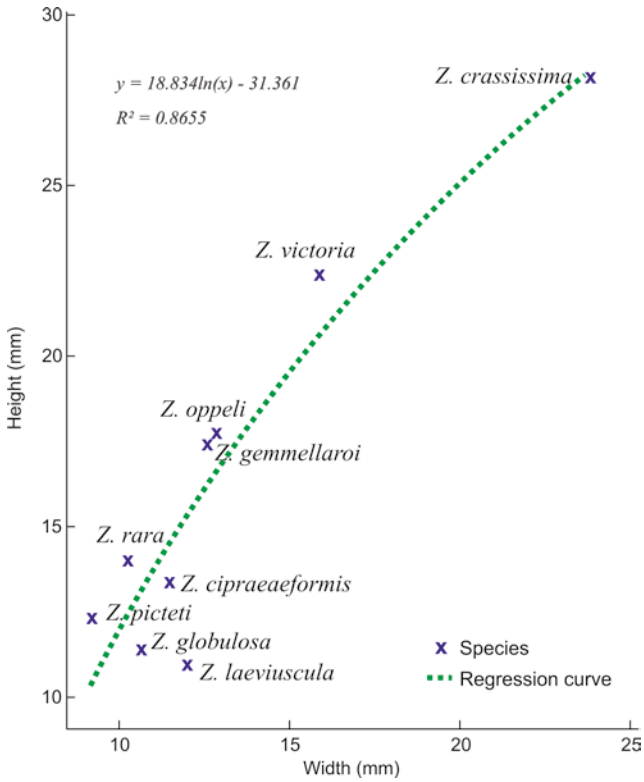

Fig. 8. Height/width ratio in species of *Zittelia*. Each point represents the mean of all specimens of the given species.

However, he did not provide any illustration or detailed description, referring only to its similarity with the specimens of Zittel (1873). Given the morphological similarity among *Zittelia* species, this record must be regarded with a degree of caution.

We assume that the specimen SNSB-BSPG AS III 898, designated herein as the lectotype, was illustrated by Zittel (1873, pl. 40, figs 12a, b) and is reproduced in the present study in Figure 6. Two other specimens, i.e., SNSB-BSPG AS III 909 and 897 (Figs 7A, B and 7E, F), probably were used to compose the illustration published by Zittel (1873, pl. 40, figs 11a, b) and reproduced in Figure 6 herein.

Stratigraphic and geographic occurrence: Tithonian–?Berriasian of Štramberk and Koňákov (Czechia).

Zittelia gemmellaroi Zittel, 1873
Fig. 9

*1873 *Zittelia Gemmellaroi* sp. nov. – Zittel, p. 208, pl. 40, fig. 10.

1909 *Zittelia globosa* sp. nov. – Brösamlen, p. 317, pl. 22, fig. 39.

1997 *Zittelia globosa* Broesamlen – Hägele, p. 108.

2017 *Columbellaria* cf. *corallina* (Quenstedt, 1852) – Werner et al., p. 32, pl. 3, figs A–C.

2019 *Columbellaria corallina* (Quenstedt) – Gründel *et al*., p. 133, pl. 9, figs 11–17.

2019 *Columbellaria globosa* (Brösamlen) – Gründel *et al*., p. 136, pl. 10, figs 2, 3.

2019 *Columbellaria* sp. 1 – Gründel *et al*., p. 136, pl. 9, fig. 18, pl. 10, fig. 1.

2024 *Columbellaria corallina* (Quenstedt, 1852) – Gründel and Nützel, p. 50, pl. 10, figs 12–15.

Remarks: The species differs from *Z. picteti* in its more convex whorls, a more inflated upper third of the ultimate whorl, and a more curved aperture, which starts to curve in the middle, whereas in *Z. picteti*, the aperture is straight and curved only in the posterior part. Additionally, we assign to *Z. gemmellaroi* specimens from Saal, Germany, recently described by Werner *et al.* (2017), Gründel *et al.* (2019), and Gründel and Nützel (2024), which exhibit a smooth columellar lip with characteristic sinuosity in the abapical part. The preservation of the material from Saal is better than that of the specimens, described by Zittel (1873) and Brösamlen (1909), which allowed the retention of faint but noticeable denticles on the inner surface of the outer lip (Gründel *et al.*, 2019, pl. 9, fig. 14). Although size of the specimens from Sall exceed Zittel's (1873) and Brösamlen's (1909) specimens (19 and 20 mm vs. 11 and 13 mm), their ornamentation and shell outline clearly correspond to the diagnostic features of *Z. gemmellaroi*.

Zittel (1873) investigated three specimens of *Z. gemmellaroi* from Czechia, and Brösamlen (1909) examined four specimens of Z. *globosa* from the White Jurassic of Swabia, Germany, both indicating differences from *Z. picteti*. The differences between Z. *globosa* and *Z. gemmellaroi*, as noted by Brösamlen (1909) are not sufficient, in our the opinion, to justify its recognition as a separate species and we consider *Z. globosa* to be a junior subjective synonym of *Z. gemmellaroi*.

Stratigraphic and geographic occurrence: Upper Kimmeridgian of Saal and Nattheim (Germany); Tithonian–?Berriasian of Štramberk (Czechia), Wilamowice (as Willamowitz in Zittel, 1873) and Iskrzyczyn (as Iskritschin in Zittel, 1873; Poland).

Zittelia globulosa Zittel, 1873
Figs 10, 11

*1873 *Zittelia globulosa* sp. nov. – Zittel, p. 207, pl. 40, figs 14, 15.

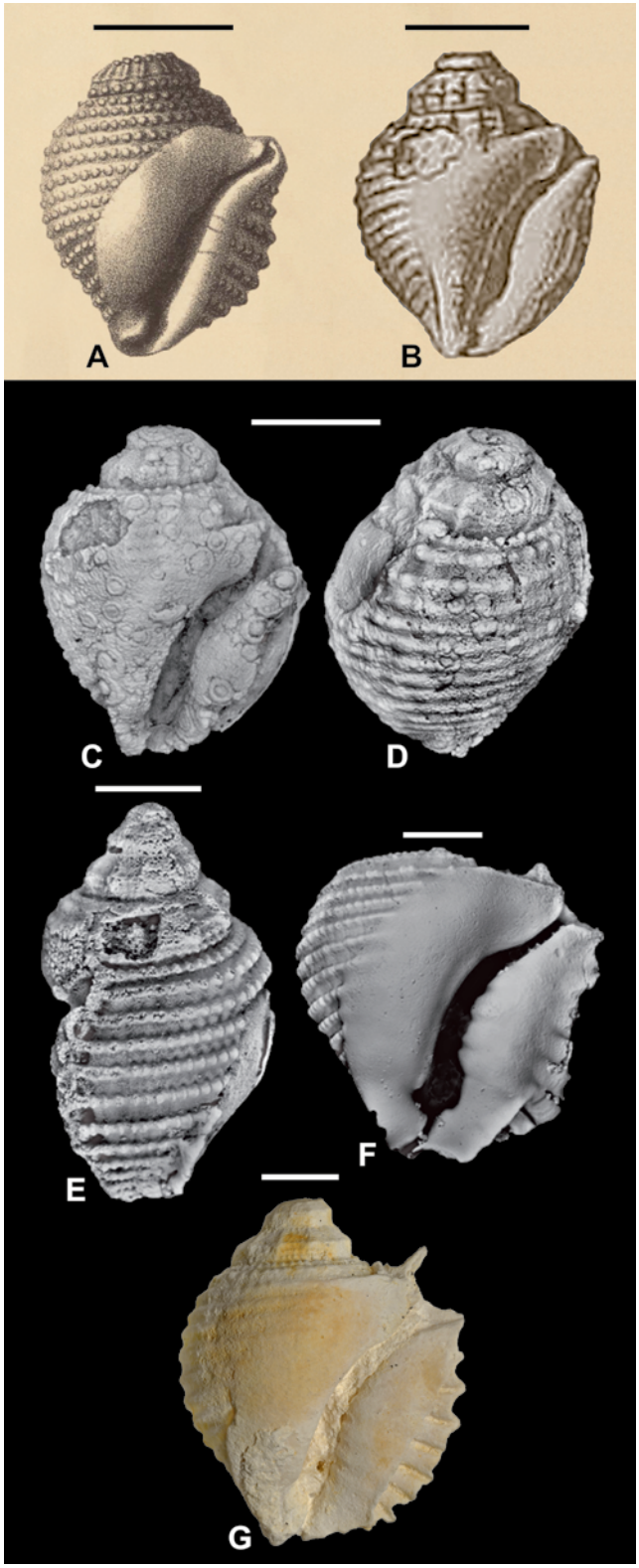

Fig. 9. *Zittelia gemmellaroi* Zittel, 1873. **A**. Reproduction of Zittel's drawing (1873, pl. 40, fig. 10c), height 11 mm; Tithonian–?Berriasian, Štramberk, Czechia. **B**. Reproduction from Brösamlen (1909, pl. 22, fig. 39), height 13 mm; Tithonian, Nattheim, Germany. **C–D**. Reproduction from Gründel *et al.* (2019, pl. 10, figs 2, 3), lectotype of *Zittelia gemmellaroi* Zittel, 1873, SMNS 60070. **E–F**. Reproduction from Gründel *et al.* (2019, pl. 9, figs 11, 14 as *Columbellaria corallina* (Quenstedt, 1852), SNSB-BSPG 2016 IV 124 and SNSB-BSPG 2016 IV 125), height 20 and 19 mm respectively; upper Kimmeridgian, Saal, Germany. **G.** SNSB-BSPG 2016 XXI 1, height 25 mm; upper Kimmeridgian; Saal, Germany. This specimen was also figured by Werner *et al.* (2017, figs 3A–C). Approximate (A–F) scale bars represent 5 mm.

Material: 2 specimens from Štramberk, Czechia (SNSB-BSPG AS III 900, 901).

Description: Shell thick, subglobular; apex not preserved; teleoconch consists of 4 convex whorls separated by moderately incised suture; on the penultimate whorl 13–14 axial ribs visible, while spiral ornamentation remains unknown; last whorl large, its height being approximately four-fifths of the entire shell height; last whorl ornamented with approximately 10 strong spiral cords (the nodular pattern in Zittel's (1873) illustrations is not visible on the examined specimens); peristome siphonostomatous, thickened; aperture narrow, slit-like; outer lip thickened and bent outward.

Remarks: The ornamentation is preserved on one specimen, where it is faintly visible. Zittel (1873) noted its distinction from *Z. crassissima* in the smaller size (Tab. 5) and different shell outline. He also stated that both the columellar and outer lip lack denticles. However, the aperture of the available specimens (Fig. 10) is covered with sediment, so its morphology remains unknown.

Table 5

Measurements (mm) of *Zittelia globulosa* Zittel, 1873.

Specimen number	H	W	PA
SNSB-BSPG AS III 900	11.37	10.76	94°
SNSB-BSPG AS III 901	11.41	10.45	83°

There is some confusion as to the number of specimens investigated by Zittel (1873) – he either had four specimens, including three internal moulds from Wilamowice, or only three specimens, including two internal moulds from Wilamowice. At SNSB-BSPG two specimens are present.

We assume that the specimens SNSB-BSPG AS III 900 and 901 (Fig. 11) probably were used to compose the illustration published by Zittel (1873, pl. 40, fig. 14a–c), which is reproduced herein (Fig. 10). Given the uncertainty about the type series and the poor preservation of both specimens we refrained from selecting a lectotype.

Stratigraphic and geographic occurrence: Tithonian–?Berriasian of Štramberk (Czechia).

Zittelia laeviuscula Zittel, 1873
Figs 12, 13

*1873 *Zittelia laeviuscula* sp. nov. – Zittel, p. 207, pl. 40, figs 16–18.

Material: 6 specimens: 5 from Štramberk, Czechia (lectotype SNSB-BSPG AS III 902 designated herein, SNSB-BSPG AS III 904, 905, 906, 907), and 1 from Wilamowice, Poland (SNSB-BSPG AS III 903).

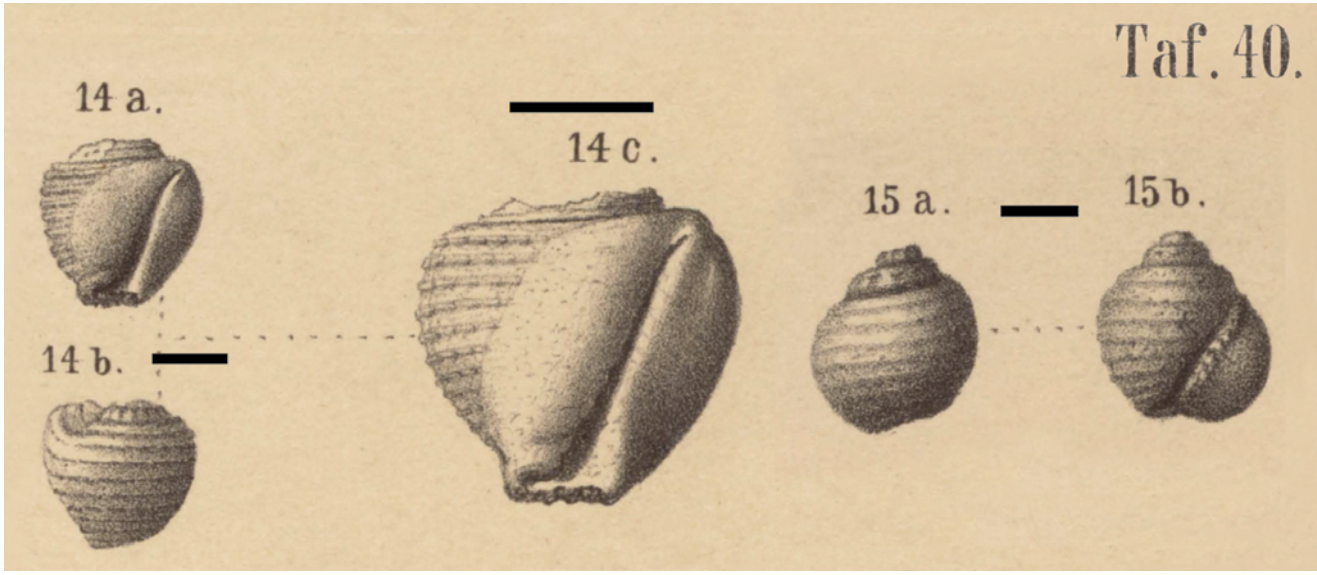

Fig. 10. Reproduction of Zittel's (1873) drawings of two specimens of *Zittelia globulosa* Zittel, 1873 from Štramberk, Czechia (14) and Wilamowice (15), Poland. The repository of the specimen from Wilamowice (15) is unknown. An approximate scale bars represent 5 mm.

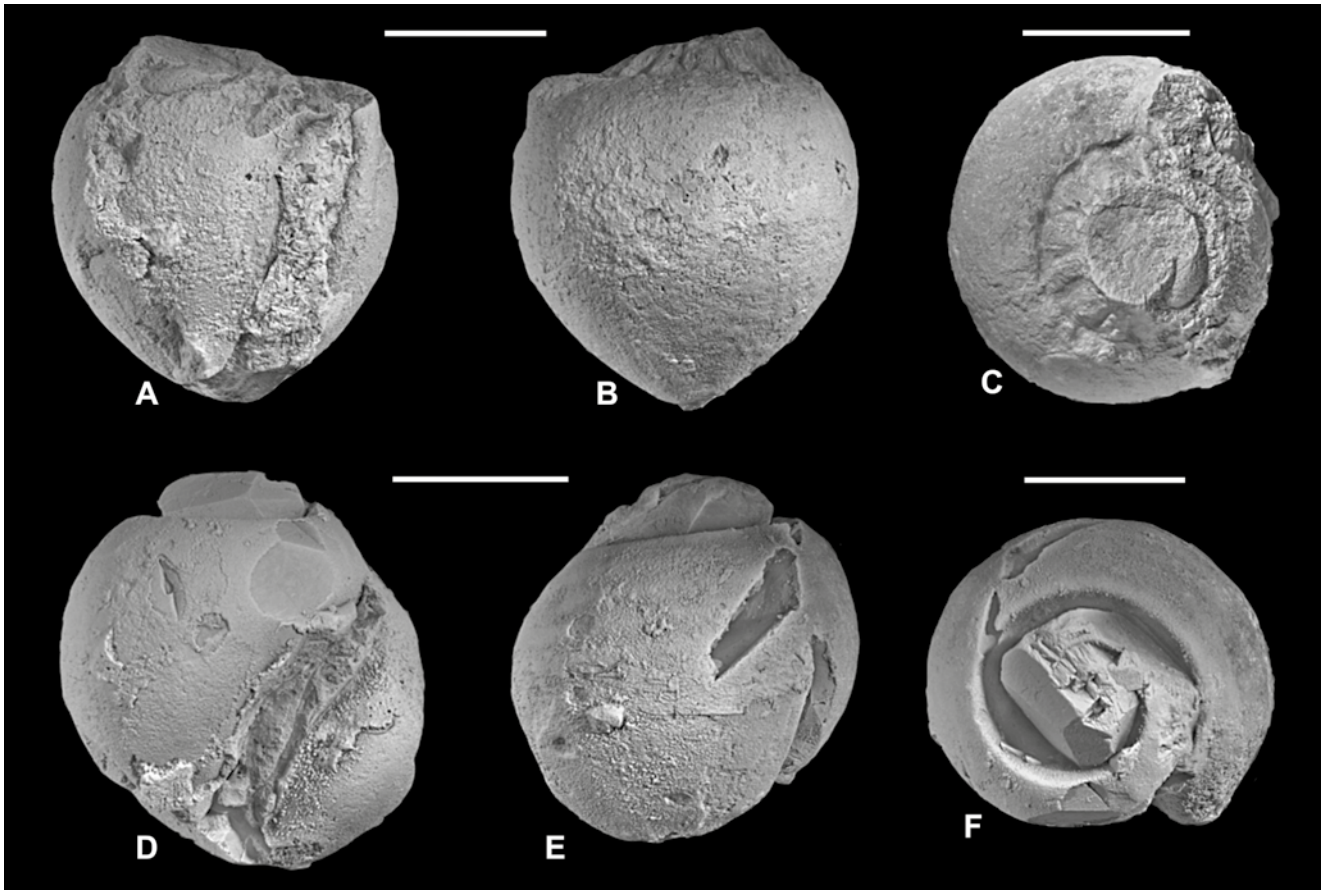

Fig. 11. *Zittelia globulosa* Zittel, 1873, from the Tithonian–?Berriasian of Štramberk, Czechia. **A–C**. SNSB-BSPG AS III 900; A – apertural view, B – abapertural view; C – apical view. **D–F**. SNSB-BSPG AS III 901; D – apertural view; E – abapertural view; F – apical view. Scale bars represent 5 mm.

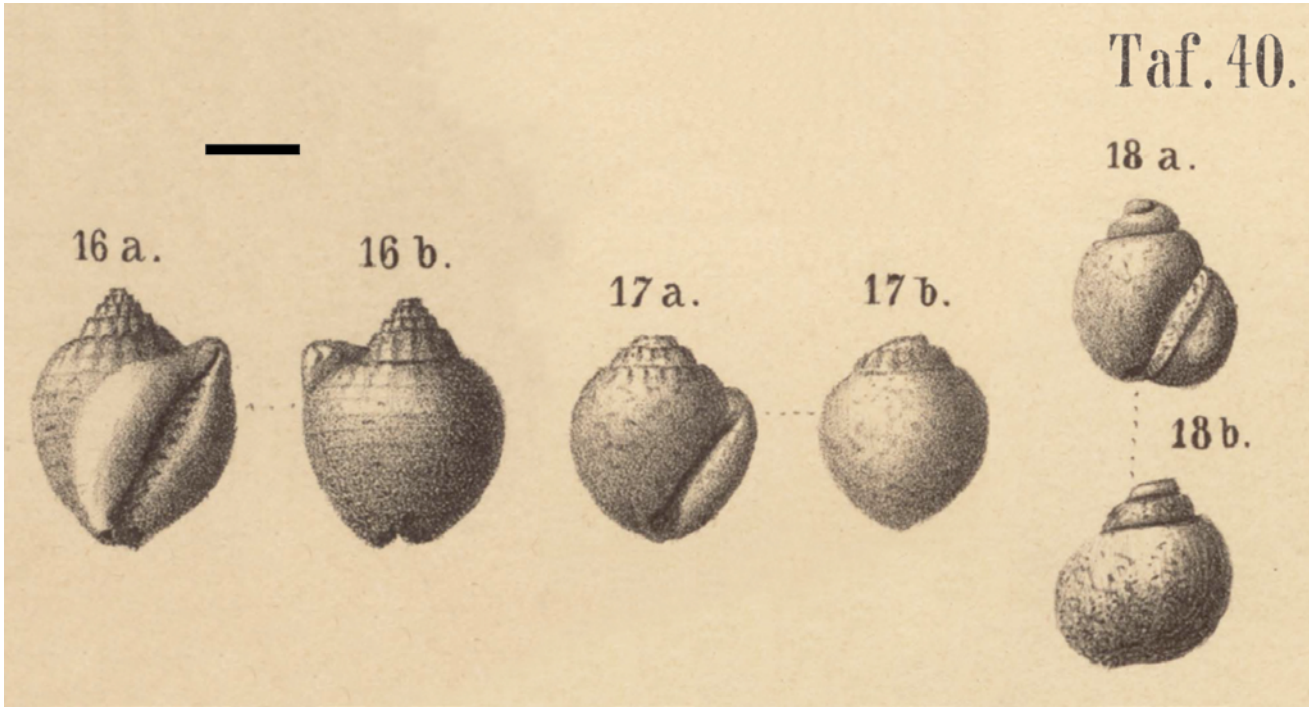

Fig. 12. Reproductions of Zittel's (1873) drawings of *Zittelia laeviuscula* Zittel, 1873 from Štramberk (16) and Koňákov (17), Czechia, and Wilamowice (18), Poland, illustrating different types of preservation. The place of storage of the specimen from Koňákov (17) is unknown. An approximate scale bar represents 5 mm.

Description: Shell thick, oval; apex not preserved; teleoconch consists of 4–5 convex whorls, separated by a moderately incised suture; spire elevated, blunt; spire whorls, angulated at middle of whorl face, ornamented with axial ribs and spiral cords; axial ribs opisthocyrt and wide, numbering 12–14 on the penultimate whorl; spiral ornamentation of two orders with the thickest spiral cord situated about on the middle of the whorls; last whorl large, its height being about three-quarters of the shell height; last whorl ornamented with spiral cords and axial ribs of almost equal thickness; peristome siphonostomatous, thickened; aperture narrow, slit-like; it terminates with short anterior canal and relatively long inclined posterior canal expanded at the end; columellar lip widely expanded, callous, smooth with sinuosity in the abapical part; outer lip denticulate, thickened, and bent outward.

Remarks: Two specimens (SNSB-BSPG AS III 906 and 907) are distinguished from others by a wider last whorl, a larger pleural angle (Tab. 6), and the presence of ornamentation. Zittel (1873) noted that the absence of ornamentation in other specimens was due to their preservation, while the wider last whorl could be an intraspecific variation.

The species differs from *Z. cipraeaeformis* in having a higher spire and a greater number of spiral cords on the last whorl. It also differs from *Z. picteti* in having a wider shell and a narrow, elongated posterior canal. Finally, it differs from *Z. crassissima* in having a straight aperture and a higher spire.

Zittel (1873) examined twelve specimen, of which six are stored at SNSB-BSPG.

We suspect that the illustration published by Zittel (1873, pl. 40, fig. 16a, b) is a composite of two specimens. The shell outline and spire ornamentation demonstrate a high degree of correspondence with specimen SNSB-BSPG AS III 902 (Figs 13A, B), which is designated here as the lectotype, whereas the aperture morphology appears to have been drawn from specimen SNSB-BSPG AS III 906 (Figs 13H, I).

Stratigraphic and geographic occurrence: Tithonian–?Berriasian of Štramberk (Czechia) and Wilamowice (Poland).

Table 6

Measurements (mm) of *Zittelia laeviuscula* Zittel, 1873.

Specimen number	H	W	PA
Lectotype SNSB-BSPG AS III 902	14.46	11.75	88°
SNSB-BSPG AS III 903	12.13	10.71	88°
SNSB-BSPG AS III 904	10.67	10.92	–
SNSB-BSPG AS III 905	11.97	9.97	95°
SNSB-BSPG AS III 906	12.29	12.84	106°
SNSB-BSPG AS III 907	10.19	9.60	112°

Zittelia oppeli (Étallon, 1859)
Figs 14, 15

1859 *Columbellina Oppeli* sp. nov. – Étallon, p. 120.

*1865 *Columbellina Sofia* – Guirand and Ogérien, p. 385, text-figs 32, 33.

1867 *Columbellina Sofia* (Guir. et Ogér.) – Ogérien, p. 592, text-figs 203, 204.

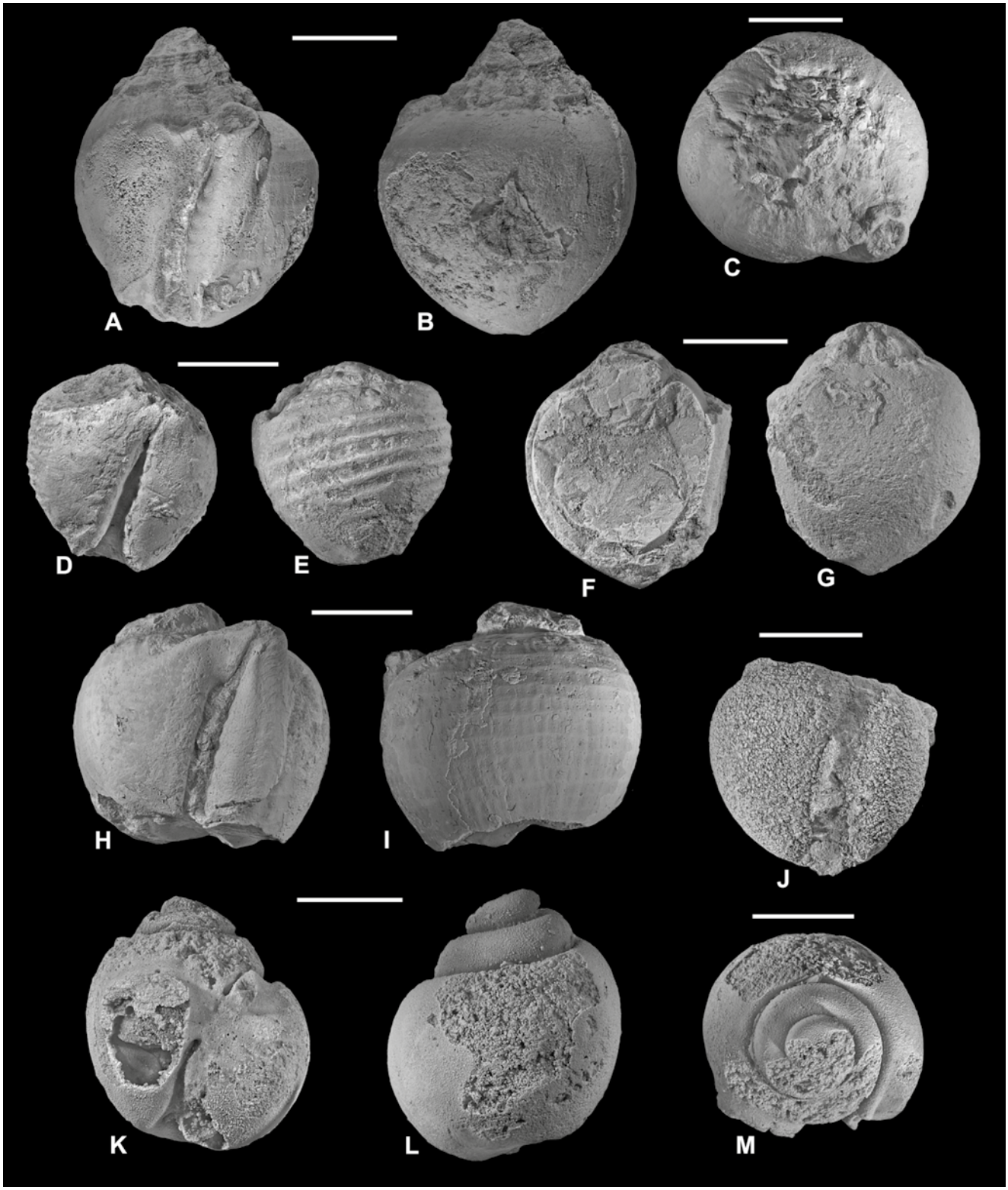

Fig. 13. *Zittelia laeviuscula* Zittel, 1873 from the Tithonian–?Berriasian of Štramberk, Czechia (A–J) and Wilamowice (Willamowitz), Poland (K–M). **A–C**. Lectotype SNSB-BSPG AS III 902 (designated herein); A – apertural view; B – abapertural view; C – apical view. **D–E.** SNSB-BSPG AS III 907; D – apertural view; E – abapertural view. **F–G.** SNSB-BSPG AS III 905; F – apertural view; G – abapertural view. **H–I.** SNSB-BSPG AS III 906; H – apertural view; I – abapertural view. **J**. SNSB-BSPG AS III 904, apertural view. **K–M.** SNSB-BSPG AS III 903; K – apertural view; L – abapertural view; M – apical view. Scale bars represent 5 mm.

1884 *Zittelia Sophia* Ogérien – Fischer, p. 657, fig. 410.

1886 *Zittelia Oppeli* (Étallon) Gemellaro – de Loriol, p. 62, pl. 4, figs 4–8.

1904 *Zittelia Oppeli* Étallon – Cossmann, p. 112, pl. 7, fig. 7.

1913 *Columbellina (Zittelia) Oppeli* Étallon – Cossmann, p. 36, pl. 2, figs 48–50.

1913 *Zittelia Oppeli* (Et.) – Favre (in Joukowsky and Favre 1913), p. 440, pl. 28, figs 13, 14.

Material: 13 specimens from Valfin, France (MDC 20014062.1-13).

Description: Shell thick, oval, with relatively high, acute spire; earliest whorls not preserved; teleoconch consists of 7–8 preserved convex whorls, separated by a moderately incised suture; spire whorls ornamented with axial ribs and spiral cords, angulated at middle of whorl face; axial ribs opisthocyrt and the most prominent in the middle part of whorls, where blunt, adapically oriented small spines occur, numbering 12–14 on the penultimate whorl on angulation; spiral ornamentation of thin cords of two orders, with more prominent subsutural and peripheral rows of nodes; last whorl large, its height being about three-quarters of the shell height and ornamented with 9–10 nodular spiral cords; the spacing between the cords approximately equal to their thickness, and nodules on the cords almost round; three spiral cords in the middle part visibly larger than the others; peristome siphonostomatous, thickened; aperture narrow, slit-like; anterior canal short; posterior canal expanded at the end; columellar lip widely expanded, smooth with sinuosity in the abapical part; outer lip denticulate, thickened, and bent outward.

Remarks: *Z. oppeli* has a higher spire (Tab. 7) than other species of *Zittelia* (Fig. 4B) and seems to be the most closely related to the species of *Colombellina* in terms of shell shape and ornamentation. Similarly to *Z. cipraeaeformis*, it exhibits a groove, but the sinuosity is slightly smaller.

Table 7

Measurements (mm) of *Zittelia oppeli* (Étallon, 1859).

Specimen number	H	W	PA
MDC 20014062.1	16.77	11.54	75°
MDC 20014062.2	17.88	12.58	73°
MDC 20014062.3	18.58	14.26	74°

It differs from *Z. picteti* in having a higher spire and the ornamentation of the last whorl.

Étallon (1859) did not illustrate the species, providing only a description. He also did not indicate the number of studied specimens, noting that the species is common. A few years later, Guirand and Ogérien (1865) described *Columbellina* (sic!) *sofia*, which was collected in large numbers from the type locality. De Loriol (1886), in addition to his own material, examined the collections of previous researchers and concluded that these two species are synonyms and belong to *Zittelia*. Favre (in Joukowsky and Favre, 1913) identified four specimens as *Z. oppeli* from the Tithonian of Salève, France, expanding the stratigraphic and geographical distribution of the species.

Stratigraphic and geographic occurrence: Kimmeridgian of Valfin and Rixouse (France); Tithonian of Salève (France).

Zittelia picteti Gemmellaro, 1869
Figs 3B, 16

*1869 *Zittelia Picteti* sp. nov. – Gemmellaro, p. 87, pl. 15, figs 4–6.

1897 *Zittelia Picteti* Gemmellaro – Roman, p. 287, pl. 2, fig. 4, 4a (non 5, 5a).

1913 *Zittelia Picteti* (Et.) – Favre (in Joukowsky and Favre, 1913), p. 440, pl. 28, figs 15–18.

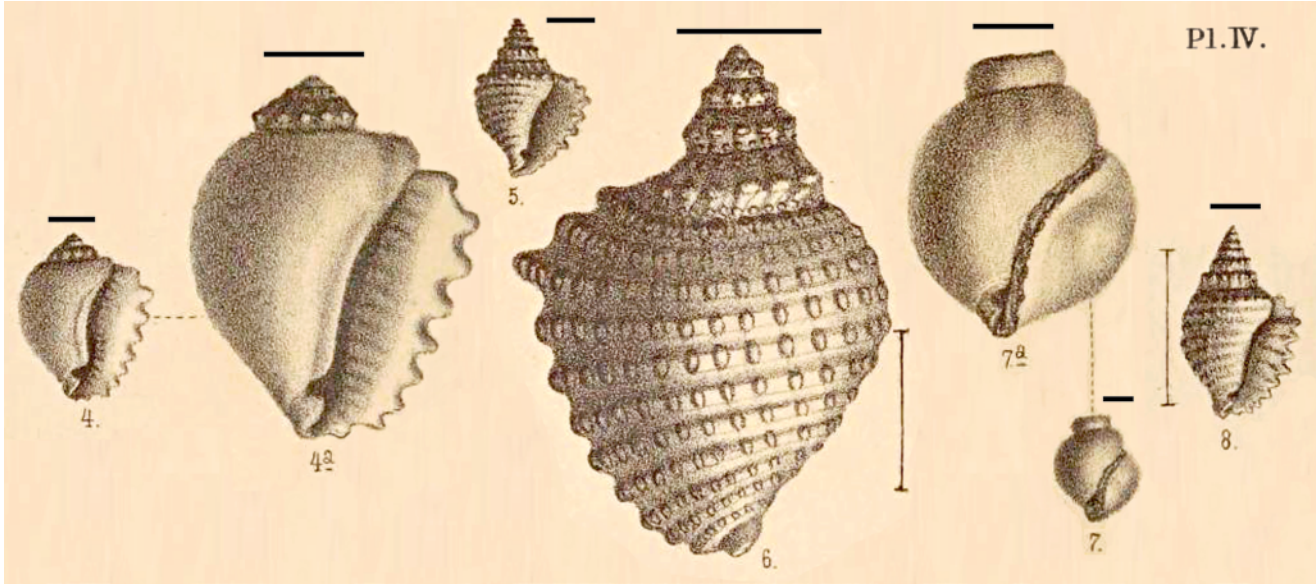

Fig. 14. Reproductions of Loriol's (1886) drawings of *Zittelia oppeli* (Étallon, 1859) from the Kimmeridgian of Valfin, France. The specimen number 5 is MDC 20014062.1 and is figured herein (Fig. 15A–C). An approximate scale bars represent 5 mm.

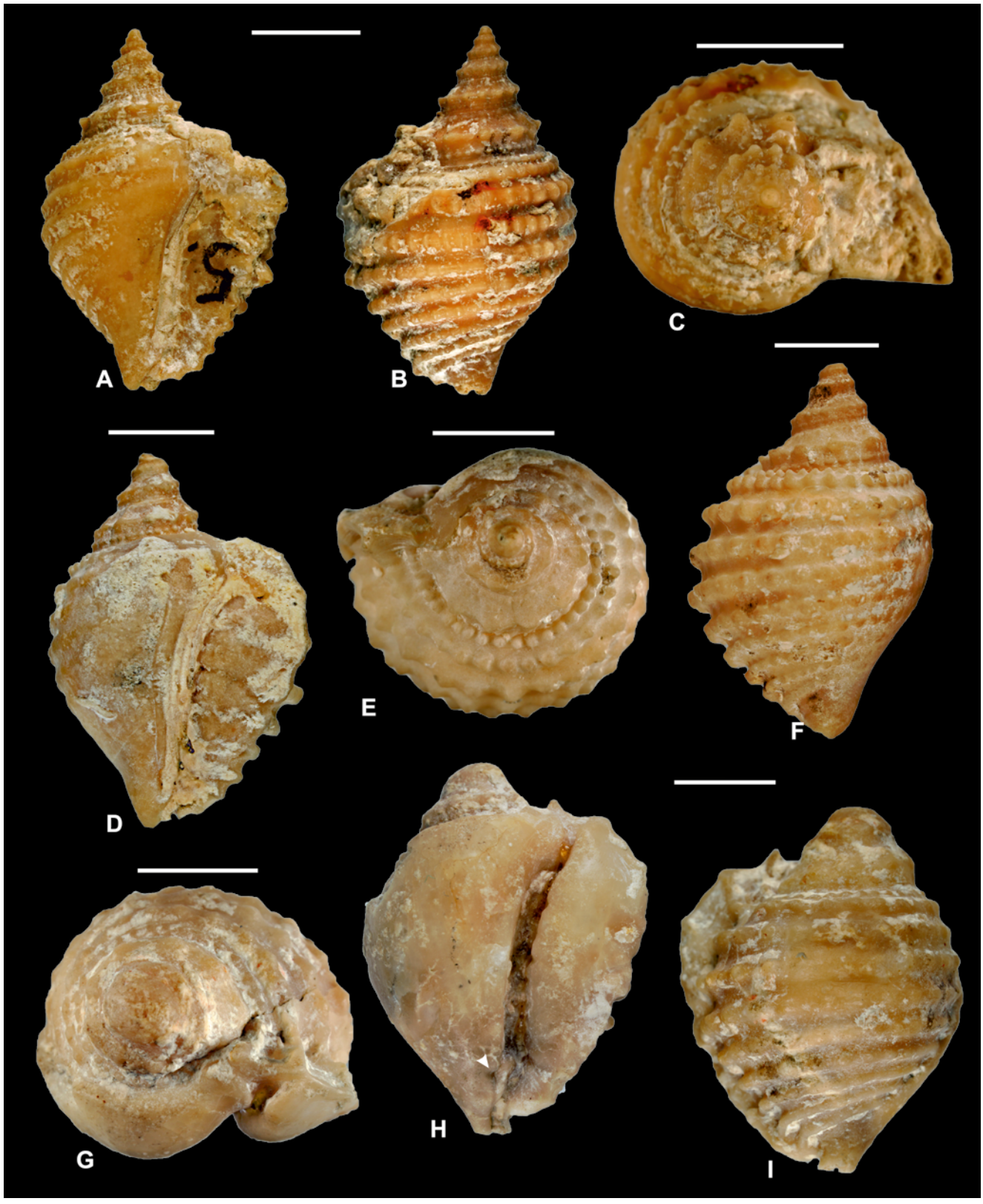

Fig. 15. *Zittelia oppeli* (Étallon, 1859) from the Kimmeridgian of Valfin, France. **A–C.** MDC 20014062.1, this specimen corresponds the figure illustrated by de Loriol (1886, pl. 4, fig. 5), as evidenced by the inscribed number 5 on the shell; A – apertural view; B – abapertural view; C – apical view. **D–F**. MDC 20014062.2; D – apertural view; E – apical view; F – abapertural view. **G–I**. MDC 20014062.3; G – apical view; H – apertural view, arrow indicates sinuosity; I – abapertural view. Scale bars represent 5 mm.

? 1931 *Zittelia Picteti* Gemmellaro – Tsan-hsun, p. 36, pl. 3, fig. 1.

Material: 2 specimens from Carini near Palermo, Sicily, Italy (lectotype MGUP-20-362.1 (designated herein), and MGUP-20-362.2).

Description: Shell thick, oval, with low spire; apex not preserved; teleoconch consists of 5 convex whorls separated by incised suture; spire whorls ornamented with wide axial ribs numbering 10–12 on the penultimate whorl; last whorl large, its height being about three-quarters of the shell height; the last whorl ornamented with 14–16 spiral cords with nodules; the spacing between the cords approximately equal to their thickness; the nodules are nearly round in shape and densely arranged; peristome siphonostomatous, thickened; aperture narrow, slit-like, and curved in the posterior part; anterior canal short; posterior canal slightly expanded at the end; columellar lip smooth, widely expanded, with sinuosity in the abapical part; outer lip thickened and bent outward.

Remarks: It differs from *Z. cipraeaeformis* in its oval shell instead of a globular one, a greater number of spiral ribs on the last whorl, and a less expanded columellar lip. It also differs from *Z. oppeli* in having more numerous spiral ribs on the last whorl, a lower shell (Tab. 8), and a straighter aperture. It can be distinguished from *Z. gemmellaroi* by its less convex last whorl and a straighter, less curved aperture.

Table 8

Measurements (mm) of *Zittelia picteti* Gemmellaro, 1869.

Specimen number	H	W	PA
Lectotype MGUP-20-362.1	12.28	9.27	77°
MGUP-20-362.2	12.36	9.06	75°

Joukowsky and Favre (1913) synonymised *Z. globosa* with *Z. picteti*. However, on the basis of a comparison between the type material of *Zittelia picteti*, described by Gemmellaro (1869) and the lectotype of *Z. globosa*, originally described by Brösamlen (1909) and redescribed by Gründel *et al.* (2019), it is concluded that these two represent separate species.

Gemmellaro (1869) observed that this species is rare (he reports two specimens). Favre (Joukowsky and Favre, 1913) studied 25 specimens from the Tithonian of Salève, France, noting significant variations in shell shape, suggesting that the less inflated shells represent younger individuals. Tsan-hsun (1931) referred to this taxon three specimens he studied from the Tithonian of southern France, but the validity of these identifications is questionable, due to the lack of data on aperture morphology.

Stratigraphic and geographic occurrence: Tithonian–?Valanginian of Carini (Sicily, Italy) and Salève (France).

Zittelia rara (Gründel, Hostettler & Menkveld-Gfeller, 2022)
Fig. 17

*2022 *Columbellaria rara* sp. n. – Gründel, Hostettler and Menkveld-Gfeller, p. 57, pl. 10, figs 12–16, pl. 11, figs 1–3.

Remarks: This species is the earliest documented representative of *Zittelia*. Gründel *et al.* (2022) diagnosed this species on the basis of two specimens with shell heights of 13 mm and 15 mm, respectively. In the original description, Gründel *et al.* (2022) did not mention the presence of a sinuosity; however, in the figures of the aperture (Gründel *et al.,* 2022, pl. 10, figs 12, 15), a slight depression is visible in the abapical part of the aperture, where sinuosity is usually present. The tightly adhering columellar lip without denticles further reinforces its affinity with *Zittelia* rather than with *Colombellina* (*Collumbellaria* in Gründel *et al.,* 2022).

Zittelia rara differs from *Z. oppeli* by a wider shell, a narrower columellar lip, a lower number of spiral cords on the last whorl and a greater distance between them, and a wider aperture. It differs from *Z. picteti* in a lower number of spiral ribs on the last whorl, as well as a curved and wider aperture.

Stratigraphic and geographic occurrence: Middle Oxfordian (coral facies of the St-Ursanne Formation) of Fabrique de Chaux, St-Ursanne (Switzerland).

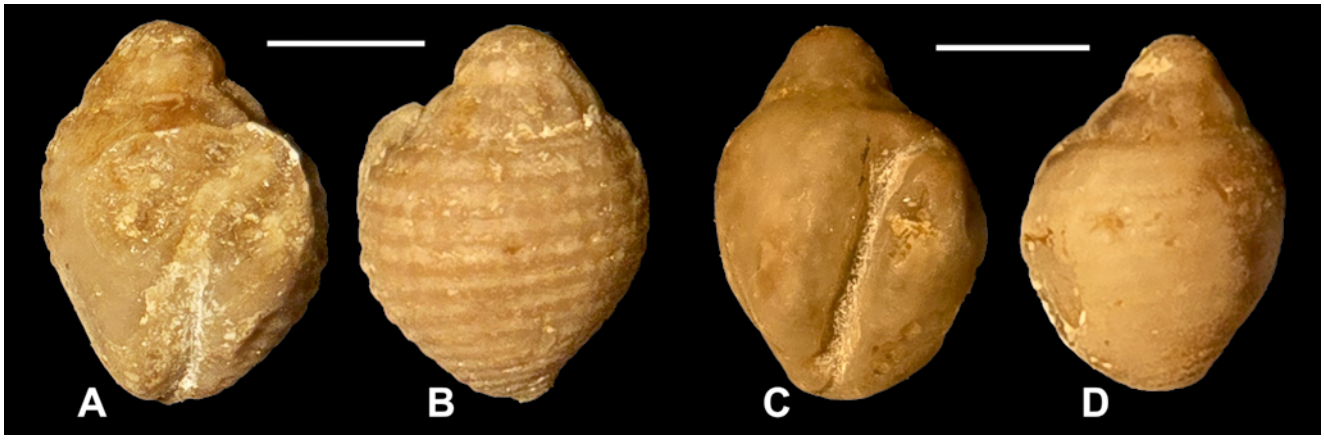

Fig. 16. *Zittelia picteti* Gemmellaro, 1869, Tithonian–?Valanginian, Carini near Palermo, Sicily, Italy. **A–B**. Lectotype MGUP-20-362.1 (designated herein); A – apertural view; B – abapertural view. **C–D**. MGUP-20-362.2; C – apertural view; D – abapertural view. Scale bars represent 5 mm.

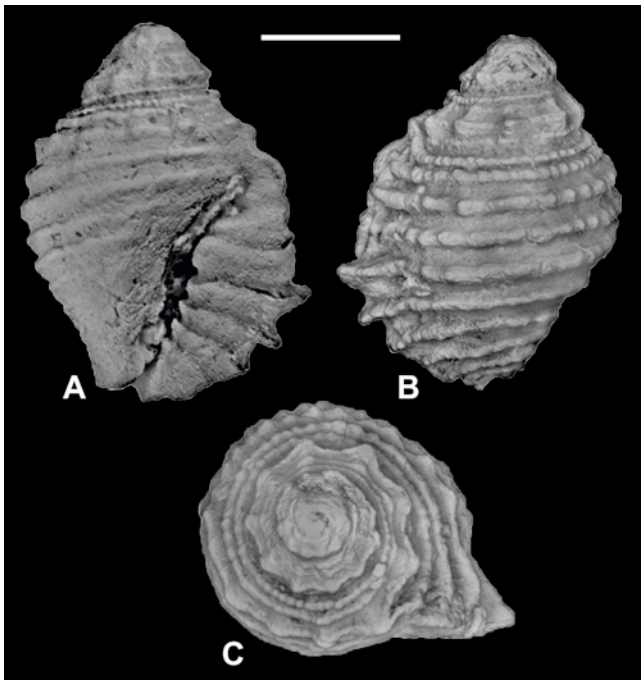

Fig. 17. Reproduction of *Zittelia rara* (Gründel, Hostettler & Menkveld-Gfeller, 2022) (Gründel *et al.*, 2022, pl. 10, figs 12, 13, pl. 11, fig. 1 as *Columbellaria rara*) from the middle Oxfordian (coral facies of the St-Ursanne Formation) of St-Ursanne, Switzerland. **A.** Apertural view. **B.** Abapertural view. **C.** Apical view. An approximate scale bar represents 5 mm.

Zittelia victoria (Guirand & Ogérien, 1865)
Figs 18, 19

*1865 *Columbellina Victoria* – Guirand et Ogérien, p. 386, text-figs 34, 35.

1867 *Columbellina Victoria* (Guir. et Ogér.) – Ogérien, p. 592, text-figs 205, 206.

1873 *Columbellaria Victoria* Guirand & Ogérien – Zittel, p. 202.

1886 *Zittelia Victoria*, Guirand et Ogérien – de Loriol, p. 64, pl. 4, fig. 9.

1904 *Columbellina* (*Zittelia*) *Victoria* (Guir. et Ogér.) – Cossmann, p. 112, pl. 7, fig. 6.

1913 *Columbellina* (*Zittelia*) *Victoriae* Guirand et Ogérien – Cossmann, p. 37, text-fig. 13.

Material: 3 specimens from Valfin, France (lectotype MDC 20014042.1 (designated herein), MDC 20014042.2, and 20014042.3).

Description: Shell thick, oval, with relatively high spire; apex not preserved; teleoconch consists of 5 preserved convex whorls separated by moderately incised suture; spire whorls ornamented with axial ribs and spiral cords; the axial ribs wide and slightly opisthocyrt, numbering 12–14 on the penultimate whorl; spiral ornamentation of nodular cords, one of which occurring almost in the middle of the whorls and the other two located towards the abapical suture; close to the adapical suture a subsutural cord occurs; last whorl large, its height being about four-fifths of the shell height and ornamented with 13–15 nodular spiral cords; the

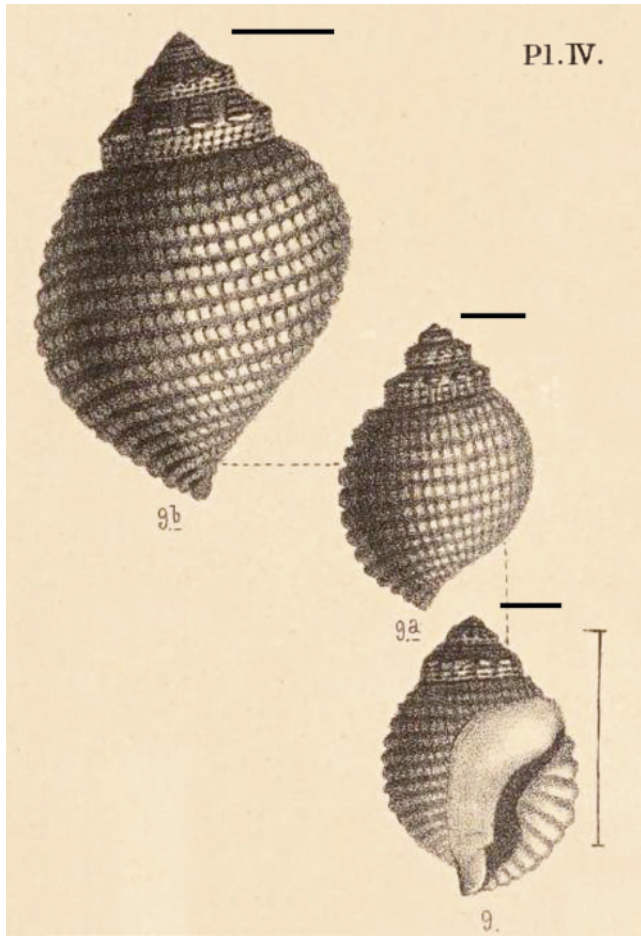

Fig. 18. Reproduction of Loriol's (1886) drawings of *Zittelia victoria* (Guirand & Ogérien, 1865) from the Kimmeridgian of Valfin, France. This is the same specimen as MDC 20014042.1 and is designated herein as the lectotype (Fig. 19A–C). An approximate scale bars represent 5 mm.

distances between the cords are approximately equal to their thickness, and the nodules on the cords are tightly arranged, oval in shape, and elongated vertically; peristome siphonostomatous, thickened; aperture narrow, slit-like and curved; anterior canal short; posterior canal expanded at the end; columellar lip widely expanded, smooth with sinuosity in the abapical part; outer lip denticulate, thickened, and bent outward.

Remarks: This species is clearly distinguishable from *Z. oppeli* in the greater number of spiral cords and wider shape (Tab. 9). It differs from *Z. picteti* in its curved aperture and cords with smaller nodes.

Table 9

Measurements (mm) of *Zittelia victoria* (Guirand & Ogérien, 1865).

Specimen number	H	W	PA
Lectotype MDC 20014042.1	22.94	16.06	74°
MDC 20014042.2	21.16	15.82	77°
MDC 20014042.3	23.19	15.01	–

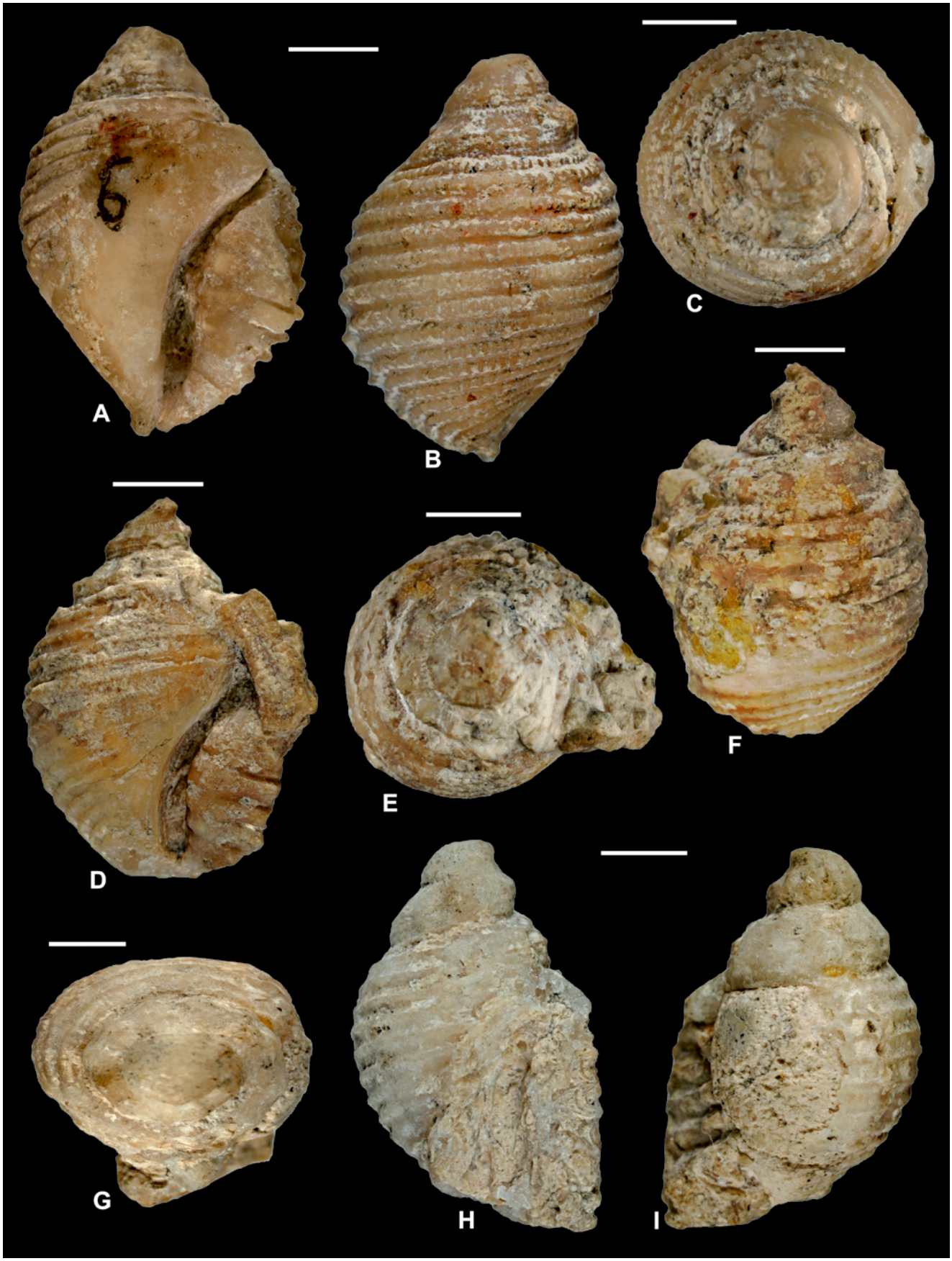

Fig. 19. *Zittelia victoria* (Guirand & Ogérien, 1865) from the Kimmeridgian of Valfin, France. **A–C.** Lectotype MDC 20014042.1 (designated herein); A – apertural view; B – abapertural view; C – apical view. **D–F**. MDC 20014062.2; D – apertural view; E – apical view, F – abapertural view. **G–I**. MDC 20014062.3; G – apical view; H – apertural view; I – abapertural view. Scale bars represent 5 mm.

Three specimens, described herein from the collection of Guirand and Ogérien (1865), were also studied by de Loriol (1886). It was also this species and perhaps these very specimens that Cossmann (1904, 1913) used to emend the diagnosis of *Zittelia*.

Stratigraphic and geographic occurrence: Kimmeridgian of Valfin (France).

DISCUSSION

Comparison with related taxa

Colombellina d'Orbigny, 1842
Pseudocassis Pictet and Campiche, 1863
Cypraeidae Rafinesque, 1815

The differences between *Zittelia* and *Colombellina* are discussed in the systematic part above. It is worth noting that there has been no comprehensive revision of *Zittelia* since its original description by Gemmellaro (1869) and some remarks by Cossmann (1904, p. 112), which may have contributed to the misunderstanding of its diagnostic character states and subsequently led to a premature synonymization of *Zittelia* with *Columbellaria* (Gründel *et al.*, 2019) – a genus that we consider to be a synonym of *Colombellina*. Previously, Cossmann (1904, 1913) included *Columbellaria* and *Zittelia* as subgenera of *Colombellina*; however, in his later work (Cossmann, 1916), he did not adhere to this classification and used them at the rank of genus. The uncertainty concerning the distinction between these two genera is caused by the significant degree of morphological similarity between them; in particular both have thick shells with granular ornamentation, a siphonostomatous and thickened peristome, and a narrow aperture. A further common characteristic is the presence of an adapical subsutural cord, which is particularly well expressed in species of *Zittelia* from the upper Oxfordian (*Z. rara*) and Kimmeridgian (*Z. victoria, Z. oppeli*), and also has been documented in species of *Colombellina*. In two species, *Z. globulosa* and *Z. laeviuscula*, the subsutural cord has not been observed, probably due to their eroded shells (Figs 11, 13).

Pseudocassis Pictet and Campiche, 1863

The Cretaceous genus *Pseudocassis* has a cypraeiform shell, resembling that of *Zittelia*. *Pseudocassis* was originally introduced as a monotypic genus, based on the type species *P. helveticus* (Pictet and Campiche, 1863, p. 363, pl. 74, figs 2, 3) from the Lower Cretaceous of Sainte-Croix (Switzerland). Although preserved as composite moulds, distinctive features, particularly the aperture morphology, enabled Pictet and Campiche (1863) to confidently assert that its specimens did not belong to any previously known species. Gemmellaro (1869, p. 86) pointed out that although *Zittelia* is morphologically similar to *Pseudocassis*, it differs in the position of the spire and the presence of anterior and posterior aperture tortuosity. According to Gemmellaro (1869, p. 86), these distinctions indicate a significant separation between these two genera, justifying their placement in different gastropod families.

Later, Zittel (1873) considered *Pseudocassis* to be a synonym of *Zittelia*, but the type species of this genus does not display any sign of the sinuosity that is diagnostic for *Zittelia*. Stoliczka (1867) regarded *Pseudocassis* as closely related to, but not synonymous with *Cypraea*, and proposed to include it in the subfamily Cypraeinae Rafinesque, 1815. Sayn (1932) included *Pseudocassis* in the Cypraeidae, noting differences from *Cypraea*, particularly the absence of denticulate lips. Zilch (1959) included ?*Pseudocassis* in the heterobranch Acteonidae d'Orbigny, 1843, and compared the apertural narrowing inwards by the outer lip (as in the cypraeids) to a narrow slit.

Pseudocassis has been documented only from a few occurrences: the Barremian–Aptian (Lower Cretaceous) of Switzerland (Pictet and Campiche, 1863) and France (Sayn, 1932), as well as the Miocene (Neogene) of Great Britain (Bell, 1917, 1918). Because all specimens studied are preserved as internal moulds, their identity is rather dubious, and their systematic position of higher rank and phylogenetic relationship remain unclear, and the taxon might be actually a nomen dubium.

Cypraeidae Rafinesque, 1815

Zittelia resembles members of the family Cypraeidae but unlike them, *Zittelia* is never convolute, i.e., the last whorl does not cover all previous ones. Differences between *Zittelia* and *Cypraea* Linnaeus, 1758, highlighted by Gemmellaro (1869) are the higher spire and a distinct aperture morphology in *Zittelia*. Out of all known species of *Zittelia*, only *Z. cipraeaeformis* has such a low spire that is not visible from the ventral side, whereas in other species, particularly those from the Oxfordian and Kimmeridgian, the spire is moderately elevated above the last whorl (Fig. 20A1). At the same time, the elongated, slit-like aperture brings *Zittelia* closer to *Cypraea* than to remaining colombellinids. Apart from several similar characteristics shared between *Zittelia* and the earliest cypraeid *Coffeacypraea*, some *Zittelia* exhibit a groove (Fig. 20A1, C1) – a feature referred to as an incipient flange – observed in some cypraeids (Nützel *et al.*, 2025, fig. 6). However, this does not appear to be a stable trait and has been documented in only two species, *Z. cipraeaeformis* and *Z. oppeli*. It is also probable that *Coffeacypraea* possesses a sinuosity, since in the figure presented by Capasso (2024, p. 166, fig. 2) from the Tithonian of Capri, Italy, a weak depression is visible at the abapical part of the aperture. It remains uncertain, however, whether it is a true shell character or a result of erosion or shell damage. Interestingly, Sayn (1932, p. 32, text-fig. 10, pl. 3, figs 8, 9) noted the presence of the sinuosity in *Zittelia drumensis* (that we interpret as a species of *Coffeacypraea*) from the Barremian–Aptian (Lower Cretaceous) of Barcelonne (France), what led him to assign this specimen to *Zittelia*. In our opinion, this feature indicates a clear relationship of *Zittelia* and the cypraeids.

Evolutionary relationships

A gradual transition in the shell outline in the species of *Zittelia* is observed during the Late Jurassic. It changes from an oval shape in the Oxfordian and Kimmeridgian to a globular form in the Tithonian (Fig. 20). Additional

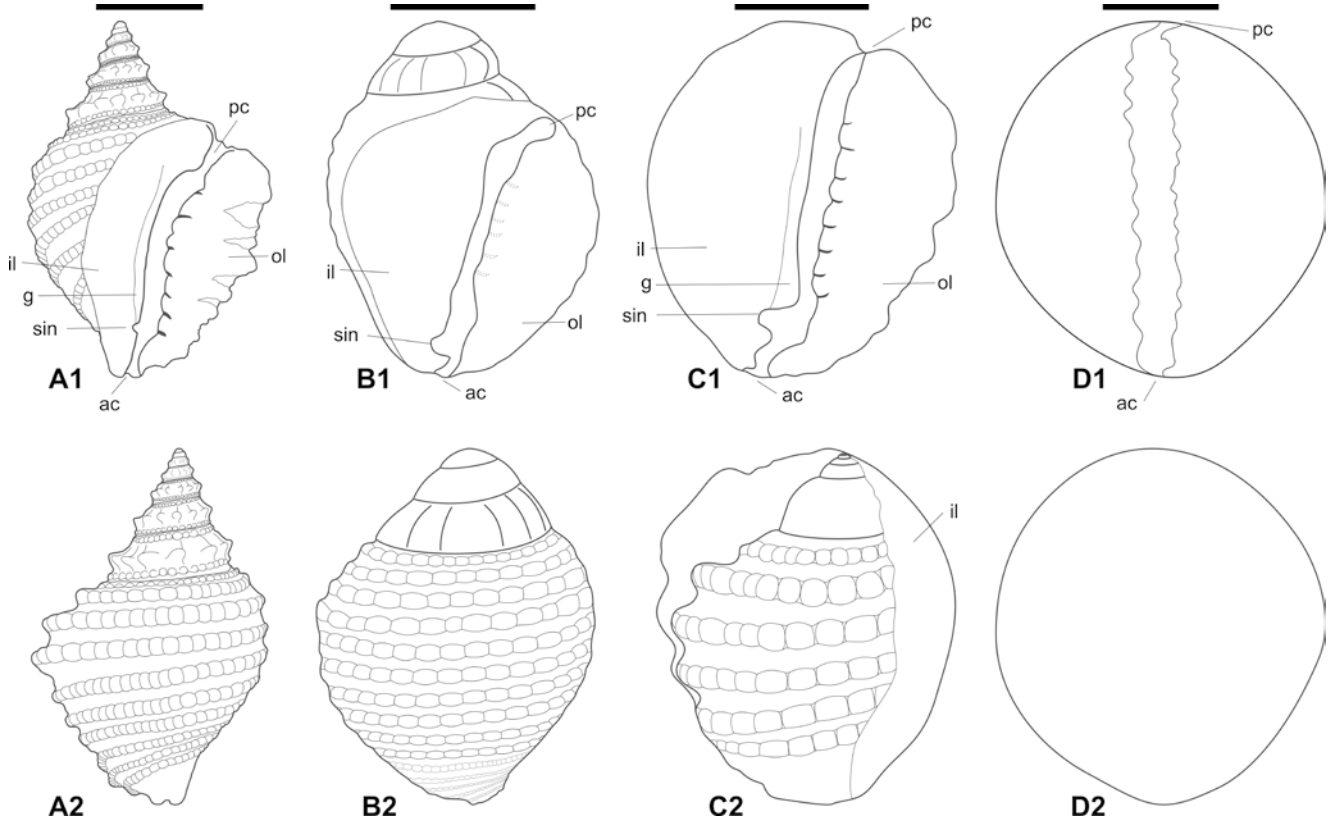

Fig. 20. Morphological changes in *Zittelia* (A, B, C) from the Kimmeridgian (A) to the Tithonian (B, C) and comparison with *Coffeacypraea* (D). **A**. *Zittelia oppeli* (Étallon, 1859), Kimmeridgian of France (Valfin). **B**. *Zittelia picteti* Gemmellaro, 1869, Tithonian of Italy (Carini near Palermo, Sicily), **C**. *Zittelia cipraeaeformis* Gemmellaro, 1869, Tithonian of Italy (Carini near Palermo, Sicily), **D**. *Coffeacypraea tithonica* (Di Stefano, 1882), Tithonian, Upper Jurassic of the castle mountain of Termini Imerese near Palermo, Sicily, Italy. In aperture (A1–D1) and lateral (A2–D2) views. Abbreviations: ac – anterior canal, g – groove, il – inner lip, ol – outer lip, pc – posterior canal, sin – sinuosity. Scale bars represent 5 mm.

morphological changes are also evident, including the elongation of the aperture, enlargement of the last whorl and reduction of the spire, as well as the expansion of the peristome, where the columellar and outer lips extend over the spire, and covering more than half of it in *Z. cipraeaeformis* (Fig. 20C2). As a result, the spire is not visible on the ventral side of the shell, being concealed by the expanded lips. This indicates that the mantle could have enveloped a significant portion of the shell. In recent cypraeids, adult forms have a convolute shell, with the last whorl enclosing all previous whorls and forming a narrowly elongate, slit-like aperture with anterior and posterior canals, while larval shells are obtusely conical with reticulate ornament and have planktotrophic larval development (Nützel *et al.*, 2025, fig. 1). The morphology of the colombellinid protoconch remains unknown so far, but the tendency of the last whorl to enclose the spire whorls is documented here (Figs 4, 20C).

In the Late Jurassic *Zittelia* and *Coffeacypraea,* the position of the posterior canal is on the right (labral) side of the shell axis. In Early Cretaceous cypraeids, the posterior canal has already shifted to the left, where it also occurs in their Recent counterparts. It might be hypothesized, therefore, that a gradual shift of the posterior canal from the right side of the shell axis to its left side occurred between the Late Jurassic (Tithonian) and Early Cretaceous (Barremian; Nützel *et al.,* 2025, fig. 6, tab. 1).

The sinuosity that clearly distinguishes *Zittelia* from *Colombellina*, has neither been mentioned nor depicted in the Cretaceous Cypraeidae (Sayn, 1932; Roman and Mazeran, 1920; Groves, 1990, 2004; Groves *et al.*, 2011). However, in the Eocene cypraeid *Cypraeorbis,* Darragh (2011, fig. 1) noted a similar structure, termed the infracolumellar groove, located at the abapical end of the aperture (Nützel *et al.*, 2025, fig. 6E1), which might be homologous to the abapical sinuosity.

It is highly probable that the infracolumellar groove at the abapical end of the aperture, observed in some Cenozoic and Recent Cypraeidae, may have evolved from the sinuosity in *Zittelia* and may thus represent a derived trait. However, this character does not consistently appear within all cypraeids. Nevertheless, its repetitive occurrence, along with the strongly expanded lips in *Zittelia*, may be considered as strong support for the relationship between the latter genus and cypraeids.

Palaeoecological insights

The distribution of *Zittelia* (Fig. 2) indicates its restricted occurrence in peri-Tethyan carbonate facies. All the confirmed records so far are Late Jurassic in age, with the possibility that some (Sicily, Štramberk) also are of earliest Cretaceous age. All findings of *Zittelia* are associated with

shallow-water limestones, deposited on extensive carbonate platforms. The Panormide carbonate platform, remnants of which crop out on Sicily, was several to hundreds of km wide and comprised peritidal, lagoonal, reef complex and fore-reef settings (Basilone and Sulli, 2016). The carbonate platform at Štramberk, although not as extensive as the Panormide carbonate platform, was also variegated and encompassed different, mostly peri-reefal facies (Vaňková *et al.*, 2019). We speculate that these reefs and the surrounding facies were the habitat of *Zittelia*, which does not occur in the more proximal, lagoonal and peritidal carbonates that instead were dominated by nerineid and acteonellid gastropods (e. g., Kollmann, 2014). Interestingly, the co-occurrence of *Zittelia* and earliest cypraeids in the latest Jurassic of Sicily, Italy, may indicate that the Late Jurassic reefs and associated lagoons of the Tethys were a centre of diversification for the Colombellinidae and the emergence of the Cypraeoidea.

The earliest record of *Z. rara* in the middle Oxfordian of Switzerland (the coral facies of the St-Ursanne Formation), followed by its occurrence in the Kimmeridgian of France and later in several European localities during the Tithonian, may indicate possible migration routes but data are probably still too sparse for such conclusions. *Zittelia* reached its highest point of diversification during the Tithonian and became extinct in the earliest Early Cretaceous (Fig. 1).

CONCLUSIONS

This review of the genus *Zittelia* revealed that the genus comprises 9 species from southern and central Europe. The earliest record of *Zittelia* is documented from the middle Oxfordian and the genus attained the greatest diversity during the Tithonian–?Valanginian. No stratigraphically well-documented occurrences of *Zittelia* younger than the Jurassic have been recorded so far. Lectotypes of some species, based on the revision of the type collections, were designated.

We observed transitional forms between *Zittelia* and *Cypraea*, which display a proportional increase of the last whorl, the elongation of the aperture and the expansion of the columellar lip. *Zittelia cipraeaeformis* from the Tithonian–?Valanginian is morphologically most similar to cypraeids, while *Z. rara* from the middle Oxfordian and *Z. oppeli* from the Kimmeridgian display a profound similarity to the species of *Colombellina* from the Jurassic.

The co-occurrence of *Zittelia* and the earliest cypraeids in the Upper Jurassic–?lowermost Cretaceous of Sicily, Italy, may indicate that the Late Jurassic–?earliest Cretaceous reefs and associated peri-reefal facies of the Tethys were centres of diversification of the Colombellinidae and the sites of emergence of the first representatives of the Cypraeoidea.

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